Gain control in the auditory system: Absolute identification of intensity within and across the two ears

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A number of studies have suggested that the auditory system employs nonlinear gain control to modulate its response to a broad range of stimulus intensities (e.g., Parker, Murphy, & Schneider, 2002), but the precise location and nature of this mechanism remains uncertain. To address these issues, we investigated the extent to which gain control in one ear was influenced by auditory events in the other ear. Listeners were asked to identify which of four sounds, varying in intensity (25, 30, 35, and 40 dB [SPL]), had been presented to the left ear. Subsequent test sets included an 80-dB (SPL) stimulus presented to either the left (ipsilateral) or the right (contralateral) ear. Ipsilateral presentations of the 80-dB (SPL) stimulus produced a greater reduction in identification accuracy among the original four sounds than did contralateral presentations, but both presentations caused a reduction in gain. In a second experiment, the perceived laterality of a sound was manipulated by presenting the same sound to both ears with an interaural time delay. When the 80-dB (SPL) stimulus was added to the set of quiet sounds (which were presented to both ears but were perceived to be in the left ear because of the interaural time delay), identification accuracy was reduced by the same amount, independently of whether the 80-dB (SPL) stimulus was perceived only in the ipsilateral ear or only in the contralateral ear.

Although the response range of individual primary auditory afferents in mammals is quite limited (e.g., 15–40 dB for the cat; Kiang, Watanabe, Thomas, & Clark, 1965), behaviorally, mammals can respond to intensity differences over a considerably larger range (e.g., >100 dB for the cat; Heffner & Heffner, 1985). To explain how a limited response range in primary auditory afferents can eventually yield a much larger behavioral dynamic range, many investigators have proposed the existence of a nonlinear auditory amplification system (a nonlinear amplifier) capable of expanding the dynamic range of hearing (Parker & Schneider, 1994; Robles & Ruggero, 2001; Schneider & Parker, 1990; Yates, 1995). Moreover, recent results have suggested that the gain of this nonlinear amplifier is under top-down control (e.g., Parker, Murphy, & Schneider, 2002). That is, the amount of amplification depends on such factors as the listener's expectations concerning the sound intensities and/or the range of stimuli expected. However, how and at what level this top-down control is exerted is not yet known. Here, we explore how gain is affected in the auditory system, specifically exploring whether the acoustic events in one ear can affect sensitivity to sounds in the contralateral ear.

Locus of the Nonlinear Amplifier

A number of electrophysiological and biomechanical studies have shown that there is a mechanism within the cochlea (called the *cochlear amplifier*) that amplifies very

low-intensity stimuli, thereby increasing sensitivity and extending the range over which the auditory system can respond (for reviews, see Brownell, 1999; Rubles & Ruggero, 2001; Yates, 1995). However, given the complexity of the auditory system, it is also possible that gain adjustments are imposed at more central levels, ranging from the brainstem to the cortex. Hence, the cochlear amplifier may be only a component of a general system that uses nonlinear amplification to extend its effective dynamic range.

Top-Down Gain Control

Behavioral evidence has demonstrated that listeners are able to use top-down knowledge to accommodate an anticipated range of acoustic intensities (Parker et al., 2002; Parker & Schneider, 1994). Using an absolute identification paradigm, Parker et al. asked listeners to identify which one of four tones (e.g., 25, 30, 35, and 40 dB [SPL], 1000-Hz tones) was presented on a trial by pressing one of four buttons (e.g., Button 1 for the 25-dB [SPL] tone, Button 2 for the 30-dB [SPL] tone, etc.). After learning the button-to-tone mappings in a short practice block with feedback, the participants completed a test block in which they had to continue to identify which of these four tones was presented on each trial.

In some of the subsequent test blocks, a more intense fifth tone (ranging from 45 to 90 dB [SPL]) was added to the original four baseline stimuli. The participants were then asked to identify which one of the five test tones

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(e.g., 25, 30, 35, 40, and 70 dB [SPL], 1000-Hz tones) was presented on a trial by pressing one of five buttons. When the fifth tone was in the same frequency channel as the four baseline tones, the accuracy with which those four tones were identified was reduced. This reduction in accuracy could be due, in part, to a higher processing load at the decision-making level. To clarify, in a signal detection model, four criteria are required to distinguish one stimulus from another when there are five stimuli, whereas only three criteria are needed to distinguish four stimuli. The increased processing load that accompanies the addition of a criterion could affect the identification of the four baseline stimuli (e.g., by increasing memory variance in Durlach & Braida's, 1969, model of intensity discrimination). Therefore, some performance decrement was expected in the ability to identify the four baseline tones in Parker et al.'s (2002) study when a fifth tone of the same frequency was added to the baseline set of four tones, independently of that fifth tone's intensity level.

The intensity level of the added fifth tone was found to be critical. In Parker et al. (2002), the intensity of the added fifth tone ranged from 45 to 90 dB (SPL). As the intensity level of the added stimulus increased, relative to the baseline tones, identification performance among the four baseline tones decreased. This result is the opposite of what would be expected on the basis of a cognitive load hypothesis (performance accuracy for the four baseline stimuli should, if anything, increase as it becomes easier to discriminate between the fifth stimulus and the four baseline stimuli).

In contrast, when a fifth stimulus of lesser intensity than four higher intensity baseline tones (e.g., 84.5, 86.5, 88.5, and 90.5 dB [SPL]) was added to the test set, identification accuracy was unaffected by the amount of decibel separation between the fifth tone and the lowest of the four baseline stimuli, once the degree of separation exceeded 6 dB. This result suggests that the decrease in identification accuracy for the low-intensity baseline tones that resulted when a more intense fifth stimulus was added to the set was not due to a simple range effect (Braida & Durlach, 1972). Increasing stimulus range decreased identification accuracy only when the added tone was more intense than the low-intensity baseline set of four tones, but not when the intensity of the added tone was more than 6 dB quieter than that of the high-intensity baseline set.

Parker et al. (2002) interpreted this pattern of results as indicating that expectations and knowledge influenced the gain of the nonlinear auditory amplifier. According to their interpretation, when only low-intensity tones were presented, the listeners increased their sensitivity to these stimuli by increasing the gain of the auditory amplifier. However, when a fifth, higher intensity tone was added to the set, the gain of the amplifier presumably had to be reduced, in order to adjust to the higher intensities being processed in the auditory system. Because of the nonlinearities in the system, this reduction in gain decreased identification accuracy for the baseline tones. Hence, as the intensity of the added fifth tone was increased, gain was progressively reduced, resulting in an increasingly larger loss in identification accuracy among the four baseline tones. Conversely, when the baseline set of four stim-

uli consisted of high-intensity tones, there was no need to change the gain to accommodate a lower intensity fifth tone. Hence, according to this model, the auditory system employs nonlinear gain control to accommodate the range and expected values of stimulus intensities.

A third experiment demonstrated the critical role that knowledge and expectation play in the modulation of gain (Parker et al., 2002). Participants were asked to make loudness discriminations of two low-intensity tones. Prior to each presentation of these test tones, a high-intensity (95-dB [SPL]) *warning tone* was presented. Although this method greatly increased the frequency of exposure the participants had to a high-intensity stimulus, it did not affect discriminability of the two low-intensity tones. This finding suggests that the listeners were able to rapidly readjust the amplifier's gain in anticipation of particular acoustic events. In other words, they used their top-down knowledge about when the warning tone was to occur in order to anticipate the appropriate level of gain for the warning and test tones. In the previous, absolute identification experiment, the participants did not know when the high-intensity stimulus would occur and, presumably, had to keep the gain at a low level at all times, thereby reducing identification accuracy among the baseline set of low-intensity stimuli. Hence, knowledge about when high-intensity stimuli are likely to occur may, in part, allow the auditory system to rapidly modulate the level of gain of the amplifier to maximize identification performance.

Other research has shown that listeners' judgments concerning loudness are modulated by the range of intensities experienced (Marks, 1994; Marks & Warner, 1991; Schneider & Parker, 1990), a phenomenon often referred to as *loudness recalibration* (Marks, 1994) or *induced loudness reduction* (Scharf, Buus, & Nieder, 2002). These studies show that loudness judgments concerning a set of sounds are, in general, reduced when more intense sounds having identical or overlapping spectral content are present (Charron & Botte, 1988; Scharf, Wagner, & Nieder, 2005). Hence, it appears that the presence of high-intensity sounds reduces both the loudnesses of a set of low intensity sounds and their discriminability.

Influence of Binaural Factors on Gain Control

Parker et al. (2002) used only monaural stimulation, and other investigations of intensity discrimination in which the absolute identification paradigm has been used have typically employed either monaural or diotic (i.e., identical auditory presentations to both ears) presentations (e.g., Durlach & Braida, 1969). When stimulation is either monaural or diotic, it is difficult to evaluate whether gain is controlled peripherally or centrally. Previous research in which induced loudness reduction across the ears has been investigated has demonstrated that the loudness of a stimulus presented to one ear is modulated by the level of a contralateral stimulus (Marks, 1996; Scharf, Nieder, Buus, & Cazals, 2003). In these experiments, listeners were asked to judge the loudness of a tone, relative to a comparison tone that had been presented in either the same or the opposite ear, relative to the test tone. When a high-intensity comparison tone was presented to the ipsi-

lateral ear, it reduced the loudness of the test tone more than when the high intensity tone was presented to the contralateral ear. Nevertheless, there still was a measurable contralateral influence. Marks suggested that this contralateral influence reflects “that the underlying process involves some kind of central mediation” (Marks, 1996, p. 479). A central mechanism would presumably monitor the relative inputs from each ear and use those levels to calibrate the loudness of sounds from both ears. This recalibration could be central only (and not affect gain control in the contralateral ear), or it might exert its influence by changing gain peripherally in the contralateral ear. If gain were to change in the contralateral ear, we would expect reduced identification accuracy for the set of sounds presented to the contralateral ear. On the other hand, if it just recalibrated loudness centrally, we might not observe any change in the identification of sounds presented to the contralateral ear.

There is, however, evidence from studies of evoked otoacoustic emissions (EOAEs) that strongly suggest that contralateral acoustic events can influence peripheral events in the ipsilateral ear (Maison, Micheyl, Andéol, Gallégo, & Collet, 2000; Morand-Villeneuve et al., 2002). To evoke a cochlear response using this method, a series of tone pips is presented to one ear. In response to this stimulation, the cochlea of that ear becomes active and produces acoustic energy at or near the frequency of the tone pips. (Because these emissions are produced by the action of the outer hair cells, any modulation of their activity reflects a change in peripheral function.) With regard to the influence of the acoustic events in one ear causing a contralateral change in gain, it was found that the magnitude of EOAEs was reduced when a broadband noise was presented to the contralateral ear during the presentation of the tone pips. The amount of suppression of the EOAE on the ipsilateral side increased as the amplitude of the contralateral broadband noise was increased (Maison et al., 2000; Morand-Villeneuve et al., 2002). Hence, the level of gain in an ear seems to be dependent on the acoustic stimulation in both ipsilateral and contralateral channels. This evidence suggests that gain in one ear is modulated by sounds presented to the opposite ear. It remains to be seen, however, whether such contralateral influences will reduce accuracy in an identification paradigm.

In the present experiments, we presented a set of four stimuli to the left ear (broadband noises at 25, 30, 35, and 40 dB [SPL]).¹ This baseline stimulus set was sometimes modified by the addition of 45- or 80-dB (SPL) noises presented to either the left or the right ear. Hence, set size was increased to five stimuli, with each stimulus occurring with equal frequency. This manipulation allowed us to evaluate how the expectation of high-intensity ipsilateral and contralateral presentations affects auditory gain in the left ear.

If identification is affected only by events in that ear (depends only on cochlear mechanisms in that ear), presenting a loud sound to the contralateral ear should have no effect on the accuracy with which the four low-intensity sounds are identified. Hence, a null effect would be consistent with the hypothesis that the cochlear gain control system is self-contained within the periphery of the audi-

tory system. Alternatively, if contralateral and ipsilateral presentations of the added fifth stimulus had identical effects on identification accuracy, this would suggest that gain was more centrally mediated. Finally, a pattern of intermediate effects between these two extremes could help us to determine how and at what level top-down effects are being exerted.

EXPERIMENT 1

Ipsilateral and Contralateral Influences on Gain Control

To examine ipsilateral and contralateral influences on gain control, we asked the participants in Experiment 1 to identify which one of a set of four or five sounds was presented on a trial by pressing the appropriate response button. The baseline set of stimuli in this experiment were four monaurally presented (left ear), low-intensity noises (25, 30, 35, and 40 dB [SPL]). Identification accuracy for these baseline stimuli was also determined in four additional conditions. In these conditions, the baseline set was augmented by adding either a 45-dB (SPL) or an 80-dB (SPL) stimulus to either the ipsilateral or the contralateral ear. As has been demonstrated in previous research, augmenting the baseline set of stimuli by adding a 45-dB (SPL) stimulus would be expected to have only a small effect, if any, on the gain of the nonlinear amplifier (e.g., Parker et al., 2002). Therefore, when this stimulus is presented contralaterally, it should have a negligible effect on performance, because it is processed in a separate auditory channel (contralateral ear) and without sufficient intensity to affect the level of gain. Any effect that this 45-dB (SPL) stimulus has when it is presented ipsilaterally (i.e., in the same auditory channel) would then serve as a measure of the effect of increasing the cognitive load occasioned by having to identify five, as opposed to four, within-channel stimuli. If gain control is local (i.e., cochlear), we should observe a decrease in performance in the baseline set of four low-intensity stimuli when an 80-dB (SPL) ipsilateral stimulus is added to the set, but no change in performance when the same stimulus is added contralaterally. However, if the addition of occasional loud sounds (one out of every five trials) affects gain more centrally, the decrement in performance observed when the 80-dB (SPL) stimulus is presented ipsilaterally should be the same as that found when it is presented contralaterally.

Method

Participants. The 28 students, who were recruited from the University of Toronto at Mississauga and paid for their participation, had audiograms in the normal range. Only those individuals who scored between 60% and 90% for accuracy in the baseline condition were allowed to participate in the rest of the experiment ($n = 24$; 13 women and 11 men; mean age = 21.5 years, $SD = 1.9$ years), with 4 individuals unable to pass the screening. This screening was used to ensure that all the participants were able to perform the task at levels well above chance but below ceiling.

Apparatus and Stimuli. The baseline set of four stimuli consisted of four levels (25, 30, 35, and 40 dB [SPL]) of a 0.5-sec burst of bandlimited Gaussian noise (0–10 kHz), which were always presented to the left ear. Four additional sets were created by augmenting the base set with (1) an ipsilateral 45-dB (SPL) noise (Ips-45),

(2) a contralateral 45-dB (SPL) noise (Cont-45), (3) an ipsilateral 80-dB (SPL) noise (Ips-80), and (4) a contralateral 80-dB (SPL) noise (Cont-80). In each test set, all the stimuli occurred with equal frequency. All the stimuli were generated online at a 20-kHz sampling rate and were presented using a Tucker Davis Technologies (T/D) II sound system over EAR insert earphones (EAR 410-3001). These insert earphones were designed to provide 80 dB of contralateral attenuation and were used to minimize the effects of contralateral bone conduction. Responses were recorded using a button box that fed into the T/D II system. A red light-emitting diode (LED) was located above each button.

Procedure. The participants initiated each trial by pressing a button. Two seconds later, they were presented with one of the stimuli from the set in question ($n = 4$ or 5). They then identified the stimulus by pressing the appropriate button. Immediately after pressing a button, feedback was provided by illuminating the LED above the button that corresponded to the presented stimulus.

Each stimulus set was divided into six blocks: a practice block and five test blocks. The blocks consisted of 10 presentations of each of the stimuli in the set. A different random order was used for each block. Each six-block set was presented in a single session, with multiple sessions being presented within a day. The baseline stimulus set was always presented first. The presentation order of the remaining four stimulus sets was counterbalanced across participants. A mixed factors ANOVA was performed to determine whether the 24 counterbalanced orders affected performance on the stimulus sets. Because there was no main effect of order and no interaction between stimulus set and order, the subsequent results were collapsed across counterbalancing order.

Each six-block session took approximately 45 min to complete.

The response interval on each trial was 2.5 sec in duration. If no response was recorded within the response interval, the trial block was restarted. The participants were informed of this time limit and were strongly encouraged to respond within the allotted time.

All testing was conducted within a double-walled IAC sound-attenuating chamber. Data analysis was performed only on the five fully completed test blocks making up a particular stimulus condition.

Results and Discussion

Our major interest in this experiment was the degree to which the added fifth stimulus would affect the participants' abilities to identify the four stimuli common to all the stimulus sets (25-, 30-, 35-, and 40-dB [SPL] broad-

band noise bursts). To that end, pressing the response button corresponding to the added fifth stimulus when any of the four baseline stimuli were presented was counted as a 40-dB (SPL) response (as in Parker et al., 2002). Hence, when the 40-dB (SPL) stimulus was presented, if the participant identified it as either the fourth or the fifth stimulus, the response was counted as correct. The tendency to confuse the 40-dB stimulus with the fifth stimulus was extremely rare, except when the 45-dB stimulus was added ipsilaterally. In that condition, the 40-dB stimulus was identified as the 45-dB stimulus on 13% of the trials on which it was presented. All of the following analyses exclusively examine performance with the four baseline stimuli, even when a fifth stimulus was added to the set. It may be noted, however, that identification performance did tend to be quite good with the added fifth stimuli. The accuracy with which the added fifth stimulus was correctly identified as such was 77%, 94%, 97%, and 98% for Stimulus Sets Ips-45, Cont-45, Ips-80, and Cont-80, respectively.

Figure 1 indicates that the addition of a contralateral 45-dB (SPL) stimulus had no effect on the accuracy with which the four baseline stimuli presented to the left ear were identified. This is what we would expect for a stimulus that is not in the same channel as the four baseline stimuli and not of sufficient intensity in the contralateral ear to noticeably affect the gain in the left ear. Figure 1 also shows that presenting an ipsilateral 45-dB (SPL) stimulus produced approximately the same decrement in accuracy for the four baseline stimuli presented to the left ear as that produced by a contralateral 80-dB (SPL) stimulus. Finally, the addition of an intense stimulus (80 dB [SPL]) to the ipsilateral ear produced the largest decrement in accuracy, consistent with the results from Parker et al. (2002).

This description of the pattern of results was confirmed by a single-factor ANOVA, which indicated a significant effect of condition [$F(4,92) = 22.334$, $MS_e = 0.004$, $p < .001$], and by a series of Newman-Keuls post hoc comparisons. As can be seen in Figure 1, identification

Figure 1. Absolute identification accuracy for the baseline stimuli (25, 30, 35, and 40 dB SPL) in Experiment 1 for each of the listening conditions. Results are given with standard error bars.

performance was best with the baseline condition and the Cont-45 condition. Paired comparisons between these two conditions revealed no difference between them ($p > .5$). The baseline condition was found to differ from all of the other conditions (baseline vs. Ips-45, $p < .01$; baseline vs. Ips-80, $p < .01$; baseline vs. Cont-80, $p < .01$). The Cont-45 condition was also found to be different from all the other conditions, except the baseline condition (Cont-45 vs. Ips-45, $p < .01$; Cont-45 vs. Ips-80, $p < .01$; Cont-45 vs. Cont-80, $p < .01$). Accuracy was lowest in the Ips-80 condition, relative to all the other conditions (Ips-80 vs. Ips-45, $p < .01$; Ips-80 vs. Cont-45, $p < .01$; Ips-80 vs. Cont-80, $p < .01$).

To confirm that an ipsilateral 80-dB (SPL) stimulus was more deleterious to performance than was a contralateral 80-dB (SPL) stimulus, the Ips-80 and Cont-80 conditions were replicated with an additional 12 participants. As can be seen in Figure 2, performance was best for the four baseline stimuli in the baseline condition, less accurate for the baseline stimuli in the Cont-80 condition, and most degraded in the Ips-80 condition. An ANOVA confirmed that these differences were statistically reliable [$F(2,22) = 14.204$, $MS_e = 0.006$, $p < .01$]. Newman-Keuls tests indicated that all pairwise comparisons were significant at $p < .05$. Hence, this additional experiment replicated the effects found when ipsilateral and contralateral 80-dB (SPL) noises were added to the stimulus set.

A comparison of baseline performance with the Cont-80 and Ips-80 conditions indicated that the occasional presentation of an intense stimulus within the test set (one fifth of the trials) produced a decrement in identification accuracy, with the magnitude of that decrement being greater for ipsilateral than for contralateral presentations. Because insert earphones were used (80-dB attenuation of bone-conducted sound to the contralateral ear) in these

tests, the decrement found in the Cont-80 condition cannot be attributed to leakage of sound from the contralateral to the ipsilateral ear. Moreover, adding a contralateral 45-dB (SPL) noise to the baseline set did not affect identification accuracy in the ipsilateral ear. Hence, the Cont-80 effect does not seem to be attributable to the increase in cognitive load due to the addition of a stimulus to a different channel but suggests that occasional intense contralateral stimulation can affect the gain of the auditory amplifier in the ipsilateral pathways. However, the question of how and at what level contralateral experience affects the degree of nonlinear amplification in the ipsilateral pathways requires further clarification.

One possibility is that the degree to which a loud sound suppresses amplification in a channel depends on its perceived lateralization. According to this model, a loud sound perceived to be on the same side as the baseline four stimuli would have a more substantial suppression effect on amplification and, thus, identification accuracy than would a similarly loud sound that was perceived to be on the contralateral side. Alternatively it may be that the effect is independent of the perceived lateral position of the loud sound and depends solely on the amount of stimulation in each ear. In Experiment 2, we tested these two alternative explanations by manipulating the perceived lateralization of the stimuli, while actually presenting the same stimuli to both ears.

EXPERIMENT 2

Perceived Lateralization of Presentations to the Left and Right Ears

In a reverberant environment, a listener's ears are stimulated not only by the direct wavefront emanating from a source, but also by sound reflections off of the surfaces in

Figure 2. Absolute identification accuracy for the baseline stimuli (25, 30, 35, and 40 dB [SPL]) in the replication experiment for Experiment 1 for each of the listening conditions. Results are given with standard error bars.

the environment. If the time delay between the direct and the reflected waves is sufficiently short, listeners perceive only one sound located at or near the sound source. In other words, the direct (first-arriving) wave takes precedence over the reflections. In the laboratory, we can simulate this effect by presenting the same sound to both ears, but with an interaural delay of 2–5 msec. Under these conditions, the listener will lateralize the sound to the location of the leading wave. By changing which ear is leading, we can vary the perceived lateralization of the sound without changing the amount of stimulation delivered to each ear (for reviews of the precedence effect, see Litovsky, Colburn, Yost, & Guzman, 1999; Zurek, 1987). The lateralization paradigm employed here will be referred to as interaural-delay-induced lateralization (IDIL).²

In this second experiment, we presented the same stimulus to both ears but changed its perceived lateral position, using IDIL. When the stimulus that was presented to the left ear preceded the identical stimulus presented to the right ear by 2 msec, the listener perceived the sound to be on the left, and vice versa. If the effect of an intense stimulus depends only on its perceived lateral position (i.e., on the channel it is perceived to be in), we would expect that the results in the following experiment would mimic those in Experiment 1. That is, if the baseline set of four low-intensity stimuli are perceived to be on the left (using IDIL) and the 80-dB (SPL) stimulus is perceived to be on the right (again using IDIL), there should be less of a reduction in identification accuracy than if the 80-dB (SPL) stimulus is perceived to be on the left (same side as the baseline stimuli). In contrast, if the identification decrement produced by a high-intensity stimulus depends only on the degree of stimulation in a given ear, we would expect to find equal-sized decrements, independently of the perceived lateral position of the intense sound, because the intense sound was actually presented to both ears.

Method

Participants. The 16 students, who were recruited from the University of Toronto at Mississauga and paid for their participation, had audiograms in the normal range. Only those individuals who scored between 60% and 90% for accuracy in the baseline condition were allowed to participate in the rest of the experiment ($n = 12$; 6 women and 6 men; mean age = 21.8 years, $SD = 2.6$ years), with 4 individuals unable to pass the screening. This screening was used to ensure that all the participants were able to perform the task at levels well above chance but below ceiling.

Apparatus and Stimuli. All of the materials used in Experiment 2 were identical to those used in Experiment 1. The stimuli were also similar to those in Experiment 1, with the following exceptions. All of the stimuli were presented using the IDIL to control their perceived lateralization. Specifically, identical broadband noise bursts (10-kHz bandwidth, 0.5-sec duration) were presented to both the left and the right ears. In the IDIL_Baseline condition, the left-ear noise burst was always presented 2 msec before the right-ear noise burst, giving the subjective impression of a sound on the left. The four intensities used for the baseline set were 25, 30, 35, and 40 dB (SPL). In the IDIL_Cont-80 condition, a fifth stimulus whose intensity was 80 dB (SPL) in both ears was added to the baseline set of four stimuli. However, for presentations of this stimulus, the right-ear noise preceded the left-ear noise by 2 msec, so that the 80-dB (SPL) stimulus was perceived to be on the right, or in the contralateral ear (IDIL_Cont-80). In the third condition, the

80-dB (SPL) stimulus in the left ear preceded the identical stimulus in the right ear by 2 msec, in order to cause a subjective impression that the loud sound was presented ipsilaterally (IDIL_Ips-80). Postexperimental debriefing confirmed previous findings (e.g., Li, Qi, He, Alain, & Schneider, 2005) that a 2-msec delay produces a very clear and consistent lateralization.

Procedure. The procedure in Experiment 2 was identical to that used in the replication conditions in Experiment 1. Hence, only three presentation conditions were used: IDIL_Baseline, IDIL_Ips-80, and IDIL_Cont-80. The participants used the same absolute identification paradigm for identifying which of the possible stimuli within a test set had been presented ($n = 4$ or 5). Initially, the participants were tested in the IDIL_Baseline condition, followed by the other two conditions. The presentation order of the IDIL_Ips-80 and IDIL_Cont-80 conditions was counterbalanced across participants.

A mixed factors ANOVA was performed to determine whether the counterbalanced order would affect performance on the stimulus sets. As in Experiment 1, there was no main effect of order and no interaction between stimulus set and order. Subsequently, the results of Experiment 2 were collapsed across counterbalancing order. In addition, responses to the added fifth stimulus were treated in the same way as in Experiment 1.

All testing was conducted within a double-walled sound-attenuating chamber. Data analysis was performed only on the five fully completed test blocks making up a particular stimulus condition.

Results and Discussion

As in Experiment 1, the same correction procedure was used when the fifth stimulus was chosen after a presentation of one of the four low-intensity stimuli in computing identification accuracy for the base set of four stimuli. Accuracy levels were 99.7% in the IDIL_Cont-80 condition and 98.7% in the IDIL_Ips-80 condition, indicating that the 80-dB (SPL) stimulus was correctly identified almost all of the time.

Figure 3 shows that when IDIL was used to vary the perceived lateralization of the 80-dB (SPL) stimulus, performance accuracy was independent of its perceived ear of presentation. Performance was degraded an approximately equal amount in the IDIL_Ips-80 and the IDIL_Cont-80 conditions, and both conditions cause performance to be worse than that in the IDIL_Baseline condition. This description of the pattern of results was confirmed by a single-factor ANOVA and a series of Newman-Keuls post hoc comparisons. Performance was better in the IDIL_Baseline condition than in the other two conditions [$F(2,22) = 64.251$, $MS_e = 0.002$, $p < .0001$]. Paired comparisons confirmed these differences (IDIL_Baseline vs. IDIL_Cont-80, $p < .01$; IDIL_Baseline vs. IDIL_Ips-80, $p < .01$). No difference was found between the IDIL_Ips-80 and the IDIL_Cont-80 conditions ($p > .05$).

In this experiment, both the IDIL_Ips-80 and the IDIL_Cont-80 conditions presented a high-intensity stimulus to each ear, with the perceived lateral position of the intense stimulus being in the left ear in the IDIL_Ips-80 condition and in the right ear in the IDIL_Cont-80 condition. If gain control depended primarily on the perceived lateral position of the intense sound, we would expect a greater reduction in identification accuracy when the 80-dB (SPL) stimulus was perceived to be in the ipsilateral versus the contralateral ear, relative to the baseline stimuli. Because perceived laterality had no effect on identification accuracy, this result seems to suggest that gain was primarily

Figure 3. Absolute identification accuracy for the baseline stimuli (25, 30, 35, and 40 dB [SPL]) in Experiment 2 for each of the listening conditions. Results are given with standard error bars.

modulated by the actual intensities presented to each ear, which were always the same in this experiment.

An additional analysis was completed to examine this hypothesis by comparing the three conditions in the replication of Experiment 1 (Baseline, Ips-80, and Contr-80) with the analogous three conditions in Experiment 2 (IDIL_Baseline, IDIL_Ips-80, and IDIL_Cont-80). If identification accuracy is determined by the actual intensity experienced by the ear, we would expect to find an interaction between the type of experiment (monaural Experiment 1 vs. IDIL Experiment 2) and the perceived lateral position of the sound. Indeed, there was a significant interaction between type of presentation (monaural vs. IDIL) and lateral position [$F(2,44) = 3.217$, $MS_e = 0.004$, $p = .05$]. Subsequent Neuman-Keuls comparisons revealed no difference between the baseline in Experiment 1 and the IDIL_Baseline condition in Experiment 2 ($p > .05$); no difference between the Ips-80 condition in Experiment 1 and the IDIL_Ips-80 condition in Experiment 2 ($p > .05$), but a significant difference between the Cont-80 condition in Experiment 1 and the IDIL_Cont-80 condition in Experiment 2 ($p < .05$). This finding is consistent with the notion that gain is modulated by the intensity of the stimulus presented to each ear, and not by its perceived lateral position. Hence, the gain control effect found in these experiments appears to be independent of the perceived locus of the added high-intensity sound.

GENERAL DISCUSSION

Experiment 1 demonstrated that a high-intensity contralateral stimulus has a smaller effect on ipsilateral levels of performance than does a high-intensity ipsilateral stimulus. This finding may reflect a difference in the level of the gain setting of the cochlear amplifier. The differential effects of the high-intensity ipsilateral and contralateral stimuli on the baseline set of low-intensity ipsi-

lateral stimuli are consistent with the results of previous research in which it has been demonstrated that ipsilateral presentations of high-intensity stimuli produces a larger change in loudness perception than do contralateral presentations of high-intensity stimuli (Marks, 1996; Scharf et al., 2003). However, when perceived lateral position was manipulated using the IDIL paradigm, identification performance on the four baseline stimuli (which were lateralized to the left, using IDIL) was unaffected by the perceived laterality (also induced by IDIL) of the 80-dB (SPL) sound. Thus, these data do not seem consistent with the notion of a centrally mediated control of loudness perception (e.g., Marks, 1996), in the sense that it is not the perceived lateralization of the stimuli in the left or right ear that leads to recalibration but, rather, the intensities of the stimuli processed in those ears. It would be interesting to use the IDIL procedure to determine whether the loudness of a stimulus perceived to be in the left ear is affected as much by a high-intensity sound perceived to be in the contralateral ear as it is by the same sound when it is perceived to be in the ipsilateral ear. To the extent that induced loudness reduction and changes in identification accuracy reflect the operation of the same mechanism, we would expect that the presentation of a high-intensity stimulus lateralized to the contralateral ear (using IDIL) would produce the same change in loudness as a high-intensity stimulus lateralized to the ipsilateral ear.

In general, there is accumulating evidence that both loudness and identification are affected by the range of sound intensities that are either experienced or expected in the auditory system. This raises the interesting question as to whether the effects of context on loudness and on intensity identification accuracy are mediated by the same mechanisms. It has been well documented that the loudness of sounds is influenced by the range and/or intensity levels (both ipsilateral and contralateral) that are experienced during a session (e.g., Arie & Marks, 2003a,

2003b; Mapes-Riordan & Yost, 1999). For example, the occurrence of an intense sound can produce a 10-dB or more reduction in the loudness of a less intense sound (induced loudness reduction; see Scharf et al., 2003, for a review). What is not clear is the relationship between induced loudness reduction and reduced identification accuracy for soft sounds when an intense sound is occasionally presented.

One possibility is that both induced loudness reduction and reduced identification accuracy are mediated by a nonlinear gain control mechanism in the auditory system that is under top-down control (Parker et al., 2002; Parker & Schneider, 1994; Schneider & Parker, 1990). When only low intensities are experienced or expected, the gain is set to a high value so as to ensure that the sounds are heard and to improve discriminability among them. However, when high-intensity sounds are experienced or expected, gain will be reduced through nonlinear compression, to keep the auditory system from saturating. The net effect of lowering the gain will be a reduction in loudness and poorer identification of low-intensity sounds. However, there is at least one study that suggests that the effects of context on loudness and identification may not be so tightly linked.

Arieh and Marks (2003a) had participants judge which of two sequentially presented tones was louder. In their baseline conditions, only two tones were presented: a target tone that was fixed at 60 dB (SPL), followed by a comparison tone that was systematically varied in intensity. The participants indicated whether the comparison tone was softer or louder than the target tone. In the subsequent experimental condition, the two tones were preceded by an 80-dB (SPL) *recalibration tone*. The presence of the recalibration tone dramatically reduced the loudness of the comparison tone (up to 11 dB). Interestingly, this recalibration occurred independently of the instructions to ignore the *recalibration tone*. By way of contrast, in Parker et al.'s (2002) study, a loud (95-dB [SPL]) *warning tone* that preceded the two tones on each trial had a negligible effect on identification accuracy. Parker et al. interpreted the results as indicating that the predictability of the warning tone allowed for a rapid adjustment of the gain control mechanism. Hence, when the participants were asked to match the loudness of one tone to that of another, the expectation and presence of a loud tone preceding a loudness match dramatically reduced the loudness of the comparison tone, whereas the presence of a high-intensity tone preceding an identification of stimulus intensity had no effect on accuracy. One possible explanation for the discrepancy between these studies is that there was no need for the participants to make a rapid adjustment in gain for loudness matching but an adjustment was necessary for intensity identification. It is also possible that loudness recalibration is governed by mechanisms that are different from those that control intensity identification. Further experiments will be required to determine which explanation is more appropriate.

CONCLUSIONS

The accuracy with which the four baseline stimuli were identified was reduced when an 80-dB (SPL) stimulus was added either ipsilaterally or contralaterally to the base set, with the reduction in accuracy being greater for the ipsilateral than for the contralateral condition. The present results help to identify the nature of the gain control mechanism and the level(s) of the nervous system at which it operates. Experiment 1 demonstrated that the inclusion of high-intensity contralateral stimuli can affect the ipsilateral level of sensitivity. Hence, the degree of amplification in an ear is affected (albeit to a much lesser extent) by events occurring in the contralateral ear, indicating a degree of bilateral control. Because the earliest level at which information from the two ears converges in the auditory system is at the level of the superior olive, we know that the gain control mechanism must engage neural circuitry at this level or above. Moreover, the fact that acoustic stimulation to one ear reduces evoked otoacoustic emissions to a stimulus in the contralateral ear (Maison et al., 2000; Morand-Villeneuve et al., 2002) suggests that the cochlear amplifier itself is subject to top-down control. (To the extent to which EOAEs represent the activity of the outer hair cells, the existence of a contralateral effect on their activity strongly supports the notion that there is top-down control over auditory gain at the level of the cochlea.)

Although the results of Experiments 1 and 2, coupled with the aforementioned influence of contralateral acoustic events on EOAEs, indicate that the earliest level at which top-down control can be exerted is at the level of the superior olive, these experiments do not preclude the involvement of higher level (i.e., cortical) mechanisms. However, Experiment 2 suggested that it is the experienced intensity in each ear, and not the perceived lateral position of the sounds, that is most salient to determining the level of gain. This result seems to indicate that gain control is asserted prior to the calculation of a sound's loudness and/or its perceived place in the auditory scene (Bregman, 1990).

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NOTES

1. Noises were used in this research because of the lateralization manipulation in Experiment 2. The use of correlated broadband noise across the two ears has been found to cause much stronger and more compelling lateralization than does the use of identical tones.

2. Traditional experiments that test the precedence effect over headphones simulate an original sound arriving first at one ear, then at the other, followed by a second sound (simulating the echo) that arrives at the two ears in the order opposite to that for the original sound. By presenting four sounds over headphones, a listener experiences an approximation of a sound and its echo as they would occur in a real environment (without headphones). The present research presents only two sounds, with a slight interaural delay. Although this method still causes the first-arriving wave front to take precedence, it does not fully capture the classic precedence effect—hence, the use of the descriptive phrase IDIL.

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