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Research paper

The continuity illusion adapts to the auditory scene

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ABSTRACT

The human auditory system is efficient at restoring sounds of interest. In noisy environments, for example, an interrupted target sound may be illusorily heard as continuing smoothly when a loud noise masks the interruptions. In quiet environments, however, sudden interruptions might signal important events. In that case, restoration of the target sound would be disadvantageous. Achieving useful perceptual stability may require the restoration mechanism to adapt its output to current perceptual demands, a hypothesis which has not yet been fully evaluated. In this study, we investigated whether auditory restoration depends on preceding auditory scenes, and we report evidence that restoration adapts to the perceived continuity of target sounds and to the loudness of interrupting sounds. In the first experiment, listeners adapted to illusory and non-illusory tone sweeps (targets) and interrupting noise, and we observed that the perceived continuity of the target and the loudness of the interrupting noise influenced the extent of subsequent restorations. A second experiment revealed that these adaptation effects were unrelated to the adapted spectra, indicating that non-sensory representations of the perceived auditory scene were involved. We argue that auditory restoration is a dynamic illusory phenomenon which recalibrates continuity hearing to different acoustic environments.

1. Introduction

A major challenge for the auditory system is to ensure stability of relevant sound objects in the presence of environmental noise. This stability is facilitated by perceptual filling mechanisms that may restore noisy interruptions in a foreground sound, thereby creating a continuity illusion of the foreground. In a loud scene, for example, an interrupted voice can be illusorily heard as continuing through noise (Miller and Licklider, 1950), which may help to restore the actual speech signal and improve its intelligibility (Warren, 1970; Powers and Wilcox, 1977; Bashford et al., 1992).

Since its discovery (Miller and Licklider, 1950) the continuity illusion has been investigated extensively under several names such as pulsation threshold (Houtgast, 1972), temporal induction (Warren et al., 1972), contextual concatenation (Warren, 1984), amodal completion (Miller et al., 2001), and illusory filling (Petkov et al., 2003; for reviews, see Bregman, 1990; Warren, 1999). Early research revealed that the continuity illusion depends on the masking of the gaps in the interrupted sound (Houtgast, 1972; Warren et al., 1972), or on the absence of sensory evidence for these gaps (Warren et al., 1972; Dannenbring, 1976; Bregman and Dannenbring, 1977). Another determining factor is the similarity of the sound fragments that surround a noisy interruption. For example, when the fragments of an interrupted sweep have the same frequency trajectory or when they are proximate to each other in frequency and time, they are more likely to be grouped and to produce a continuity illusion (Ciocca and Bregman, 1987). Thus, the relevance of the fragment that follows the interruption implies that the continuity illusion depends on the acoustic context (Warren, 1983; Ciocca and Bregman, 1987). Furthermore, it has been observed that the continuity illusion may fade out or fade in during long noise interruptions (Wrightson and Warren, 1981; Warren et al., 1994). This apparent partial extension of the fragmented sound during the interruption indicates that the illusion is not an all-or-none phenomenon, but a perceptual continuum (Bregman, 1990).

More recent research on the continuity illusion has extended the previous findings and stressed the relevance of acoustic onsets and offsets (edges). When a sweep intersects with a silent interruption of a longer sweep, the gap may be misattributed to the shorter sweep while the longer sweep may appear illusorily continuous (Nakajima et al., 2000). Furthermore, two spectrally segregated sweeps that partly overlap in time may be illusorily perceived as a single continuous sweep, accompanied by an additional illusory tone during the overlap (Remijn et al., 2001; Remijn and Nakajima, 2005). This effect is observed irrespective of the presence or absence of masking noise, and persists even when the spectral gap is wider than one critical band (Fletcher, 1940), indicating the involvement of non-peripheral mechanisms.

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These findings are consistent with the previous results (see previous paragraph) and support a model of auditory grouping proposed by Nakajima et al. (2000). According to this model, the illusory continuity of a sound may emerge from the perceptual binding of spectro-temporally proximate edges of different sounds.

An aspect of the continuity illusion which has received not much attention so far is the stability of the illusion across different acoustic environments. This aspect is relevant as restoration of a given sound may be desired under certain circumstances, but not under other circumstances. For example, in quiet environments, an abrupt interference by a loud sound from the background might reflect a meaningful event and thus it should *not* be smoothed into a sound of interest in the actual foreground. To achieve appropriate levels of perceptual stability, the restoration mechanism would need to adapt its output to current environmental demands.

Auditory adaptation phenomena illustrating how hearing depends on recent acoustic input have been well described in the literature. For example, the same sound may be perceived as substantially softer when a louder sound is presented shortly before (Marks, 1994). Such contrastive aftereffects have been commonly interpreted in terms of adaptation or habituation, which can be understood as reductions in behavioral or neurophysiologic responses caused by prior or ongoing stimulation. Aftereffects may occur for various low-level stimulus properties and in various sensory modalities as evidenced by previous research. Exposure to sounds was shown to induce temporary changes in the ability to discriminate intensities (Zeng et al., 1991; Zeng and Turner, 1992; Carlyon and Beveridge, 1993; Plack et al., 1995; Zeng and Shannon, 1995; Plack, 1996; Oberfeld, 2007, 2008) or to detect target sounds in noise (Penner, 1974; Kidd and Feth, 1982; Viemeister and Bacon, 1982; Wright et al., 1993). Furthermore, amplitude- or frequency-modulations (AMs or FMs, respectively) of preceding sounds were found to temporarily increase detection thresholds for AMs or FMs of subsequent sounds (Kay and Matthews, 1972; Green and Kay, 1973, 1974; Regan and Tansley, 1979; Tansley and Suffield, 1983; Moody et al., 1984; Wojtczak and Viemeister, 2003, 2005).

These and other (Rosenblith et al., 1947; Zwicker, 1964) auditory aftereffects may reflect a ubiquitous mechanism that enables the auditory system to adapt to current probabilities in the acoustic environment. Further findings of adaptation to non-illusory higher-level sound properties such as sound source location (Frissen et al., 2003, 2005; Phillips and Hall, 2005), phonemic category (Eimas and Corbit, 1973; Cooper, 1974; Diehl et al., 1978; Samuel and Newport, 1979; Simon and Studdert-Kennedy, 1978; Ohde and Sharf, 1979; Sawusch and Jusczyk, 1981; Landahl and Blumstein, 1982) or voice gender (Schweinberger et al., 2008) have extended this hypothesis. Therefore, hearing might depend not only on the acoustic input but also on its perceptual interpretation. Such a perceptual adaptation mechanism could have ecological value because it potentially improves the ability to discriminate rare sound objects in the perceived auditory scene.

To assess whether this adaptation also applies to auditory restoration, we investigated whether the continuity of tone sweeps (targets) or the masking potential of interrupting noise influence subsequent restorations of fragmented target sounds. Listeners were presented with series of schematic auditory scenes, consisting of sweeps, noise, or both (restoration condition), and rated their continuity. An ambiguous scene (probe) created a bistable restoration condition which was presented after different series of unambiguous scenes (adaptors). In the first experiment, listeners were adapted to illusory continuous, truly continuous, or discontinuous sweeps, and to loud or soft noise. We obtained evidence that auditory restoration adapts to the perceived continuity of the sweeps and also to the loudness of the interrupting noise. In a second experiment, we investigated whether this adaptation is specific to the spectra of the adapting sounds. Listeners adapted to sweeps or noise whose spectra did not overlap with the portion of the spectrum required for illusory restoration. We found that auditory restoration adapts even when the adapted and restored spectra are incongruent, and we observed that the masking potential of the noise has little impact. The results indicate that auditory restoration depends on the perceived continuity and the loudness of preceding sounds, irrespective of their frequency content. We argue that these aftereffects can be explained by adaptation to abstract, non-sensory representations of the auditory scene.

2. Materials and methods

2.1. Participants

Twenty six volunteers (age: 24 ± 3 years, mean ± standard deviation [SD]) with normal hearing abilities, mainly students from Maastricht University, participated in the study after providing informed consent. Two different groups of 12 listeners participated in experiment 1 and 2, respectively, and two other listeners participated in both experiments. Participants were uninformed about the background of the study, except for two (one of the authors and one research assistant). The local ethical committee approved the procedure.

2.2. Stimuli

An auditory scene was simulated by stimuli of 5000-ms duration (Fig. 1A) consisting of a tone sweep, white noise, or both (Fig. 1B and C). The tone's frequency was logarithmically increased from 1 to 3 kHz and its amplitude was pulsed at 2 Hz, resulting in an ascending sweep which was repeatedly interrupted by silence. For experiment 1 (Fig. 1B), the noise was band-passed from 0.9 to 3.6 kHz (two octaves, 3-dB cutoff frequencies) so that the noise covered the sweep's spectrum. To enable the probing of restoration in these spectra, the noise was inserted in the silent gaps of the sweep such that the onsets and offsets of noise and gaps were synchronized. All onsets and offsets were linearly ramped with 10-ms rise–fall times. For experiment 2 (Fig. 1C), some sweep and noise spectra were modified such that they did not overlap with the probe spectrum described above. The sweep's frequency was logarithmically decreased from 0.8 to 0.3 kHz, resulting in a pitch modulation which was reversed relative to that in experiment 1. The noise was band-passed from 0.45 to 7.2 kHz (four octaves) and band-stopped (notched) from 0.9 to 3.6 kHz (two octaves). Stimuli were sampled at 44.1 kHz with 16 bit resolution using Matlab 7.0.1 (The MathWorks Inc., Natick, MA). Stimuli were presented diotically at maximal 80 dB sound pressure level (SPL) using Presentation 9.30 software (Neurobehavioral Systems, Inc., Albany, CA, USA), a Creative Sound Blaster Audigy 2ZS sound card (Creative Technology, Ltd., Singapore), and a Sennheiser HMD 25-1 headset (Sennheiser electronic, Wedemark, Germany).

2.3. Design and task

For each experiment, three pairs of adaptors were designed to test listeners for adaptation to three different aspects of the simulated auditory scenes (Fig. 1B and C). In the "noise-interrupted sweep" conditions, the interrupted ascending sweep was alternated with noise. For experiment 1 (Fig. 1B), the overall noise level was varied (signal-to-noise ratio (SNR) = −20 or 8 dB, respectively) and the noise and sweep spectra overlapped. For experiment 2 (Fig. 1C), the overall noise level was held constant at the higher value (SNR = −20 dB), and the noise spectrum was either congruent or incongruent with the sweep spectrum. Thus, the noise was

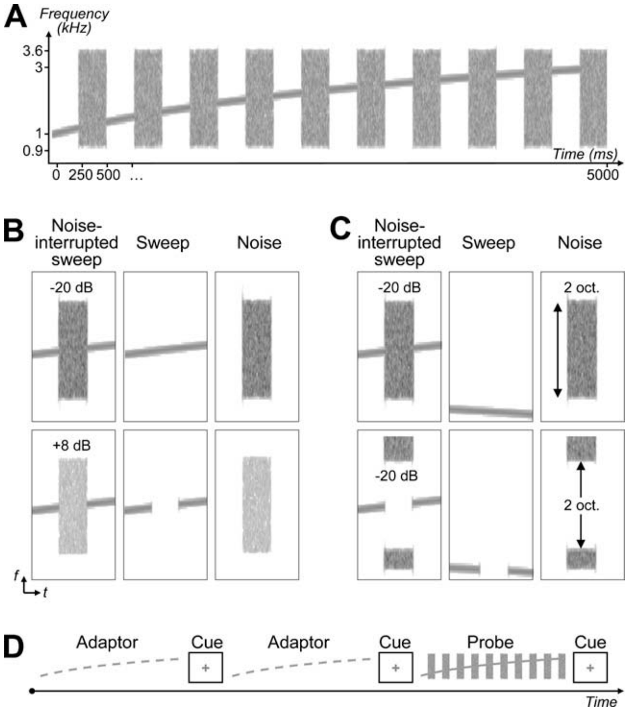

Fig. 1. Stimulus and experimental design. (A) Sound spectrogram and acoustic settings of a schematic auditory scene consisting of a discontinuous sweep repeatedly interrupted by noise. The interrupted target sound tends to be perceptually restored when the noise masks the interruptions, yielding a continuity illusion. Noise of an individually defined intermediate loudness was used to create an ambiguous masking condition (probe) under which restoration becomes bistable. (B) Truncated spectrograms of the six adaptation stimuli (adaptors) presented in experiment 1. Sweeps of differently heard continuity and noise of different masking potential were presented either simultaneously (left column) or separately (middle and right col.). For experiment 2 (C), the spectra of some adaptors were modified such that they were incongruent with the probe spectrum (A). dB-values indicate SNR; oct., octaves. (D) Adaptation, probe, and response intervals (the latter denoted by a visual cue) within a single trial sketched for a "sweep" condition in experiment 1. Listeners rated stimulus continuity on a four-point scale.

eligible to either mask the sweep or not in each experiment and, therefore, these stimuli were expected to adapt listeners to illusory continuity or true discontinuity of the target sound (see introduction). In the "sweep" conditions, the sweep was either uninterrupted (i.e. the sweep's amplitude was not pulsed) or interrupted by silence, and no noise was present. The sweep's spectrum and pitch modulation were either congruent (exp. 1) or incongruent (exp. 2) with those of the probe. These stimuli were designed to evoke adaptation to different target sounds that were physically continuous or discontinuous, in the absence of noise. The sweep level remained constant throughout both experiments. The "noise" conditions were identical to the "noise-interrupted sweep" conditions, except that no sweep was presented. These stimuli were expected to adapt listeners to noise of high or low masking potential, either at covarying (exp. 1) or fixed (exp. 2) overall noise level, in the absence of the sweep.

Participants were seated in a sound-attenuated chamber and performed a forced-choice task. They were given written instructions to rate each stimulus' overall continuity by pressing a button on a four-point scale (labeled as ">75% continuous, >50% continuous, >50% discontinuous, >75% discontinuous"). For the noise-interrupted sweep conditions, participants were instructed to attend to the sweeps and to ignore the noise, rendering these sounds the perceived foreground and background, respectively (Thurlow, 1957). Response intervals were indicated by a visual cross turning green at the stimulus offset. Before the main experiments, the participants' ability to hear continuity illusions and perform the task was assessed in 12 training trials. Individual continuity illusion thresholds were estimated based on the method of limits (Fechner, 1860): Multiple series of noise-interrupted ascending sweeps were presented in which the SNR was either gradually decreased from +1.5 dB, or increased from −20 dB, in average steps of 1.5 dB. Thresholds were estimated as the average SNR at which listeners' ratings switched from non-illusory discontinuity to illusory continuity, or vice versa. These thresholds were offset by an average step of −1.5 dB and implemented as intermediate noise levels to define individual, putative ambiguous, probe stimuli (Fig. 1A). These stimuli were expected to evoke bistable hearing of the target's continuity, as observed during informal pilot experiments.

In the main experiments, each trial was comprised of an adaptation interval during which one of the six unambiguous adaptors (Fig. 1B and C) was presented twice, followed by a test interval during which the ambiguous probe was presented (Fig. 1D). The inter-stimulus interval (ISI) was fixed at 100 ms. Each of the six conditions was presented three times in randomized blocks of 4.5-min duration. Five individually randomized blocks were presented in total and listeners were allowed to take breaks in between. One listener's data revealed bistable adaptor ratings during two successive blocks in experiment 1. These data likely reflected a fluctuation in vigilance and were discarded, which did not affect the overall results (Fig. 3A, subject S12).

2.4. Statistical analysis

For each experiment, each listener's continuity rating data were averaged across the 15 trials presented for each condition. The average ratings were statistically analyzed using a general linear model and a two-way analysis of variance (ANOVA) for repeated measures in SPSS 12.0.1 (SPSS inc., Chicago, ILL, USA). The conditions "noise-interrupted sweep", "sweep", and "noise" (Fig. 1B and C) were included in the model as a single within-subject factor with three levels (labeled as adaptor *type*). The experimental manipulations of the different adaptor types were included in another within-subject factor with two levels (labeled as adaptor *level*). Interactions between these two factors were tested with *F*-tests. For testing simple effects, pairwise comparisons between individual conditions were analyzed using two-tailed paired samples *t*-tests. Differences between experiments were analyzed with two-tailed independent samples *t*-tests. Aftereffects were computed by subtracting the average probe ratings at each adaptor *level* separately for each adaptor *type*. The relative contributions of the separated adaptor *types* (sweeps, noise) to the aftereffects of the simultaneous adaptor *type* (noise-interrupted sweeps) were estimated using a linear regression model. The model's fit was assessed with an ANOVA and an *F*-test. Significance of the estimated regression coefficients was assessed with two-tailed one-sample *t*-tests. For all group analyses, inflated type-I error probabilities caused by multiple comparisons were corrected for using Bonferroni's method.

3. Results

3.1. Threshold

The average continuity illusion threshold was estimated as −6.6 ± 2.7 dB (mean ± SD) across listeners. Thresholds estimated from descending and ascending SNR continua differed significantly (−4.7 and −8.5 dB, respectively; $t_{25} = 3.88$, $p < .001$). Listeners' reported ability to detect true discontinuities thus improved after being presented repeated continuity illusions, and vice versa, consistent with the notion of continuity adaptation.

3.2. Adaptor continuity ratings

Group analysis of listeners' adaptor continuity ratings revealed consistent results for experiment 1 and 2 (Fig. 2A and B). The midpoint of the continuity rating scale was considered to be the point at which auditory restoration became bistable (Fig. 2, large tick marks). As expected, all adaptors were rated significantly different from this point (exp. 1: all $|t_{13}| > 8.50$, all $p < 10^{-6}$; exp. 2: all $|t_{13}| > 8.02$, all $p < 10^{-6}$). Noise-interrupted sweeps were rated illusorily continuous when the noise masked the gaps in the sweep (exp. 1: $t_{13} = 18.12$, $p < 10^{-10}$; exp. 2: $t_{13} = 14.23$, $p < 10^{-9}$; Fig. 2A and B, col. 1, 2), consistent with our previous results (Riecke et al., 2008). Truly interrupted and uninterrupted sweeps alone were rated as discontinuous and continuous, respectively (exp. 1: $t_{13} = 32.44$, $p < 10^{-14}$; exp. 2: 19.51, $p < 10^{-11}$; Fig. 2A and B, col. 3, 4). Noise alone was rated as discontinuous, irrespective of its overall level (exp. 1: $t_{13} = -1.42$, $p = .18$) and masking potential (exp. 2: $t_{13} = -0.46$, $p = .66$; Fig. 2A and B, col. 5, 6). Therefore, these stimuli adapted listeners to hearing strong sweep continuity or discontinuity in the presence or absence of masking or unmasking noise.

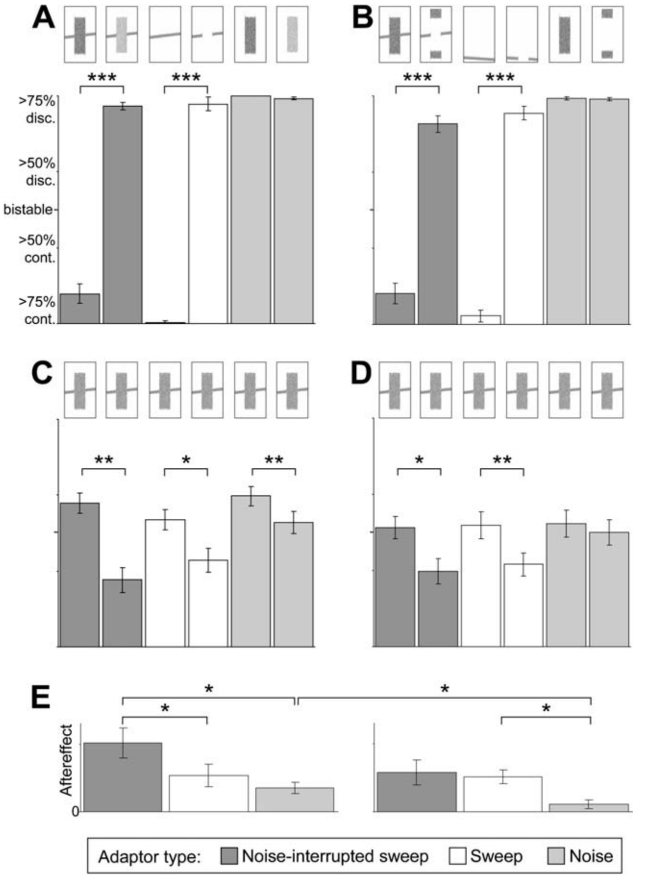

Fig. 2. Results from group analysis for experiment 1 and 2. (A, B) Mean continuity ratings of all adaptors (indicated by the truncated spectrograms) ± standard error (SE) across listeners ($N = 14$ each) for experiment 1 (A) and 2 (B). The adaptors evoked unambiguous continuity ratings. (C, D) Mean continuity ratings of the probe ± SE across listeners after hearing twice the adaptors depicted above (A, B). The true or illusory continuity of preceding sweeps exhibited aftereffects on continuity ratings of the same subsequent ambiguous target, indicating adaptation to continuity (B, C, col. 1–4). Preceding loud noise supported discontinuity ratings of the ambiguous target, indicating adaptation to noise level (C, col. 5, 6). (E) Mean differential continuity ratings of the probe ± SE across listeners representing contrastive aftereffects of the three adaptor types in experiment 1 (left) and 2 (right). Adaptation to continuity (col. 2) affected adapted and non-adapted portions of the spectrum. The aftereffects of the noise (col. 3) indicate adaptation to loudness rather than to masking potential. The aftereffects of illusory sweeps (col. 1) were mainly explained by the aftereffects of non-illusory sweeps (col. 2), indicating adaptation to restoration. All ratings are plotted on the same four-point scales. disc., discontinuous; cont. continuous; middle tick marks, presumed point of bistability; asterisks, significance levels (0.05, 0.005, or 0.0005) corrected for multiple comparisons.

3.3. Probe continuity ratings

Group analysis of listeners' continuity ratings of the same ambiguous probe (Fig. 3A and B) revealed similar results for experiment 1 and 2 (Fig. 2C and D). The probe was rated as significantly different from the presumed point of bistability when the preceding adaptors comprised a sweep and were perceived as discontinuous (noise-interrupted sweeps: $t_{13} = -3.02$, $p < .01$ (exp. 1) and $t_{13} = -3.05$, $p < .009$ (exp. 2); interrupted sweeps: $t_{13} = -2.23$, $p < .04$ (exp. 1) and $t_{13} = -2.78$, $p < .02$ (exp. 2); Fig. 2C and D, col. 1–4). Regarding differences between the individual adaptation conditions, the *type* and *level* of the adaptors exhibited an interaction (exp. 1: $F_{2,\,12} = 8.16$, $p < .006$; exp. 2: $F_{2,\,12} = 4.87$, $p < .03$), and the adaptor *level* exhibited simple effects for noise-interrupted sweeps (exp. 1: $t_{13} = -4.63$, $p < .0005$; exp. 2: $t_{13} = -3.18$, $p < .007$; Fig. 2C and D, col. 1, 2) and for sweeps alone (exp. 1: $t_{13} = -3.23$, $p < .007$; exp. 2: $t_{13} = -5.03$, $p < .0003$; Fig. 2C and D, col. 3, 4). Notably, the effect of the adaptor *level* on the adaptor ratings (Fig. 2A and B) *versus* the subsequent probe ratings (Fig. 2C and D) was reversed: Adaptation to discontinuous sweep percepts biased listeners to rate the probe as more illusorily continuous, and

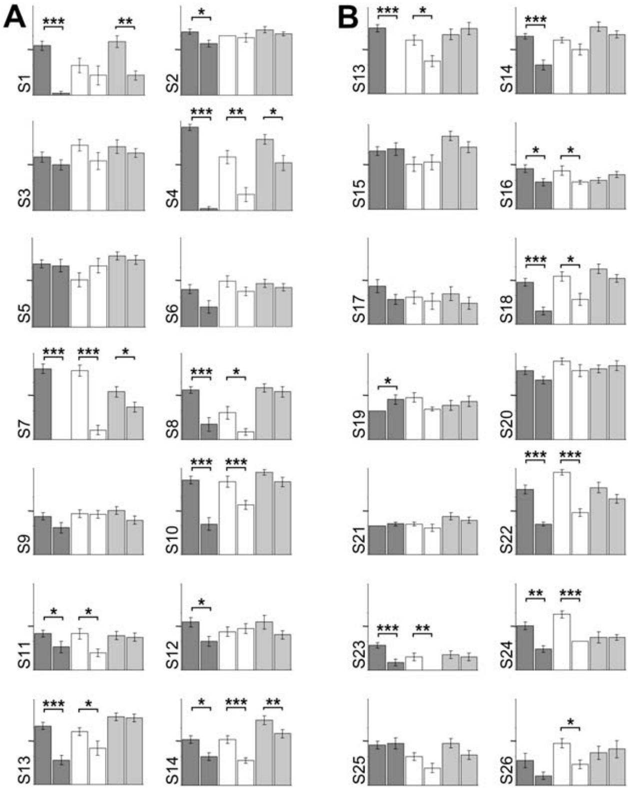

Fig. 3. Results from single-subject analysis for experiment 1 and 2. (A, B) Mean continuity ratings of the probe ± SE across trial repetitions for all listeners in experiment 1 (A) and 2 (B). 15 out of 26 listeners showed consistent significant aftereffects of perceived sweep continuity (col. 1, 2). Note that two listeners (S13, S14) participated in both experiments. For details, see Fig. 2.

vice versa for adaptation to continuous sweep percepts (Fig. 2C and D, col. 1–4). Therefore, prior presentation of these stimuli induced contrastive aftereffects on how listeners rated the same ambiguous probe, consistent with the notion of adaptation (see introduction). For the noise alone, the adaptor *level* exhibited simple effects on (exp. 1: $t_{13} = -4.20$, $p < .001$) or induced trends in (exp. 2: $t_{13} = -1.74$, $p = .11$; Fig. 2C and D, col. 5, 6) the probe ratings, partially consistent with the aftereffects observed for the noise-interrupted sweeps. Adaptation to loud masking noise biased listeners to rate the ambiguous probe as more discontinuous than adaptation to soft unmasking noise (Fig. 2C, col. 5, 6), whereas adaptation to masking or unmasking fixed-level noise did not affect these ratings significantly (Fig. 2D, col. 5, 6).

3.4. Comparison of different aftereffects

To assess the effects of varying the adaptor spectra, the aftereffects of each adaptor *type* were compared across the two experiments (Fig. 2E). This analysis revealed that spectral changes in the sweep adaptor did not affect the aftereffects of sweep continuity ($t_{26} = 0.13$, $p = .90$), indicating that these aftereffects did not depend on which part of the spectrum was adapted. The aftereffects of the noise's masking potential were significantly stronger when the overall noise level covaried with the masking potential, compared to when the overall level remained fixed ($t_{26} = 2.27$, $p < .03$). A similar trend was observed when the noise interrupted the sweep ($t_{26} = 1.54$, $p = .13$). Therefore, the aftereffects of noise depended on the overall noise level rather than on its masking potential.

Aftereffects were generally stronger for noise-interrupted sweeps than for noise (exp. 1: $t_{13} = 3.68$, $p < .003$; exp. 2: $t_{13} = 2.32$, $p < .04$) or congruent sweeps alone (exp. 1: $t_{13} = 3.58$, $p < .003$). Linear regression was used to unravel the relation between the different aftereffects (Fig. 2E, col. 1–3). For experiment 1, the aftereffects of noise-interrupted sweeps were largely explained by a weighted sum of the individual aftereffects (sweeps: $t = 4.70$, $p < .001$; noise: $t = 2.92$, $p < .01$; model fit: $R^2 = .79$, $F_{2,\ 11} = 20.74$, $p < .0002$), whereas for experiment 2 only the aftereffects of sweeps were explanatory ($R^2 = .34$, $F_{1,\ 12} = 6.20$, $p < .03$). Therefore, the aftereffects of noise-interrupted sweeps were more related to the perceived continuity of the sweeps than to the acoustic properties of the noise. The aftereffects of sweeps and noise were not significantly correlated (exp. 1: Pearson's $R = .28$, $p = .17$; exp. 2: $R = -.06$, $p = .42$), suggesting that two adaptation mechanisms were differentially involved.

4. Discussion

We investigated whether the continuity of simple target sounds and the masking potential of noise influence illusory restorations of subsequent interrupted target sounds. Our results show that preceding sweeps and noise both determine the extent of illusory restoration. First, we observed that interrupted sweeps increased the degree of subsequent restorations, whereas uninterrupted sweeps made restoration less likely. Second, loud noise reduced the extent of subsequent restorations, whereas soft noise increased their likelihood. These aftereffects are indicative of adaptation to continuity and noise level, respectively. We further investigated whether these two factors affect restorations of sounds that are spectrally incongruent with the adapting sounds. We found that continuity adaptation influenced the degree of restorations of non-adapted parts of the spectrum, and that the masking potential of interrupting noise had little impact. In summary, these results show that restoration adapts to the continuity and loudness of preceding sounds irrespectively of their frequency content.

Our conclusions are corroborated by two further observations. First, adaptation to restoration conditions (simultaneously presented sweeps and noise) revealed that continuity illusions reduced the extent of subsequent restorations, while true discontinuity percepts made restoration more likely. These aftereffects of preceding continuity illusions were largely explained by the aftereffects of true continuity percepts, indicating that listeners adapted to the restored rather than physical continuity. Second, the aftereffects of preceding continuity illusions further scaled with the loudness of the interrupting noise, suggesting that two adaptation mechanisms were differentially involved.

4.1. Previous studies on auditory adaptation

Recent studies on non-illusory phenomena have consistently reported that auditory adaptation applies to higher-level sound properties. It has been shown that listeners' judgments of the identity of a phoneme, the gender of a voice, or the spatial location of a tone depend on prior exposure to the respective sound categories (see introduction). It was commonly observed that the adaptive effects were influenced slightly by preceding sound-frequencies. Tones, for example, were reported to affect the localization of subsequent tones, even when the consecutive tone frequencies differed by two or four octaves (Frissen et al., 2003, 2005). Similarly, gender categorizations of voices may be determined by preceding voices, but not by preceding tones of different frequencies (Schweinberger et al., 2008). These results suggested that changes in auditory categorization may reflect adaptive changes in abstract, non-sensory sound representations. Our results consistently show that aftereffects on restoration are almost unaffected by the adapted sound-frequencies, supporting the previous notion that non-sensory sound representations may have adapted.

There is also evidence that preceding sounds may influence the loudness of subsequent sounds (Marks, 1988; Mapes-Riordan and Yost, 1999; Scharf et al., 2002). Adaptation to loud tones may cause loudness reductions of 10 dB or more in subsequent softer tones (Marks, 1993; Arieh and Marks, 2003a; Nieder et al., 2003; Oberfeld, 2007), especially for adaptor levels of 60–80 dB (Mapes-Riordan and Yost, 1999) and for tones of similar frequency (Marks and Warner, 1991; Marks, 1994; Wagner and Scharf, 2006). Loudness reductions may emerge about 200 ms after the adapting sound and may persist for several seconds (Arieh and Marks, 2003b; Arieh et al., 2005; Wagner and Scharf, 2006; Nieder et al., 2007). These values are compatible with the sound levels and time scales in our study, and therefore loudness adaptation may account for the noise level aftereffects that we observed. Specifically, the loud noise could have reduced the loudness of subsequent noise, thereby enhancing the relative audibility of the partially masked gaps, and suppressing the restoration of the target.

4.2. Contextual factors influencing auditory restoration

A common view on auditory restoration states that the putative underlying mechanisms analyze incoming sounds for their relative spectrum levels, i.e. for whether the interrupting sound masks the foreground gaps. Depending on the gaps' relative audibility, the gaps may or may not be filled by the interrupting sound, which yields a foreground percept that can be categorized as either illusorily continuous or truly discontinuous (for review, see Bregman, 1990; Warren, 1999).

Our data demonstrate that the extent of restoration of an interrupted target sound depends on preceding continuity illusions and other factors which generally influence continuity perception, i.e. true target continuity and noise levels. The absence of frequency selectivity that we observed raises doubts on the possibility that adaptation modulated the sensory input to the restoration mechanisms. This finding, together with the observed adaptation to perceived continuity, supports the notion that the perceptual output of auditory restoration was affected by the preceding sounds. In other words, adaptation probably did not influence the processing of low-level acoustic properties, but the integration of the target and noise spectra, and the categorization of the resulting percept. Modulations of restoration may induce adaptive changes in the audibility of the continuity illusion, whereas modulations of categorization may cause adaptive shifts in an implicit continuity criterion.

Even though these factors cannot be fully disentangled from our data, explanations by continuity criterion shifts alone seem unlikely. First, larger criterion shifts would be expected after stronger continuity ratings, producing stronger bias towards discontinuity ratings. Our results are inconsistent with this prediction since truly continuous sweeps induced significantly weaker bias than illusory continuous sweeps, even though the former were rated significantly more continuous. Second, similar criterion shifts and response biases would be expected after similarly rated adaptors. This prediction is also incompatible with our data given the different biases induced by the *indifferently* rated noise adaptors. These aftereffects more likely reflected loudness adaptation (see previous paragraph) which has been shown to influence perceived sound levels rather than categorization criteria (Arieh and Marks, 2003a). Finally, debriefings indicated that our listeners were unaware of being repeatedly presented with the same ambiguous sound, and our impression was that adaptation influenced the ability to perceptually integrate the noise with the target.

In summary, these considerations suggest that listeners did not rate continuity simply based on previous button presses. It is possible that preceding sounds induced adaptive changes in restoration and thereby shifted listeners' continuity criteria, or vice versa. Preceding sounds may have altered schemas of auditory continuity, thereby recalibrating listeners' perceptual interpretation of the ambiguous illusory sound (Bregman, 1990). Further experiments including appropriate control conditions and analysis in terms of signal detection may help disentangle these possibilities.

4.3. Potential neural mechanisms for perceived continuity adaptation

Previous research has shown that auditory restoration may involve activity in primary auditory cortical neurons which typically respond to gaps in sounds. The responses of such neurons may be suppressed when a noise facilitates restoration (Petkov et al., 2007; for review see Recanzone and Sutter, 2008) and may further scale with changes in the illusory continuity of an interrupted sound (Riecke et al., 2007). Other neurons in primary auditory cortex were shown to adapt for several seconds (Ulanovsky et al., 2003, 2004; Barlett and Wang, 2005; Werner-Reiss et al., 2006) and alter their responses to consecutive tones, even when the adapted tone frequency differed by one octave (Barlett and Wang, 2005).

It may be possible that neurons in primary auditory cortex change their responses also after continuity adaptation, thereby modulating the detectability of subsequent gaps. Furthermore, their output could be gated by top-down factors, such as by adaptive schemas of continuity, which bias the perceptual interpretation of ambiguous gaps. At present, these potential mechanisms remain speculative and neural correlates of the observed adaptation effects are yet to be determined. The present study provides a useful basis for controlling continuity illusions without confounding stimulus changes, ideally suited for neurophysiologic investigations of auditory restoration.

5. Conclusions

Auditory restoration seems to be a flexible phenomenon which adapts to foreground continuities and background levels in the perceived auditory scene. Ten seconds of adaptation are sufficient to affect restorations within the following five seconds. We propose that the tracking of sounds of interest during noisy interruptions may improve after hearing discontinuities. Potentially relevant interruptions, however, may become more salient after hearing ongoing foregrounds or loud noise. These enhancing effects may help optimizing continuity perception and facilitate useful hearing in different acoustic environments.

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