Dominance of persistence over adaptation in forward masking

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Abstract

Persistence of excitation and neural adaptation are competing theories proposed to explain the mechanisms underlying psychophysical forward masking. Previous research has been directed towards finding models that accurately describe the phenomenon but cannot account for the underlying explanation. The current study was designed to determine which theory best accounts for results obtained from behavioral gap duration adjustment tasks. Thirteen adults adjusted the gap within asymmetrical noise markers to be subjectively equal to the gap within equal-intensity-noise markers. The duration of the perceived gap between the asymmetrical markers is expected to vary depending on which theory dominates perception. The persistence of excitation mechanism would lead to longer duration gaps when the second noise marker is lower in intensity than the preceding. Neural adaptation would result in matched gaps that are shorter in duration when the second noise marker was lower in level. The outcome of our data analysis is consistent with the persistence of excitation as a dominant mechanism in forward masking.

Keywords Psychoacoustics · Adaptation and aftereffects · Audition

Introduction

Forward masking is a phenomenon that occurs when the threshold of a signal is increased due to the presence of a preceding stimulus (Oxenham, 2001; Plack & Oxenham, 1998; Widin & Viemeister, 1979). Two theories, persistence of excitation (Plomp, 1964; Oxenham & Moore, 1994) and neural adaptation (Nelson & Swain, 1996), have been proposed to explain existing psychophysical forward-masking data. The persistence of excitation theory, also known as the temporal integration theory, states that forward masking occurs because of persisting neural activity in the auditory

system after the physical offset of the masker (Fastl, 1977; Moore, Glasberg, Plack, & Biswas, 1988; Penner, 1977; Plack & Oxenham, 1998; Plomp, 1964). The neural adaptation theory supports the notion of reduced neural activity in the auditory system following a masker as a cause of forward masking (Relkin & Turner, 1988; Smith, 1977, 1979). Motivation for the current study stems from the lacking discriminability between the roles of the two proposed theories.

The evidence for persistence of excitation first came from the study in which Plomp (1964) measured the smallest detectable silent gap between two noise pulses. He varied the relative intensity of the noise pulses and found that individuals required longer silent gaps when the second noise pulse was lower in intensity than the first. Based on this result, he concluded that auditory sensation persists for approximately 200–300 ms post offset of a signal before it decays. Later studies have revealed similar findings when using ramped (rising intensity) and damped (falling intensity) signals. Data have consistently shown that ramped signals are perceived to be longer in duration (DiGiovanni & Schlauch, 2007; Grassi & Darwin, 2006; Schlauch, DiGiovanni, Olson, & Donlin, 2001a; Schlauch, Ries, & DiGiovanni, 2001b) and louder (Irino & Patterson, 1996; Neuhoff, 1998; Stecker & Hafter, 2000) compared to damped sounds. Specifically, ramped sounds were found to be 1.5 to 2 times longer and needed to be 2 to 3 dB lower than damped sounds to be perceived as equal (Ries, Schlauch, & DiGiovanni, 2008; Schlauch, Ries, & DiGiovanni, 2001b). This supports the notion that sounds

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ending at higher intensities will result in more persistent neural firing than sounds ending at lower intensities. While the majority of evidence supporting persistence of excitation comes from behavioral data, physiological data have also been collected. A recent experiment by Wang, Qin, Chimoto, Tazunoki, and Sato (2014) explored the physiologic response within cats' higher auditory cortex neurons when exposed to ramped and damped sounds. The stimuli presented mirrored the stimuli used in the Ries et al. (2008) study. Wang and colleagues focused their study on excitatory responses from edge cells in the cats' auditory cortex because they are sensitive to amplitude changes in sounds; in other words, they respond to rapid temporal attack and decay. Responses from the edge cells in cats were found to be 1.4 times longer and 1.2 times larger for ramped sounds than damped sounds (Wang et al., 2014). These results reinforce existing psychophysical data (Ries et al., 2008) and provide insight to a higher-up physiological mechanism driving the nature of the perception of ramped and damped sounds in humans, ultimately supporting the persistence of excitation theory.

Reduction in the neural activity of the auditory system following a masker, known as neural adaptation, is another theory proposed to account for forward masking (Relkin & Turner, 1988; Smith, 1977, 1979; Nelson & Swain, 1996). Evidence for the adaptation theory of forward masking mostly stems from psychoacoustic and neurophysiologic data obtained from the peripheral and central auditory pathways. Relkin and Turner (1988) noted a 50 dB increase in the detection threshold of a signal following a masker when measured behaviorally through psychoacoustic studies. They suggested that 21 dB of the 50 dB threshold increase could be attributed to adaptation at the level of the auditory nerve. To address forward masking in the central auditory system, Nelson, Smith, and Young (2009) measured the growth of forward masking in marmoset inferior colliculi. About ninety percent of the results revealed inhibitory responses following the offset of a masker as the main contributor towards forward masking. At high intensity levels, and in the other ten percent of their results, persistence of excitation was found in only a few neurons. Overall, Nelson et al. (2009) concluded that the physiological forward masking data they collected at the level of the inferior colliculus was best explained by neural adaptation.

Further support for forward masking existing at higher levels of the auditory system, not exclusive to either theory, comes from a study by Shannon (1990) exploring forward masking in cochlear implant patients. Shannon (1990) reported that cochlear implant patients have a similar forward masking pattern to those with normal hearing. Since individuals with cochlear implants do not have a normally-functioning peripheral auditory system, these data show that forward masking must also occur at more central levels of the auditory pathway. Furthermore, early studies completed by Elliot (1962) and Deatherage and Evans (1969) reveal the

presence of forward masking in dichotic listening conditions. Reevaluating the effects of forward masking seen in binaural tasks will strengthen the argument of the role of higher-level mechanisms. To account for the potential central components of forward masking, both binaural and monaural tasks were developed for the current study.

Most research has focused on the development of models and theories that can explain data obtained from forward masking studies. However, findings illuminating the relative roles of possible mechanisms contributing to forward masking is lacking. Oxenham (2001) sought to determine which model explaining forward masking, adaptation or integration, would best fit forward masking data. Signal detection thresholds were obtained from four participants and the means and standard deviations were recorded. Researchers then fit these values to the models. Both models were able to account for at least part of forward masking if minor adjustments were made to each, so the dominant theory was not clearly identifiable. Another similarly-motivated study compared simulated forward masking using the temporal-window model and the adaptation-loop model (Ewert, Hau, & Dau, 2007). Each study made similar conclusions: models designed to fit neural adaptation or persistence of excitation can each accurately explain the collected data. Both Oxenham (2001) and Ewert et al. (2007) discuss the inconsistency in which the two theories are compared. In both cases, data were collected and then fit to a model rather than using the theories to describe the outcome of the data. With the number of variables that can be tuned to fit a data set, it was not surprising that both models could accurately predict the data. A novelty of the current paper is that the pattern of data will be determined by the dominant theory.

Plomp's (1964) approach was interesting in that it revealed a forward masking effect in a gap detection paradigm. With his task and most others, the overall effect can be observed and quantified, but not attributed to a particular mechanism or theory. In Plomp's case, the small gap detection thresholds do not allow an interpretation to be made. However, Plomp's paradigm might be adapted to achieve this end. According to Oxenham (2001), should adaptation drive forward masking, the detection of the signal following a masker would be determined by the components at the end of that signal. The onset of the stimuli becomes *less detectable* due to the reduction in neural response following the offset of the preceding masker. In this case, there would be inhibition of neural firing following the offset of the first noise marker, which would result in an increased perceptual gap until the second noise marker was perceived and may even alter the perceived length of the second stimulus. It is important to understand that this perception would be agnostic to the method of measurement. For example, if one stimulus impacts the perception of the following stimulus with a silent gap, as discussed by Oxenham (2001), adaptation would render that

gap as being perceived as longer since the second stimulus onset would be perceived as occurring later. Similarly, if persistence holds true, then the first stimulus would be perceived as extending beyond its physical end. As such, the perception of the gap would be relatively shorter than the physical duration would suggest. Therefore, the pattern of results from this type of comparison can inform which theory, adaptation or persistence, has a stronger effect.

To determine which mechanism is dominant, two adjustment tasks were created for the present study. In both gap duration-matching tasks, participants were asked to adjust the gap between asymmetrical noise markers (i.e., the level of first noise marker being higher than the second noise marker) to be subjectively equal to that of the gap within symmetrical noise markers (i.e., the level of noise before and after the gap being the same). To address central involvement of forward masking, gap duration matching was performed in a monaural condition (noise markers presented to one ear) and a binaural condition, in which the first stimulus was presented to the right ear and the second to the left ear.

The pattern of results will determine which theory best describes this auditory system phenomena. Should the neural adaptation theory be dominant, reduced neural firing following the offset of the initial stimulus would extend into the silent gap and potentially the onset of the second stimulus. If the neural adaptation theory was dominant, participants would require a smaller gap within the asymmetrical stimuli than symmetrical stimuli to achieve subjective equality. As the gap becomes shortened, this reduction may extend beyond the silent gap resulting in altered perception of the second stimuli (i.e., the onset may become less detectable). The persistence of excitation theory suggests that following the presentation of the first noise marker, there will be a continuation of excitation. This continuation would “run into” the gap prior to the second noise marker and in turn, the second marker would become an extension of the first. Since the symmetric stimuli have a clear gap, the participant would need to increase the gap duration between the asymmetric stimuli to achieve perceptual equality. In the instance of an audible gap, it would be so short between the two asymmetric stimuli that the participant would still require an increase in duration to be equal to the symmetric gap. Figure 1 is a visual representation of these two proposed concepts. Based on psychoacoustic data from ramped and damped sound perception (e.g., Ries et al., 2008) and recent evidence of persistence of excitation in the auditory cortex (Wang et al., 2014), the authors hypothesized that the disparity in physical gap length required for participants to match perceived gap length within asymmetric stimulus pairs would increase as the intensity of the second noise marker within the asymmetric pair decreased. This result would support persistence of excitation as the appropriate theory to describe the underlying physiological mechanism for forward masking in gap duration matching tasks.

Method

Participants

Thirteen adults with a mean age of 27 years ($SD=4.6$ years; 4 males) with normal hearing (bilateral hearing thresholds of 15 dB HL or less across the octave frequencies from 250 to 8000 Hz) participated in the monaural matching task. Twelve of these participants also took part in the binaural matching task. Informed consent was obtained and all participants were compensated for their time. All participants were trained for at least two hours prior to formal data collection.

Stimuli and procedure

Band-limited, broad-band noise markers (low-pass filtered at 8,000 Hz) were used. Stimuli were generated digitally at a sampling rate of 24,414 Hz, using a real-time signal processor (Tucker-Davis Technologies, RP 2.1) interfaced with a computer (Dell Dimension, Dim 4550). Stimuli were passed through a programmable attenuator (Tucker-Davis Technologies, PA5) and a headphone driver (Tucker-Davis Technologies, HB7) before being presented via insert earphones (ER-2A, Etymotic Research). The experiments were conducted in a double walled sound-treated booth (IAC Model 1204-A, Industrial Acoustics Corp.). Stimulus presentation and response collection were automated using custom written Matlab programs (The MathWorks, Inc).

Before the duration matching task, participants' thresholds for the noise markers were obtained separately for each ear using a two-interval forced-choice adaptive procedure that estimated a 70.7% psychometric threshold point (Levitt, 1971). The stimulus duration of each interval was 500 ms including 5 ms raised cosine onset and offset ramps. The intensity of the noise was adaptively varied following 2-down, 1-up rule using a step size of 4 dB during the first 4 reversals, and reduced to 1 dB throughout the remaining 8 intervals. After each run, the threshold at the last eight reversals were averaged to obtain a threshold estimate. A total of 3 runs per ear were completed and the geometric mean of threshold estimates was computed to obtain the threshold.

Procedure for monaural gap duration matching task

The method of adjustment procedure was used for the gap-duration matching task. Participants adjusted the gap between asymmetric stimuli to be subjectively equal to that of the standard symmetric stimuli. The durations of the gaps in the standard stimuli were chosen such that the gaps were perceived clearly. Gap-duration matches were obtained from the right ear in three conditions. In all conditions, the level of the standard noise markers and the first noise marker of the comparison stimuli was set to 30 dB SL. The first condition was the

Fig. 1 Comparison of the adaptation theory and the persistence of excitation theory as they pertain to gap duration matching tasks. The first column represents symmetrical stimuli noise markers (30-30 dB SL), the second shows asymmetric stimuli (i.e. 30-25 dB SL or 30-20 dB SL), the third depicts the hypothesized perceived gap dependent on which mechanism dominates, and the fourth describes the manner in which the gap is adjusted to be perceptually equal to the symmetrical stimuli. The top sequence, a, is a visual representation of the role the adaptation theory. The dotted line dips below the second stimulus to

represent a reduction in neural firing; the perceived gap is longer because presumably the reduction in neural firing would render the onset of the second stimulus imperceptible. In order for the gap between the two markers to be perceptually equal to that of the symmetric, it must be decreased. The bottom sequence, b, represents the persistence of excitation theory. Neural firing following the first noise marker persists into the gap and the second marker, making an audible gap very short. In order for this gap to be perceived, the participant must extend the time between the two markers

control condition, in which the level of the first and second comparison noise markers was 30 dB SL (hereafter called 30-30 dB SL), with matching performed for standard gaps of 10, 20, 30, 40, 60, 70 and 90 ms. The second condition was 30-25 dB SL with standard gaps of 15, 20, 25, 30, 40, 60, 70 and 90 ms. The third condition was 30-20 dB SL with standard gaps of 35, 40, 45, 50, 60, 70 and 90 ms. The durations of the noise markers in each observation interval were randomly chosen within an 80 ms range centered at 400 ms to eliminate overall duration and the duration of the second noise pulse as cues. Minimum gap durations per condition increased as the second stimulus decreased in intensity relative to the first to ensure an audible silent gap was present. As the second stimuli intensity decreases within an asymmetric pair, the forward masking from the initial stimuli is greater so the initial gap must be longer (i.e., a silent interval of 10 msec may not be perceived in the 30-20 dB SL condition). The inter-stimulus interval between the standard and variable noise-marker pairs was 400 ms. Participants used a dial displayed on a computer screen to adjust the gap durations within the variable stimulus pair. They were instructed to initially adjust the variable gap set such that the gap within the variable markers was clearly longer than within the standard markers. The participant would then adjust the variable gap to a clearly shorter and shorter gap. In this manner, the participant would increment towards the perceived equal gap duration. Finally, when

satisfied with their adjustments, they pressed a button on the screen to store the response. Participants were allowed to listen to the symmetric and asymmetric stimulus pairs as many times as they desired by clicking on the screen. Duration matching was conducted in two ways, the forward procedure where the standard stimuli were presented first and the reverse procedure where the standard stimuli were presented second; this was done to control for procedural bias (Stevens, 1956). Each subject completed 20 matches for each condition. A total of 440 matches per participant were obtained for each of the forward and reverse procedures. The starting gap duration and the number of dial rotations before the hard-stop (i.e., the point at which the moving the dial no longer resulted in a gap change) was reached were randomized for each adjustment sequence to render such cues unreliable.

Procedure for binaural gap duration matching task

For this experiment, the first marker of both the standard and variable marker pairs was presented to the right ear and the second was presented to the left ear. Otherwise the procedure was the same as for monaural matching. Each participant completed 10 matches for each condition. A total of 220 matches per participant were obtained for each of the forward and reverse procedures.

Results

Prior to analysis, forward and reverse procedures were averaged. There were no systematic differences between these two procedures. Differences between the averaged matched gaps and standard gaps were calculated for all levels of the three conditions for both the monaural and binaural tasks. These values served as the “standard-match” measure. Linear regression analyses were then conducted for each condition to investigate the relationship between each “standard-match” difference and the standard gap duration. Slopes for each condition of the binaural and monaural tasks were obtained from these initial linear regression analyses. The primary outcome of this study was derived from a slope comparison across conditions; doing so offered numerous advantages. A slope comparison allowed for increased statistical power by including all points for each condition in the comparison. Critically, given the low levels of the stimuli, not all listening conditions contained the same standard durations. As such, a direct, point-by-point, comparison among conditions would not be possible. With a slope comparison, no difference in slopes would be expected if neither mechanism was captured by the paradigm. Similarly, a dominance of the adaptation mechanism would result in a positive slope, whereas a dominating persistence mechanism would result in a negative slope. In both cases, the slope difference would be greater in conditions with greater differences in stimuli level. Wuensch (2016) described the process of computing the standard error of the differences between slopes to obtain a “*t*” test statistic as an alternative method that can be used to determine the magnitude of differences between groups or conditions. To determine significant differences between slopes for the present study an omnibus univariate analyses of variances (ANOVA) was conducted followed by individual paired contrast, post-hoc analyses.

Slopes and goodness-of-fit statistics are shown in Table 1 for both tasks. Fig. 2 shows the mean data for the monaural task for all three conditions as a function of standard gap duration. Results of binaural duration matching are plotted as a function of standard gap in Fig. 3. The ordinate is the difference between the matched gap and the standard gap. Differences greater than zero indicate that participants

Table 1 Regression slopes and goodness-of-fit statistics by condition for monaural and binaural tasks

Condition	Monaural matching task			Binaural matching task		
	Slope	SE of slope	R ²	Slope	SE of slope	R ²
30-30 dB SL	-0.16	0.02	0.93	-0.33	0.06	0.87
30-25 dB SL	-0.30	0.01	0.99	-0.36	0.03	0.95
30-20 dB SL	-0.49	0.03	0.98	-0.55	0.05	0.96

Fig. 2 Differences between the matched gap in the comparison and standard stimuli as a function of the standard gap in the monaural task. The symbols represent mean differences with bars representing the 95% confidence intervals. Regression lines are shown

required a duration longer than that of the standard gap for perceptual equivalence. For the monaural duration matching task, slopes for all the three conditions were significantly different. The effect sizes of the relationships between the three monaural gap conditions were: $d = 0.511$, 0.5 and 0.82 respectively. Compared to standard condition (30-30 dB SL), the slopes for the 30-25 dB SL condition, $F(1,280) = 15.5$, $p < 0.01$, and the 30-20 dB SL condition, $F(1,280) = 48.9$, $p < 0.01$, were significantly steeper (i.e., more negative). The slope for 30-20 dB SL condition was also significantly steeper than for the 30-25 dB SL condition, $F(1,280) = 15.5$, $p < 0.01$. Results for the binaural matching condition revealed no significant difference in slope between the 30-30 dB SL and 30-25 dB SL conditions, $F(1,258) = 0.36$, $p = 0.55$. However the

Fig. 3 Differences between the matched gap in the comparison and standard stimuli as a function of the standard gap in the binaural task. The symbols represent mean differences with bars representing the 95% confidence intervals. Regression lines are shown

slope for 30-20 dB SL condition was significantly steeper than for the 30-30 dB SL, $F(1,258) = 8.6$, $p < 0.01$, and 30-25 dB SL, $F(1,258) = 6.1$, $p < 0.05$, conditions. The effect sizes of the relationships between the three binaural gap conditions were: $d = 0.2$, 0.633 and 0.82 for 30-30 dB SL, 30-25 dB SL, and 30-20 dB SL, respectively. Post hoc power analyses for all binaural and monaural gap conditions revealed power greater than 0.80 .

Discussion

The current study evaluated two existing theories of forward masking, adaptation and persistence of excitation, aiming to determine which concept best accounts for this auditory phenomenon. The authors hypothesized that persistence of neural firing following the offset of an initial noise marker is more dominant. The results of the gap-duration matching experiments were consistent with our hypothesis; when the second noise marker was lower in level than the preceding, adjusted gaps set to be perceptually equal to the standard gap were longer in duration. The increase in duration suggests that the offset of the first marker extended into the perception of the following noise marker. Therefore, the persistence of excitation theory is most fitting to describe forward masking in gap duration adjustment tasks.

Steeper slopes are indicative of longer duration adjusted gaps relative to the standard gap and suggest persistence of excitation as the dominant theory. A decreased level of the second stimulus in the variable presentation (30-20) resulted in a steeper change of “standard-match” difference, as predicted by a persistence mechanism. This pattern of results was seen in both monaural and binaural conditions. If only the slope magnitudes are considered, the monaural and binaural conditions appear similar. The slopes for the 30-25 is almost identical in the monaural and binaural conditions, as was the 30-20 condition, suggesting a strong role of central mechanisms.

An additional perspective is observed when the differences between the slopes for each condition are analyzed. The 30-25 and 30-20 slope differed from 30-30 to a much smaller degree in the binaural condition, noting that some difference remains. In this case, the monaural condition demonstrated a much greater effect than the binaural condition. Similarly, Elliot (1962) and Deatherage and Evan (1969) showed a greater threshold shift in forward masked detection in monaural conditions versus dichotic conditions. The current data, therefore, agree well with previous findings, which further supports that the method used in this study is assessing the mechanisms responsible for forward masking. While it is difficult to discern which analysis is more proper, the agreement with previous findings are hard to ignore. Regardless of whether the slopes are viewed independently or in comparison with each

other, the results broadly support our hypothesis that persistence has a stronger role over adaption in perception.

Our data support the existence of persistence of excitation, yet as the intervals between the two signals increase, we see less of a forward masking effect. The decrease in the effect of forward masking as the masking interval increases has been explained by Elliot (1962). When evaluating forward masking, as the interval increases, the effect of forward masking decreases and ultimately approaches zero, especially in dichotic listening conditions (Elliot, 1962; Deatherage & Evans, 1969). Not only do these findings explain the decrease in the magnitude of the slopes as the inter-stimulus interval increased, they reinforce the legitimacy of using gap detection adjustment tasks to explore the mechanism driving forward masking since the same patterns of results were seen in traditional forward masking studies (Elliot, 1962).

There is also less direct support for persistence of excitation using ramped and damped sounds (Ries et al., 2008). Due to the perceived elongation in duration and increase in level of ramped compared to damped sounds, Ries et al. argued that persistence of excitation best accounted for the perceptual difference between the stimuli. The results of the present and previous studies, nevertheless, do not rule out the possibility that adaptation contributes to forward masking to some degree. It is possible to explain simple detection of tones in forward masking experiments using adaptation in the auditory nerve (Relkin & Turner, 1988) or adaptation at the level of inferior colliculus (Nelson et al., 2009). These explanations are isolated to individual components of the auditory system. The present data strongly suggest, however, that persistence is the dominant mechanism. Further, perception of signal duration (Fastl, 1977; Schlauch et al., 2001b) and duration matching, as used in the present study, presumably are determined broadly throughout the auditory system. Given that an auditory stimulus activates much of the neural auditory system, it is possible that effects of both adaptation and persistence mechanisms are occurring concomitantly. However, the study demonstrates which mechanism dominates by using a gap duration matching task. In this study, the results support persistence as the dominant mechanism.

Conclusion

Overall, the data obtained from the present study provide evidence supporting the persistence of excitation as the dominant theory of forward masking for gap discrimination tasks. Even though existing literature is not conclusive about where in the auditory system persistence occurs, our data support the concept that auditory sensation invoked by sound continues after the stimulus offset. Various psychophysical experiments and models have shown support for the persistence of excitation (e.g., Fastl, 1977). Studies focused on perceptual duration

and intensity levels of ramped and damped stimuli have consistently found that ramped sounds are perceived to be longer than damped sounds (Ries et al., 2008; Schlauch et al., 2001a). Recent physiological evidence in the auditory cortex for persistence of excitation supports the perceptual difference in ramped and damped sound (Wang et al., 2014). Taken together, these results indicate that the persistence of excitation theory best explains forward masking during gap discrimination tasks and may be responsible for forward masking.

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