

Emotion and the auditory brainstem response to speech

Jade Q. Wang^{a,b,*}, Trent Nicol^{a,c}, Erika Skoe^{a,c}, Mikko Sams^d, Nina Kraus^{a,b,c,e,f}

^a Auditory Neuroscience Laboratory, Northwestern University, 2240 Campus Drive, Evanston, IL 60208, USA

^b Institute for Neuroscience, Northwestern University, USA

^c Roxelyn and Richard Pepper Department of Communication Sciences and Disorders, Northwestern University, USA

^d Laboratory of Computational Engineering, Helsinki University of Technology, FI-02015 TKK, Helsinki, Finland

^e Neurobiology and Physiology, Northwestern University, USA

^f Otolaryngology, Northwestern University, USA

ARTICLE INFO

Article history:

Received 12 January 2009

Received in revised form 30 August 2009

Accepted 9 December 2009

Keywords:

Emotion

Auditory brainstem response

Speech

IAPS

EEG

Evoked response

ABSTRACT

Effects of emotion have been reported as early as 20 ms after an auditory stimulus onset for negative valence, and bivalent effects between 30 and 130 ms. To understand how emotional state influences the listener's brainstem evoked responses to speech, subjects looked at emotion-evoking pictures while listening to an unchanging auditory stimulus (danny). The pictures (positive, negative, or neutral valence) were selected from the IAPS database and controlled for dominance and arousal. Utilizing an array of measurements to assess subcortical modulation, we have found that emotion does not substantially alter brainstem responses although there is a subtle effect of background noise suppression in both emotional conditions.

Published by Elsevier Ireland Ltd.

Emotion is clearly a powerful modulator of human experience (for a review, see Dolan [13]), and converging evidence from diverse methodologies has demonstrated its impact on sensory processing of visual [2,6,9,11,16,22,30,47,51–53,62] and audiovisual stimuli [1,59]. Emotion reduces the cost of additional distracting features, facilitating visual search [14]; moreover, for low-contrast stimuli, emotional cues improve the detection threshold [46]. In the auditory modality, there is a growing body of literature in support of emotional influence [15,33,39,56,64], which has been shown as early as 20 ms after the stimulus onset for negative valence, and valence-dependent effects between 30 and 130 ms [59]. Furthermore, there are data showing attentional and perceptual modulation of transient and periodic sound processing in the human auditory nerve and brainstem [7,18,24,41]. In this study, we examine the possibility that emotion could impact the human auditory brainstem response to speech.

The extent of emotional modulation in humans needs elucidation. Modulation of the auditory system has been demonstrated from the cortex to the level of the cochlear hair cells in the auditory periphery [5,17,26,57,59,60]. Direct and widespread projections exist by which emotion, typically attributed to limbic areas, can

modulate the afferent auditory stream [31]. Retrograde trace labeling has established these projections from the basal nucleus of the amygdala to the inferior colliculus (IC) [43], an auditory relay station that plays a nontrivial role in the generation of the auditory brainstem response (ABR) [23,45]. Lesion studies have shown that the IC is necessary for amygdala activation by auditory stimulation [48], and that emotionally aversive inputs from the IC receive serotonergic modulation from the amygdala [42]. In rats, effects of emotion on the afferent auditory stream have been measured in the IC [8]. If emotion influences the human ABR, this would corroborate the existence and role of these reciprocal IC–amygdala connections in humans.

The ABR to the speech exhibits a remarkable fidelity to the stimulus [4,29,49], so much that specific acoustic components of speech are clearly observable in the response [19]. Early processing in the auditory periphery of humans was once believed to be relatively unaffected by attention, arousal or other “higher” level functions [21]. It is this independence from such factors that has allowed ABR measurements to achieve widespread acceptance as objective, non-invasive measures of the integrity of low-level auditory anatomy and physiology [28]. Nevertheless, in the past decade, the response has proven not to be entirely immune to non-auditory factors. As a highly replicable within-subject measure, subtle response differences can be detected, such as those brought about by attention modulation, influence from other modalities, and experience ([44]; reviewed in [58]). The ABR is influenced by musi-

* Corresponding author at: Northwestern University, Frances Searle Building, 2240 Campus Drive, Evanston, IL 60201, USA.

E-mail address: jadewang@u.northwestern.edu (J.Q. Wang).

cal experience [3,56,65–67], visual influences (lip-reading) [44] online context dependence (Chandrasekaran et al., Neuron 2009), short-term training [50,54], and lifelong language experience [4,10,25,32,35,45,61,63,68]. Furthermore, Galbraith et al. showed that the brainstem frequency following response (FFR)—phase-locked activity to periodic elements in the stimulus—is increased in overall amplitude by selective attention in humans [18,20]. Based on this literature, if emotion has an influence on the ABR, one would expect to observe higher magnitude in the time domain, sharper and larger peaks in the frequency domain, and/or stronger phase-locking in the emotional conditions.

Lee et al. used the International Affective Picture System (IAPS) to establish an effect of emotional valence on visual processing with fMRI [40]. IAPS pictures have been normed for emotional dimensions (valence: pleasant, unpleasant, or neutral; arousal, etc.), and have previously been used to demonstrate the effects of emotional state on the auditory evoked mismatch response [36]. A laterality effect (left hemisphere responds more to positive valence, and the right more to negative) was replicated in the auditory system with EEG [59], with the earliest effect of emotion occurring in the middle latency response range (20 ms), typically attributed to the thalamus and thalamo-cortical pathways [34]. Thus, to investigate the effects of emotion on auditory brainstem processing in humans, we used the IAPS pictures to elicit emotional states visually while neural responses to an unchanging speech sound were measured. The absence of an emotional influence on the ABR would indicate the absence of modulation via IC–amygdala connections. Utilizing an array of measurements to assess subcortical modulation, we found that emotion does not substantially alter the brainstem activity although there is a subtle valence-independent effect of background noise suppression in the frequency domain was noted.

Subjects. 11 adults (3 female), 20–30 years old, right-handed, normal vision and hearing.

Auditory stimulus. The acoustic stimulus was an emotionally neutral, fully voiced, 457 ms “Danny” [dæni], spoken by a female speaker (average fundamental frequency, $F_0 = 189.8$ Hz). The specific recording was chosen for the steady F_0 within the first syllable ($F_0 \sim 200$ Hz, see Fig. 3). In both the stimulus and the response, the F_0 and its integer harmonics are readily observable in the amplitude spectrum.

Visual stimuli. Visual stimuli were color pictures chosen from the International Affective Picture System (IAPS) [36], which contains approximately 1000 pictures which have been experimentally normed for valence and arousal [27]. Pictures were evaluated very similarly by different subject groups and elicited emotional responses [12,27,37,38]. In this study, three emotional categories were used: negative (e.g. mutilations), neutral (e.g. mushrooms) and positive (e.g. pleasant sceneries). Within a category, images (30 each) were controlled for arousal level.

Stimulus presentation. Visual stimuli were presented in monovalent (positive, negative, or neutral) blocks (random order), followed by a 5-min cool-down period to attenuate the emotional effects of each block. Auditory stimuli were concurrently presented at 1.67/s, for a total of 3240 sweeps/emotional condition (half at each polarity). Stimuli were presented with Presentation (NeuroBehavioral Systems, Inc.), which synchronizes the stimulus with the AEP recording system. Visual stimuli were projected onto a 97 cm × 122 cm screen using an LCD projector in a soundproof room, with the subject seated 3 m away. Auditory stimuli were presented binaurally at a comfortable listening level (70 dB peak SPL) through ER-3 ear inserts (Etymotic, Inc.).

Data collection. EEG: Responses were recorded in continuous mode with a PC-based AEP system running Neuroscan Acquire 4 (Neuroscan, Compumedics, Inc.) software through a SynAmp2 amplifier (Neuroscan, Compumedics, Inc.). Brainstem potentials were collected at a 20,000 Hz sampling rate, with a montage of Cz,

right ear (reference), and forehead (ground) using Ag–AgCl scalp electrodes. **Perception:** Subjects were asked to rate experiences evoked by the stimuli using standardized nine-point valence and salience (or arousal) scales following each monovalent block. The valence scale spans from 1 (maximally positive) to 9 (maximally negative), and the salience scale spans from 1 (maximally salient) to 9 (minimally salient).

Data analysis: EEG data were band-pass filtered from 100 to 2000 Hz, epoched from –100 to 500 ms relative to the stimulus onset artifact rejected from –50 to 50 μ V, and sweeps from both polarities were summed. Latencies of four reliable onset peaks, amplitudes of major spectral peaks, and robustness of phaselocking were analyzed. The vowel portions (/æ/ and /i/ of “danny”) were analyzed separately, with time ranges chosen based on morphological features of the stimulus waveform and grand average response waveform. The lengths of the vowel-evoked responses were virtually identical to those in the stimulus. In the stimulus, /a/ was defined as 22.4–212.2 ms (with spectral peaks at 201, 403, 609, 811, 1014, and 1217 Hz), and /i/ as 258.5–456.8 ms (with spectral peaks at 172, 338, 505, 673, 840, 1009, and 1175 Hz). In the response, /a/ was defined as 30–219.3 ms, and /i/ as 263.9–469.7 ms. Response spectra were obtained by fast Fourier transform, and average spectral amplitudes were calculated for 50 Hz bins centered at spectral peak for each vowel. Additionally, to calculate the robustness of phaselocking, autocorrelations, which quantify periodicity, were performed. Short-time autocorrelation (using 40-ms time bins, with 2-ms overlap) functions were calculated for each vowel segment. The maximum autocorrelation value was recorded for each bin and then averaged over the duration of the vowel, with higher values indicating greater periodicity and therefore greater phaselocking [35,63]. Signal processing and statistical analyses were performed using Matlab and Microsoft Excel.

Overall, emotion did not alter the brainstem transcription of specific acoustic elements of the speech signal. Although the visual stimuli were successful in eliciting an emotional response from the subjects (mean \pm SE; valence: neutral 5.6 ± 0.3 , negative 8.6 ± 1.5 , positive 1.5 ± 0.2 ; salience: neutral 6.7 ± 0.6 , negative 1.5 ± 0.2 , positive 3.1 ± 0.3), emotion caused neither latency nor amplitude differences. In the onset region, there were four highly reliable peaks: the onset peak, its trough, and the peak and trough that follow it (Fig. 1, inset). Those four peaks (labeled 1–4) were identified for each subject, and the latencies did not differ between emotional conditions (Table 1). The average peak autocorrelation r -values in either vowel region did not differ between emotional conditions, suggesting that the strength of the response phaselocking was not influenced by emotion (Fig. 3).

However, emotion created a subtle effect of background noise suppression in the frequency domain. The analysis of the background noise at frequencies between the spectral peaks revealed the neutral condition to have higher amplitude as compared to the emotional conditions in several frequency bins (Fig. 2b). This was

Table 1

Emotion does not affect onset peak latency. Four reliable peaks in the onset region (Fig. 1, inset) were picked, and p -values for t -tests between conditions are shown above. Except for weak trends in peak 2, emotion did not cause any significant differences in latency.

	Peak 1	Peak 2	Peak 3	Peak 4
Latency (ms)				
Positive	9.16	10.69	12.69	15.15
Neutral	9.20	11.03	12.26	14.58
Negative	9.19	10.69	12.17	14.12
p -Values				
Positive vs. neutral	0.201	0.064	0.280	0.329
Negative vs. neutral	0.607	0.085	0.754	0.297
Positive vs. negative	0.437	1	0.201	0.139

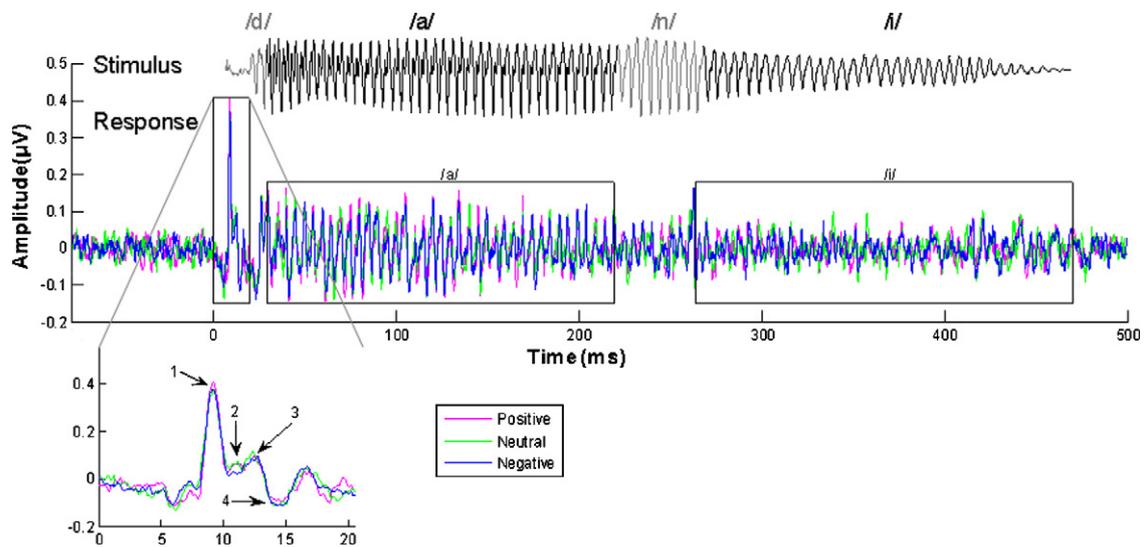


Fig. 1. Auditory brainstem response to speech. The morphological properties of the stimulus (danny) can be seen in the brainstem response. The onset region is shown enlarged beneath, with the onset peaks labeled.

more evident in the /i/ region than the /a/ region. There was one bin for which the negative and neutral conditions differed significantly. Upon closer inspection, it was determined that this difference was due to differences in peak width, not amplitude, with the negative condition possessing a sharper peak than the neutral. Moreover, a spectral analysis of the pre-stimulus period revealed no differences

between conditions, ruling out an auditory stimulus-independent state effect on the background EEG.

Here we have found that emotion does not affect the brainstem response according to a number of key indices of modulation. However, there is a slight, subtle valence-independent effect of background noise suppression in the emotional conditions.

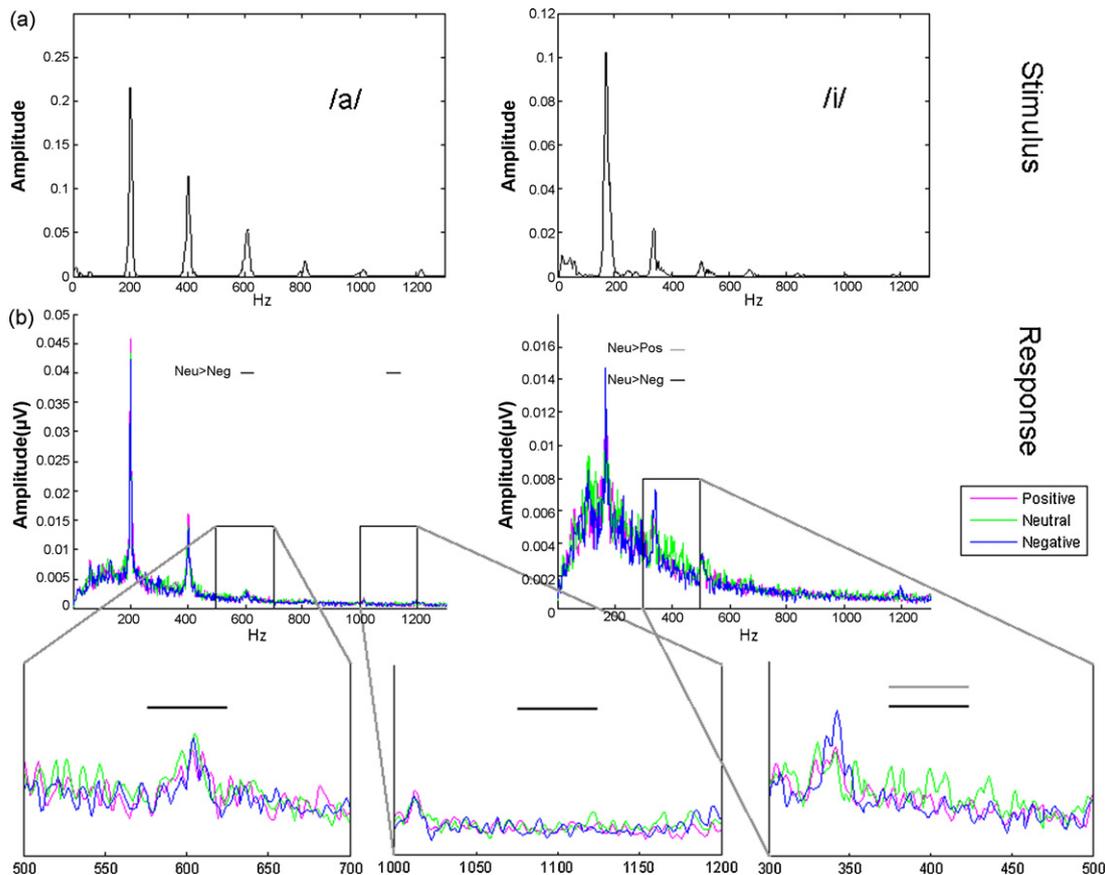


Fig. 2. Emotion reduces background spectral magnitude. (a) *Stimuli*. The vowel portions of the stimuli are separated and the peaks in the spectra identified. (b) *Response*. Average spectral amplitudes are calculated in 50 Hz bins around peaks in the stimuli and their midpoints. Horizontal bars indicate regions where Neutral has higher amplitude than an emotional condition ($p < 0.05$, positive = grey; negative = black). Except for the peak at 609 Hz ($p = 0.01$), in which negative is narrower than neutral at a peak, all other significant differences are centered on midpoints between peaks.

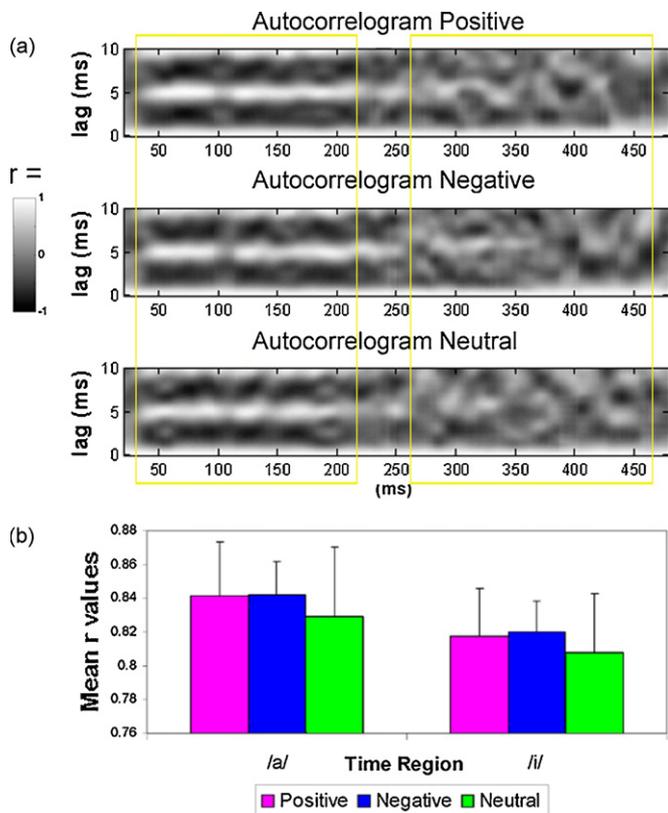


Fig. 3. Emotion does not affect response phaselocking. (a) The maximum autocorrelations r -values were calculated in 40 ms overlapping bins, and averaged for each vowel region (indicated by boxes). (b) Mean r -values did not differ between emotional conditions, but did differ between vowels.

Although the fidelity of the ABR to speech is high (readily observable in Fig. 1), when the vowel portions of the stimuli (/a/ and /i/ of “danny”) were analyzed in the frequency domain, there is a suppression of background noise which may lead to increasing the relative prominence of stimulus-relevant information (Figs. 2 and 3). In sum, the results indicated that emotion leaves the auditory brainstem response largely unaltered, but has a minor noise suppression effect.

In a previous study, we found that emotion affects cortical auditory-evoked potentials to the same stimulus as early as 20 ms after the onset of the stimulus, and in a valence-dependent manner starting 10 ms after that [59]. Most of the participants (55%) whose brainstem data are shown here participated in the cortical study. However, due to the practical limitations of collecting simultaneous cortical and brainstem responses (e.g. cortical responses require slower repetition rate and brainstem responses require greater number of sweeps), these datasets were collected in separate test sessions.

There are a number of potential reasons for the minimal modulation of the ABR by emotion observed here. It is possible that the reciprocal IC–amygdala pathways are differentially activated when emotion is visually vs. auditorily elicited. Speculatively, it stands to reason that there may be an advantage if the source of emotion is elicited through the same modality as the pathway being modulated, unlike our experimental design. Furthermore, a higher level of emotional arousal might be needed to evoke emotional modulation of the auditory brainstem response. However, the subjects’ self-reports suggest that the emotional states (more along the valence dimension than the arousal dimension) were at an amply high intensity. There is also a trend in peak 2 (Table 1 and Fig. 1, the trough following the onset peak) of the neutral condition being later

than both emotional conditions and it is possible that a significant effect would have emerged with a larger number of subjects.

When the vowel portions of the responses were analyzed separately in the frequency domain, there was a subtle but appreciable suppression of background noise in the emotional conditions regardless of valence (Fig. 2). Due to electrical activity arising from muscle tension, one might expect a state effect from emotion, with some states evoking a higher level of random neural activity (i.e. background noise) compared to others. However, in the pre-stimulus period, there were no differences between emotional conditions, ruling out the possibility of attributing the background suppression to a stimulus-independent state effect. An analysis of background activity during the response (i.e. spectral activity not occurring at stimulus-specific spectral peaks) revealed that the patterns of differences were non-identical between the two vowels, but in both, the amplitude during the neutral condition exceeded that of the emotional conditions. Since the differences tended to occur between the peaks in the response spectra, the net effect is a lower noise floor in the emotional conditions. That the quantity of background noise was non-identical for the two vowels could be attributed to the fact that the F_0 for the first vowel (/a/) was relatively steady whereas it was falling for the second vowel (/i/), thereby increasing its acoustic complexity. As demonstrated by Song et al., the effects of lifelong and short-term training on brainstem activity occurred primarily in response to the dipping tone [55], which, of four Mandarin tones, it is the tone with the highest degree of acoustic complexity [55,63] and to the most complex portion of an emotional vocal sound [56]. That is, experience-dependent effects may be sensitive to the most acoustically complex elements of the signal. In conclusion, the results indicated that the auditory brainstem response remains largely unaltered, yet exhibits a minor noise suppression effect, by emotional state.

Acknowledgement

This work was supported by a National Research Service Award Predoctoral Fellowship (F31 DC009140) from the National Institutes of Health. We thank the participants of the study, and other members of the Auditory Neuroscience Laboratory for input into this project.

References

- [1] J.L. Armony, R.J. Dolan, Modulation of auditory neural responses by a visual context in human fear conditioning, *Neuroreport* 12 (2001) 3407–3411.
- [2] M. Balconi, U. Pozzoli, Face-selective processing and the effect of pleasant and unpleasant emotional expressions on ERP correlates, *Int. J. Psychophysiol.* 49 (2003) 67–74.
- [3] G. Musacchia, M. Sams, E. Skoe, N. Kraus, Musicians have enhanced subcortical auditory and audiovisual processing of speech and music, *Proceedings of the National Academy of Sciences* 104 (2007) 15894.
- [4] N. Kraus, T. Nicol, Brainstem origins for cortical ‘what’ and ‘where’ pathways in the auditory system, *Trends in Neurosci.* 4 (2005) 5.
- [5] S.W. Bao, E.F. Chang, J.D. Davis, K.T. Gobeske, M.M. Merzenich, Progressive degradation and subsequent refinement of acoustic representations in the adult auditory cortex, *J. Neurosci.* 23 (2003) 10765–10775.
- [6] M. Batty, M.J. Taylor, Early processing of the six basic facial emotional expressions, *Cogn. Brain Res.* 17 (2003) 613–620.
- [7] L.O. Bauer, R.L. Bayles, Precortical filtering and selective attention - an evoked-potential analysis, *Biol. Psychol.* 30 (1990) 21–33.
- [8] M.L. Brandao, N.C. Coimbra, M.Y. Osaki, Changes in the auditory-evoked potentials induced by fear-evoking stimulations, *Physiol. Behav.* 72 (2001) 365–372.
- [9] S. Campanella, P. Quinet, R. Bruyer, M. Crommelinck, J.M. Guerit, Categorical perception of happiness and fear facial expressions: an ERP study, *J. Cogn. Neurosci.* 14 (2002) 210–227.
- [10] J. Cunningham, T. Nicol, S.G. Zecker, A. Bradlow, N. Kraus, Neurobiologic responses to speech in noise in children with learning problems: deficits and strategies for improvement, *Clin. Neurophysiol.* 112 (2001) 758–767.
- [11] R.J. Davidson, H.A. Slagter, Probing emotion in the developing brain: functional neuroimaging in the assessment of the neural substrates of emotion in normal and disordered children and adolescents, *Ment. Retard. Dev. Disabil. Res. Rev.* 6 (2000) 166–170.

- [12] W.J. Davis, M.A. Rahman, L.J. Smith, A. Burns, L. Senecal, D. McArthur, J.A. Halpern, A. Perlmutter, W. Sickels, W. Wagner, Properties of Human Affect Induced by Static Color Slides (Iaps) - Dimensional, Categorical and Electromyographic Analysis, *Biol. Psychol.* 41 (1995) 229–253.
- [13] R.J. Dolan, Emotion, Cognition, and Behavior, *Science* 298 (2002) 1191–1194.
- [14] J.D. Eastwood, D. Smilek, P.M. Merikle, Differential attentional guidance by unattended faces expressing positive and negative emotion, *Percept. Psychophys.* 63 (2001) 1004–1013.
- [15] H. Erhan, J.C. Borod, C.E. Tenke, G.E. Bruder, Identification of emotion in a dichotic listening task: event-related brain potential and behavioral findings, *Brain Cogn.* 37 (1998) 286–307.
- [16] H. Fischer, C.I. Wright, P.J. Whalen, S.C. McInerney, L.M. Shin, S.L. Rauch, Brain habituation during repeated exposure to fearful and neutral faces: a functional MRI study, *Brain Res. Bull.* 59 (2003) 387–392.
- [17] J. Fritz, S. Shamma, M. Elhilali, D. Klein, Rapid task-related plasticity of spectrotemporal receptive fields in primary auditory cortex, *Nat. Neurosci.* 6 (2003) 1216–1223.
- [18] G.C. Galbraith, P.W. Arbagey, R. Branski, N. Comerci, P.M. Rector, Intelligible speech encoded in the human brain stem frequency-following response, *Neuroreport* 6 (1995) 2363.
- [19] G.C. Galbraith, S.M. Bhuta, A.K. Choate, J.M. Kitahara, T.A. Mullen, Brain stem frequency-following response to dichotic vowels during attention, *Neuroreport* 9 (1998) 1889–1893.
- [20] G.C. Galbraith, D.M. Olfman, T.M. Huffman, Selective attention affects human brain stem frequency-following response, *Neuroreport* 14 (2003) 735.
- [21] M.H. Giard, L. Collet, P. Bouchet, J. Pernier, Auditory selective attention in the human cochlea, *Brain Res.* 633 (1994) 353–356.
- [22] A. Holmes, P. Vuilleumier, M. Eimer, The processing of emotional facial expression is gated by spatial attention: evidence from event-related brain potentials, *Cogn. Brain Res.* 16 (2003) 174–184.
- [23] L.J. Hood, Clinical applications of the auditory brainstem response, Singular Pub. Group, San Diego, 1998.
- [24] J. Hoormann, M. Falkenstein, J. Hohnsbein, Effect of selective attention on the latency of human frequency-following potentials, *Neuroreport* 5 (1994) 1609–1612.
- [25] J. Hornickel, E. Skoe, T. Nicol, S. Zecker, N. Kraus, Subcortical Differentiation of Voiced Stop Consonants: Relationships to Reading and Speech in Noise Perception, *Proceedings of the National Academy of Science* 106 (2009) 13022–13027.
- [26] D.R.F. Irvine, R. Rajan, M. Brown, Injury- and use-related plasticity in adult auditory cortex, *Audiol. Neuro-Otol.* 6 (2001) 192–195.
- [27] T. Ito, J.T. Cacioppo, P.J. Lang, Eliciting affect using the international affective picture system: Trajectories through evaluative space, *Pers. Soc. Psychol. Bull.* 24 (1998) 855–879.
- [28] J.T. Jacobson, *The Auditory Brainstem Response*, Taylor & Francis, 1985.
- [29] E. Skoe, N. Kraus, Auditory brainstem response to complex sounds: a tutorial, *Ear and Hearing*, (in press).
- [30] W. Joost, M. Bach, J. Schulte-Monting, Influence of mood on visually evoked potentials: a prospective longitudinal study, *Int. J. Psychophysiol.* 12 (1992) 147–153.
- [31] J.H. Kaas, T.A. Hackett, M.J. Tramo, Auditory processing in primate cerebral cortex, *Curr. Opin. Neurobiol.* 9 (1999) 164–170.
- [32] C. King, C.M. Warrier, E. Hayes, N. Kraus, Deficits in auditory brainstem pathway encoding of speech sounds in children with learning problems, *Neurosci. Lett.* 319 (2002) 111–115.
- [33] J.P. Kline, G.E. Schwartz, D.F. Fitzpatrick, S.E. Hendricks, Defensiveness anxiety and the amplitude/intensity function of auditory-evoked potentials, *Int. J. Psychophysiol.* 15 (1993) 7–14.
- [34] N. Kraus, T. McGee, The middle latency response generating system, *Electroencephalogr. Clin. Neurophysiol. Suppl.* 44 (1995) 93–101.
- [35] A. Krishnan, Y. Xu, J. Gandour, P. Cariani, Encoding of pitch in the human brainstem is sensitive to language experience, *Cogn. Brain Res.* 25 (2005) 161–168.
- [36] P. Lang, D.V. Öhman, The international affective picture system [photographic slides], (1988).
- [37] P.J. Lang, M.K. Greenwald, M.M. Bradley, H. AO, Looking at pictures - affective, facial, visceral, and behavioral reactions, *Psychophysiol.* 30 (1993) 261–273.
- [38] P.J. Lang, M.M. Bradley, B.N. Cuthbert, Emotion, attention, and the startle reflex, *Psychol. Rev.* 97 (1990) 377–395.
- [39] J.E. Ledoux, A. Sakaguchi, D.J. Reis, Subcortical Efferent Projections of the Medial Geniculate-Nucleus Mediate Emotional Responses Conditioned to Acoustic Stimuli, *J. Neurosci.* 4 (1984) 683–698.
- [40] G.P. Lee, K.J. Meador, D.W. Loring, J.D. Allison, W.S. Brown, L.K. Paul, J.J. Pillai, T.B. Lavin, Neural substrates of emotion as revealed by functional magnetic resonance imaging, *Cogn. Behav. Neurol.* 17 (2004) 9–17.
- [41] J.H. Lukas, The role of efferent inhibition in human auditory attention - an examination of the auditory brain-stem potentials, *Int J Neurosci* 12 (1981) 137–145.
- [42] C.E. Macedo, G. Cuadra, V. Molina, M.L. Brandao, Aversive stimulation of the inferior colliculus changes dopamine and serotonin extracellular levels in the frontal cortex: Modulation by the basolateral nucleus of amygdala, *Synapse* 55 (2005) 58–66.
- [43] R.A. Marsh, Z.M. Fuzessery, C.D. Grose, J.J. Wenstrup, Projection to the Inferior Colliculus from the Basal Nucleus of the Amygdala, *J. Neurosci.* 22 (2002) 10449–10460.
- [44] G. Musacchia, M. Sams, T. Nicol, N. Kraus, Seeing speech affects acoustic information processing in the human brainstem, *Exp. Brain Res.* (2005) 1–10.
- [45] B. Chandrasekaran, N. Kraus, The scalp-recorded brainstem response to speech: Neural origins plast. *Psychophysiol.* (Articles online in advance of print) (2009).
- [46] E.A. Phelps, S. Ling, M. Carrasco, Research Article Emotion Facilitates Perception and Potentiates the Perceptual Benefits of Attention, *Psychol. Sci.* 17 (2006) 292.
- [47] D. Pizzagalli, T. Koenig, M. Regard, D. Lehmann, Faces and emotions: brain electric field sources during covert emotional processing, *Neuropsychologia* 36 (1998) 323–332.
- [48] A. Poremba, R.C. Saunders, A.M. Crane, M. Cook, L. Sokoloff, M. Mishkin, Functional Mapping of the Primate Auditory System, *Science* 299 (2003) 568–571.
- [49] N. Russo, T. Nicol, G. Musacchia, N. Kraus, Brainstem responses to speech syllables, *Clin. Neurophysiol.* 115 (2004) 2021–2030.
- [50] N.M. Russo, T.G. Nicol, S.G. Zecker, E.A. Hayes, N. Kraus, Auditory training improves neural timing in the human brainstem, *Behav. Brain Res.* 156 (2005) 95–103.
- [51] W. Sato, T. Kochiyama, S. Yoshikawa, M. Matsumura, Emotional expression boosts early visual processing of the face: ERP recording and its decomposition by independent component analysis, *Neuroreport* 12 (2001) 709–714.
- [52] H.T. Schupp, M. Junghofer, A.I. Weike, A.O. Hamm, Emotional facilitation of sensory processing in the visual cortex, *Psychol. Sci.* 14 (2003) 7–13.
- [53] H.T. Schupp, M. Junghofer, A.I. Weike, A.O. Hamm, Attention and emotion: an ERP analysis of facilitated emotional stimulus processing, *Neuroreport* 14 (2003) 1107–1110.
- [54] J.H. Song, E. Skoe, P.C.M. Wong, N. Kraus, Plasticity in the Adult Human Auditory Brainstem following Short-term Linguistic Training, *J. Cogn. Neurosci.* 20 (2008) 1892–1902.
- [55] J.H. Song, E. Skoe, P.C.M. Wong, N. Kraus, Plasticity in the adult human auditory brainstem following short-term linguistic training, *Human Brain Mapping Conference*, Chicago, IL, 2007.
- [56] D.L. Strait, E. Skoe, N. Kraus, R. Ashley, Musical experience and neural efficiency: effects of training on subcortical processing of vocal expressions of emotion, *Eur. J. Neurosci.* (2009).
- [57] N. Suga, Z.J. Xiao, X.F. Ma, W.Q. Ji, Plasticity and corticofugal modulation for hearing in adult animals, *Neuron* 36 (2002) 9–18.
- [58] T. Tzounopoulos, N. Kraus, Learning To Encode Timing: Mechanisms of Plasticity in the Auditory Brainstem, *Neuron* 62 (2009) 463–469.
- [59] J.Q. Wang, T. Nicol, E. Skoe, M. Sams, N. Kraus, Emotion Modulates Early Auditory Response to Speech, *J. Cogn. Neurosci.* 21 (2009) 2121–2128.
- [60] N.M. Weinberger, W. Hopkins, D.M. Diamond, Physiological plasticity of single neurons in auditory cortex of the cat during acquisition of the pupillary conditioned response: I. Primary field, *Behav. Neurosci.* 98 (1984) 171–188.
- [61] B. Wible, T. Nicol, N. Kraus, Correlation between brainstem and cortical auditory processes in normal and language-impaired children, *Brain* 128 (2005) 417–423.
- [62] L.M. Williams, B.J. Liddell, J. Rathjen, K.J. Brown, J. Gray, M. Phillips, A. Young, E. Gordon, Mapping the time course of nonconscious and conscious perception of fear: an integration of central and peripheral measures, *Hum. Brain Mapp.* 21 (2004) 64–74.
- [63] P.C.M. Wong, E. Skoe, N.M. Russo, T. Dees, N. Kraus, Musical experience shapes human brainstem encoding of linguistic pitch patterns, *Nat. Neurosci.* 10 (2007) 420.
- [64] L.L. Young Jr., J.S. Horner, A comparison of averaged evoked response amplitudes using nonaffective and affective verbal stimuli, *J. Speech Hear. Res.* 14 (1971) 295–300.
- [65] J. de Boer, A.R.D. Thornton, Neural Correlates of Perceptual Learning in the Auditory Brainstem: Efferent Activity Predicts and Reflects Improvement at a Speech-in-Noise Discrimination Task, *J. Neurosci.* 28 (2008) 4929.
- [66] K.M. Lee, E. Skoe, N. Kraus, R. Ashley, Selective Subcortical Enhancement of Musical Intervals in Musicians, *J. Neurosci.* 29 (2009) 5832–5840.
- [67] A. Parbery-Clark, E. Skoe, N. Kraus, Musical Experience Limits the Degradative Effects of Background Noise on the Neural Processing of Sound, *J. Neurosci.* 29 (2009) 14100–14107.
- [68] K. Banai, J. Hornickel, E. Skoe, T. Nicol, S. Zecker, N. Kraus, Reading and Subcortical Auditory Function, *Cereb. Cortex* 19 (2009) 2699–2707.