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REPORT

Hemispheric asymmetries in children's perception of nonlinguistic human affective sounds

Seth D. Pollak,[1] Lori L. Holt[2] and Alison B. Wismer Fries[3]

1. Department of Psychology, University of Wisconsin at Madison, USA
2. Department of Psychology, Carnegie Mellon University and the Center for the Neural Basis of Cognition, USA
3. Department of Psychology and Waisman Center, University of Wisconsin at Madison, USA

Abstract

In the present work, we developed a database of nonlinguistic sounds that mirror prosodic characteristics typical of language and thus carry affective information, but do not convey linguistic information. In a dichotic-listening task, we used these novel stimuli as a means of disambiguating the relative contributions of linguistic and affective processing across the hemispheres. This method was applied to both children and adults with the goal of investigating the role of developing cognitive resource capacity on affective processing. Results suggest that children's limited computational resources influence how they process affective information and rule out attentional biases as a factor in children's perceptual asymmetries for nonlinguistic affective sounds. These data further suggest that investigation of perception of nonlinguistic affective sounds is a valuable tool in assessing interhemispheric asymmetries in affective processing, especially in parceling out linguistic contributions to hemispheric differences.

Introduction

Little is known about developmental changes in the neural systems that subserve perception of emotional cues in the environment. One affective system, associated with activation of the right hemisphere parietotemporal area, appears to influence emotional arousal and recognition. Patients with lesions to this area have difficulty comprehending emotional tone of voice (Tucker, 1981; Tucker, Watson & Heilman, 1977) and recognizing facial displays of emotion (DeKosky, Heilman, Bowers & Valenstein, 1980). A second affective system appears to differentially involve the anterior (frontal) portions of both the RH and left hemisphere (LH) in the *experience*, as opposed to the *recognition*, of affect (Davidson, 1995; Silberman & Weingartner, 1986). For example, higher relative electroencephalographic (EEG) activation over LH frontal regions is associated with cheerful emotional states whereas higher relative activation over RH frontal regions is apparent during depressed emotional states (Davidson, 1995). Frontal EEG also predicts individual differences in emotional reactivity in that greater left-sided activation is associated with increased intensity of positive affect in response to amusing film clips (Tomarken, Davidson & Henriques, 1990). Likewise, patients with anterior RH damage tend to display euphoric emotions, whereas patients with anterior LH damage are more often sad (Gainotti, 1972).

Of particular interest is that the anterior prefrontal cortex directly communicates with posterior perceptual processing regions through amygdaloid projections (Amaral, Price, Pitkanen & Carmichael, 1992). Similarly, investigations of adult subjects have concluded that there are reciprocal relations between anterior and posterior regions such that increased activation of one region is associated with decreased activation of the other (e.g. Davidson & Hugdahl, 1996; Knight, 1991; Tucker, Stenslie, Roth & Shearer, 1981). This observation is interesting considered from a developmental perspective because there is indirect evidence that white matter connections between anterior and posterior regions develop slowly over age (Thatcher, 1994, 1996). For this reason, in children, activation of both anterior and posterior affective processes within one hemisphere may lead to quite different patterns of information processing than in adults.

Here, we examine this possibility using a behavioral approach that has proven useful in inferring processes associated with each hemisphere. In the dichotic listening (DL) technique, different information is simultaneously presented to each ear. This methodology takes advantage

Address for correspondence: Seth Pollak, Department of Psychology, 1202 West Johnson Street, University of Wisconsin at Madison, Madison, WI 53706-1696, USA; e-mail: spollak@wisc.edu

of the fact that the auditory pathways are crossed such that contralateral information is carried between the right ear (RE) and the LH and between the left ear (LE) and the RH. Although the ipsilateral pathways also carry sensory information, they are less efficient. Thus, when different information is presented to each ear, the neural architecture of the auditory system prevents subjects from simultaneously analyzing the information presented to both information channels with equal efficiency. This results in an ear asymmetry with respect to the message subjects report hearing; one ear maintains an 'advantage' such that its message is more readily perceived by a listener. When subjects report hearing the message played to the LE (LE advantage) greater activation of the RH may be inferred; likewise, reports of the message presented to the RE (RE advantage) suggest activation of the LH (Kimura, 1961). In summary, asymmetric hemispheric activation is inferred by a contralateral ear advantage (e.g. an activated LH results in a stronger RE advantage). DL performance has been correlated with more precise neurophysiological measures (Davidson & Hugdahl, 1996; Zattore, 1989).

Most prior DL studies examining emotion processing have used affectively charged words, or words spoken with prosodic inflection (see, Borod, Pick & Hall, 2000; Pollak & Wismer Fries, 2001; Shipley-Brown, Dingwall, Berlin, Yeni-Komshian & Gordon-Salant, 1988; Van Strien & Heijt, 1995; Van Strien & Morpurgo, 1992) as stimuli. Since receptive language abilities typically are left-lateralized (in right-handed individuals), linguistic stimuli may have an unequal effect on inference of affective processing across the hemispheres because the eliciting stimuli are both affective and linguistic. Thus, it is difficult to tease apart the relative contributions of LH language processing and putative affective processing. One goal of the present study is to examine the processes related to the recognition of emotional cues, while attenuating activation of language processing systems. To do so, we developed a database of nonlinguistic sounds that mirror prosodic characteristics typical of language and thus carry affective information, but do not convey linguistic information. Although less frequently studied than the visual perception of emotion or the semantic content of speech, perception of nonlinguistic acoustic events is an important aspect of human communication and such sounds carry a great deal of affective information. Using these stimuli in a DL task, we aim to disentangle the relative roles of linguistic and affective processing.

We also seek to better understand developmental changes in affective processing. As noted above, intrahemispheric interaction between anterior and posterior emotion systems may be different in mature and immature participants. Supportive of this view, Pollak and Wismer Fries (2001) employed a DL task with emotional words to demonstrate that activation of multiple affective processes within a single hemisphere results in a processing advantage for the opposite hemisphere in children, but not in adults. Other studies have also indicated that activation of multiple specialized processes within one hemisphere may produce a processing advantage for the opposite hemisphere when processing loads are high or computationally complex (Banich, 1995; Banich & Belger, 1990; Hellige, Bloch & Taylor, 1988). In light of the possibility that recognition of emotionally charged stimuli may be constrained by children's developing cognitive resource capacity, a second goal of the present study is to examine whether activation of multiple affective processes within one hemisphere differentially affects information processing in less mature participants as compared to adults when affective semantic content is present but linguistic information is not.

Hypotheses

As shown in Figure 1, the key distinctions between conditions are ear of presentation and the emotional valence of the nonlinguistic token. We predicted that perceptual asymmetries for adults and children would follow contralateral pathways (solid arrows). Dashed lines indicate ipsilateral, less efficient, pathways. Thus, neither adults nor children were expected to show perceptual asymmetries when negative stimuli were presented to the RE because relevant affective processing is purely ipsilateral and thus less efficient. As shown by the lack of arrows originating from the ear to which neutral stimuli were presented, affectively neutral stimuli were not expected to activate either anterior or posterior affective systems. Owing to the fact that there is a contralateral advantage in processing efficiency in the DL task and to the fact that the RH anterior system processes negative experience, positive stimuli presented to the LE should best activate the right *posterior* system resulting in a left ear advantage. However, when the same stimuli are presented to the RE, the left *anterior* system should be best activated resulting in a right ear advantage.

With respect to our developmental hypothesis, we expected that children and adults would show different asymmetries when negative stimuli were presented to the LE. As shown in Figure 1, this is the single condition where both anterior affective and posterior processes are activated within the same hemisphere. In adults, activation of these two processes in the RH was expected to produce an LE advantage. However, we predicted a potential cost of having both anterior and posterior systems active within a single hemisphere for immature subjects. If presentation

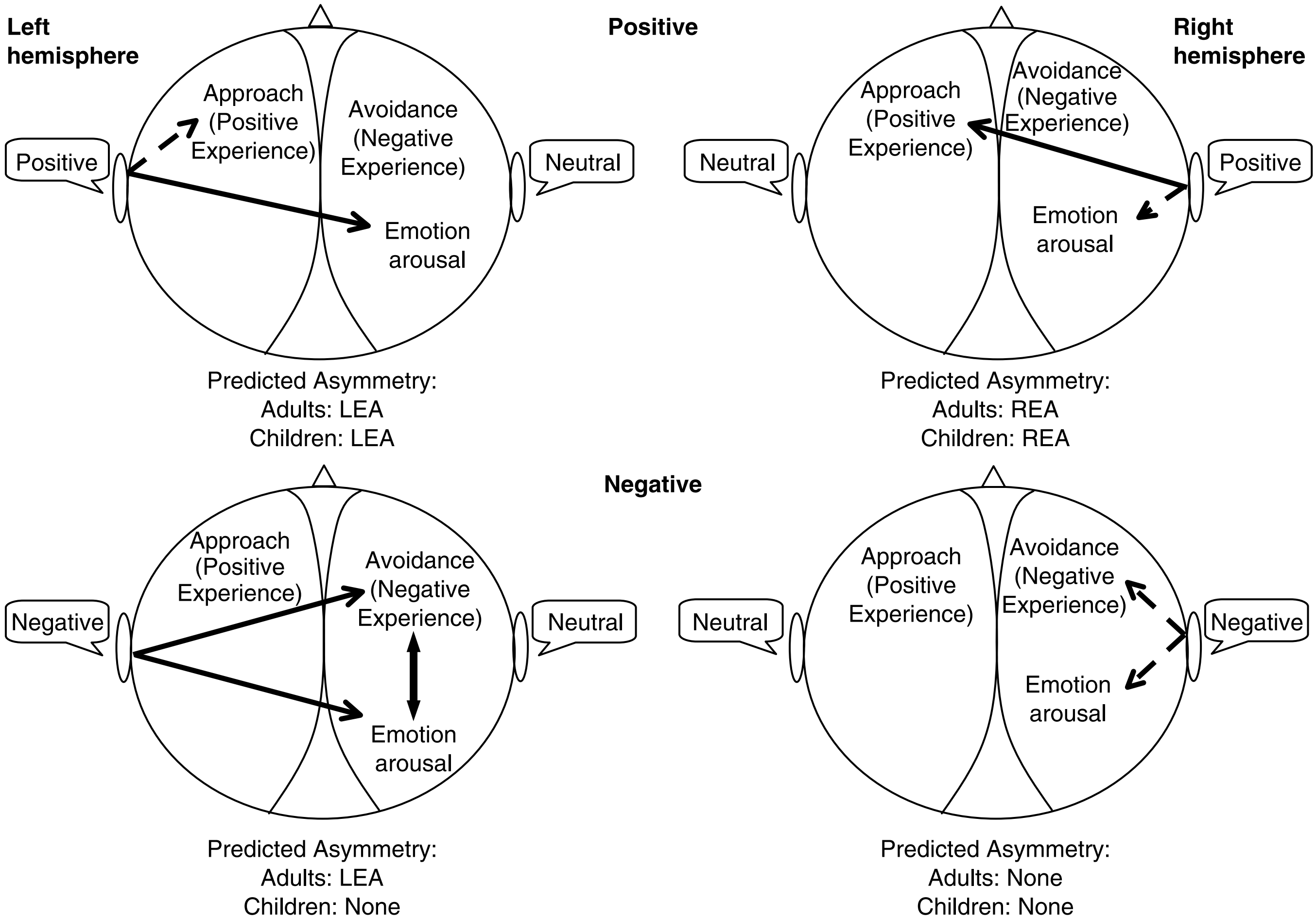

Figure 1 *Schematic of hypothesized pathways involved in the emotion DL task. Solid arrows represent contralateral pathways that are expected to determine perceptual asymmetries. Dashed lines indicate other affective systems activated by the stimuli, albeit less effectively. Experimental conditions that assess response to positive affective stimuli are illustrated in the top two panels whereas those corresponding to negative affective stimuli are shown below. LEA = left ear advantage; REA = right ear advantage.*

of negative stimuli to the LE/RH leads to a computational overload of the RH in less mature subjects, we would expect increased activation of the LH, resulting in no ear advantage. Since this overload effect is expected to be strongest in younger children, the present study includes a group of children who are just old enough to complete the experimental task with reasonable accuracy.

Experiment 1

Method

Participants

Twelve (8 female) right-handed adults (*M* age = 23 years, 7 months, SD = 2 years, 1 month) and 18 (9 female) right-handed children (*M* age = 6 years, 2 months, SD = 6 months) participated in this experiment. The Edinburgh Handedness Inventory (Oldfield, 1971) was used to determine handedness of participants. Subjects were free of hearing problems and head colds which might interfere with normal hearing. All participants also had two right-handed biological parents. Adult participants or parents of child participants provided written informed consent, and children provided oral assent prior to their participation.

Materials and stimulus development

A female actor produced 59 emotional sounds. Sounds were recorded using a Computerized Speech Laboratory (Kay Elemetrics) and a high-quality Shure microphone (XLR for balanced input and protection from noise)

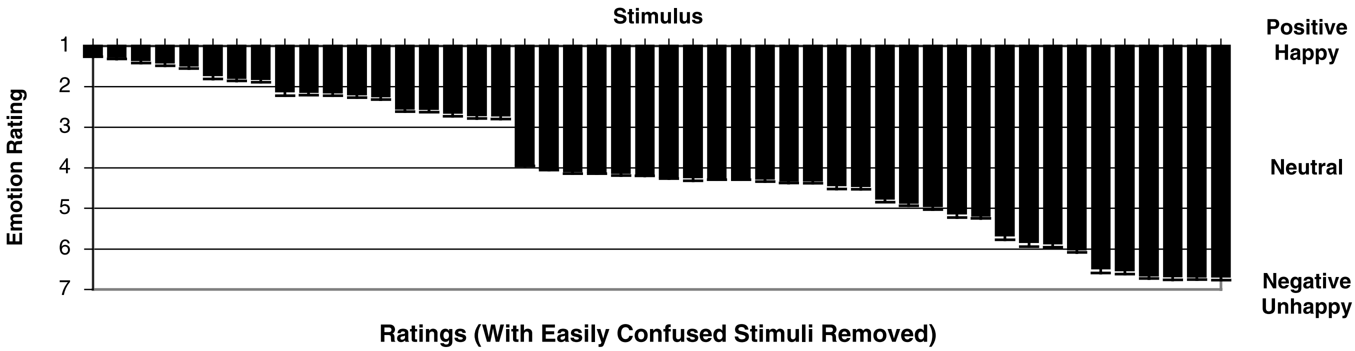

Figure 2 *Affective ratings of non-linguistic human sound stimuli. An emotion rating of '1' indicates a Positive/Happy sound and a rating of '7' indicates a Negative/Unhappy sound.*

placed approximately 12 inches from the speaker's mouth. Each target sound was recorded several times to ensure that representative tokens could be chosen. Sounds were recorded at a sampling rate of 10 kHz with 16-bit resolution. The sounds produced by the actor had no linguistic semantic content, but conveyed affective information. For example, the actor spoke single vowels like 'ahhhh', 'oooo' and 'ohhhh' in a neutral voice, a positive voice and a negative voice and produced giggles, grunts, sighs, cries and groans.

These sounds were rated for affect by 34 (25 female) native English-speaking adults with normal hearing. Listeners heard each of 59 stimuli five times (295 total responses) and rated each token along a 7-alternative rating scale by pushing one of seven labeled buttons on a hand-held electronic response box. Labels on the response box depicted happy, neutral and sad faces on a small line drawing figure. The endpoints (1 and 7) were also labeled with the words 'Positive/Happy' and 'Negative/Unhappy', respectively. In addition, the middle button (4) was labeled with the word 'Neutral'. Subjects were encouraged to use the entire scale, with at least some sounds rated a '1' (Positive/Happy) and some sounds rated a '7' (Negative/Unhappy). Subjects were tested in individual sound-attenuated chambers during a single 45-minute experimental session.

The order of the stimulus presentation was randomized and stimulus presentation and response collection were under the control of an 80486-25 microcomputer. Following D/A conversion (Ariel DSP-16), stimuli were low-pass filtered (4.8 cutoff frequency, Frequency Devices, #677), RMS matched in amplitude, amplified (Stewart HDA4) and presented to subjects via headphones (Beyer DT-100) at a level of 70 dB SPL(A). For several long samples of giggles and cries, smaller segments were excised to edit sounds at zero crossings so that no onset or offset artifacts were introduced. Stimulus duration varied from 364 ms to 1.4 sec ($\underline{X}$ = 879 ms, SD = 284 ms).

Each listener's ratings were submitted to an analysis of 'confusability' across affective categories to determine that stimuli rated as negative by one subject were not rated as positive by other subjects and thus to provide a measure of certainty that a particular stimulus falls into a given emotion class. Maximum and minimum ratings for each sound were calculated across listeners. From these ratings, a Confusion Index (Max Rating – Min Rating) was calculated for each sound. Sounds were judged to be easily confusable across positive and negative affective categories if this index was greater than 3. Based on listeners' evaluation of these sounds, 11 easily-confused stimuli were removed from the stimulus set.

Figure 2 presents the mean rating of each of the remaining 48 stimuli, ordered from lowest (most positive) rating to highest (most negative) rating. Stimuli with ratings of 1.0–3.0 were defined to be 'Positive' stimuli ($N = 18$). Those with ratings of 5.0–7.0 were designated 'Negative' stimuli ($N = 12$). Stimuli with ratings of 3.1–4.9 were defined as 'Neutral' ($N = 18$). These stimuli formed the basis for the dichotic pairs used in Experiment 1.

Each dichotic stimulus was formed by compiling two stimuli from the set of 48 affective sound stimuli, one to the left channel (presented to the left ear) and one in the right channel (for presentation to the right ear). In each case, the affect conveyed by the stimulus differed between ears. For example, a Positive-Neutral stimulus was a sound rated as positive by adult listeners (rating <3.0 along the 7-point scale) presented to one ear and a sound rated as neutral (rating falling between 3.1 and 4.9) presented to the other. A second, matched dichotic stimulus comprised identical acoustic stimuli, but with ear of presentation reversed, was also created. The two classes of dichotic stimuli varied in their affective category (Positive-Neutral and Negative-Neutral).

Prior to combination as dichotic stimuli, individual sounds were low-pass filtered (4.8 kHz cutoff frequency) to remove any high-frequency noise that may have been picked up in recording. All stimuli across the positive, negative and neutral sets were matched in total RMS energy. In addition, pairs of stimuli comprising a dichotic stimulus were mated in duration by slicing pitch periods. Care was taken to ensure that slices occurred at zero crossings and did not corrupt the acoustic signal. Acoustic analyses ensured the integrity of the stimulus after manipulation of duration. To further assure that duration matching did not fundamentally change stimuli, pairs were chosen based on closest natural duration. The average duration for the three classes of stimuli (Positive, Negative and Neutral) is 890, 880 and 810 ms, respectively. Stimuli were saved at a 22050 Hz sampling rate.

Procedure

The DL task consisted of two trial blocks. Each trial block consisted of 4 pairs of each of the following dichotic pairs (presented as left ear–right ear input): positive-neutral, neutral-positive, negative-neutral and neutral-negative, for a total of 32 trials. Participants were presented with equal numbers of positive, negative and neutral sounds to the right and left ears. Dichotic pairs were randomized and not repeated within trial blocks. Participants listened to dichotic sound pairs through high-resolution headphones at a comfortable sound level of approximately 75 dB. Headphones were reversed after each block to minimize channel effects. An IBM PC computer equipped with an ELO Graphics touch-screen delivered stimuli and collected responses. Listeners were instructed to listen carefully and decide if the sound was happy, neither happy nor unhappy, or unhappy. Participants were not explicitly told about the dichotic nature of the stimuli; rather, the instructions emphasized that the stimuli might sound odd, and were told, 'We are interested in how you think the person making the sound probably feels.' Participants indicated their perception of the emotion conveyed in the stimuli by selecting one of three (happy, sad, neutral) cartoon schematic faces (representing the left ear input, the right ear input and a foil) that appeared on the computer screen 50 ms after stimulus presentation. The placement of the cartoon faces was counterbalanced so that the left ear inputs, right ear inputs and foils appeared in random order across the computer screen. Participants were required to make a response for each trial. Each response was followed by a 2.5-second interstimulus interval.

Results

Percentages of subjects' left and right ear identifications in each emotion and stimulus condition are presented numerically in Table 1, with a summary statistic presented graphically in Figure 3. Because the difference in accuracy for the right and left ear is correlated with the subject's overall performance level (Chapman & Chapman, 1988), we calculated an asymmetry score, the *f*-index, as (R – L) / (R + L), where R stands for sounds recognized from the right ear and L refers to sounds recognized from the left ear. REAs were determined to be present when the *f*-index value was positive and significantly differed from zero, LEAs were determined to be present when the *f*-index value was negative and significantly differed from zero, and values that did not differ from zero were taken to reflect absence of a perceptual asymmetry. Perceptual asymmetries were evaluated by a repeated measures analysis of variance on *f*-index scores

Table 1 *Asymmetry values for Experiment 1 by emotion and stimulus conditions*

	Adults				Children			
Stimulus condition	POR	POL	Error	*f*-index	POR	POL	Error	*f*-index
Negative to LE/RH								
M	.23	.75	.02	–.53*	.32	.39	.29	.02
SD	.19	.19	.04	.41	.18	.21	.24	.51
Negative to RE/LH								
M	.54	.41	.05	.14	.39	.31	.30	.02
SD	.37	.39	.06	.83	.25	.18	.24	.62
Positive to LE/RH								
M	.22	.77	.01	–.54*	.22	.71	.07	–.49*
SD	.28	.28	.02	.56	.24	.30	.11	.58
Positive to RE/LH								
M	.75	.20	.05	.56*	.72	.19	.09	.56*
SD	.26	.20	.09	.44	.28	.22	.11	.52

Note: * indicates difference from zero is significant at $p < .05$. LE = left ear, RE = right ear, LH = left hemisphere, RH = right hemisphere, POR = percent right ear identifications, POL = percent left ear identifications. *M* = mean, SD = standard deviation.

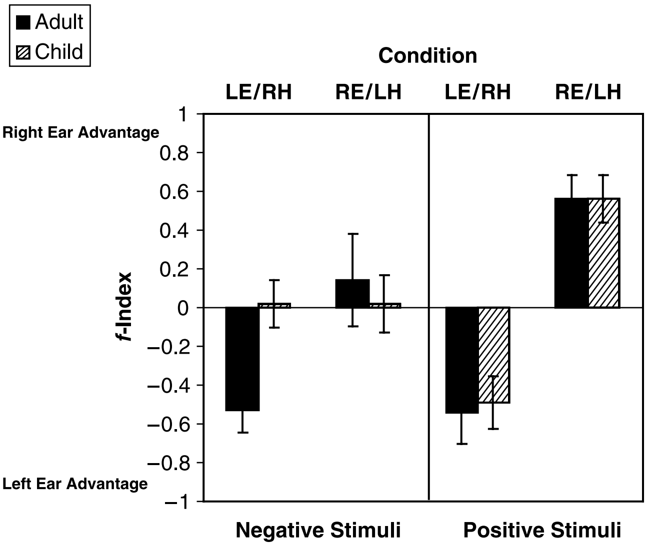

Figure 3 *Average* f*-index values and standard deviations for children and adults across affective stimuli (Negative and Positive) and ear of presentation (LE/RH and RE/LH). Negative values indicate an LEA whereas positive values indicate an REA. Only the LE/RH condition for Negative affective stimuli exhibited a difference between child and adult listeners.*

with condition (negative to LE, negative to RE, positive to LE, positive to RE) as a within-subject factor and subject's sex as a between-subject factor. The Greenhouse-Geisser values are reported for F tests to correct for repeated measures.

Across age groups, the magnitude of perceptual asymmetries differed by condition, $F(3, 84) = 17.57$, $p < .01$. Planned contrasts were consistent with our expectation that perceptual asymmetries for adults and children would differ only when negative stimuli were presented to subjects' LE/RH, $F(1, 29) = 7.52$, $p < .01$. There were no age differences in performance when negative stimuli were presented to listener's RE/LH, or when positive stimuli were presented to the LE/RH or RE/LH, all Fs < 1.

Adults displayed a right ear (LH) advantage when positive stimuli were presented to the RE/LH, but a left ear (RH) advantage when those same stimuli were presented to the LE/RH. Adults also had a left ear (RH) advantage when negative stimuli were presented to the LE/RH. As predicted, no hemispheric asymmetry emerged when these same negative stimuli were presented to the RE/LH. This same pattern of results emerged for children with one exception. In contrast to adults, who displayed a left ear (RH) advantage when negative stimuli were presented to the LE/RH, children did not show a perceptual asymmetry.

Conclusion

We predicted that presentation of negative stimuli to the LE/RH would lead to a computational overload of the RH and an increased activation of the LH in less mature subjects because this is the only condition where *both* anterior and posterior affective systems are purportedly simultaneously activated within the same hemisphere. Results from Experiment 1 support this prediction. Whereas adults showed an LEA, children's cognitive resources may become taxed by such activation, precluding an RH processing advantage and resulting in no observed perceptual asymmetry under this condition. The present study eliminates the potential confound of receptive language versus emotion activation, thus providing a clearer understanding of the overload hypothesis and confirming the use of nonlinguistic affective stimuli as effective in laterality tasks.

One alternative hypothesis for the present findings is that the exaggerated acoustic characteristics typical of positive sounds may have disproportionately captured subjects' attention. In this regard, it could be the case that for positive stimuli, listeners simply heard and reported the most perceptually salient information, regardless of ear of presentation. Based upon this reasoning, it is also possible that failure to find perceptual asymmetries for the negative stimuli emerged because the acoustic characteristics typical of negative stimuli were less salient to children than the neutral sounds. Consistent with this idea, children's error rates for dichotic pairs containing negative sounds were notably higher than those of adults. While we would expect 6 year olds to make more errors than college students, it is unclear whether their error rates reflect affective processing differences. Experiment 2 was conducted to examine this possibility.

Experiment 2

Experiment 2 employed the same procedures and stimuli as Experiment 1, with one alteration. In this experiment, each affective acoustic token was dichotically paired with a time-reversed version of itself rather than with one of the neutral stimuli used in Experiment 1. Playing each stimulus in reverse maintained low-level perceptual attributes of the stimuli, while eliminating affective information. Thus, each positive and negative stimulus sound served as its own control, the backwards version serving as the 'neutral' stimulus in the sound pair. It was expected that the pattern of perceptual asymmetries found for children in Experiment 1 would be replicated.

Method

Participants

Ten (4 female) right-handed children (*M* age = 6 years, 5 months, SD = 3 months) participated in this experiment. None of these children had participated in the previous experiment.

Materials

New dichotic pairs were formed in which positive stimuli were played forward in the left channel, backward in the right channel and also in which the same stimuli were played backward in the left channel, forward in the right channel. The same procedures were followed for the negative stimuli. Channels were RMS matched in overall amplitude prior to presentation. Care was taken to ensure that forward and backward sounds were aligned in time according to their natural zero-crossings in amplitude. All other stimulus manipulation and presentation characteristics were identical to those of Experiment 1.

Procedure

The procedures used were similar to those used in Experiment 1, with the following exceptions. Two blocks with seven tokens of each of the four sound pair types (positive/negative forward to LE–backwards to RE, positive/negative backwards to LE–forward to RE) were presented to children for a total of 56 trials. The second trial block repeated the tokens from the first block in a different random order.

Results

As shown in Table 2, children displayed the same pattern of results as was found in Experiment 1. Consistent with Experiment 1, children displayed an REA when forward-oriented positive stimuli were presented to the RE/LH and an LEA when forward-oriented positive stimuli were presented to the LE/RH. Also identical to Experiment 1, no perceptual asymmetry emerged when forward-oriented negative stimuli were presented to either the LE/RH or the RE/LH. Error rates were higher for this experiment; yet the increased task difficulty did not affect the overall pattern of perceptual asymmetries.

Table 2 *Asymmetry values for Experiment 2 by emotion and stimulus conditions*

Stimulus condition	POR	POL	Error	*f*-index
Negative to LE/RH				
M	.34	.45	.21	−.15
SD	.22	.20	.13	.45
Negative to RE/LH				
M	.41	.29	.30	.16
SD	.21	.19	.21	.38
Positive to LE/RH				
M	.29	.57	.14	−.33*
SD	.13	.12	.08	.28
Positive to RE/LH				
M	.58	.25	.17	.39*
SD	.15	.09	.14	.21

Note: * indicates difference from zero is significant at $p < .05$. LE = left ear, RE = right ear, LH = left hemisphere, RH = right hemisphere, POR = percent right ear identifications, POL = percent left ear identifications. *M* = mean, SD = standard deviation.

Conclusion

These results replicate the pattern of perceptual asymmetries found for children in Experiment 1. When paired with time-reversed versions of themselves, positive and negative stimuli elicit the same qualitative pattern of DL results as when they were paired with affectively neutral stimuli in Experiment 1. Therefore, these perceptual asymmetries are unlikely to be secondary to attentional factors resulting from differences in acoustic characteristics among positive, negative and neutral stimuli.

Experiment 3

Another alternative interpretation of the data obtained in the previous experiments is that children simply do less well at perceiving negative affective stimuli, given that children were performing at chance levels when negative emotions were presented to either ear. Ancillary support for our claims would be provided if children could accurately identify negative stimuli as being negative when hearing the stimulus set one sound at a time. Experiment 3 employed the same stimuli as Experiment 1, with one methodological alteration. In this experiment, each affective acoustic token used in Experiment 1 was presented diotically. Diotic presentation of each stimulus allowed us to determine if children could accurately identify negative stimuli when hearing a single stimulus presented to both ears.

Method

Participants

Fifteen (6 female) right-handed children (*M* age = 6 years, 4 months, SD = 3 months) participated in this experiment. None of these children had participated in the previous experiments.

Materials

Stimuli were the same as those used in Experiments 1 and 2. For the present experiment, only a single sound was presented on each trial so identical sounds were sent to each channel (LE and RE) of the headphones. There was no dichotic competition.

Procedure

Children heard each of the 12 negative and 18 positive stimuli two times (60 total trials) in one trial block. After hearing each sound, participants were asked to decide if the sound was positive, neutral or negative. Participants indicated their perception of the emotion conveyed in the stimuli as described in Experiment 1.

Results

Children correctly identified nearly all of the positive sounds (X = .96, SD = .02) and a similarly high proportion of the negative sounds (X = .94, SD = .05). This accuracy difference between stimuli did not differ significantly, $t(14) < 1$, n.s.

Conclusion

The results from Experiment 3 indicate that children accurately perceived both the negative and positive stimuli. These data suggest that the results of Experiment 1 are not secondary to differences in task difficulty between stimulus sets, but likely reflect processing differences between conditions.

General discussion

Perceptual asymmetries in the processing of information are considered by many to be a reflection of the organization of the brain, through which fundamental operations of different brain regions become integrated (Levy, 1972; Schneirla, 1959). Of continuing interest are questions regarding how different mental operations become integrated and organized over development. The present data are consistent with the hypothesis that both anterior-mediated and posterior-mediated processes are implicated in emotion perception in adults and children. Moreover, in less mature participants, activation of both anterior and posterior affective processes within one hemisphere lead to patterns of information processing quite different from those of adults. The present data suggest that in children, higher anterior activation may occur without decreased posterior activation in the same hemisphere – at least in the processing of affective stimuli. In tandem with indirect evidence that white matter connections between anterior and posterior regions develop slowly over age, it is anatomically feasible that the developmental changes in the circuitry between these systems is extensive (Thatcher, 1994, 1996).

The present data point to the importance of developmental processes in the emergence and organization of affective processing systems. Affect processing appears to be a regulatory, adaptive process that is critically dependent upon the integrated neural functioning of multiple neural networks. Thus, understanding of the control of emotional processes requires understanding of how hemispheric specialization develops, including both experience-dependent and experience-independent factors in cerebral organization.

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