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Local and Global Auditory Processing: Behavioral and ERP Evidence

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Abstract

Differential processing of local and global visual features is well established. Global precedence effects, differences in event-related potentials (ERPs) elicited when attention is focused on local versus global levels, and hemispheric specialization for local and global features all indicate that relative scale of detail is an important distinction in visual processing. Observing analogous differential processing of local and global auditory information would suggest that scale of detail is a general organizational principle of the brain. However, to date the research on auditory local and global processing has primarily focused on music perception or on the perceptual analysis of relatively higher and lower frequencies. The study described here suggests that *temporal* aspects of auditory stimuli better capture the local-global distinction. By combining short (40 ms) frequency modulated tones in series to create global auditory patterns (500 ms), we independently varied whether pitch increased or decreased over short time spans (local) and longer time spans (global). Accuracy and reaction time measures revealed better performance for global judgments and asymmetric interference that were modulated by amount of pitch change. ERPs recorded while participants listened to identical sounds and indicated the direction of pitch change at the local or global levels provided evidence for differential processing similar to that found in ERP studies employing hierarchical visual stimuli. ERP measures failed to provide evidence for lateralization of local and global auditory perception, but differences in distributions suggest preferential processing in more ventral and dorsal areas respectively.

Keywords

selective attention; event-related potential; temporal; congruency; lateralization; pitch

Visual perception can vary drastically across different spatial scales. A compelling demonstration of how scale affects visual analysis is provided by the tension between local and global elements in portraits by the artist Chuck Close. For many of his pictures, face recognition only occurs when attention is focused on low spatial frequency information at the global level. Data from various methodologies support the view that visual information at relatively small and large spatial scales is differentially processed in the human brain. It has also been suggested that this local-global distinction may define a general organizational principle (Ivry & Robertson, 1998; Sergent, 1982). However, a lack of robust evidence for

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differential local and global processing in other modalities and across other stimulus dimensions limits the extent to which organizational scale can be considered to reflect an important neural division of labor.

Visual local and global processing

Navon (1977) introduced hierarchical figures in which local parts (e.g., S) are repeated and arranged to form global configurations (e.g., H). Viewers are both faster to identify targets at the global level and show more interference of global organization on detecting local targets when the information at the two levels is incongruent. These two effects were termed global precedence and were used to argue that perception occurs in a “whole” to “part” sequence. Global precedence effects are also found in studies employing selective attention designs; global discrimination requires less time and is less affected by what is presented at the local level (Koivisto & Revonsuo, 2004; Pomerantz, 1983). Global precedence effects are found with a wide variety of stimuli presented at a range of visual angles (Boer & Keuss, 1982; De Lillo, Spinozzi, Truppa, & Naylor, 2005; Hoffman, 1980; Koivisto & Revonsuo, 2004; Navon, 1977, 1981, 1991) but at the extremes can be mediated by attention, size and shape of the items, and level of processing (Blanca & Alarcón, 2002; Kinchla, Solis-Macias, & Hoffman, 1983; Shedden & Reid, 2001). Furthermore, the two measures of global precedence can be dissociated (Han, Yund, & Woods, 2003; Heinze & Münte, 1993; Lamb & Robertson, 1989; Lamb, Robertson, & Knight, 1989). Global precedence effects provide strong evidence that local and global visual information can be processed at different rates; data showing dissociation between global precedence measures suggest the two levels may be processed in distinct neural systems.

Electrophysiological methods provide a means to study the time course of differential local and global processing. Studies employing divided attention tasks indicate that a posteriorly distributed negativity peaking around 250 ms after stimulus onset (N250) is the earliest component to be affected by target level (Heinze, Hinrichs, Scholz, Burchert, & Mangun, 1998; Heinze & Münte, 1993; Johannes, Wieringa, Matzke, & Münte, 1996). A later study reported that the amplitude of a much earlier component, the posteriorly distributed positivity peaking around 100 ms after stimulus onset (P100), is also modulated by target level (Han, He, & Woods, 2000a). Not surprisingly, evidence for early processing differences of local and global information is more consistent in studies employing selective attention designs. When viewers focus their attention on local features, hierarchical figures typically elicit larger P100s and larger N250s (Han, Fan, Chen, & Zhuo, 1997, 1999; Han, He, Yund, & Woods, 2001; Han, Liu, Yund, & Woods, 2000b). Additionally, the posterior N250 to targets at the local level has been shown to have a shorter latency when information at the local and global levels are similar, but no such relationship is found for targets at the global level (Han & Chen, 1996; Han et al., 1999; Han et al., 2000a; Johannes et al., 1996).

Perhaps the most compelling distinction between local and global visual processing is the differential lateralization in the brain. Behavioral, neuropsychological, and neuroimaging studies with neurally intact and lesioned adults indicate that local information is preferentially processed in the left hemisphere and global information in the right hemisphere. For example, patients with left parietal or temporal damage create drawings with less local detail and have more difficulty identifying local features in hierarchical figures, whereas patients with right hemisphere damage in homologous areas draw pictures that lack global organization, have difficulty identifying global items in hierarchical figures, and lack global precedence effects (Lamb et al., 1989; Lamb, Robertson, & Knight, 1990; Robertson & Lamb, 1991; Robertson, Lamb, & Knight, 1988). PET studies have shown lateralized activation when viewers selectively attend to local or global features of visual stimuli (Fink et al., 1997). An fMRI study of selective attention found greater activation in right occipito-temporal regions when viewers

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attended to the global level and equivalent activity in left occipito-temporal regions when viewers sustained attention at the local level (Martinez et al., 1997).

Although ERPs offer the possibility of determining *in time* which stages of local and global processing are lateralized in the brain, the electrophysiological evidence is mixed. Many studies employing selective or divided attention tasks, central or lateralized presentation of stimuli, and varied or consistent information at unattended levels report no evidence of lateralized processing for local versus global information (Han et al., 1997, 1999; Han & He, 2003; Han et al., 2000a; Heinze et al., 1998; Johannes et al., 1996). However, there is some evidence for lateralization – in the predicted direction – of later components (N250 and P300) under conditions of divided attention (Heinze et al., 1998; Heinze & Münte, 1993), when information at the other level could result in response conflicts (Volberg & Hübner, 2004), when level to be attended was cued immediately before presentation (Yamaguchi, Yamagata, & Kobayashi, 2000), and when targets were compared to nontargets at the two levels (Proverbio, Minniti, & Zani, 1998). Evidence for lateralization of earlier ERP components (P100) has only been reported for a paradigm in which the information at the unattended level was invariable and unrelated to the discrimination task (Evans, Shedden, Hevenor, & Hahn, 2000).

Across the different methods employed to study local and global visual processing, several factors have been shown to affect the relative speed, the asymmetric interference, and the lateralization of processing. First, local and global levels of processing have to be described in relation to each other rather than on some absolute scale (Christman, Kitterle, & Hellige, 1991; Polster & Rapcsak, 1994). Second, the timing of lateralization and other differences in neural processing at local and global levels is modulated by whether attention is divided across levels or directed specifically to one level, as described above. Third, level of processing impacts lateralization (Grabowska & Nowicka, 1996; Sergent, 1982). For processing spatial gradients, there are visual field effects on reaction times if viewers are asked to identify specific gradients but not if they are asked to detect them (Kitterle, Christman, & Hellige, 1990). Finally, temporal characteristics of visually presented stimuli have been shown to impact lateralization of local and global spatial processing. When checkerboards of high and low spatial frequency are flickered at fast and slow rates, visually evoked potentials are larger over the left hemisphere for fast rates and larger over the right hemisphere for slower rates (Mecacci & Spinelli, 1987; Rebain, Mecacci, Bagot, & Bonnet, 1989).

Local and global processing in other modalities

The distinction between local and global visual processing has been well documented and is an important starting point for exploring relative scale as a more general organizational principle of the brain. A small body of research has addressed the issue of how the local versus global processing distinction applies to other domains. For example, the games ‘Go’ and ‘Chess’ have been hypothesized to differentially employ local and global strategies (Chen et al., 2003). Studies of haptic processing have revealed that global shape information affects object identification at an earlier age than local features (Morrongiello, Humphrey, Timney, Choi, & Rocca, 1994), that young infants process more global information for objects explored with their left hands and more local information for explorations made with their right hands (Streri, 2002), and that the relative importance of local and global processing changes over time during object manipulation (Lakatos & Marks, 1999). However, audition has been considered to be the test-case for whether or not the local and global processing distinction applies directly to modalities other than vision (Dowling, 1978; Horváth, Czigler, Sussman, & Winkler, 2001; Justus & List, 2005; Lassonde et al., 1999; Peretz, 1990; Schiavetto, Cortese, & Alain, 1999).

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Auditory local and global processing

Local and global rules of auditory patterns have typically been defined in terms of adjacency (Bregman, 1990). For example, violations of adjacent (local) and nonadjacent (global) rules elicit mismatch (MMN) responses with similar distributions (Horváth et al., 2001). This finding has been used to suggest that processing of auditory information at these levels is not lateralized, but it may simply reflect insensitivity to lateralized processing by the MMN measure. Local and global auditory distinctions have also been made for listening to music. Listeners are asked to determine if two unfamiliar melodies are the same or not when differences can occur at the local level, defined as a difference in the pitch of one note which maintains overall pitch contours of the melody, or at the global level, defined as a violation of the overall pitch contours. Evidence from a few patients with right lateralized lesions indicate they are relatively unimpaired at detecting local pitch deviations in comparison to patients with left hemisphere lesions (Peretz, 1990). A case study of a child with a right temporal lobe lesion showed both no typical global interference on local processing of visual perception and no global precedence for discriminating melodies (Lassonde et al., 1999). In an ERP study using similar global and local melody violations, Schiavetto et al. (1999) found that global violations elicited larger N2s and P3s whereas local violations modulated the P3 component only. These data were interpreted to support a global precedence effect for auditory perception.

More recent research challenges the way in which local and global levels have been defined in the auditory modality (Justus & List, 2005). For visual stimuli, parts and wholes are typically defined spatially, and information from both levels is presented simultaneously within a few degrees of visual angle. For sounds, local and global levels have often been defined by temporal adjacencies or direction of pitch deviance, and local parts are presented individually with varying amounts of intervening silence. Citing arguments that frequency and time are fundamental features of auditory objects, Justus and List (2005) report level-priming in divided attention tasks in which local and global features are defined by their relatively higher or lower pitch *and* by their relatively shorter or longer time scale. This research suggests that auditory hierarchical stimuli can be defined by both pitch and time, just as evidence for visual local and global processing indicates it can be defined by relative scale, spatial frequency, and time.

Lateralization of auditory processing

A controversy parallel to that of defining local and global levels of sounds has arisen in the literature concerning cortical lateralization of auditory processing. Although there is a great deal of evidence for hemispheric specialization of auditory processing from dichotic listening, neuropsychological, neuroimaging, and electrophysiological studies (for review, see Tervaniemi & Hugdahl, 2003), no single domain-specific (e.g., language-music) nor parameter-specific (e.g., temporal-spectral) distinction can account for all of the data. The same can be argued of relative temporal scale, but there is strong evidence that rate of change contributes to lateralization of auditory processing in areas other than primary auditory cortex. Auditory tasks that require high temporal resolution are typically left lateralized in at least some cortical areas (Belin et al., 1998; Celsis, et al., 1999; Fiez et al., 1995; Johnsrude, Zatorre, Milner, & Evans, 1997; Nicholls, 1996). It has also been argued that left lateralization of speech perception may arise from the preferential processing of rapid auditory changes in the left hemisphere (Tallal, Merzenich, Miller, & Jenkins, 1998; Tallal, Miller, & Fitch, 1993). In contrast, there is evidence for greater right lateralization of processing when auditory tasks require pitch discriminations over longer time periods. For example, higher pitch-direction thresholds were found in patients with right (but not left) auditory cortex lesions for two 100 ms tones presented with 800 ms between them (Johnsrude, Penhune, & Zatorre, 2000). Both PET and fMRI studies provide evidence for right lateralization of processing slow (500 ms) frequency modulated sweeps (Brechmann, Baumgart, & Scheich, 2002; Poeppel, et al.,

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2004). Similarly, the results of an fMRI study showed greater activation in the left hemisphere when participants listened to meaningless speech that contained the rapid frequency changes of normal phonological information and greater activation in the right hemisphere when the same participants listened to the slower, global changes in fundamental frequency that communicate prosody (Meyer, Alter, Friederici, Lohmann, & von Cramon, 2002). Evidence for differential lateralization of processing different aspects of speech purely as a function of the temporal structure of the signal has been extended in recent findings (Hesling, Dilharreguy, Clement, Bordessoules, & Allard, 2005; Luo & Poeppel, manuscript).

Across these studies, there is some evidence for preferential processing of fast auditory changes in the left hemisphere and for slow changes in the right hemisphere (Poeppel, 2003). However, the results from visual studies clearly indicate that it is *relative* scale (of size, spatial frequency, and rate of change) that affects lateralization of processing. A few neuroimaging studies employing both rapid and slower frequency transitions implicate relative scale in the lateralization of auditory processing as well. In a parametric study of temporal and spectral complexity, Zatorre and Belin (2001) found increases in fMRI activation in left auditory cortex as the rate of frequency change was increased. In PET and fMRI studies, faster frequency transitions (40ms) have been shown to preferentially drive left auditory cortex and slower transitions (200ms) have resulted in greater right superior temporal sulcus activation (Boemio, Fromm, Braun, & Poeppel, 2005; Belin, et al., 1998). When participants made phonetic discriminations for speech stimuli, greater PET activation was found in the left hemisphere; greater right hemisphere activation was found when listeners made pitch discriminations for the identical stimuli during the same session (Zatorre, Evans, Meyer, & Gjedde, 1992).

Auditory selective attention

Top-down influences, in addition to differences in stimulus parameters, can impact the organization of auditory processing. There is extensive evidence that early perceptual processes are modulated by selecting specific sounds for attentive processing on the basis of a simple feature such as location or pitch (e.g., Hansen & Hillyard, 1980; Hillyard, 1981; Schröger & Eimer, 1997; Schwent, Snyder, & Hillyard, 1976). More recent evidence indicates that temporally selective attention also affects perceptual processing. Attention can be directed to specific points in time such that people are faster and more accurate given valid than invalid temporal cues (Coull, Frith, Büchel, & Nobre, 2000; Coull & Nobre, 1998; Griffin, Miniussi, & Nobre, 2002; Miniussi, Wilding, Coull, & Nobre, 1999). Furthermore, temporally selective attention has been shown to modulate early auditory processing in a manner similar to spatially selective attention; sounds presented at attended times elicit larger amplitude auditory onset ERP components (Lange, Rösler, & Röder, 2003; Sanders & Astheimer, 2006). However, it is also important to distinguish between auditory selective attention designs in which listeners use a simple feature to determine which sounds they will attend (including the studies cited above) and designs in which listeners are asked to attend to different features while processing the same sounds. Behavioral studies have shown that selectively attending to different time *scales* impacts auditory perception. Listeners who selectively attend to shorter (more local) and longer (more global) time ranges while processing rhythmic sound trains show different patterns of responses in sequence monitoring tasks (Jones, Moynihan, MacKenzie, & Puente, 2002; Klein & Jones, 1996; Large & Jones, 1999). Neuroimaging studies have provided evidence for differential lateralization of auditory processing when listeners selectively attend to different features of the same physical stimuli (Brechmann & Scheich, 2005; Zatorre, et al., 1992). Considered together, these studies raise the untested hypothesis that selectively attending to relatively local and global time scales will affect the lateralization of auditory processing in the brain.

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Attention to local and global auditory features

Based on evidence in both the auditory and visual modalities, we selected stimuli, tasks, and measurements to maximize detection of differential local and global processing of auditory stimuli. First, auditory local and global levels were defined in terms of time scale. The supramodal nature of time, the importance of temporal information for auditory identification, the precision of auditory temporal representations (Kraus & Nicol, 2003; Rupp, Gutschalk, Sebastian, & Scherg, 2002; Wang, Lu, & Liang, 2003), the ability of naive listeners to selectively attend to specific time points, and the neuroimaging evidence suggesting hemispheric specialization for auditory processing might be driven by differences in temporal scale, all point to time as a reasonable dimension in which relatively local and global features can be defined. The local-global distinction was defined such that local elements changed over short time periods (40 ms) and global elements over longer time periods (500 ms). These specific durations were chosen to match those that resulted in differential lateralization in neuroimaging studies and to parallel (and exaggerate) segmental and syllabic level timing in speech perception. Second, to test for any interactions of sound frequency with temporal characteristics, stimuli were presented across a broad range of high and low pitches. Third, a selective attention design in which participants were asked to make a difficult pitch change direction decision was employed to modulate early perception of stimuli and ensure deep processing. Finally, ERP measurements were made to provide the temporal resolution necessary to determine the earliest time at which attention to the local or global level impacts processing of auditory stimuli.

MATERIALS AND METHODS

Participants

All participants were adult (ages 18–35 years) native English speakers with normal hearing and normal or corrected to normal vision, who reported no neurological disorders or psychoactive medications and were strongly right-handed as assessed by the Edinburgh Inventory for handedness (Oldfield, 1971). Twelve individuals were recruited for Experiment 1; twelve others participated in Experiment 2. Twenty-four people (14 women) who had not been in either behavioral study participated in the ERP experiment. All participants gave informed consent and were paid for their time.

Stimuli

Three 40 ms sinusoidal FM sweeps were combined with 190 ms of silence between each sweep to make 500 ms sequences (Figure 1). Local pitch direction was defined by change in the FM sweeps and global pitch direction by change in center frequency across sweeps. All three FM sweeps in a sequence changed in the same direction and center frequency across the three sweeps increased or decreased by equal increments. The FM tones were combined such that local pitch change could be in the same direction as global pitch change (congruent) or in the opposite direction (incongruent). In the first behavioral experiment, each FM sweep increased or decreased in pitch by 1 octave and the center frequency of the first and third FM tone in a sequence differed by 1 octave. The difference in center frequency of the first and third FM tones was decreased to 1/2 octave for the second behavioral experiment and was further decreased to 1/5 octave for the ERP study. This pattern of frequency changes was presented around 8 different center frequencies such that the lowest frequency used for the ERP study was 333 Hz and the highest was 2400 Hz (Table 1).

Procedure

Participants were introduced to the stimuli by hearing all of the sounds that fit a specific category. For example, some listeners were first instructed that all of the sounds they would

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hear increased in pitch across the whole sequence while the word “WHOLE” appeared on the computer monitor in front of them. Then all 16 sounds that increased in global pitch were presented 4 times in random order with 1 s interstimulus intervals. The same procedure was repeated for the sounds that decreased in global pitch, increased in local pitch, and decreased in local pitch. Once all four categories were introduced, the examples were repeated once. Order of category presentation was balanced across subjects.

Following this introduction phase, a brief practice session with feedback was given. In 4 blocks (2 local, 2 global) the word “WHOLE” or “PART” was shown on the screen. Following that word, a single sound stimulus was presented and listeners were asked to press a button to indicate if pitch increased or decreased across the whole sound or parts that made up the sound. The word “RIGHT” or “WRONG” was presented to give subjects feedback immediately after their button press. In the behavioral experiments, practice was limited to 10 trials in each block. For the ERP experiment, every block of practice included 32 trials so that participants heard every stimulus an equal number of times before testing.

Participants in the behavioral experiments then directed their attention to the local or global level in 4 blocks of 64 trials each (2 presentations of each stimulus) with no feedback. For the ERP study, the number of blocks was doubled for a total of 512 trials. During the testing phase of the ERP experiment, a fixation point was presented 800–1200 ms before the onset of each sound and remained on the monitor for 800–1200 ms after the offset of the sound. Participants were instructed to look directly at the fixation point, avoid blinking and other movements, and refrain from giving any response while the fixation point was on the screen.

Accuracy and reaction times were recorded for behavioral experiments; only accuracy was measured for the ERP experiment since all responses were delayed. Reaction times were calculated from the onset of sound sequences for correct responses only. Behavioral measures were analyzed with 2 x 2 x 2 x 8 within-subjects ANOVAs. Factors were attended level (local, global), congruency (congruent, incongruent), local pitch change direction (up, down), and average pitch of sequence (eight levels).

ERP recording and analysis

All participants were fitted with a 61-channel cap containing tin electrodes (Electro-Cap International). Scalp electrode locations are shown in Figure 2. Impedances at all electrode sites included in analyses were maintained below 3 k s for the duration of the experiment. EEG was amplified by isolated bioelectric amplifiers (SA Inst. Co) with a bandpass of .01 – 100 Hz and sampling rate of 250 Hz. Electro-oculogram was recorded from additional electrodes below, to the right, and to the left of the eyes as well as the most anterior cap electrodes above the eyes. Trials during which blinks or eye movements occurred were rejected before averaging. Individual amplitude cutoffs were determined by measuring peak-to-peak amplitudes in eye channels for trials containing the smallest observable blink and eye movement. All electrodes were referenced to a right mastoid location during recording and later re-referenced to the average mastoid (all figures show mastoid referenced data). Additional analyses on ERP data that were referenced to the average of all scalp electrodes were also performed. A 60 Hz notch filter was applied during the individual data averaging procedure. For all conditions, EEG was averaged from 200 ms before to 800 ms after onset of the sounds. The 200 ms pre-stimulus interval was used as a baseline.

Eight dependent variables were measured: mean amplitude and local positive peak latency between 40 and 70 ms (P1), mean amplitude and local negative peak latency between 110 and 150 ms (N1), mean amplitude and local positive peak latency between 180 and 240 ms (P2), and mean amplitudes 250 – 700 ms, and 350 – 700 ms. Omnibus repeated measures ANOVAs (Greenhouse-Geisser adjusted) were conducted on each of these variables. Factors for these

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analyses were level (local, global), congruency (congruent, incongruent), laterality and hemisphere of electrode (left lateral, medial, right lateral), and anterior/posterior position of electrodes (six levels). Electrodes included in each level of the electrode position factors are indicated in Figure 2. Additional ANOVAs included one of four other factors: Local pitch change direction (up, down), average pitch (eight levels), accuracy Group (median split on overall accuracy), or congruency group (median split on size of behavioral congruency effect).

RESULTS

Behavior

Accuracy and reaction times for indicating the direction of local and global pitch change when direction at the two levels was congruent and incongruent are shown in Figure 3. When the center frequency of the first and third FM sweeps differed by 1 octave performance on the global task was accurate (M = 99.2%) and fast (M = 798 ms) in comparison to performance on the local task (M = 54.0%, M = 941 ms). For the local task, accuracy did not differ from chance ($p > .50$). The interaction between level and congruency on accuracy ($F(1,11) = 232$, $p < .001$) may reflect an impact of global direction on guesses for the difficult local task. Since typical listeners can accurately indicate the direction of 40 ms FM sweeps presented in isolation, chance performance on the local task was attributed to the large global pitch differences that were reduced in subsequent experiments.

Reducing the amount of global pitch change to 1/2 octave both decreased global task accuracy to below ceiling (M = 91.1) and increased local task accuracy to above chance (M = 61.4%), but performance on the global task was still clearly more accurate ($t(11) = 11.20$, $p < .001$). Asymmetric interference on accuracy resulted in an interaction between level and congruency ($F(1,11) = 84.81$, $p < .001$) as well as no congruency effect at the global level ($p > .50$) and a significant effect at the local level ($t(11) = 11.89$, $p < .001$). Responses were also faster during the global task (M = 948 ms) than the local task (M = 1074 ms; $t(11) = 15.33$). There was an overall congruency effect on reaction times such that responses to congruent stimuli (M = 962 ms) were faster than responses to incongruent stimuli (M = 1061 ms), but this effect was larger for the local task ($F(1,11) = 16.72$, $p < .001$). Additionally, reaction times were longer with the global pitch change over only 1/2 octave compared to 1 octave ($t(11) = 14.01$, $p < .001$).

Further reducing the global pitch change to only 1/5 octave did not decrease accuracy on the global task (M = 92.0%) but did increase accuracy on the local task (M = 81.4%). Listeners were still more accurate on the global than local task ($t(23) = 4.29$, $p < .001$) and were more accurate on congruent (M = 90%) than incongruent trials (M = 82%; $t(23) = 7.52$, $p < .001$). However, the congruency effect was evident when listeners attended to either the local level or the global level (level x congruency interaction: $p > .20$). Reaction times were not recorded during the ERP experiment since all responses were delayed until after a response cue.

Overall pitch of the stimuli affected performance during the ERP experiment ($F(7,161) = 5.58$, $p < .01$) such that listeners were more accurate at determining pitch change direction for midrange frequencies than extremes. There was no evidence of differences in accuracy for relatively higher and lower pitches or interactions between overall pitch and attention to temporally defined local and global levels from any of the experiments (p’s > .20). However, when center frequency difference was limited to 1/5 octave, accuracy was higher on both the local and global tasks when local pitch change direction was up ($t(23) = 3.87$, $p < .01$).

ERP components

The first of three FM sweeps in the 500 ms series elicited a typical positive-negative-positive sequence of ERP components (Figure 4). The first positivity peaked at 55 ms after stimulus

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onset (P1) and was broadly distributed though larger in amplitude at medial and right lateral electrode sites (laterality and hemisphere: F(2,46) = 6.04, p < .001). Statistical significance of subsequent distribution analyses for all comparisons is shown in Table 2. The first negativity peaked at 132 ms (N1) and was largest at medial and right lateral sites (laterality and hemisphere: F(2,46) = 8.56, p < .001) over central and anterior regions (anterior/posterior: F (5,115) = 92.91, p < .001). N1 amplitude was larger for up FM sweeps than for down sweeps (F(1,23) = 8.38, p < .01). This difference in amplitude for local pitch change direction mirrored the distribution of the N1 itself – larger over medial and right lateral sites (local pitch change direction x laterality and hemisphere: F(2,46) = 10.01, p < .001) and over central and anterior regions (local pitch change direction x anterior/posterior: F(5,115) = 6.71, p < .001). N1 amplitude was also modulated by overall pitch (F(7,161) = 9.43, p < .001) such that responses across the scalp were smaller in amplitude for midrange frequencies than extremes. The following positivity peaked at 209 ms (P2) and was largest at medial and central sites (laterality and hemisphere: F(2,46) = 33.29, p < .001; anterior/posterior: F(5,115) = 6.15, p < .001). The P2 was also larger for up FM sweeps than for down sweeps (F(1,23) = 8.89, p < .01). This series of peaks (P1-N1-P2) was followed by a sustained component that was negative over anterior regions and positive over posterior areas (anterior/posterior: F(5,115) = 94.72, p < .001). Superimposed on this sustained component were clear negative peaks (N1s) occurring 124 ms after the onset of the second 40 ms FM sweep (N1(2nd)), and 140 ms after the onset of the third FM sweep (N1(3rd)).

ERP attention effects

Selectively attending to the local or global level modulated the amplitude of the later sustained component (Figure 4). Attending to the global level resulted in a larger negativity between 250 and 700 ms (task: F(1,23) = 51.17, p < .001). This effect was broadly distributed across the head, but was largest at medial (task x laterality and hemisphere: F(2,46) = 29.15, p < .001) and posterior sites (task x anterior/posterior: F(5,115) = 11.81, p < .001). This larger negativity when attending to the global level could also be measured as larger N1s elicited by the second FM sweep (task: F(1,23) = 23.4, p < .001) and the third FM sweep (task: F(1,23) = 30.62, p < .001). However, the N1s elicited by the onsets of each of the FMs were larger over anterior electrodes whereas the differences in ERPs elicited during the local and global tasks were larger over posterior sites.

As described above, the earliest components (P1 and N1) were larger over the right hemisphere, but this distribution was not modulated by attention to the local or global level (Figure 5) or overall pitch of the stimuli. The later components (P2 and sustained component) and attention effects were largest at medial sites with no evidence of lateralization. Referencing auditory evoked potentials to mastoids results in more medial distributions as was seen in the current study and could mask small lateralized effects. Therefore, all data were also referenced to individuals' averages across the scalp. This analysis resulted in more lateral distributions of both components and the local/global attention effect. However, there was no evidence that attention to the local or global level or pitch of the stimuli affected lateralization of components or effects.

ERP congruency effects

ERPs showed asymmetric congruency effects (Figure 6) even though the behavioral measure with these specific acoustic parameters did not. While listeners attended to local pitch changes, congruency at the global level resulted in a more negative response over anterior sites and a more positive response over posterior sites between 350 and 700 ms (congruency x anterior/posterior: F(5,115) = 3.97, p < .01). There was no evidence of lateralization of this congruency effect. When attention was directed to global pitch change, direction of the local FM sweeps

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had no effect (p's > .50). The difference in congruency effects for the two tasks differed (task x congruency x anterior/posterior, F(5,115) = 4.71, p < .01).

Relationship between behavioral and ERP effects

Some of the participants in the ERP experiment were highly accurate at determining pitch change direction at both levels (N = 12, M = 96.3%) and others were less accurate (N = 12, M = 71.1%). Across all 24 participants, there was no significant relationship between overall accuracy and size of the congruency effect on performance (p > .40). Therefore, median-splits based on the two criteria resulted in distinct divisions of data. However, the ERP effects of attention to the local or global level and of congruency at the local level during global processing were similar for groups with higher and lower overall accuracy and with larger and smaller behavioral congruency effects (p's > .30)

DISCUSSION

Performance on the auditory tasks with varied acoustic parameters and ERPs elicited when listeners attended to different levels support the hypothesis that auditory information presented at temporally local and global levels is differentially processed in the human brain. Listeners are more accurate and faster at determining the direction of smaller pitch changes over larger time scales (slow rate of change) than the direction of larger pitch changes over smaller time scales (fast rate of change). The amount and direction of pitch change at the global level has a large impact on processing at the local level; the opposite is not true. Selectively attending to the local or global level to perform a discrimination task modulates ERPs elicited by physically identical sounds. The differences in ERPs elicited by sounds during temporally local and global attention tasks are in some ways remarkably similar to the effects of selectively attending to spatially local and global visual features. In both paradigms, attention to local features results in larger early positive peaks and posteriorly distributed modulations of later components. Importantly, the similarities in behavioral and ERP measures of local and global processing of auditory and visual stimuli suggest that *time scale*, unlike spatial extent, is a meaningful way to define level of detail for hierarchical information in both modalities.

ERP selective attention effects

Ample evidence exists that selectively attending to a subset of sounds on the basis of a simple feature (e.g., location, time, or pitch) results in differential sensorineural processing of attended and unattended stimuli (Hansen & Hillyard, 1983; Hink & Hillyard, 1976; Lange, et al., 2003; Sanders & Astheimer, 2006; Schwent, et al., 1976; Woods, Alho, & Algazi, 1994). This approach assumes that once sounds are selected for attentive processing, all of the features that make up the attended auditory objects are processed in an attentive manner. The current study is the first report that selectively attending to different levels of a feature (i.e., relatively short and long time scales) while listening to physically identical and uniformly attended sounds also modulates auditory evoked potentials. Importantly, both the behavioral and ERP data support the conclusion that participants in this study were attending to different time scales rather than sounds presented at different times. If participants had adopted the strategy of selectively attending to the first FM tone during the local task and to all three sweeps during the global task, a pattern of results different from what was observed would be expected.

The finding that attention to different time scales affects how sounds are processed in the brain is consistent with findings that neurons in auditory cortex of animals show sensitivity to the speed of frequency modulations (Heil, Rajan, & Irvine, 1992; Kowalski, Versnel, & Shamma, 1995; Mendelson & Cynader, 1985; Schulze, Ohl, Heil, & Scheich, 1997). Attention to time scale could impact auditory processing by increasing the activity in populations of neurons responsive to a specific rate of frequency modulation or by increasing the number of neurons

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tuned to a specific rate of change. However, it is likely that even if selective attention to a feature were modulating processing in primary auditory cortex, it would be acting on re-afferent activity, as has been shown for visually selective attention (Di Russo, Martínez, & Hillyard, 2003; Khoe, Freeman, Woldorff, & Mangun, 2006). Furthermore, differential processing of sounds within the small spatial extent of auditory cortex is more likely to result in auditory evoked potentials that differ in amplitude. The difference in distribution between auditory onset components (in response to each of the three FM tones in a sequence) and the selective attention effects observed in the current study are more consistent with differential processing in areas beyond auditory cortex. The hypothesis that auditory information at different time scales is preferentially processed at different locations in the brain is discussed in more detail below.

Global precedence effects

In their most banal sense, global precedence effects merely reflect that larger images are easier to identify than smaller images and, in the current study, that slower auditory changes are easier to identify than faster ones. However, asymmetric interference effects reveal more about perception. Reducing the amount of global pitch change for auditory stimuli improved listeners' ability to determine local pitch change direction when information at the two levels was incongruent: a reduction in the amount of interference or influence on guesses when the amount of global pitch change in the opposite direction was reduced. Importantly, reducing the amount of global pitch change also improved performance at the local level when information at the two levels was congruent. Listeners were more accurate at determining local pitch change direction on congruent trials when the center frequency of the first and third FM sweep differed by only 0.2 octaves in comparison to 0.5 octaves. This finding indicates that amount of global pitch change affects local perception directly. It is also interesting to note that the amount of interference of local pitch change direction on global processing was modulated by amount of global pitch change when local change remained constant. The global precedence effects observed in the current study are consistent with visual spatial processing findings that behavioral measures of global precedence are generally seen across a range of stimulus parameters (De Lillo, et al., 2005; Hoffman, 1980; Navon, 1981, 1991) and that these effects can be reduced by increasing the difficulty of the global perception task (Amirkhiabani & Lovegrove, 1996; Antes & Mann, 1894).

Asymmetric interference effects were evident in evoked responses even under conditions in which congruency effects on accuracy were similar at the local and global levels. Superficially, the timing of local-on-global interference effects as indexed by ERPs for visual hierarchical figures (Han & Chen, 1996; Han et al., 1999; Han et al., 2000a; Johannes et al., 1996) and auditory stimuli is very similar. However, visual interference effects are observed around 250 ms after the simultaneous onset of both local and global information. For auditory hierarchical figures interference effects were evident by 350 ms after the onset of the first FM tone and only 110 ms after the onset of the second FM tone when global pitch direction information first became available. The relatively short latency of interference effects in the current study suggests that global pattern representations are being formed during, rather than after, the presentations of 500 ms sequences and that these global representations can affect early (within 100 ms) sensorineural processing.

Across several conditions and measures, *auditory temporal global precedence effects* are very similar to *visual spatial global precedence effects* in that: 1) they are found for a broad range of stimulus parameters, 2) they can be eliminated under extreme conditions, 3) effects found in more sensitive dependent variables can be absent in others, and 4) better performance at the global level and asymmetric interference can be dissociated. These similarities suggest conclusions based on visual global precedence effects may also apply to auditory processing.

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Local and global information can be processed at different rates and in distinct neural systems operating in parallel.

Lateralization

Directing attention to the local or global level of hierarchically organized auditory stimuli results in differential processing in the brain. However, there is no evidence from the current study for preferential processing of local and global information in the left and right hemispheres. This finding is not particularly surprising in light of the lack of lateralized effects in most ERP studies of local and global visual processing with similar designs (Han et al., 1997, 1999; Han & He, 2003; Han et al., 2000a; Johannes et al., 1996). If further evidence supports the conclusion that the temporal definition of local and global auditory processing adopted here is most similar to the spatial distinction made in the visual modality, more spatially sensitive neuroimaging and neuropsychological studies could serve as a stronger tests of lateralized local and global auditory processing.

However, lateralization is not a requirement for an auditory local-global distinction to be meaningful. An equally plausible hypothesis concerning spatial separation of local and global auditory processing is that local information might be preferentially processed in ventral areas and global information in more dorsal areas. Human auditory cortex, like visual cortex, is functionally organized in a hierarchical manner such that core areas are activated by simple stimuli (e.g., pure tones) whereas belt and parabelt areas preferentially respond to more complex sounds (Binder et al., 1997; Hall et al., 2002; Price et al., 1996; Wessinger et al., 2001). Evidence that corticocortical connections from different belt and parabelt areas diverge into a primarily anterior and a primarily posterior stream (Kaas, Hackett, & Tramo, 1999; Romanski et al., 1999) has been used to argue that there are two major functional divisions of auditory processing beyond auditory cortex (Rauschecker, 1998; Rauschecker, Tian, & Hauser, 1995). Although this division for auditory processing has been compared to ‘what’ and ‘where’ visual processing streams (Alain, Arnott, Hevenor, Graham & Grady, 2001; Hart, Palmer, & Hall, 2004; Rauschecker, 1998; Rauschecker & Tian, 2000; Read, Winer, & Schreiner, 2002), more evidence is needed to clearly differentiate between the auditory domains or acoustic features that functionally define auditory ventral and dorsal pathways. The anterior-posterior differences in distribution for attention to local and global auditory information in the current study are consistent with a ventral-dorsal pathway distinction, but different techniques would also be needed to draw conclusions concerning this spatial hypothesis.

Relatively high and low pitch

As outlined previously, the three dimensions that could be used to define local and global auditory processing are space, frequency, and time. The manner in which sounds are localized precludes the perception of distinct sources in different locations if the sounds do not also differ in temporal or spectral characteristics. Therefore, hierarchical stimuli in which the same unit is repeated at different locations in the visual modality cannot be directly translated into the auditory modality. Under many conditions, simultaneously presented frequencies are also perceived as a single unified pitch such that listeners are unable to direct their attention to individual frequencies. However, listeners can separate multiple auditory *streams* that primarily differ in pitch (Bregman, Ahad, & Van Loon, 2001; Rose & Moore, 2000). Relatively higher and lower frequency may define the local and global distinction in both the auditory and visual modalities (Justus & List, 2005).

In the current study, there was no evidence for differential processing of sounds with higher and lower pitch: listeners were equally accurate and fast at determining the direction of FM sweeps and the direction of pitch change across three sweeps for the highest three and lowest three pitch ranges, ERPs in response to stimuli at the three lowest and three highest pitch ranges

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were equally right lateralized, and there were no significant differences in the amplitude or latency of measured ERP peaks in response to stimuli of higher and lower pitch. Instead, performance was better and auditory evoked potentials were smaller for stimuli in the middle pitch range. Reduced amplitude of auditory onset components for middle frequencies may relate to the spatial relationship between scalp electrodes and tonotopically organized neural activity since scalp potentials are affected more by postsynaptic potentials in nearby gyri than in sulci (Nunez & Srinivasan, 2006). Alternatively, frequency-specific refractory effects could result in reduced responses to the sounds in the middle pitch range. Since sequences with 8 different center frequencies were presented in random order, sounds in the middle of the range were more likely than those at the extremes to be preceded by other sounds with similar pitch. The average time between onsets of sounds presented in contiguous trials was less than 3.5 seconds; auditory refractory periods may extend to as long as 10 seconds (Hari et al., 1987; Knight, Hillyard, Woods, & Neville, 1980; Sams, Hari, Rif, & Knuutila, 1993; Woods, Courchesne, Hillyard, & Galambos, 1980).

The lack of pitch effects with these stimuli does not preclude defining local and global auditory processing on the basis of frequency. In this study, sounds with relatively high and low pitch were presented on separate trials. Detecting differential processing of local and global pitch ranges likely requires simultaneous presentation. Additionally, the evidence supporting a local and global auditory distinction based on time scale does not conflict with defining a similar distinction based on relative pitch. In the visual modality, there is evidence for differential processing of local and global features defined temporally and spatially. In the auditory modality, local and global processing may differ when defined by time and by frequency.

Differential processing of up and down FM sweeps

Although performance and ERP characteristics did not differ for relatively higher and lower overall pitch, effects of direction of pitch change in the 40 ms FM sweeps were seen in both. Listeners were more accurate at determining pitch change direction at both the local and global levels when the 40 ms sweeps increased in pitch. Further, N100 amplitudes were larger in response to up sweeps than down sweeps. Although not completely understood, this finding is consistent with previous research and the hypothesis that fast up FM sweeps result in more synchronous firing of auditory neurons at the level of the basilar membrane (Gordon & Poeppel, 2002).

Attention and discrimination

The effects of selectively attending to the local or global level on ERPs were the same in participants with better and worse overall performance on the tasks. This finding suggests that the ability to selectively attend to a particular temporal scale is independent from the ability to make pitch direction discriminations at the two levels. However, it may be necessary to use a somewhat difficult discrimination task (or rapid presentation of stimuli) to prevent listeners from attending to multiple levels at the same time or switching frequently between levels. Likewise, participants with larger and smaller behavioral congruency effects showed ERP congruency effects of similar magnitude. One possible explanation for the lack of correspondence between the behavioral and ERP congruency effects is that reaction times and accuracy reflect response selection in addition to perceptual processing. Local pitch direction many have influenced response selection during the global pitch direction task resulting in congruency effects across local and global selective attention. However, differences in ERPs elicited by congruent and incongruent stimuli were only found when listeners were attending to the local level. These ERP differences may index asymmetric interference on perceptual processing that occurs regardless of participant’s skill at making pitch change direction discriminations, any interference at the level of response selection, and individual strategies for reducing interference from the other level.

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General conclusions

Listeners are able to selectively attend to local and global *temporal* levels of auditory stimuli. Doing so results in differential auditory processing reflected in accuracy, reaction times, and ERPs. The patterns of evoked potential and global precedence effects are similar to those found for selectively attending to local and global spatial features in the visual modality. These results provide further evidence that the local-global distinction is important for understanding the organization of auditory processing in the human brain and that time scale is an important dimension along which local and global auditory processing is divided. Future comparisons between visual and auditory local and global processing may provide important information about the relationships between cortical structures and the functions they support across modality.

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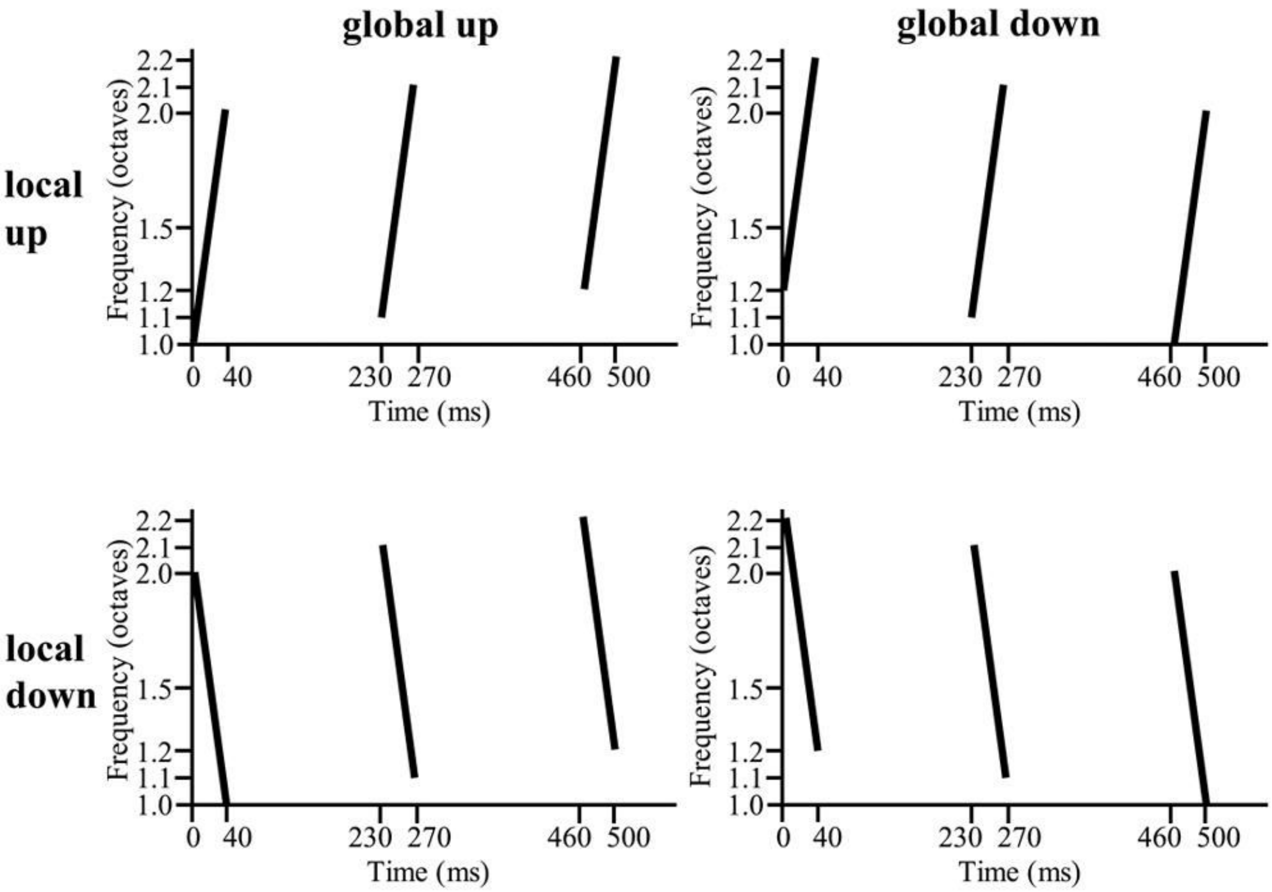

Figure 1.

Stimuli were created by combining three 40 ms up or down FM sweeps with 190 ms interstimulus intervals to form 500 ms sequences. The center frequency for the first and third sweep differed by 1 octave for experiment I, 0.5 octaves for experiment II, and 0.2 octaves for the ERP experiment (shown). Sequences were presented at 8 different frequency ranges.

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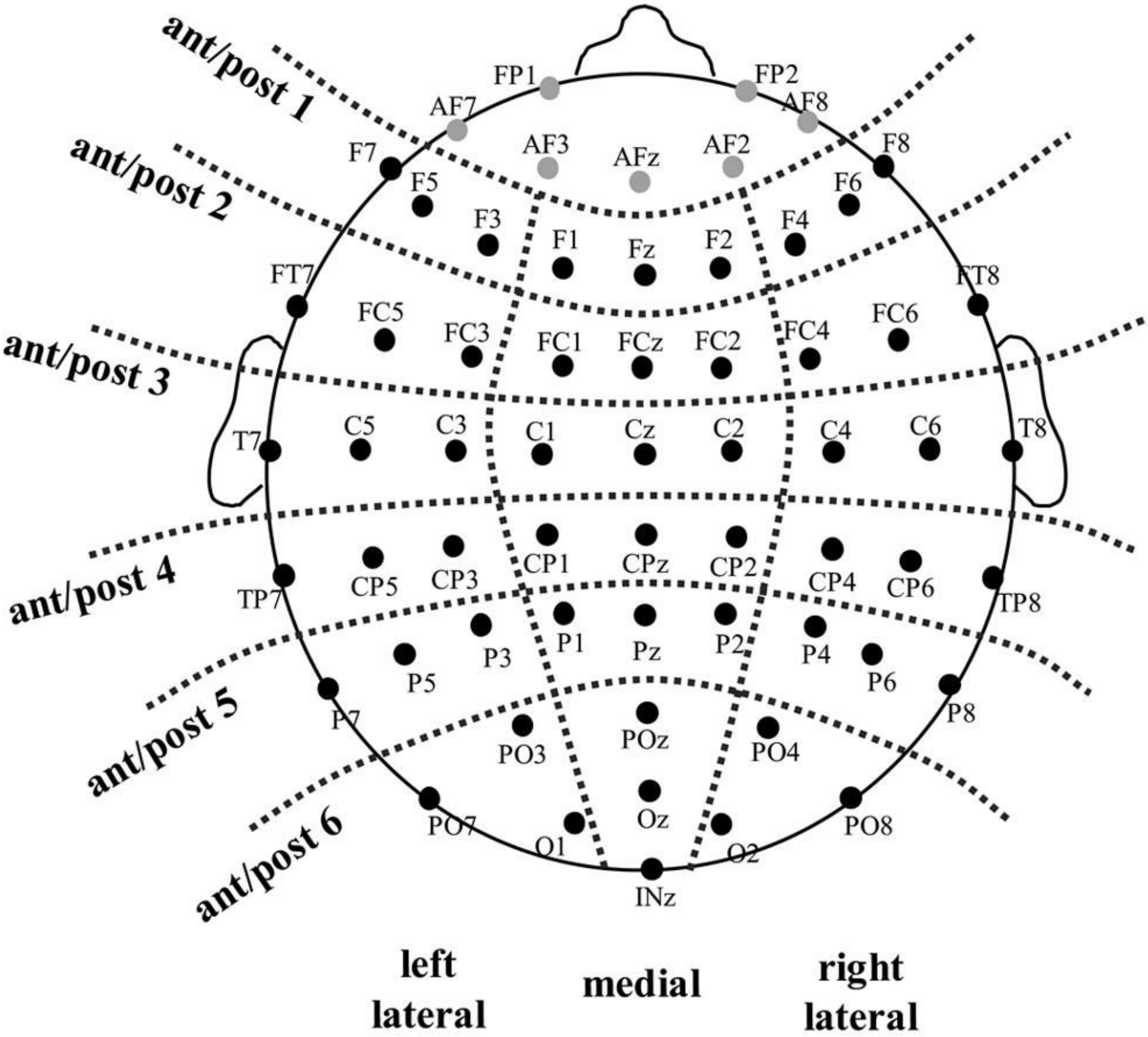

Figure 2.

EEG was recorded at 61 scalp locations (shown), left and right mastoids, and three EOG positions. Electrodes shown in grey were not included in analyses. Three levels of the electrode position factor laterality and hemisphere, 6 levels of the electrode position factor anterior/ posterior, and the electrodes included in each are labeled.

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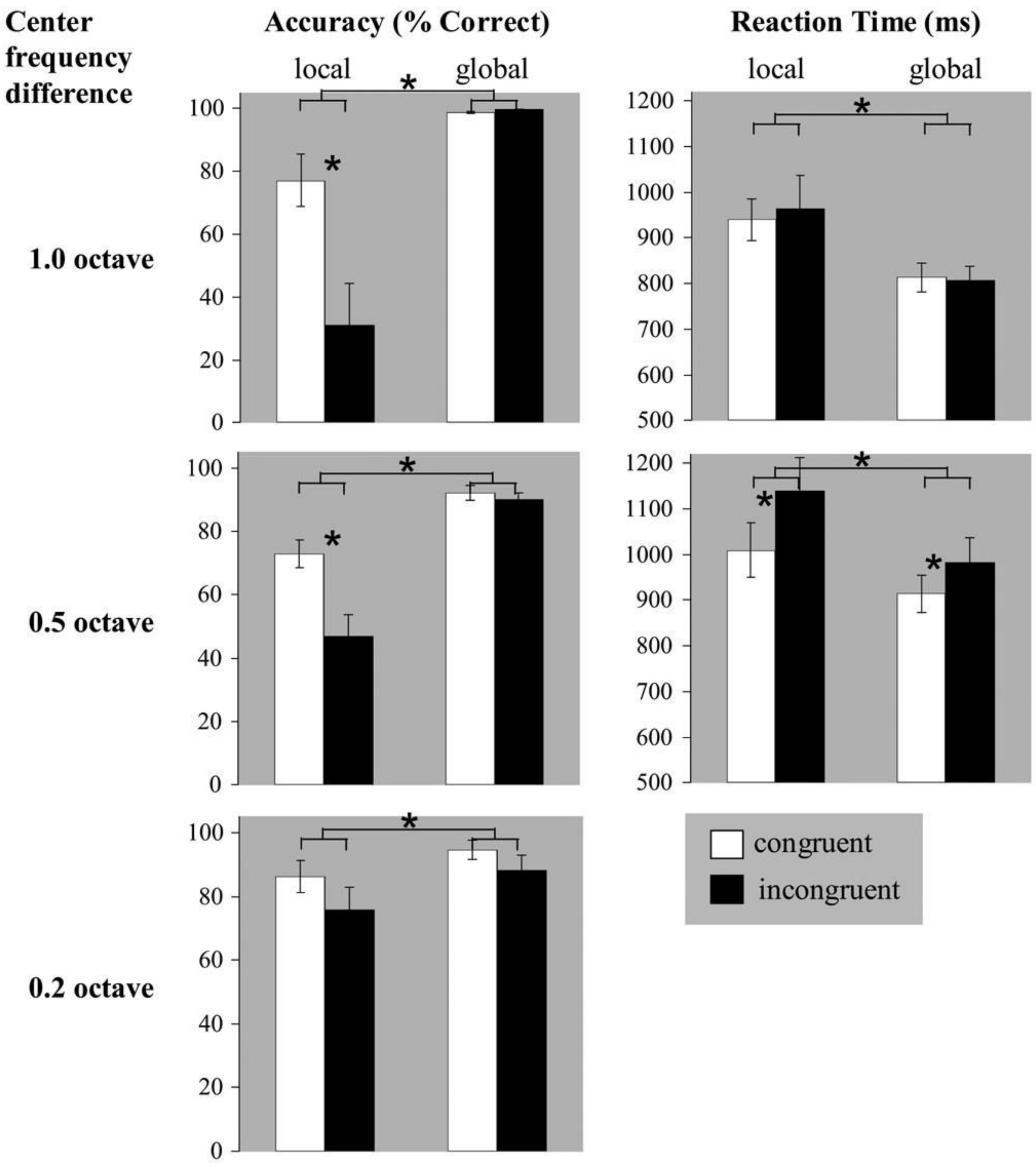

Figure 3.

Average percent correct and reaction time measured from the onset of sound sequences for correct responses were measured for the behavioral experiments. Only accuracy was measured during the ERP experiment since participants were required to delay all responses. Error bars indicate Standard Error for each condition.

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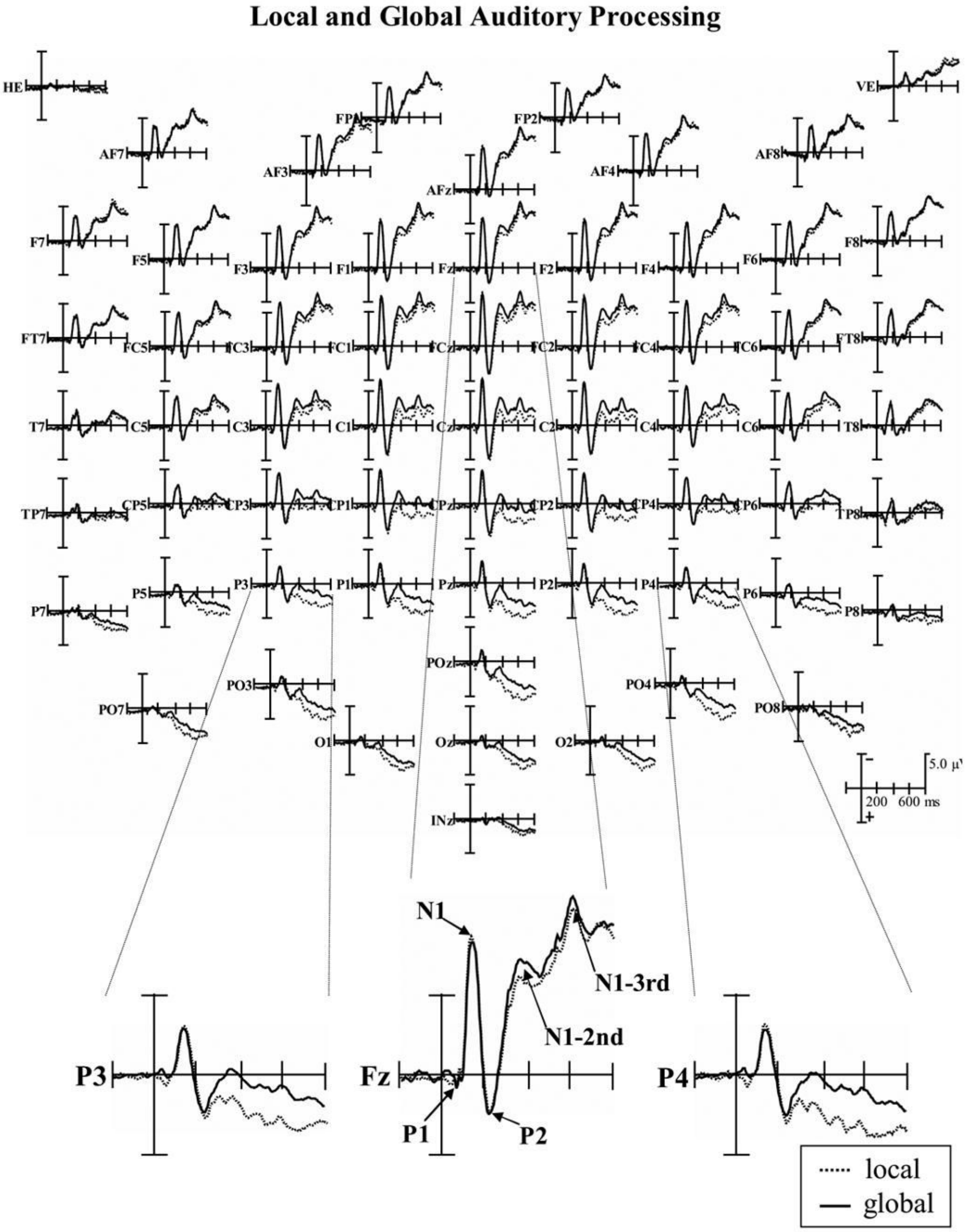

Figure 4.

ERPs elicited by the same physical stimuli when participants attended to the global level (solid lines) or local level (dashed lines). When listeners selectively attended to the local level, sound sequences elicited a larger positivity between 250 and 700 ms.

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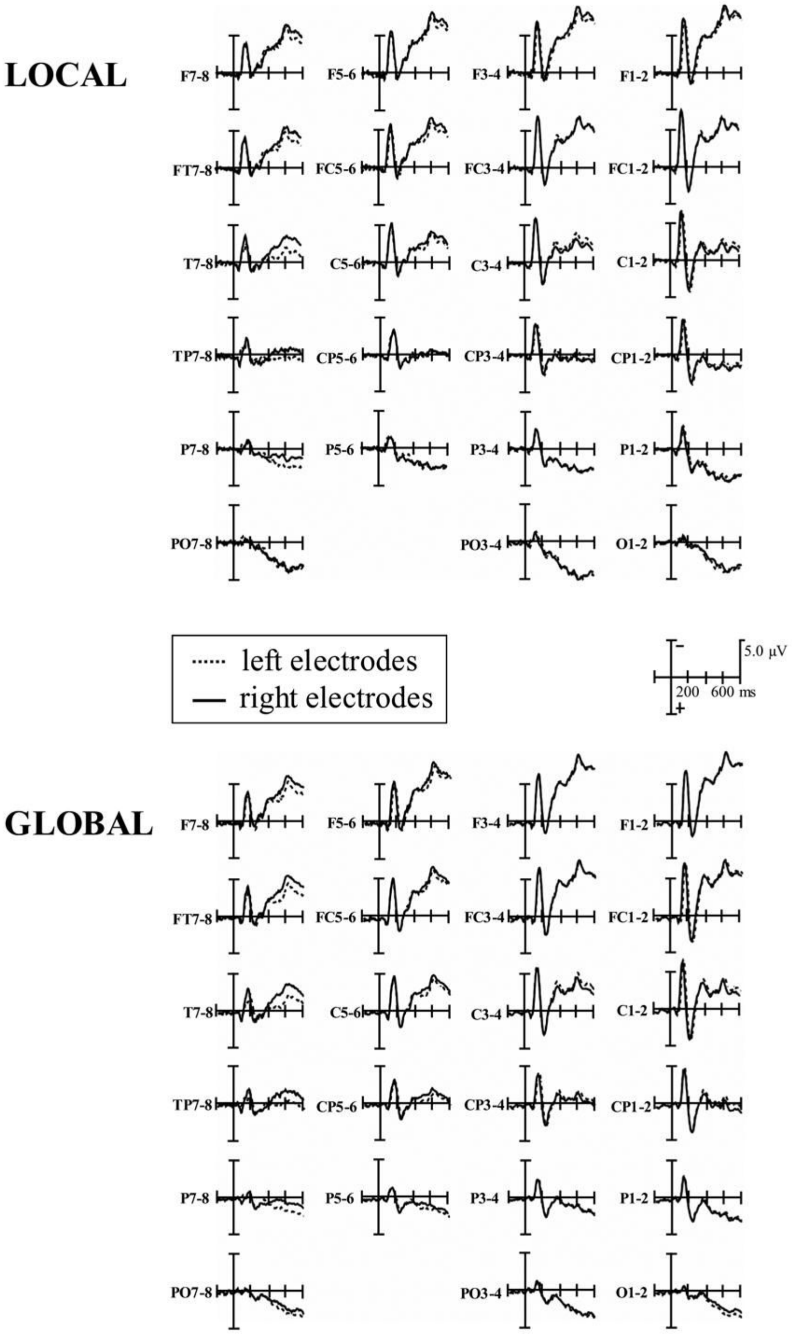

Figure 5.

ERP responses at left and corresponding right electrode sites are shown on the same axis. Responses were right lateralized regardless of task. The overall rightward lateralization may reflect an intrinsic rightward bias when dealing with pitch tracking tasks.

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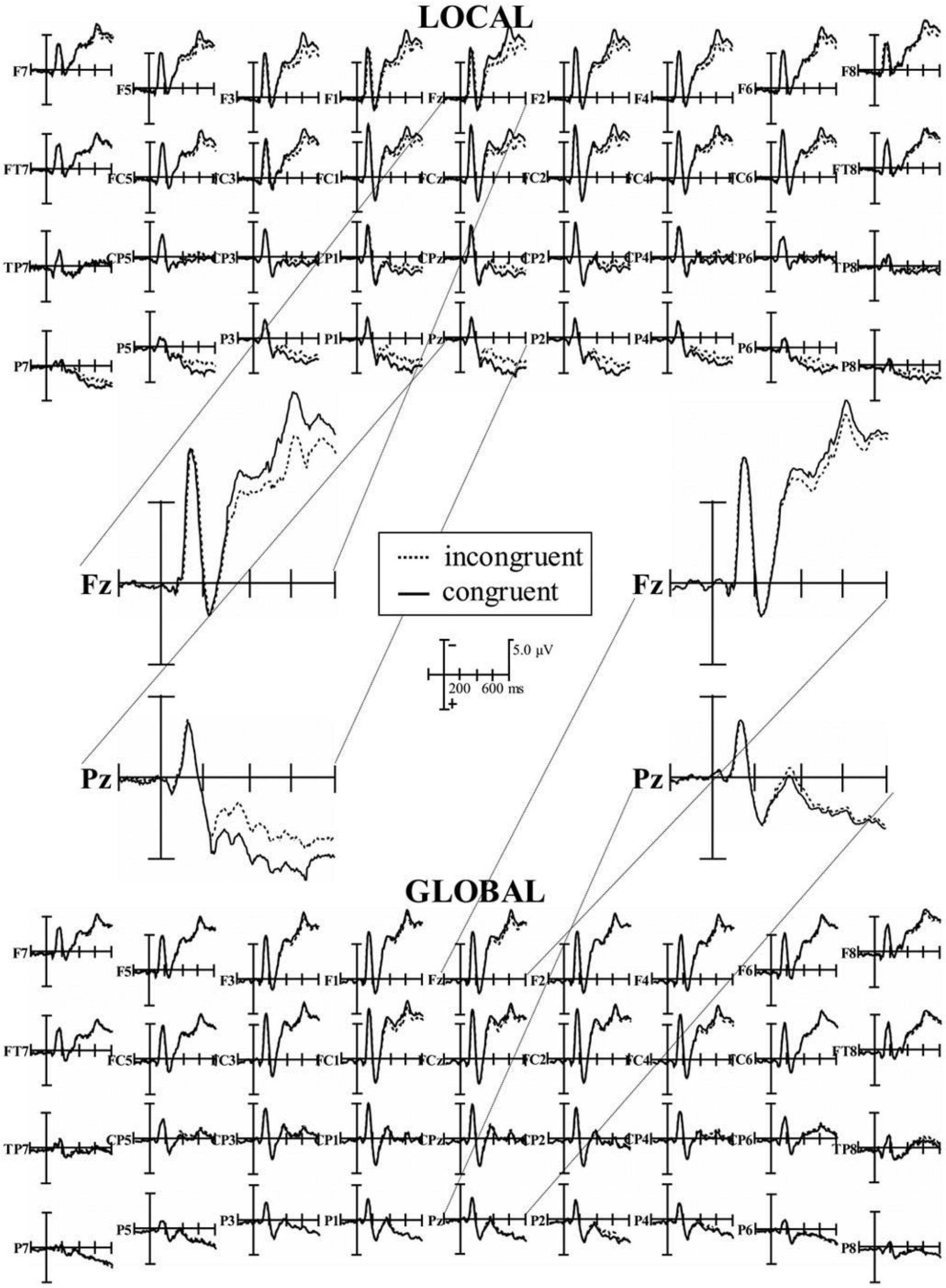

Figure 6.

ERPs for congruent and incongruent trials when participants selectively attended to the local and global levels. Congruency effects were found during attention to the local level only.

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Table 1

Frequency spans and center frequencies for the ERP study.

Pitch Level	FM sweep 1	FM sweep 2	FM sweep 3
1	333 – 666 (500)	366 – 732 (550)	400 – 800 (600)
2	400 – 800 (600)	440 – 880 (660)	480 – 960 (720)
3	466 – 932 (700)	513 – 1026 (770)	560 – 1120 (840)
4	533 – 1066 (800)	586 – 1172 (880)	640 – 1280 (960)
5	600 – 1200 (900)	660 – 1320 (990)	720 – 1440 (1080)
6	666 – 1332 (1000)	733 – 1466 (1100)	800 – 1600 (1200)
7	833 – 1666 (1250)	916 – 1832 (1375)	1000 – 2000 (1500)
8	1000 – 2000 (1500)	1100 – 2200 (1650)	1200 – 2400 (1800)

Note: Range is shown in Hz and describes both rising and falling FM sweeps. Center frequency for each sweep is in parentheses. Both 1-2-3 and 3-2-1 sequences were used to create rising and falling global pitch.

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Table 2

Distribution analyses following significant effects of hemisphere and laterality factor.

Dependent Variable	**Left lateral and Right lateral**	**Left lateral and Medial**	**Right lateral and Medial**
P1 amplitude	**	*	n.s.
N1 amplitude	*	***	**
N1 pitch direction effect	*	**	*
P2 amplitude	n.s.	***	***
Sustained attention effect	n.s.	***	***

Note: When ANOVA results included significant main effects of or interactions with the hemisphere and laterality factor, follow-up comparisons that included every two-level combination of this factor were conducted.

*** p < .001,

** p < .01,

* p < .05, n.s. = not significant (p > .05).