

Selective listening at fast stimulus rates: so much to hear, so little time*

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Selective attention may be defined as a process by which the perception of certain input in the environment is enhanced while that of other concurrent stimuli is relatively suppressed. A common example of this phenomenon in the auditory modality is the so-called 'cocktail party effect', in which a person can selectively listen to one particular speaker's voice while tuning out one or more simultaneous conversations.

Both the physiological and psychological mechanisms of selective attention can be investigated noninvasively in humans by recording event-related electrical potentials (ERPs) and/or event-related magnetic fields (ERFs) from the scalp. Figure 1 shows the three main phases of the auditory ERP: the Brainstem Evoked Responses (BERs, 0–10 msec) reflecting the sequence of evoked activity in the auditory nerve and pathways in the brainstem; the midlatency range (MLRs; 10–50 msec), which appears to reflect some of the earliest cortical activity; and the so-called late waves (60–500

msec), including the well-known N1, P2, and N2 waves.

From the latency and characteristics of various changes of the ERP as a function of the direction of attention, one can make some inferences as to how attention affects processing of stimuli, including how early in the processing such effects occur. For example, can attention affect activity as early as the BERs, or is it not until the MLR/early-cortical range, or perhaps not until several hundred msec into the late waves? For a number of years, the earliest effect of attention that has been consistently observed in the human auditory ERP has been a negative wave in the ERPs elicited by attended stimuli relative to the ERPs elicited by ignored stimuli (Hillyard et al. 1973; Naatanen et al. 1978; Hansen and Hillyard 1980). This negative difference wave, often called Nd, can onset as early as 60 msec, often overlapping the sensory-evoked N1 component, which peaks at about 100 msec.

Some of the key questions we have been interested in examining are:

1. Whether highly focused auditory selective attention in humans can affect stimulus processing at earlier latencies than 60 msec, or whether all the processing before that latency is strongly automatic.
2. Addressing a long-standing controversy as to whether (a) the Nd attention effect, at least under highly focused attentional conditions, includes

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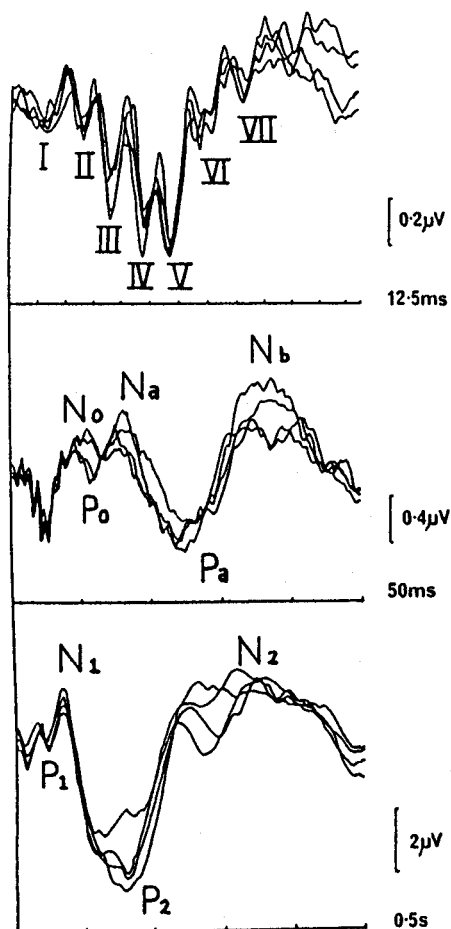


Fig. 1. The three main phases of the auditory ERP. *Top*: The BERs (0–10 msec) reflecting the sequence of evoked activity in the auditory nerve and pathways in the brainstem. *Middle*: The MLRs (10–50 msec), which appears to reflect some of the earliest cortical activity. *Bottom*: The ‘late’ or ‘longer latency’ waves (60–500 msec). (From Picton et al. 1974.)

a direct amplitude modulation of the sensory-evoked N1 component (Hillyard et al. 1973; Hillyard 1981), or (b) whether it is completely, as some have claimed (Naatanen et al. 1978; Alho et al. 1986; Naatanen 1988; 1990), a separate, additional negative wave from a completely different source than the N1 that just happens to sometimes overlap it at the scalp.

3. Determining where in the brain the auditory attention effects occur.

To address these questions, we have carried out in recent years a series of ERP and ERF dichotic listening experiments in which we attempted to optimize the experimental conditions for the se-

lective focusing of auditory attention (Woldorff et al. 1987; Woldorff and Hillyard 1991; Woldorff et al. 1991; Woldorff et al. 1993; also see Hackley et al. 1987; 1990). In these experiments, monaural tone pips are presented randomly to the two ears at a very rapid rate (typically averaging 4–5 stimuli per sec, substantially faster than in most previous studies), with the tones in one ear of a high pitch, those in the other ear of a low pitch. The stimuli are presented in random order to the two ears so the subject cannot predict which ear the next stimulus will come in. The subject’s task is, on half the runs, to listen selectively to all the tones in one ear and press a button upon detecting occasional, difficult-to-detect, target tones of slightly fainter intensity than the rest of the tones in that ear; all the tones in the other ear are to be ignored. On the other half of the runs, the subject selectively attends to the other ear, detects the fainter tones in that ear, and ignores all the tones in the first ear. The task is made deliberately difficult in these experiments to ensure that the subject has to attend very closely to all the tones in the designated ear, both the standard intensity ones and the fainter targets, in order to perform the task.

We will be mainly focusing in this paper on the data from the standard-intensity tones in these experiments. The evoked responses to the deviant target tones in these experiments also provide important data concerning auditory information processing and attention (see Woldorff et al. 1991), evoking such components as mismatch negativity (MMN) and P300; they will be briefly discussed later in this paper.

For the standard tones, the key comparison in this kind of experiment is between the ERP responses to the same physical stimulus under different attention conditions. That is, for example, to take the evoked responses to right-ear standard tones when they were attended, and compare them to the responses to right-ear standard tones when they were unattended – that is, when the left-ear was being attended. In such a comparison, not only is the physical stimulus identical, but the overall arousal is the same because attending to the left ear is about as difficult as attending to the right ear (indeed typically the standard/target intensity difference was titrated for each ear for each subject

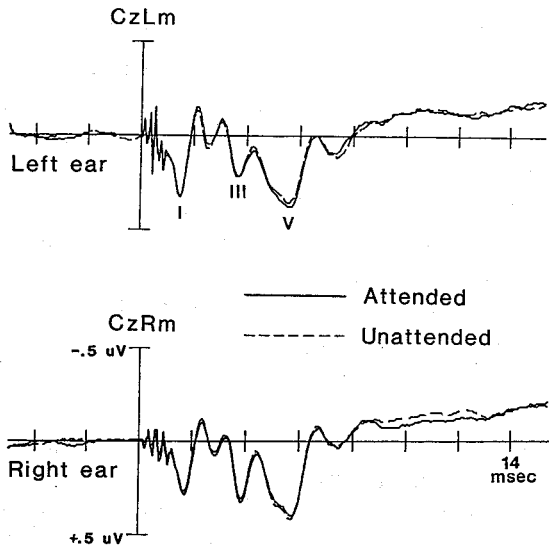


Fig. 2. Grand-averaged ($N = 10$) BERs to left-ear and right-ear tones in a fast-rate dichotic listening experiment. ISIs were from 120–320 msec. BERs to the tones when attended are superposed on the BERs to the same tones when unattended. Recordings are from site Cz referred to the ipsilateral mastoid, with bandpass 30–3000 Hz. That there was no effect of attention on these components can be seen from the close superposition of the attended and unattended waveforms. (Figure from Woldorff et al. 1987.)

so that this was the case). Thus, any differences found can be attributed to the internal shifting of attention either towards or away from these tones.

Short latency effects

Concentrating first on the very earliest components, the BERs, Fig. 2 shows the first 14 msec of the evoked responses, grand-averaged across the 10 normal subjects in one of these experiments. It is evident from the figure that it made no difference to the BER responses whether the eliciting tones were attended or unattended, and statistical analysis revealed no significant effects on either the amplitude or latency of any the BER components (Woldorff et al. 1987). Thus, despite our attempts to optimize the conditions for the selective focusing of attention, we obtained no evidence for any brainstem level gating as a mechanism of selective attention, thereby confirming previous reports (Picton and Hillyard 1974; Woods and Hillyard 1978; Picton et al. 1981).

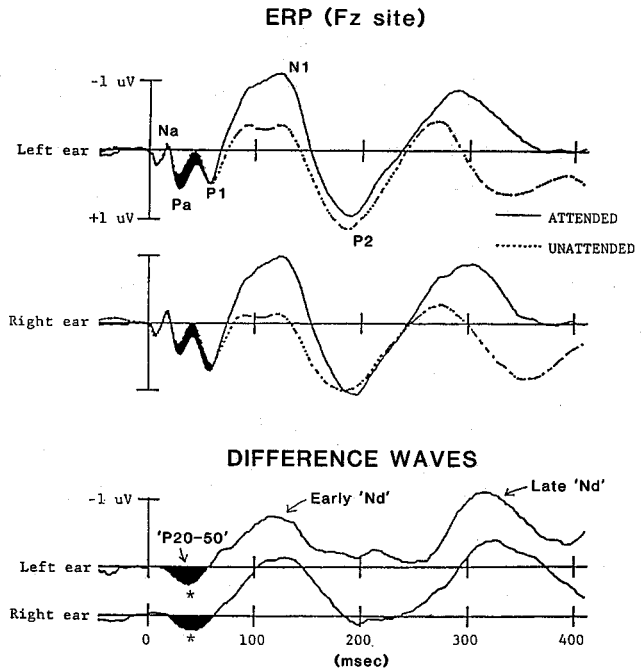


Fig. 3. Grand-averaged ($N = 10$) ERPs and attentional difference waves to left-ear and right-ear tones, when attended and when unattended, in the same fast-rate dichotic listening experiment for which the BERs are shown in Fig. 2. Recordings are from the Fz site referred to averaged mastoids, with bandpass 0.01–100 Hz. The P20–50 attention effect (darkened area) appears as an enhanced positivity between 20–50 msec in the attended-tone ERP relative to the unattended-tone ERP. This can be seen more clearly in the attentional difference waves (attended-tone ERP minus unattended-tone ERP), shown at the bottom. (Figure from Woldorff et al. 1987.)

We did, however, discover a new early attention effect under these conditions in the midlatency range (Fig. 3), with tones in the attended ear eliciting a small, but reliable, enhanced positivity from 20–50 msec relative to those same tones when they were unattended (Woldorff et al. 1987). This attention effect, which we termed the P20–50, can be seen more closely by taking the attentional difference waves of attended ERP minus unattended attended ERP (Fig. 3, bottom). Besides being obtained in several fast-rate dichotic listening experiments, this very early effect of attention was also obtained in a closely related fast-rate intermodal (auditory/visual) attention experiment (Hackley et al. 1990).

The P20–50 attention effect overlaps the

midlatency wave Pa, a component that, based on other sorts of evidence (Celesia 1976; Kraus et al. 1982; Kileny et al. 1987; Scherg et al. 1989), appears to reflect some of the earliest activity in primary auditory cortex. Thus, the occurrence of an effect of attention at this latency strongly suggests that selective processing of attended vs. unattended inputs in humans can begin by the level of primary or secondary auditory cortex.¹ Furthermore, the very early onset of this effect (20 msec following stimulus occurrence) strongly supports the psychological stimulus processing theory known as early selection, which posits that stimulus processing can be selectively tuned or biased before full analysis has occurred (reviewed in Johnston and Dark 1982; 1986; Kahneman and Treisman 1984). Moreover, this very early onset also strongly implies that this biasing must be achieved by means of a tonically maintained prestimulus set that biases the processing of stimuli in the relevant channel relative to the irrelevant one.

Longer-latency attention effects

At longer latencies, we have found a variety of attention-related ERP effects in this fast-rate dichotic listening paradigm (Woldorff and Hillyard 1991). Figure 4 shows the attended and unattended ERPs to the right-ear tones at some of the scalp sites that were used; Fig. 5 shows the corresponding ERPs for the left ear.

The first feature to notice in these plots is that there were various attention effects, so that describing them simply in terms of one negative wave, such as an Nd, would be inadequate. Moreover, these various effects appeared to involve both endogenous and exogenous components. Frontally, for example, the effect of attention was a long broad negativity, which appeared to be primarily exogenous, in that it bore little similarity to the underlying ERP components. Centrally, however, the attention effect was distinctively triphasic and highly modulatory in appearance — that is, the attention-related changes closely overlapped in time

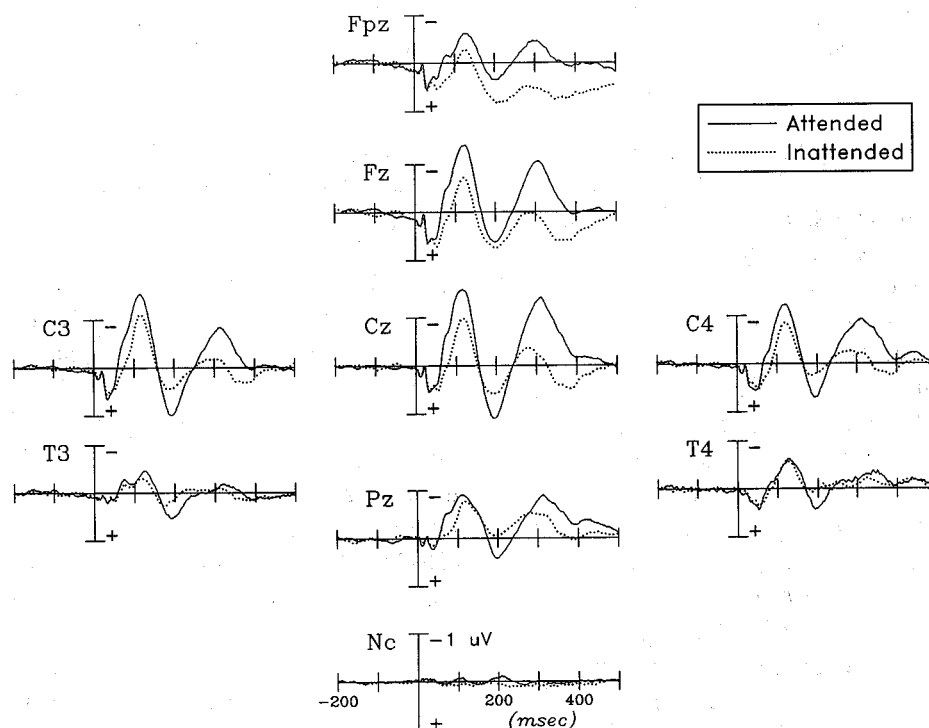


Fig. 4. ERPs for attended and unattended right-ear tones at some of the recorded sites, grand-averaged across subjects ($N = 16$), in a second fast-rate dichotic listening experiment (also with ISIs of 120–320 msec). Reference for all sites is the algebraic average of the mastoids. Bandpass was 0.1–100 Hz. Nc = balanced sterno-vertebral noncephalic. (Data from Woldorff and Hillyard 1991.)

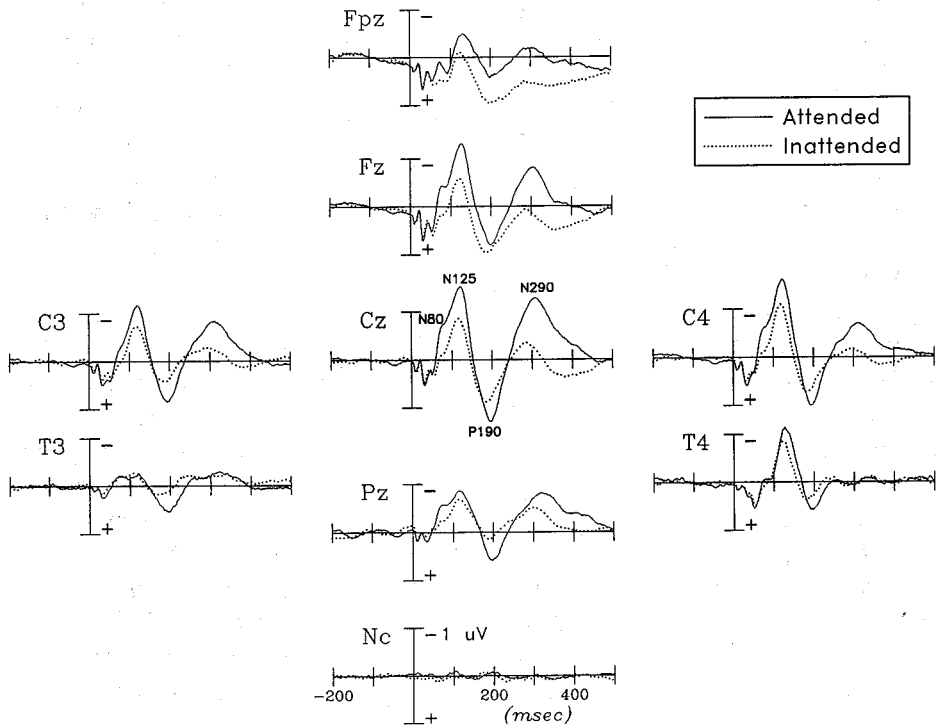


Fig. 5. Same as for Fig. 4 for left-ear tones, with some additional, more specific, labelling of several components/subcomponents seen at central sites. N80 and N125 were apparent subcomponents of the N1; P190 = P2; N290 = N2. (Data from Woldorff and Hillyard 1991.)

the underlying N1, P2, and N2 components (occurring at around 100, 200, and 300 msec, respectively). It is conceivable that this triphasic attention effect was also entirely endogenous and that the waveshape similarity and close temporal correspondence with the exogenous ERP components were completely coincidental. That is, an endogenous negativity attention effect from a different source than the N1 just happened to closely overlap the N1, that an endogenous positivity attention effect just happened to closely overlap the P2, and that an endogenous negative attention effect just happened to closely overlap the N2. However, we believe that a much more plausible explanation is that this close temporal correspondence results from the highly focused auditory attention in this experiment causing an amplitude modulation of at least some of the exogenous (sensory-evoked) components of the ERP (Woldorff et al. 1987; Woldorff and Hillyard 1991; Hackley et al. 1987; 1990). This was further supported in these studies in that the evoked N1 wave and the attention effect

overlapping it were both larger contralateral to the stimulated ear (Woldorff and Hillyard 1991).

Figure 6 shows the attentional difference waves (attended ERP minus unattended ERP) for the left-ear and right-ear tones. These traces show even more clearly the multiplicity of the attention effects – frontally, the broad negativity; centrally, the triphasic, modulatory effect. Some hints of an even greater multiplicity of attention effects in this kind of paradigm can also be seen. For example, there was a suggestion of even greater subcomponentry centrally in the N1/‘early ND’ range (60–150 msec), which appeared to correspond to similar subcomponentry of the sensory-evoked exogenous components (Fig. 5). In addition, the effect of attention at temporal sites was different still, with an enhanced positivity at 100 msec followed by a negativity at 135 or 140 msec. This appeared to be an effect on the ‘T-complex’ (Wolpaw and Penry 1975), a biphasic (positive/negative) exogenous wave believed to arise from association auditory cortex on the lateral surface

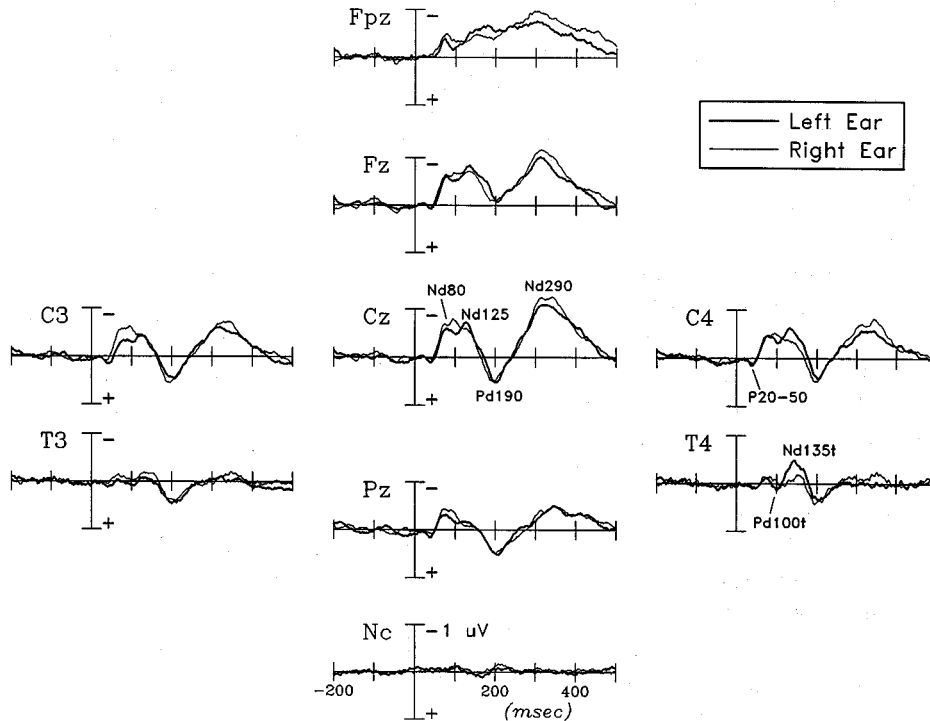


Fig. 6. Attentional difference waves (attended-tone ERP minus unattended-tone ERP) derived from the data shown in Figs 4 and 5. (Data from Woldorff and Hillyard 1991.)

of the superior temporal gyrus (Wolpaw and Penry 1975; Scherg and von Cramon 1986; Näätänen and Picton 1987).² These attentional difference waves underscore the view that (a) several different ERP attention effects were elicited in this fast-rate dichotic listening paradigm, and (b) that these effects included amplitude modulations of various of the major exogenous sensory-evoked ERP components.

Adjacent ERP overlap at fast stimulus rates

One of the factors that we found to be particularly important in engendering the selective focusing of attention and in enhancing the early selection process is the rapid presentation of stimuli (also see Schwent et al. 1976; Hillyard and Picton 1979; Hansen and Hillyard 1984). In particular, when stimuli are coming fairly slowly into two channels of input, such as when tone pips are presented randomly to the two ears, it is very difficult to stay selectively tuned in to one channel (that is, to one ear) and keep the other channel tuned out; our attention just does not stay very focused on a sparsely presented channel. However, if the tones are de-

livered quickly, it is easier to stay tuned in to an ear, or to a channel of input in general, in part because the repetitively presented channel cues help keep you tuned in, and in part because it simply becomes too difficult to attend to all the stimuli. (Thus, a principal reason for the title of this paper.) Also, fast streams of stimuli more closely simulate the continuous sounds that we often encounter and attend to in everyday life.

Although fast stimulus rates may enhance the selective focusing of attention, they pose a problem in the analysis of ERP data due to the fact that the ERP to a given stimulus is likely not to have ended by the time the next stimulus arrives. In the course of our studies, it became clear that this was a major problem for the stimulus rates at which we wanted to run. Figure 7a shows some ERP responses to standard-tone stimuli from a single subject engaged in a dichotic listening task in a pilot experiment where the interstimulus intervals (ISIs) were 130–190 msec. It is easily discerned that there was substantial distortion from adjacent ERP responses. For example, there is a clearly evoked

signal even before time 0 – i.e. before the current stimulus even occurred; moreover, the series of waves past around 350 msec appears to have resulted from subsequent stimuli.

One method to help deal with the overlap problem is to jitter, or randomly vary, the ISIs over a range, and thereby temporally ‘smear out’ the distorting overlap from the adjacent responses (Woldorff 1993). As Fig. 7a shows, an ISI jitter of only 60 msec resulted in considerable distortion of the ERP averages due to previous and subsequent response overlap. As the ISI jitter is widened (Fig. 7b), however, the adjacent stimuli occur across a wider and wider range relative to time 0, resulting in the distortion due to the ERP responses to those adjacent stimuli being more and more attenuated in the ERP averages. In the last case (Fig. 7c), where the range of ISIs was the widest (120–320 msec), the waveforms appear relatively undistorted, with, for example, a relatively flat prestimulus baseline, and without extra activity past N2. This last set of ISIs is what we used in several of our recent dichotic listening experiments, and, in fact, the data in Fig. 7c are from a single subject in one of those experiments.

Thus, it might appear that jittering the ISIs from 120–320 msec solved the problem. However, it was not entirely clear whether it had actually done so completely. Moreover, because of the implications of the early P20–50 effect (Fig. 3) for mechanisms of selective attention, particularly the implications derived from the very early latency of this effect, it was very important to be sure that the latency really was 20 msec, rather than the effect actually being the result of some combination of overlap from the late waves of the previous overlapping ERP responses.

By borrowing some principles from signal processing, a framework could be developed for analyzing the distortion of ERP averages due to adjacent response overlap (Woldorff 1993). This framework expresses the overlap distortion in terms of mathematical convolutions and uses filtering concepts to analyze the manner and degree to which jittering the ISIs or adjusting other experimental parameters or design can help mitigate the distortion that ends up in the final averages. Using such a framework, it was possible to evalu-

ate the implications of overlap in various experimental situations, such as cross-modal vs. intramodal studies, when stimuli were well randomized, when they were not, and so on. A particularly important finding that resulted from this analysis was that, contrary to popular belief, the widely used procedure of stimulus randomization used in selective attention experiments does *not* necessarily eliminate differential ERP overlap between attended and unattended ERPs (for a complete discussion, see Woldorff 1989; 1993).

Thus, this work had succeeded in proving that the P20–50 *could* have been due to differential overlap. However, the analyses also showed that intramodal auditory attention studies are considerably less vulnerable to this problem than are some other types of studies. Particularly vulnerable are cross-modal attention experiments (e.g. visual/auditory) and intramodal selective attention experiments in which the ERPs are highly lateralized (e.g. visual, somatosensory). In addition, building on this signal-processing framework led to the development of a set of algorithms, called the ‘Adjacent Response Filter Technique’ (Adjar), that could estimate and remove the residual overlap distortion from the recorded averages (Woldorff 1989; 1993). Technical details about this technique will not be presented here, but a few examples of its application will be illustrated.

An important first question that could be addressed with the Adjar technique was how much overlap distortion actually was in the overall attended and unattended ERP averages (which in the Adjar procedures are called the ‘full averages’), and thus whether this was the artifactual cause of the P20–50. Figure 8 (left panel) shows examples of these full averages before any correction. Examining these waves closely, especially during the prestimulus period where no activity should yet be occurring, reveals that indeed some residual previous response activity may have been present. The middle panel of Fig. 8 shows the Adjar-derived estimates of the overlap distorting these ERP averages. The overlap estimates show that even in these full averages, which were preceded by a variety of types of stimuli, eliciting their responses across the entire ISI jitter range of 120–320 msec, some residual overlap distortion still was present.

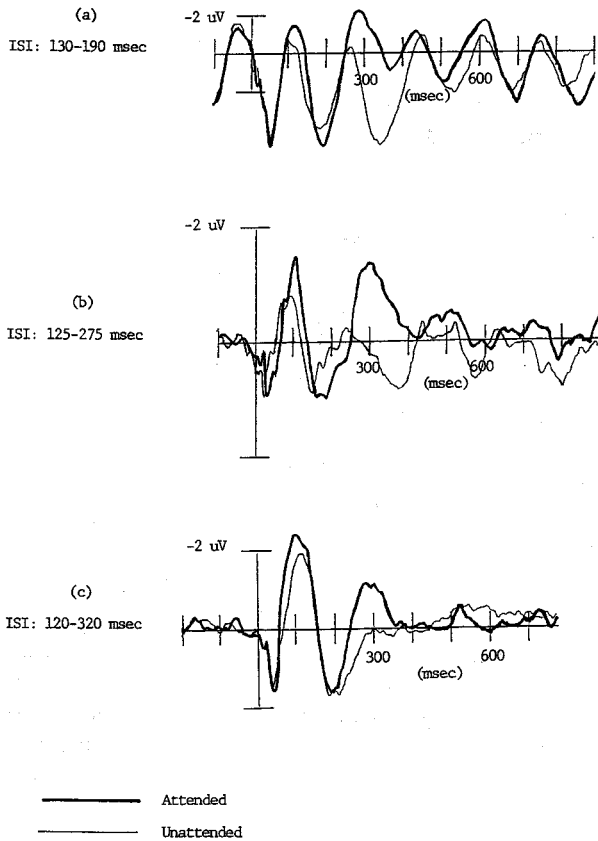


Fig. 7. Effects of ISI jitter range on the average ERP response. (a) Jitter = 130–190 msec. (b) Jitter = 125–275 msec. (c) Jitter = 120–320 msec. Data are from single subjects performing a dichotic listening task. (Figure from Woldorff 1993.)

However, as can be seen, this residual overlap was small, and, more importantly, it did not differ between the attended and unattended ERPs. Thus, after subtracting these overlap estimates from the original ERP full averages to obtain the Adjar-corrected full averages (Fig. 8, right panel), the small P20–50 was still present (Woldorff and Hillyard 1991).

Sequential analysis

The implications and capabilities of being able to remove overlap with a technique such as Adjar go beyond being able to remove the residual overlap from the overall attended and unattended ERPs. Once a means exists for removing the overlap distortion from ERPs, various questions can be investigated that were not possible to investigate before, or at least not possible to do so validly. For example, at a rapid rate of stimulation, the processing of each stimulus may vary considerably as a function of what the previous stimulus was and how recently it occurred. Observing the effects of such interactions on different ERP components could lead to substantial insight into the dynamic mechanisms of stimulus processing during selective attention. In attempting to investigate such sequence effects using ERPs, however, the problem of differential overlap distortion becomes even

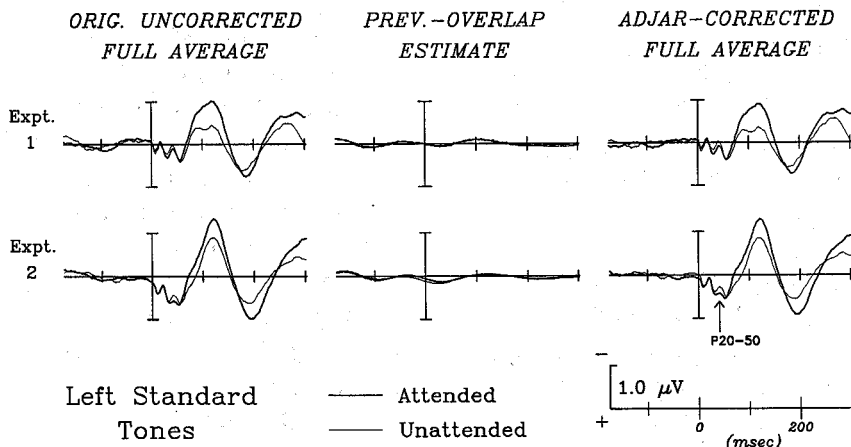


Fig. 8. Uncorrected and Adjar-corrected full average ERPs elicited by left-ear standard tones at the C3 site in two different fast-rate dichotic listening experiments, along with the corresponding summated overlap from previous responses that was estimated and removed. All waveforms are grand averages across subjects. (Data from Woldorff and Hillyard 1991.)

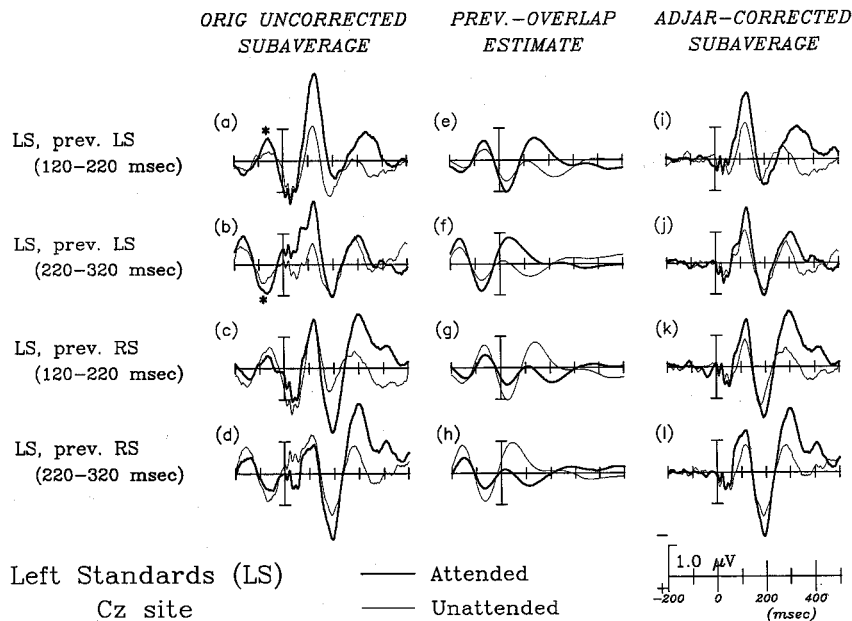


Fig. 9. Removal of previous-response overlap from ERP sequence-based subaverages. Left column shows the grand-average ($N = 16$) subaverages, before Adjar correction, for attended and for unattended left-ear standard tones, for each of four types of preceding stimuli. Note the differential distortion from the overlapping responses to these preceding stimuli. The middle column shows the Adjar-derived estimates of the distorting overlap and the right column shows the corresponding subaverages obtained after subtracting out these estimates of the distortion. LS = left standard tone; RS = right standard tone. (Figure from Woldorff and Hillyard 1991.)

more troublesome. That is because the individual ERPs must be sorted into subaverages based on different subsets of the previous stimulus types or ISI subranges.

For example, Fig. 9 (left column) shows the ERPs to left standard tones sorted as a function of whether the previous stimulus occurred in the same ear, or in the opposite ear, as well as whether it occurred in the recent half of the ISI range, or the longer half. The figure clearly shows that, when responses are overlapping, any physiological effects of the prior stimulus type on the ERP being analyzed are confounded with differential overlap resulting from the ERPs elicited by those differing previous stimuli. For instance, instead of having flat prestimulus baselines, there is clearly evoked activity from the previous responses; moreover, this previous-response activity is different for these various subaverages. The wave peaking at -70 msec in the top left panel, for example, is the partially smeared out N1 of the previous left-tone responses. In the second panel of the left column it appears longer ago, and the partially smeared P2

can be more clearly seen. This differential distortion from the previous responses clearly continues past the prestimulus period into the current waveforms, thereby making a valid analysis of those ERPs impossible.

Applying the Adjar technique to these data yields the estimates of the overlap distortion in each of these subaverages (Fig. 9, middle column). Note in the prestimulus baselines, where there should be no evoked activity appearing because the current stimulus has not even occurred yet, how well the estimates appear to approximate the distortion. These overlap estimates are then simply subtracted from the original averages to obtain the filtered, or corrected, subaverages (Fig. 9, right column), which can clearly be seen to be much less distorted by overlap. This now enables a valid analysis of the ERP responses, and the ERP attention effects, to these left standard-tone stimuli, as a function of what occurred previously and how long ago, but with the overlap distortion from those previous responses removed.

The concepts of the Adjar framework and tech-

nique, although developed for ERP analysis, are applicable more broadly. In modified form, they would be applicable to various other physiological response measures, for example, galvanic skin responses, or post-stimulus histograms of single unit firing, or even, perhaps, yet-to-be-developed evoked time-locked positron emission tomography (PET) or functional magnetic resonance imaging (fMRI) responses. These principles should be applicable essentially whenever a researcher needs or wants to collect evoked responses at short ISIs – short, that is, relative to the particular responses being measured.

Returning to these ERP data, however, consider briefly just a few of the findings revealed by the sequential analysis of the data from these fast-rate dichotic listening experiments (Woldorff and Hillyard 1991). One clear finding was that the attended responses varied considerably more than did the unattended ones (Fig. 10). The left side of Fig. 10 shows superposed the various attended left-ear ERP subaverages at two sites, when they were preceded in the same ear, or opposite ear, recently, or longer ago, all Adjard-corrected. These attended-tone waveforms clearly show substantial sequen-

tial variation, whereas the corresponding unattended-tone subaverages (right side of Fig. 10) varied substantially less. The reason for this interaction appears to be related to some complicated but revealing interactions between attention and a type of neural processing ‘refractoriness.’ (See Woldorff and Hillyard 1991, for a full discussion.) The main point to be made here is that the overall attended and unattended left-tone ERPs show only the average of these various subaverages, and this differential pattern is not seen.

Also of particular interest to examine in these data were the attention effects as a function of sequence – that is, the attentional difference waves of attended ERP minus unattended ERP, as a function of preceding stimulus type or ISI subrange. Figure 11 shows examples of such attention difference waves as a function of preceding stimulus type. Various subcomponents of the attention effects became much more distinguishable, especially in the N1/early-Nd latency range, because they were differentially affected by sequence (cf, Figs 5 and 6). These attention-related subcomponents differentiated still further when the factor of ISI was added in (Fig. 12). There were also

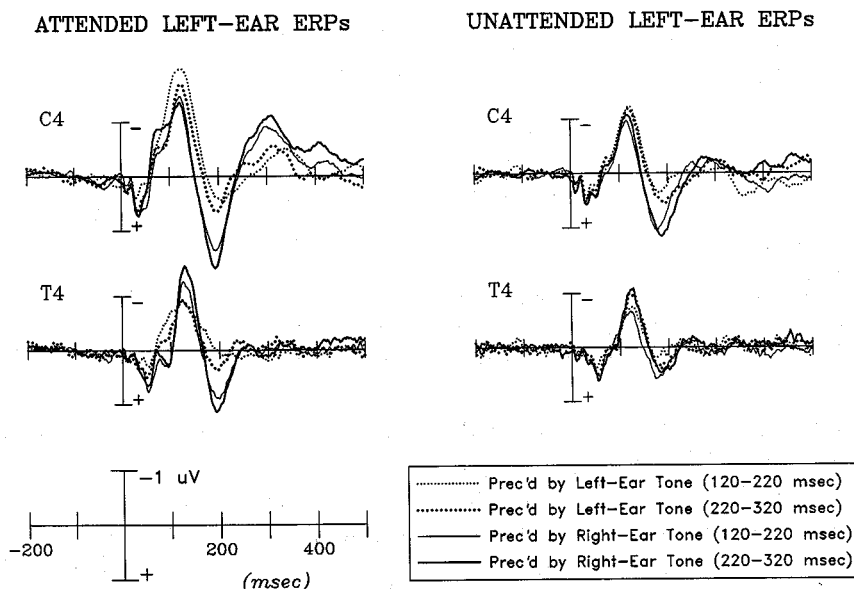


Fig. 10. Adjard-corrected left-tone ERP subaverages as a function of the type and ISI subrange of the previous stimulus. The superposition of the four attended-tone subaverages with each other and the corresponding four unattended-tone subaverages with each other shows that the ERPs to the tones when they were attended varied considerably more as a function of sequence than did ERPs to those same tones when unattended. (Figure from Woldorff and Hillyard 1991.)

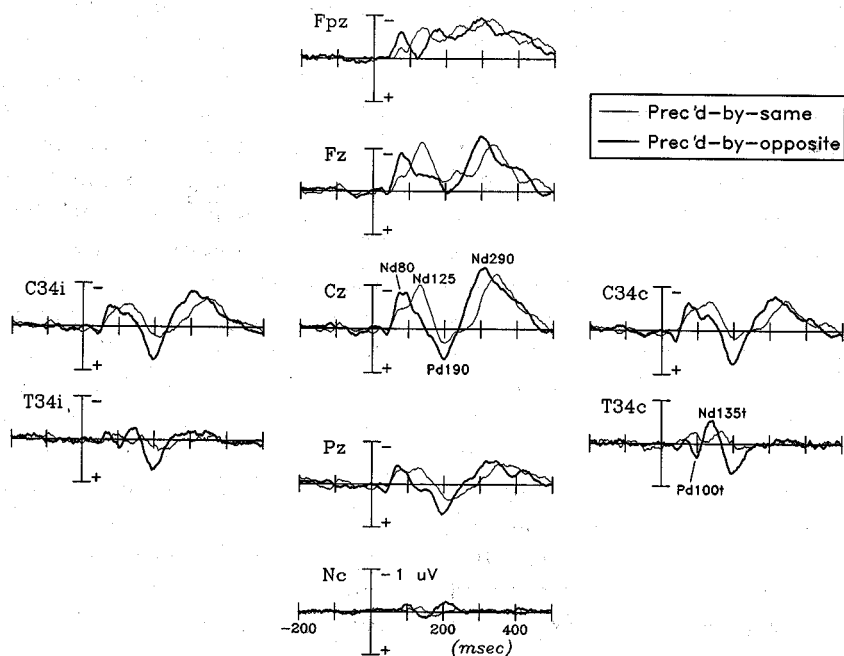


Fig. 11. Attentional difference waves (attended-tone ERP minus unattended-tone ERP) in the fast-rate dichotic listening paradigm for tones preceded in the same ear vs. preceded in the opposite ear, collapsed across ear of stimulation. For the lateral sites, 'c' indicates the site contralateral to the ear of stimulation, and 'i' indicates the ipsilateral site. Reference for all sites is the algebraic average of the mastoids. (Data from Woldorff and Hillyard 1991.)

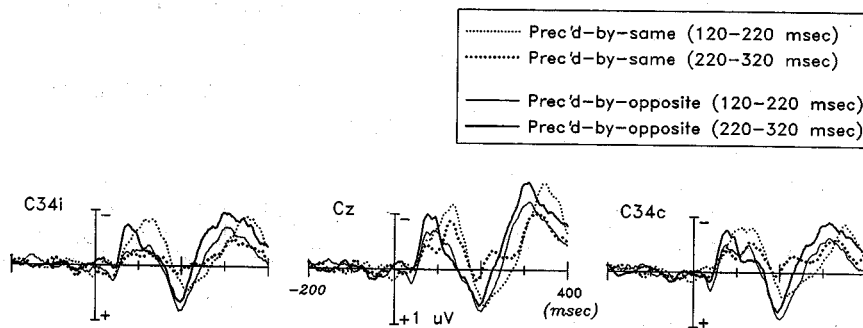


Fig. 12. Attentional difference waves at central sites as a function of both previous stimulus type and ISI subrange, collapsed across ear of stimulation. For the lateral sites, 'c' indicates the site contralateral to the ear of stimulation, and 'i' indicates the ipsilateral site. (Data from Woldorff and Hillyard 1991.)

striking interactions of attention and sequence at temporal sites (e.g. see sites T3 and T4 in Fig. 11) on the biphasic T-complex, mentioned earlier. Again, the main point here is that the overall attentional difference waves obtained from the overall attended and unattended ERP averages would show only the average of these clearly differing waveforms.

Overall, the various effects revealed by this

sequential analysis using the Adjar technique (Woldorff and Hillyard 1991) can be best summarized by saying that these analyses reinforced the view that the effects of attention included the modulation of various sensory-evoked exogenous components or subcomponents. These analyses showed further, however, that the degree to which attention could enhance these components at these fast stimulus rates appeared to be limited by a neural

refractoriness which varied as a function of sequence. In addition, a parallel sequential analysis of task performance was performed – that is, an analysis of the discrimination of the target tones in the attended channel as a function of what type of stimulus preceded the targets. This behavioral analysis revealed that the sequential variations in perceptual discrimination accuracy paralleled the sequential variations in several of the attention effect components (Woldorff and Hillyard 1991). Such results lend additional support to the view that attention can affect stimulus processing before full perceptual analysis has been completed.

Mismatch negativity (MMN)

The data presented thus far have focused on the ERPs elicited by the standard tones in these fast-rate selective listening experiments. However, the ERPs elicited by the infrequent, lesser-intensity, deviant tones in these experiments also provided important data relevant to recent theories of auditory attention. In particular, when an infrequent, physically deviant stimulus occurs in a repetitive sequence of identical stimuli, it elicits a negative wave that onsets at about 100 msec post-stimulus and peaks at around 200 msec (reviewed in Naatanen 1990). This wave, termed the MMN by Naatanen and associates, is thought to arise predominantly from the auditory cortex on the supratemporal plane (STP). In several studies, Naatanen and colleagues had asserted that the MMN is unaffected by attention and thus reflects the operation of a strongly automatic mismatch detection process (Naatanen et al. 1978; 1980; Sams et al. 1984; 1985; Naatanen 1990). Further, they have cited this effect, and its independence from attentional influence, as evidence that the physical characteristics of auditory stimuli are fully processed even when unattended.

Because conditions in our fast-rate dichotic listening experiments were optimized for the selective focusing of attention, they provided an opportunity for a strong test of Naatanen's proposals in that we could examine 1) whether an 'automatic' MMN would still be elicited by the unattended deviant tones, and 2) if so, whether it would be

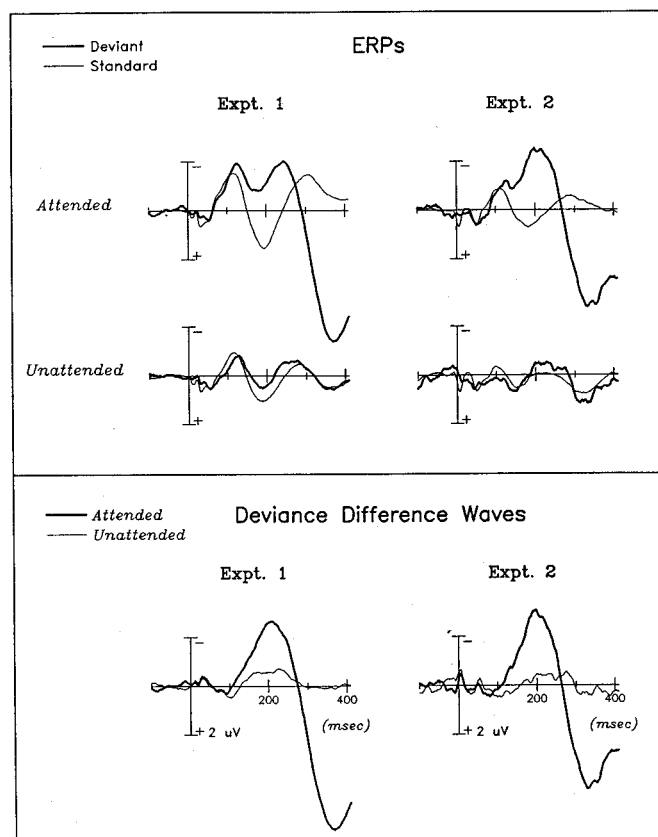


Fig. 13. Vertex (Cz) ERPs and deviance difference waves from two fast-rate dichotic listening experiments, collapsed across ear of stimulation. *Experiment 1* (left column) had ISIs of 120–320 msec, and deviant tones were intensity decrements averaging about 15 dB. *Experiment 2* (right column) had ISIs of 65–205 msec, and deviant tones were intensity decrements averaging about 20 dB. Note the deviance-related negative (DRN) at 200 msec was of similar amplitude in the two experiments, but the unattended-channel DRN/MMN, which was small in Experiment 1, was reduced even further in Experiment 2. (Figure from Woldorff et al. 1991.)

equivalent to that elicited by the attended deviants. Also, Naatanen's framework predicts, and some empirical evidence supports (see, for example, Naatanen et al. 1987), that the MMN should be larger at shorter ISIs, because the standard-tone template to which the deviant tone would be compared should be stronger. Thus, the MMNs in our fast-rate experiments should not only be of equal amplitude in the attended and unattended channels – they should also be of substantial size.

Figure 13 shows the ERPs elicited in two fast-rate dichotic listening experiments at the Cz site

(Woldorff et al. 1991). The ERPs elicited by the deviant tones (intensity decrements), when they were attended and when they were unattended, are superposed on the ERPs to the corresponding standard tones in those conditions. Focusing first on the left column (labelled Experiment 1), we see that in both attention conditions there is a negative wave in the deviant-tone ERP relative to the standard-tone ERP in the MMN latency range; in the attended condition, this was clearly much larger and was followed by the large P300 wave. The deviance-related activity can be seen more clearly by examining the deviance difference waves of deviant ERP minus standard ERP, shown in the bottom panel. In addition to the striking similarity in timing and waveshape, the attended-channel deviance-related negativity (DRN) had a distribution on the scalp that was similar to that of the much smaller unattended-channel negativity, as well as that of previously reported MMNs (Woldorff et al. 1991).

The data in Fig. 13 indicate that the unattended deviants in Experiment 1, which used ISIs of 120–320 msec, did indeed elicit a small negative wave onsetting at ~100 msec and peaking at ~200 msec, despite the fact that attention was strongly focused on the other channel. This therefore does support the part of Naatanen's proposal that states that an MMN can be elicited by deviant tones in a sequence even if they are, presumably, not attended. Importantly, however, the very similar looking DRN wave elicited by the deviant tones in the attended channel was approximately four times as large, in sharp contrast with Naatanen's claim that this deviance-related activity is not affected by attention. Moreover, it does not appear that the attended-channel DRN was unusually large, because its amplitude is typical of (or even smaller than) that found in previous MMN studies using this degree of deviance, but that the inattended one was extremely small, as if it had been drastically suppressed (or 'gated').

In a second experiment reported in Woldorff et al. 1991, the stimuli were presented at an even faster rate, with ISIs of 65–205 msec, thus presumably further enhancing the selective focusing of attention. Data from that experiment is also shown in Fig. 13 (right column, labelled Experi-

ment 2). The attended-channel DRN was again of substantial size, but now the one in the unattended-channel appeared to be so suppressed that it was barely discernible. Indeed, in this experiment it actually did not rise above noise levels.

The data for the deviant tones in these experiments thus call into question the assertion that auditory feature analysis, mismatch detection, and the associated MMN wave are wholly independent of attentional influence. On the contrary, these data provide additional evidence that one of the mechanisms of auditory selective attention is the attenuation or gating of processing in unattended channels at an early sensory level. These results thus dovetail well with the data from the standard tones.

MEG, MRI, and auditory selective attention

Another means of measuring the evoked activity in the brain is to record the magnetic counterpart to the EEG, namely the magnetoencephalography (MEG), and extract from it by signal-averaging the time-locked magnetic fields evoked by the stimuli. The magnetic event-related field (ERF) responses mainly reflect activity arising from cortical sulcal sources, being relatively blind to activity in the gyral convexities. This selective sensitivity of ERFs, together with the lesser distortion of ERFs by the skull, appears to give ERFs an advantage for source localization over ERPs (for sulcal sources only, of course) (Okada 1987; 1993; Williamson and Kaufman 1987). Because primary and secondary auditory cortex sit on the STP on the bottom bank of the Sylvian fissure, activity from those areas appears to be particularly amenable to being recorded with MEG.

Briefly, the theory (at least from a 'forward solution' standpoint) is as follows: When a focal portion of cortex is activated, it produces a current dipole that is oriented perpendicular to the cortical surface. Referring to Fig. 14, assume the diagram is a depiction of the Sylvian fissure of a subject lying on his or her side. When primary auditory cortex is activated, it would produce a current dipole oriented perpendicular to the sulcus and parallel to the skull, as shown in the figure.

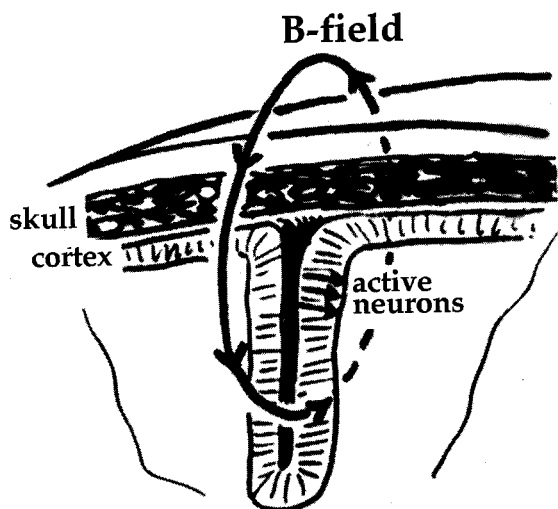


Fig. 14. Production of magnetic (B) field by activated neuronal tissue in a cortical sulcus, such as the auditory cortex on the STP. (See text for discussion.)

By the right-hand rule of currents and magnetic fields, this would produce magnetic fields at the scalp that exit the head on one side of the dipole and enter the head on the other. Thus, if one were to measure the fields perpendicular to the skull (Fig. 15), one would expect a polarity inversion

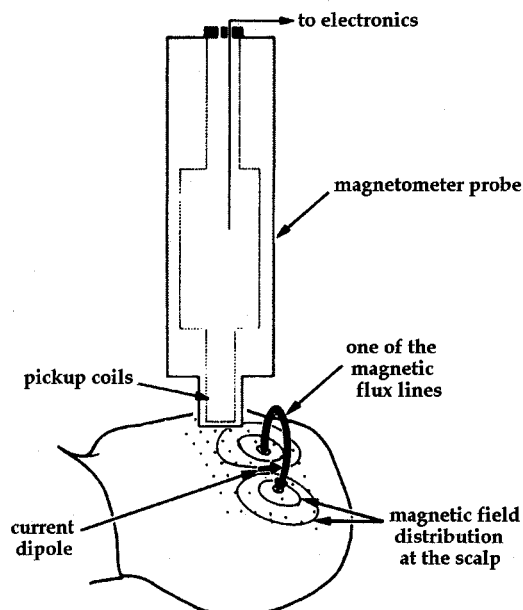


Fig. 15. Production of magnetic field distribution at the scalp by a focal current dipole, and the detection of these fields by a magnetometer.

across the dipole, a so-called 'dipolar distribution', with a maximum and a minimum on opposite sides of the dipole. From such a distribution, the location of the dipole source can be estimated. This includes the depth of the source, in that the extrema will be closer together for a near source and farther apart for a deeper source.

Such source localization has been performed with considerable accuracy in recent years for certain ERF components, such as the magnetic correlate of the auditory N1 wave, known as the M1 or M100 (Yamamoto et al. 1988; Pantev et al. 1990; Arthur et al. 1991). This has been greatly facilitated by the recent advent of large-scale, multi-channel MEG machines that allow a number of sites to be recorded simultaneously.

In a collaboration with researchers at the MEG recording facility at Scripps Clinic in La Jolla, where a prototype 37-channel magnetometer from Biotechnologies Inc. (BTI) was housed, we were able to perform an ERF study (Woldorff et al. 1993) using essentially the same fast-rate dichotic listening paradigm for which ERP results have been shown throughout this paper. The goal was to try to record the magnetic counterparts to these various ERP components and attention effects to try to determine which of them, if any, were coming from auditory cortex. Using the BTI magnetometer, we were able to record simultaneously from 37 locations from over the left hemisphere. We also simultaneously recorded three channels of EEG from over that hemisphere, from the standard 10–20 sites Cz, C3, and T3.

The evoked response waveforms, grand-averaged across the seven normal subjects in this experiment, are shown in Fig. 16a. Superposed are the ERF waveforms elicited by right standard tones when attended and when unattended. In the upper right are the corresponding, simultaneously recorded, ERPs at the C3 site. Note first the N1 attention effect in the ERP, similar to what we have seen in the previous studies, with the attentional enhancement closely overlapping in time the sensory-evoked N1. Now a corresponding effect can be seen on the magnetic counterpart to the N1, the M100 (e.g. channel 25). Of critical importance is that at the same latency (i.e. ~100 msec) at the anterior sites (e.g. site 33), there is an inversion in

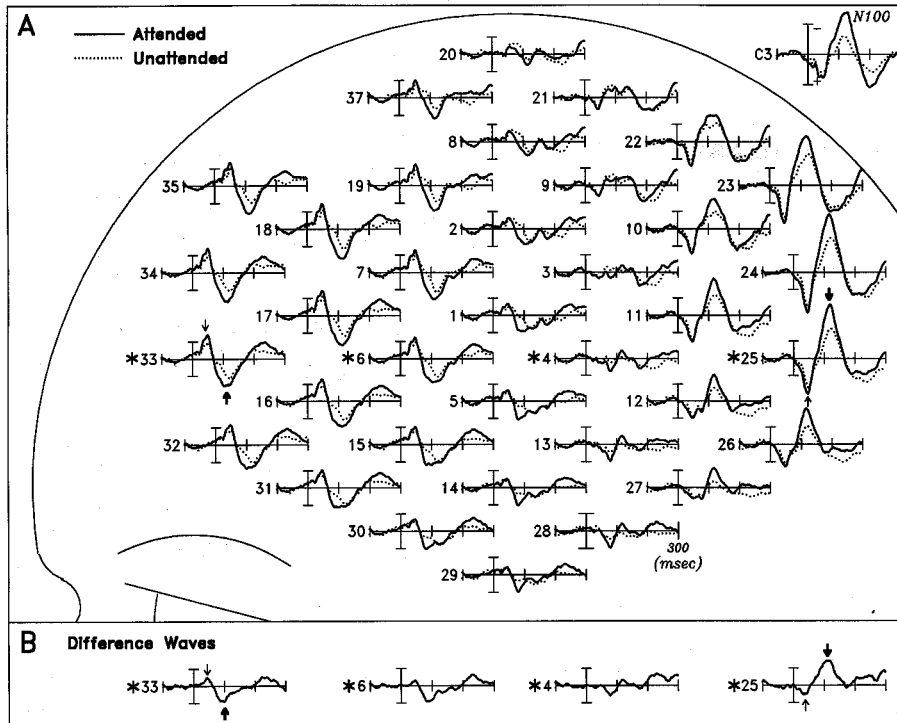


Fig. 16. (A) Grand-averaged ($N = 7$) ERF and ERP waveforms elicited by right-ear standard tones, when attended and when unattended, in the fast-rate dichotic listening experiment described in the text. The ERFs are displayed inside the head diagram at the approximate locations of the magnetic sensors over the left hemisphere. At the upper right are shown the simultaneously recorded ERPs from the C3 site. Positive (upward) values for the magnetic activity indicate that the fields were directed out of the head at that site (at that time point), and negative values indicate inward-directed fields [ERF calibration bars = ± 20 femtotesla (fT)]. ERP scalp negativity is plotted upwards (ERP calibration bars = ± 1 microvolt (uV)). Large arrows indicate the polarity-inverting M100 at sites 25 (posterior) and 33 (anterior); small arrows indicate the also polarity-inverting M50. (B) Grand-average attentional difference waves (attended ERFs minus unattended ERFs) derived from the data in (A) for four sites (asterisked in (A)) along an anterior-to-posterior line across the array. Large and small arrows indicate the polarity-inverting attention effects associated with the M100 and M50, respectively. (Figure from Woldorff et al. 1993.)

polarity of both the M100 itself *and* the attention effect on it. That is, posteriorly the magnetic fields are oriented out of the head, and anteriorly they are oriented into the head. This dipolar distribution of the M1 and M1 attention effect is consistent with a current dipole oriented vertically (leaning slightly anteriorly) and located a few cm below the center of array – that is, in the general area of primary auditory cortex on the STP (more about this below).

Figure 16a additionally reveals that the small P20–50 ERP attention effect also has a magnetic signature. This appears as a small but significant attentional enhancement of the magnetic M50 wave, an effect we have termed the ‘M20-50’ (Woldorff et al. 1993). This attention effect can be

seen better by looking at the attentional difference wave of attended minus unattended response, shown for several sites in Fig. 16b. The magnetic M20-50 attention effect can be seen as a positive wave anteriorly (e.g. channel 33) and as a negative wave posteriorly (e.g. channel 25), followed by the larger attention effect at 100 msec.

One way to estimate the location of sources of magnetic activity is to take a point in time where the activity is particularly dipolar, such as at the M100 peak, and analyze the distribution of the magnetic activity at that time. For example, Fig. 17a (top left panel) shows a topographic (isocontour) plot of the attended response magnetic activity at the peak of the attended-tone M100 from one of the subjects. Note the classic dipolar

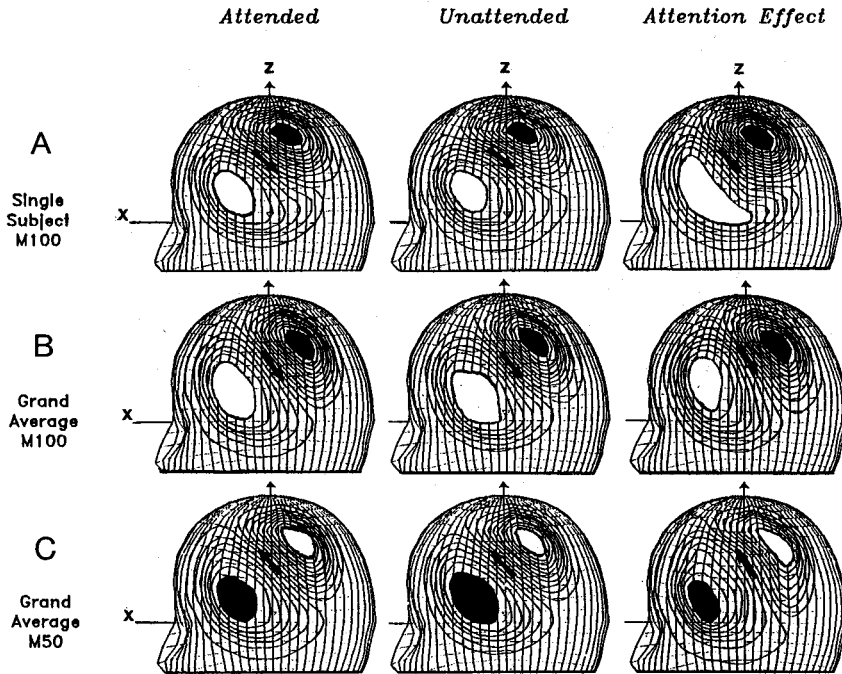


Fig. 17. Topographic plots (isocontour lines) showing magnetic field distributions for the M100 and the M50, each individually scaled to emphasize distribution rather than absolute magnitude. (A) The M100 distribution of a single subject, for the attended response, the unattended response, and the attentional difference wave. (B) Corresponding field distributions for the M100 from the grand-average waveforms. (C) Same as (B) for the M50 (thus the attention effect panel in this case corresponds to the M20-50). The distributions for each of these cases can be seen to be highly dipolar, with a maximum (shaded dark) where the magnetic field lines are directed out of the head and a minimum (shaded light) where the magnetic field lines are directed into the head. The arrow in each case indicates the orientation of the single ECD source that would produce a set of fields that would best fit the distribution. (Figure from Woldorff et al. 1993.)

distribution, with a maximum posteriorly and a minimum anteriorly. According to the right-hand rule of magnetic fields and currents, this distribution suggests that the activity is dominated by a single dipolar source oriented like the arrow. It is this distributional information that is used to estimate the location of the equivalent current dipole (ECD) model source that would produce a field distribution that would best fit this activity. Figure 17a shows the three contour plots for this subject for the attended-tone M100, for the unattended-tone M100, and for the corresponding M100-latency attention effect (that is, the differential activity between the attended and unattended responses). Note the high degree of similarity between these distributions, suggesting that their sources have similar locations and orientations. Note also how highly dipolar these distributions are, suggesting they should be well modelled by

our dipole source localization approach. Using these sets of distributional information, the estimated locations for these sources were calculated, all of which indeed fit extremely well to the dipole model, with correlations of the model fields and the data fields ranging from 0.97–0.99. The locations of these three sources for this subject were within several mm of each other, and, based on previous magnetic studies, these locations would be in the auditory cortical areas on the STP.

In addition, however, magnetic resonance images (MRIs) were obtained for four of the subjects in this study who had good dipole fits, including the one in Fig. 17A. Using the relative locations of several distinctive skull landmarks in the reference frame of the MEG and that of the MRI, the two frames of reference were put into register. This enabled determination of where in the subject's brain these estimated locations of the

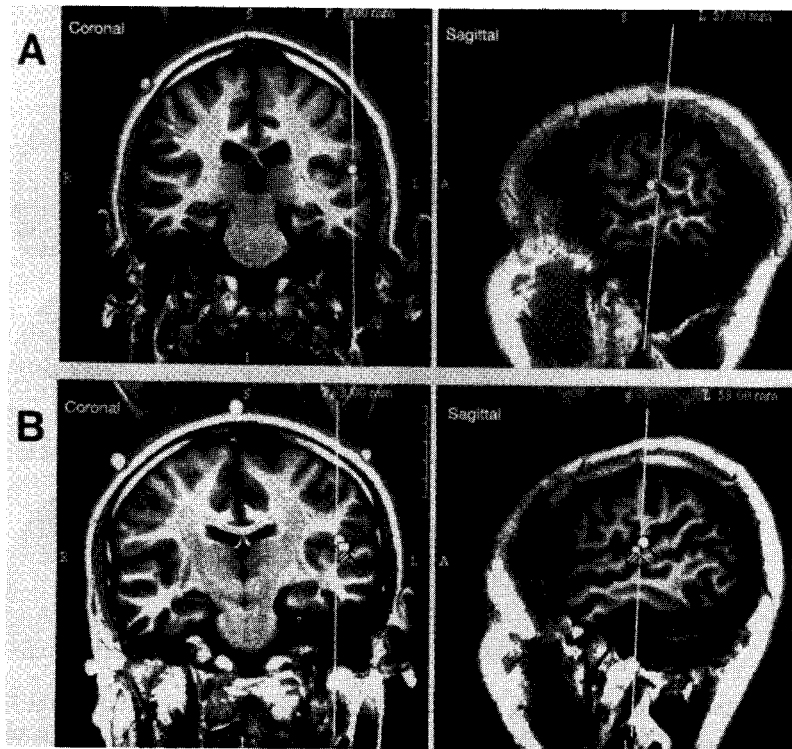


Fig. 18. (A) Coronal and sagittal MR images showing the locations and angles of the ECD sources estimated for the M100 and for the M100-latency attention effect for the subject whose ERF distributions are shown in Fig. 17A. The white square indicates the estimated location for the source of the attended M100, the hatched square the unattended M100, and the white circle the M100-latency attention effect. These estimated source locations were within mm of each other, localizing to the auditory cortex on the STP just lateral to Heschl's gyrus. The small black lines attached to each symbol indicate the angle of the estimated current dipole in each case. The long vertical white line in each image indicates the plane through which the other image is taken. (B) Same as (A) for a second subject. (Figure from Woldorff et al. 1993.)

M100 and the M100 attention effect were. Figure 18A shows a coronal and a sagittal slice, with symbols indicating the estimated locations and angles of the current dipole sources for the attended M100, the unattended M100, and the M100-latency attention effect. These three locations are practically on top of one another, all localizing just lateral to Heschl's gyri, the auditory sensory cortical area on the STP. In addition, the estimated angle of the current dipole in each case is oriented approximately perpendicular to the cortical surface of the STP, as expected by current dipole theory (Okada 1987; Williamson and Kaufman 1987). Figure 18B shows the two MRI views for a second subject, again showing the estimated dipole source locations for the attended-tone M100, the unattended-tone M100, and the M100-latency attention effect.

In this case, there is at least enough spread in the three locations to see the three symbols. Within the accuracy of these localization techniques and the signal-to-noise ratio, however, these are also essentially identical locations. The two other subjects for which MRI scans were obtained showed similar localization patterns to STP auditory cortex for the M100 and M100-latency attention effect. These MR localization results, together with the close temporal overlap, provide the strongest evidence to date that the magnetic attention effect at 100 msec arises predominantly from enhanced activity in auditory cortex on the STP and that this enhanced activity consists primarily of an attention-related modulation of the M100 neural generator.

The M20-50 (i.e. the attention effect on the mag-

netic M50) had an insufficient signal-to-noise ratio in individual subjects to be successfully fit using the source localization techniques. However, due to the consistency of the probe placements and the magnetic responses across subjects, the waveforms could be grand-averaged (Fig. 16). Figures 17B and 17C shows the field distributions of the M100 and M50 derived from the grand-averaged attended-tone, unattended-tone, and attentional-difference waveforms. All six of these distributions were highly dipolar, suggesting that the relative location of the M20-50 source could be estimated by applying the ECD source localization analysis to the grand-average data. Thus, best-fit ECDs were calculated from the grand-averaged waveforms using grand-averaged head shape information and grand-averaged probe-placement information. These analyses did yield excellent fitting ECDs (correlations of 0.98–0.995) for each of these grand-average M100 and M50 field distributions shown in Figs 17B and 17C, including those for the associated attention effects (right column). Although such source estimates could not be localized on any individual subject's MRI scan, the relative x-y-z coordinate locations in the MEG reference frame could be evaluated. Most importantly, in this reference frame, the estimated location of the grand-average M50 (for both attended and unattended tones) and the corresponding attention effect (i.e. the M20-50) were quite near to that of both the grand-average M100s and the individual subjects' M100s (localizing about 2–14 mm more medial). Because these M100 sources did localize in individual subjects to on or near Heschl's gyrus, it follows that the still earlier M20-50 attention effect also derives from this region.

Conclusions

In summary, the standard-tone data presented in this paper strongly support the view that:

1. Highly focused auditory selective attention in humans can indeed affect stimulus processing at latencies earlier than 60 msec;
2. The effect of highly focused auditory selective attention does indeed include an amplitude modulation of the sensory processing activity

that is reflected by the sensory-evoked electrical and magnetic responses; and

3. At least part of this effect of highly focused attention occurs in the early auditory cortical areas in the STP.

In addition, the deviant-tone data indicate that this early attentional modulation results in relatively reduced auditory feature analysis and mismatch detection in unattended channels relative to the attended one.

To put this into a perhaps more global cognitive neurosciences perspective, what we believe this means is that the effect of highly focused auditory selective attention in humans is not simply the addition of processing in non-modality-specific brain areas after the specific auditory analysis areas have completed their analyses. Rather, the effect of highly focused auditory selective attention includes a preset biasing of the sensory input channels. This results in an amplitude modulation, or gating, of sensory processing activity in early auditory cortex on the STP. This, in turn, results in reduced acoustic feature analysis in the unattended auditory channel(s) relative to the attended channel. Thus, these data not only provide strong support for psychological theories of attention that propose early, pre-perceptual selection of stimulus input, they also provide specific information concerning some of the neuroanatomical structures and physiological mechanisms by which such selection is accomplished.

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Notes

1. Although this very early attention effect may be a reflection of enhanced activity in primary auditory cortex, it may reflect the ramification at that level resulting from the gating of the sensory transmission at the earlier level of the thalamic relay (Skinner and Yingling 1977).
2. The T-complex effect in this experiment was not so clear as a *main* effect, but became striking and highly significant in the sequential analysis described below. However, a more robust, significant main effect on the T-complex was found in the related, visual/auditory cross-modal attention experiment reported in Hackley et al. 1990.

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