

NEUROPHYSIOLOGICAL MECHANISMS OF AUDITORY SELECTIVE ATTENTION IN HUMANS

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1. ABSTRACT

This chapter reviews the main data on the physiological substrates of auditory selective attention and their contribution to theoretical models of cognitive psychology. While event-related potentials, magnetoencephalography, and more recently neuroimaging techniques have provided fundamental information on the neural correlates of attention in the central cortical system, measurements of the frequency-following responses in the brainstem and evoked otoacoustic emissions at the cochlea strongly suggest attentional phenomena at the auditory periphery. We propose an adaptive filtering mechanism for selective auditory attention that can be flexibly and dynamically tuned depending on the attentional demand.

2. INTRODUCTION

Knowledge of the psychophysiological mechanisms of modality-specific attention closely depends on knowledge of the corresponding sensory system. In spite of extensive research these last decades on audition and sound analysis, the neural basis of automatic and controlled processing in audition remains poorly understood compared to that in the visual system. We do not pretend here to make an exhaustive list of the studies of auditory attention, but rather give some landmarks of the hypotheses, orientations, and main findings that have contributed to the knowledge of the brain mechanisms of auditory selective attention in humans.

Interestingly, the literature on this topic shows an evolution in the theoretical and experimental approaches, the questions raised, and of course the techniques used. Research in the 1960's has been characterized by the

elaboration of theoretical models of attention based on behavioral measurements. Since the pilot experiment by Hillyard *et al.* in 1973 (1), the chronometric measures provided by event-related potentials (ERPs) and later by magnetoencephalographic recordings (MEG) have enriched the psychological theories and physiological models of selective attention. These models, in turn, have been improved with the development of ERP mapping systems and electrical source analysis methods. Likewise promising is the recent use of neuroimaging techniques such as functional magnetic resonance imaging (fMRI) and positron emission tomography (PET), which provide better spatial resolution for locating the brain structures activated. However, as will be discussed, the variety of experimental paradigms and the empirical approaches frequently used have often made it difficult to interpret the findings within the framework of theoretical models of attention. On the other hand, the recent discovery of active mechanical processes in the cochlea that are directly connected with the efferent auditory system has given a new impetus to the peripheral gating hypothesis.

These various aspects of attentional research are illustrated below.

3. PSYCHOLOGICAL MODELS OF AUDITORY SELECTIVE ATTENTION

Auditory selective attention refers to the mental ability to resist distractor stimuli and select relevant information from the surrounding acoustic events, as illustrated in the "cocktail party effect". This effect has been primarily conceptualized in the so-called *structural*

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models of attention. These models hold that attentional mechanisms have a limited-capacity and can perform only one task at a time. In these models there would be a fixed location in the system for an "attentional bottleneck" beyond which the parallel processing capacity is limited. A key issue is the level of processing at which this bottleneck is located – that is, the level of processing at which auditory inputs from relevant and irrelevant channels are differentially processed (reviewed in (2)). This question has led to two competing theories: *early-selection* and *late-selection*. In *early-selection* theories the processing of unattended stimuli can be attenuated prior to full sensory analysis. In his original statement of filter theory, Broadbent (3) assumed that stimuli are briefly stored and analyzed in parallel for elementary characteristics at the pre-attentive level, with only a selected subset ("selected channel") allowed by the filter to be processed at higher levels (see also (4)). Later, Treisman (5) proposed a modified filter-attenuation version, according to which the filter only reduces the information available on a rejected channel. In turn, *late-selection* theories (6,7) propose that all stimuli are fully processed, even at a semantic level, before any selections take place. The role of attention would only be to control for access to consciousness, memory and response.

Support for either theory has depended in large part on the type of paradigm used. Kahneman and Treisman (8) have distinguished two basic experimental approaches: the filtering paradigm and the selective-set paradigm. Examples of the latter are Posner's (9) paradigm on the cost and benefits of attention and expectation and Shiffrin and Schneider's (10) visual search paradigm. The tasks investigated with these paradigms are generally easier (stimulus rate is much slower) than those used in the filtering paradigm, and the observations have often supported *late selection* theories. The filtering paradigm, in the auditory modality, typically consists of dichotic listening with subjects attending to the input arriving at the designated ear and ignoring the input to the opposite ear (11). Initial findings with the filtering paradigm suggested that very little information is processed in the unattended ear, providing an empirical basis for *early-selection*, or *filtering*, theories (3). Subsequent studies, however, showed that more analysis seems to occur in the unattended channel than had been initially thought. (For example, subjects can be aware from their own name presented in the unattended ear (12)). These observations led to the modification of the first version of Broadbent's filter theory (5), and to the emergence of the *late-selection* theories.

Another class of attention models includes the so-called *resource* or *capacity theories* of attention. These theories primarily refer to the issue of how attention can be allocated and shared between several sources or tasks, and have been particularly suitable in accounting for human performance in dual-task and divided-attention situations (reviewed in (2)). Although they entail a more global view of attentional processes, *resource models* have been less often addressed with physiological measures, in the framework of auditory selective attention, than the *structural models*. Indeed, for years two basic questions in

selective attention research have been the level of processing at which relevant and irrelevant channels are differentially processed and the extent to which unattended information is processed.

4. ERPS AND PHYSIOLOGICAL MODELS OF AUDITORY SELECTIVE ATTENTION

In these theoretical questions of the level of attentional selection, the use of ERPs has provided fundamental and decisive information. Indeed, ERPs are characterized by a double - temporal and spatial - specificity. First, as a chronometric tool, they accurately measure time events in the absence of, or before, the behavioral measures of cognitive psychology. Therefore, they can yield precise information on the temporal dynamics of mental activities. Second, being generated "somewhere in the brain", their topographic analysis provides clues about the brain structures and the neurophysiological processes involved. An early line of research focused on the temporal aspects of attentional events and has provided definitive electrophysiological support for the *early-selection* theories of attention (1, 2, 13-18). More debated, however, were the questions of how early in the sensory processing chain and by which physiological mechanisms this attentional selection occurs.

These issues were most often investigated through selective dichotic paradigms. Typically, subjects were instructed to detect occasional target stimuli in a series of tones presented to one ear, and to ignore a concurrent sequence of tones to the opposite ear. The general observation was that the ERP to tones in the attended ear was negatively shifted compared with the ERP to the same tones in the same ear when ignored. This attention-related negativity, however, has been differently interpreted, giving rise to two physiological models of auditory attention.

4.1. The "gain" theory of attention

In their pioneering experiment in 1973, Hillyard *et al.* (1) presented tone sequences at a rapid rate (variable interstimulus interval (ISI) of 250-1250ms). They found an attention effect (negative displacement of the ERP to attended tones relative to unattended) in the time range of the N1 wave around 100 ms post-stimulus. The auditory N1 wave of ERPs is known to be generated primarily in auditory cortex (19) (reviewed in (20)). Therefore, the larger N1 to attended stimuli ("N1 effect") was interpreted as an increased activity of the N1 generators, reflecting modulation of activity in the neural populations involved in the obligatory sensory analysis of acoustic stimuli in auditory cortex. The authors proposed that selective attention acts as a *filtering* or a *gain mechanism* capable of inhibiting or gating unattended stimuli, relative to attended, at an early stage of sensory analysis (about 100 ms). This model represents a physiological version of the original psychological filtering or attenuation models (3,5).

4.2. The "attentional trace" model of attention

Later, Näätänen *et al.* (21) showed that the attention-related negativity observed by Hillyard *et al.* (1)

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could be dissociated in time from the "obligatory" N1 wave. Using a longer and constant ISI (800ms), they found that the attentional negativity (measured as the negative difference "Nd" waves obtained by subtracting ERPs to ignored tones from those to the same tones when attended) began to emerge around 150ms post-stimulus and persisted for at least 500ms. Näätänen and colleagues proposed that the Nd wave (called "processing negativity"; PN) is a component of endogenous origin, representing activity in attention-specific neural systems separate from the obligatory sensory analysis (21). He suggested that the "N1 effect" observed by Hillyard's group was caused by an endogenous PN overlapping the exogenous N1, rather than by an intensification of the N1 generator process. The shorter ISI used in Hillyard's experiment could, according to Näätänen, have shortened the PN latency because subjects had to process the stimuli more rapidly.

In addition, the attentional PN wave was found to include two components: an "early PN", possibly generated in auditory association cortex, and a "late PN" of larger amplitude and longer duration at frontal sites. These observations led Näätänen (2, 18, 22) to develop the "attentional-trace" model of selective attention. According to this model, the initial selection is performed by a comparison process between a sensory input and an attentional trace in auditory cortex. This trace is defined as a voluntarily maintained representation, through a consciously controlled system, of the physical features that separate relevant stimuli from irrelevant ones. The better the match, the longer the comparison process continues. The early component of the PN would reflect this on-line comparison mechanism. The late component would be related to a frontal mechanism to control and maintain the attentional trace.

The attentional-trace model is fundamentally different from the filtering hypothesis first proposed by Hillyard. The two models differ not only in their nature, but also in their predictions and implications for auditory information processing. Unlike the attentional-trace model, physiological filtering could occur at a number of processing stages and would directly affect the transmission, analysis, and representation of stimulus information (23). The point at issue is the *nature* of the Nd (PN) wave. In the *filtering* hypothesis, the Nd could include modulations of exogenous components, in addition to whatever endogenous processing system may be invoked. In Näätänen's model, all ERP effects of selective attention would be of endogenous origin and explainable by the attentional-trace theory. The comparison process would be *the* mechanism of early selection.

4.3. Electrophysiological evidence for complex physiological processes

4.3.1. Processing of relevant inputs

The conclusions of this controversy, which has been at the origin of many ERP and MEG studies in the 1980's, may be summarized with the following: (i) at least a part of the attentional Nd wave is of endogenous origin ((24-35), reviewed in (2,18)); (ii) the Nd wave includes an

"early", modality-specific component, probably generated in auditory cortex, and a "late" frontal component (14,15,17,22,27,31,35-38); and (iii) the onset latency of the Nd wave strongly and inversely depends on the rate of stimulus delivery - the faster the stimulus rate the shorter the Nd onset latency (14,26,39,41).

These findings have been hotly defended by Näätänen (2,18) as supporting the attentional-trace theory. However, a number of parallel findings have challenged this hypothesis, showing that the morphology and/or the topography of the "early" Nd wave was more complex than that expected from a unitary ERP component that simply changed in amplitude and latency. In several dichotic listening experiments using short ISIs and difficult-to-detect targets (high attentional load), attention was found to affect multiple midlatency ERP components around 20-50ms in addition to the N1 wave around 80-100ms (15,16,43-45). The findings were replicated with MEG recordings (46) and interpreted as modulation of major subcomponents of the exogenous responses, thereby leading the author to defend the gain theory of attention.

Furthermore, data in our laboratory (35) showed that a strong attentional demand is not a necessary condition for attentional modulation of exogenous sensory components. In two dichotic listening experiments using rather long ISIs (800ms), effects of attention were expressed as three successive components of different nature. The first, an "Nd1" component (around 70-80ms) that followed the same frequency-dependent variations as the exogenous N1 distribution, was interpreted as a genuine modulation of the neural activity in tonotopically-organized supratemporal auditory cortex (Figure 1-A; Note also that N1 is known to include temporal and frontal components (47). However, attention effects were found for the temporal, but not for the frontal components of N1). The second, an endogenous attentional "Nd2" component (110-275ms) with an origin different from that of N1 in auditory cortex, was stronger in the left hemisphere regardless of the direction of attention (Figure 1-B). The third was a late attentional wave ("Nd3") with a frontal distribution, probably generated in deep structures of the frontal cortex (31,35,48).

Existence of several successive attentional waves of different nature in auditory cortex (modulation of exogenous components and endogenous activities) implies the existence of different physiological operations during attentional selection. In fact, any theory of selection would require some form of template to represent the stimulus features that separate attended and unattended input, as well as some process of comparison with the template. The multiple findings of attentional modulation of obligatory ERP components before 100ms post-stimulus - whatever the additional endogenous activities elicited - strongly strengthen the hypothesis of a sensory gain control (16) within the auditory cortex and support the filtering model of attention at a (early) cortical level. Existence of a genuine gating mechanism in cortex is not surprising, however, since in both the visual and somatosensory systems, there is strong evidence that selective attention

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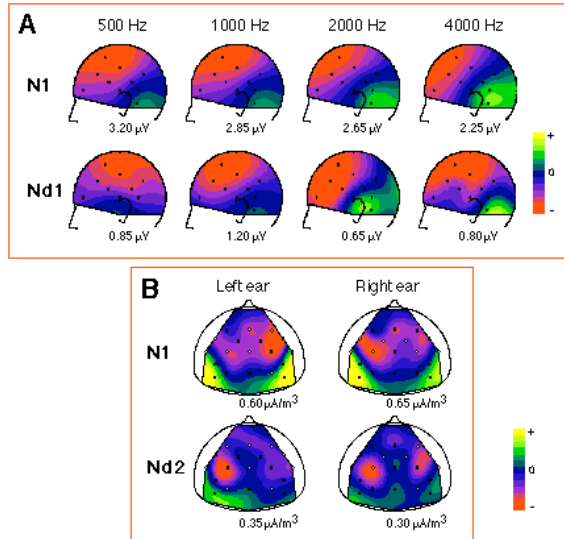


Figure 1: Attentional effects in auditory ERPs : Evidence for both a modulation of exogenous responses in auditory cortex (A), and an endogenous origin (B) of the auditory attentional waves. A. Comparison of the potential distributions of the auditory N1 wave elicited by pure tones of 500, 1000, 2000 and 4000 Hz when ignored, and of the Nd1 wave (at the same latency of 80-100 ms) reflecting the effect of attention to each of these tones. N1 and Nd1 present similar topographic variations with the tone frequencies (stronger mastoid positivities associated with more anterior frontal negativities for higher tone frequencies). This strongly suggests that Nd1 reflects an attentional modulation of the N1 generator activities in tonotopically-organized auditory cortex. B. Comparison of the scalp current density distributions of the auditory N1 wave to unattended tones with the attentional effects around 150 ms (Nd2). N1 is characterized by stronger currents in the contralateral temporal areas, whereas attention effects (Nd2) are stronger in the left hemisphere whatever the direction of attention, suggesting different origins for N1 and Nd2.

modulates exogenous components at early stages of analysis (49-51). A possibility is that under active attention conditions, the N1 generator process has a lower (more sensitive) threshold of activation and thus evokes larger activity in some of its subsystems. This interpretation would fit with, and complement, two findings from different approaches. First, auditory N1 amplitude correlates with the detection of threshold-level acoustic events (20, 52). Second, auditory selective attention to a specific range of frequencies lowers the detection threshold for the stimuli of that frequency range (53). The N1 enhancement (as well as the modulation of other exogenous midlatency components) could well be the reflection of this change of sensitivity in the auditory system under the control of higher central mechanisms (perhaps reflected by the late frontal Nd wave) (54).

4.3.2. Active rejection of irrelevant inputs

Thus far we have analyzed the attention effects in the ERPs to attended tones. However, the procedures in

most of the studies reviewed above did not allow the distinction, within the attentional effects, between a negative shift of the ERPs to attended tones (relative to a "neutral" condition) and a possible positive displacement of the ERPs to unattended tones. In other words, the data could say neither if irrelevant inputs are actively rejected nor at which level of processing such would occur. The few studies having addressed this important question have generally reported a positive-going shift in the ERPs to unattended tones, relative to a "neutral" condition, that begins approximately 100ms after the negativity to attended tones (30,32,45,55-57). The data strongly suggest that there does exist an active rejection mechanism for irrelevant acoustic inputs. Furthermore, the attentional facilitation and inhibition may be two independent processes with different temporal properties (inhibition occurring later than facilitation (45)).

5. A PERIPHERAL FILTER MECHANISM OF ATTENTION?

Thus far we have seen that the electrophysiological and MEG data on auditory selective attention can be better explained by a mechanism of sensory gain or physiological filtering at the cortical level, rather than by the attentional-trace hypothesis. Unlike the predictions of the attentional-trace model, however, an attentional filter mechanism could theoretically affect auditory processing at several stages of analysis, including at the level of the peripheral auditory system.

In fact, since the pioneering study of Hernandez-Péon in 1956 (58), the theory of peripheral gating had attracted many prominent physiologists (59-61) before being rejected for many years. Hernandez-Péon and colleagues had observed an amplitude decrease in the response to clicks recorded at the dorsal cochlear nucleus of unanesthetized cats during attention to visual, somesthetic or olfactory targets. However, their findings were later refuted on methodological grounds (62,63) (however, see (64)). Subsequently, a number of human studies attempted to show a peripheral effect of attention in the brainstem auditory evoked potentials (BAEPs) generated within the first 10ms of sensory analysis. Except the findings from Lukas in 1980 (65,66), who showed a decreased amplitude and an increased latency in waves I and V of the BAEPs during visual attention (see also (67)), most of these attempts were unsuccessful (13,68-76), and the general view was that auditory attention alters the sensory analysis of inputs only in the central auditory system.

Yet, there has been a renewal of interest for the peripheral model of attention with the recent discovery that the cochlea is the center of exquisitely sensitive active processes, and that these processes are directly connected with the efferent auditory system (reviewed in (77)). First, it was found that the cochlea can emit sounds, the "evoked otoacoustic emissions" (EOAEs), in response to auditory stimulation (78). EOAEs appear to arise from physiologically active processes of the outer hair cells in the organ of Corti (79-81) and can be easily recorded in

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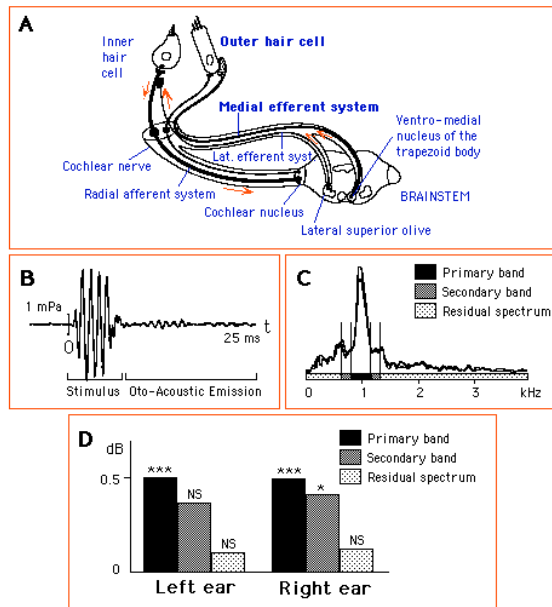


Figure 2: Effects of auditory selective attention in the evoked otoacoustic emissions (EOAEs) recorded in the human ear. A. Peripheral auditory pathways. B. EOAEs elicited by 1-kHz tone bursts in one subject. The superimposed traces show the reproducibility of the signals in three runs of 200 stimuli each in the unattended ear. Attention effects are generally not evident in the raw waveforms. C. Amplitude spectra of EOAEs from one subject attending to (full lines), or ignoring (dotted lines), the evoking stimulus (1-kHz tones). The vertical lines delimit the primary band (spectral band centered around, and within $\pm 15\%$ from, the attended frequency) and the secondary bands (same width as the primary). The spectrum amplitude in the primary band is larger for attended than unattended stimuli. D. Mean amplitude of the EOAEs to attended tones relative to unattended in three spectral bands. The effect of attention is highly significant in the primary band and decreases with increasing distance from the attended frequency.

humans using a small acoustic probe composed of an emitter and a microphone fitted in the external ear canal. The outer hair cells, whose active micromechanical properties play an important role in the transduction process (82), receive direct synapses from medial efferent neurons of the olivocochlear bundle (OCB) (83), thereby allowing the cochlear mechanics to be altered by descending inputs via the medial efferent system (84,85) (Figure 2-A). Furthermore, this alteration in the cochlear mechanics can occur in a frequency-specific manner, since the afferent and efferent fibers with the same characteristic frequencies innervate the same cochlear region and have similar tuning curves (86,87).

Thus, this cochlear-efferent system provides the functional architecture for top-down control of sensory processing at the periphery. In addition, the EOAEs have properties well suited to test attentional effects. First, they

can be elicited by stimuli of much lower intensity than brainstem potentials, and may thus reveal finer peripheral phenomena (see also below). Second, they have high signal-to-noise ratios relative to brainstem potentials, thereby permitting shorter recording sessions (Figure 2-B). This is critical in experiments requiring subjects to maintain sharply focused attention.

Indeed, several studies found that EOAE amplitudes are reduced when subjects are engaged in a visual task (88-92). The findings strongly suggested the existence of a top-down attentional control mechanism operating through centrifugal projections to the cochlea (probably through the medial efferent system). However, the procedures (comparison of the EOAE amplitudes between a passive listening condition and an active task) did not reveal whether the observed effects were due to a genuine effect of selective attention or to a change in non-specific arousal during task performance (18,89). (Note that this question also applies to previous electrophysiological studies in humans and in animals (e.g. (64,65)).

Two studies have tested these hypotheses. One, in our laboratory, used a dichotic selective listening paradigm based on those previously employed in ERP experiments (e.g. (1,16,21)), in which the stimulus and task conditions were optimized for the early selection of competing inputs (15). Subjects were presented with short tone pips of 1kHz in one ear and 2kHz in the other ear, rapidly and randomly delivered (ISI of 180-250ms). The task was to count occasional targets of slightly higher intensity in the designated ear which were difficult to discriminate from the frequent standard stimuli. The tone frequency in each ear and the ear attended were counterbalanced so that the effect of attention could be measured in four (2 frequencies x 2 ears) conditions in each subject. It was found that the EOAE amplitudes to attended tones were larger than those to the same tones in the same ear when unattended (Figure 2-C). Although the absolute magnitude of the effect was small (0.5dB), it was highly significant and observed in 41 of the 48 observations. In addition, the effect was largest in the spectral band corresponding to the attended stimulus frequency (Figure 2-D). It was concluded that selective auditory attention could already operate as a peripheral band-pass filter at the cochlear receptor level prior to the transduction process (93). (Note, however, that the paradigm did not distinguish whether the observed effects were due to an increase in the EOAE amplitude for attended tones or to a decrease for unattended tones).

The second series of experiments, conducted in another laboratory (94), did not come to these conclusions, however. In these experiments, subjects still listened to random sequences of 1 or 2kHz tone pips and were instructed to pay attention to one frequency in order to detect occasional targets of slightly higher intensity. In five of these experiments, all the tones were delivered to the same ear, whereas the 6th experiment was similar to that of Giard *et al.* (93). No effect of attention was observed in any experiment. Although a deep discussion on the methodological issues is beyond the scope of this review, we note two points that might explain the differences in the

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results of the two studies. First, in 5 of the 6 experiments both the attended and unattended stimuli were presented at the same ear (94). Previous ERP findings have shown that early effects of attention are more easily observed when the attended and unattended stimuli are separated by large differences including a different spatial origin (15,16,95). A second and more important difference between the two studies is the stimulus intensity used. Giard and colleagues (93) presented sounds of 15dB HL, whereas Michie and colleagues (94) used sounds of 60 or 70dB SPL. As noted above (and discussed by Michie), these louder sounds might have led to ceiling effects in the cochlea, preventing any observation of fine attentional modulations. This interpretation is strengthened by the fact that the efferent system has been found to be more efficient for low intensity stimulation (96-99).

Other recent findings from different approaches have provided evidence that activities of the peripheral auditory system can be modulated, in a frequency-specific manner, under the influence of higher mechanisms. In 1994, Scharf and colleagues (100) (see also (101)) reported that a patient, whose olivocochlear bundle had been surgically sectioned for severe Meniere's disease, showed better ability to detect signals in noise, regardless of whether the signals were of the attended or unattended frequency. Scharf's interpretation was that the OCB during attention may act as a sharp band-pass filter by suppressing responses to frequencies outside a narrow attentional focus. A separate study of the cat (102) showed that activation of the OCB by contralateral noise increases the response to single auditory nerve fibers to ipsilateral tones in a continuous masking noise, whereas it decreases the response of auditory nerve fibers in a quiet background. While these different findings may diverge in the models of OCB functioning, they all support the view that top-down efferent inputs can control and modify cochlear mechanics in a frequency-specific manner.

In parallel with these findings at the cochlear level, several recent studies have challenged the view that auditory attention operates only at central cortical level. Attention effects have been reported in the "frequency-following responses" (FFR) generated in the brainstem probably at a site peripheral to the inferior colliculus (103-105).

6. FUNCTIONAL BRAIN IMAGING STUDIES OF AUDITORY ATTENTION

In recent years, the rapid development of the neuroimaging techniques such as PET and fMRI, which are based on quantitative measurement of regional cerebral blood flow (rCBF) and metabolism, has provided powerful tools for localizing neural operations with high spatial resolution. Yet their actual contributions to the understanding of attentional mechanisms has been somewhat limited primarily because of their weak temporal resolution and secondly because the paradigms used have been very diverse and often not based on conceptual models. Results from these techniques are therefore difficult to compare and interpret in the framework of

attentional theories. In spite of these limitations, however, neuroimaging studies of auditory attention have provided interesting information about the involvement of auditory cortex as well as evidence for an active mechanism of rejection of irrelevant inputs.

6.1. Localization of the brain structures involved in auditory attention

Evidence for attention effects in auditory cortex has been found in several studies using fMRI (106-109) and PET (110-113). As in some ERP and EOAE experiments reviewed above, however, several of these studies compared passive listening situations with active auditory conditions (107-109, 113), making it difficult to know whether the effects were due to genuine selective attention or to changes in non-specific arousal during task performance. Other studies, based on "classical" dichotic selective listening paradigms, found increased activity in the superior temporal gyrus of auditory cortex. The effect was generally larger in the cortex contralateral to the direction of attention (106, 110-112) and was interpreted as "selective tuning of the left or right auditory cortices according to the direction of attention" (112). However, in a paradigm where attention was directed to either visual or auditory stimuli, Frith and Friston (114) did not find any auditory attention effects in auditory cortex, but rather in right mid-thalamus. The other brain structures found to be activated during auditory attentional tasks included several regions of the frontal cortex (106,111,112,115), bilateral precentral and left postcentral cortices, and the supplementary motor area (111). While attentional effects were also found in the anterior cingulate gyrus without involvement of "posterior attention structures" (115), another study found the reverse (106). As previously noted, the different paradigms used (continuous performance test in the first experiment and dichotic listening in the second) do not permit direct comparison of the findings.

6.2. Active rejection of unattended stimuli

More informative are the findings of decreased activity in auditory cortex for unattended or task-irrelevant tones, relative to relevant tones, reported in several PET studies (e.g. (113, 116)). This decreased activity in rCBF has been interpreted as physiological evidence for an active mechanism of selective inhibitory modulation of cortical processing for non-relevant inputs (116), and is to be related to the positive-going displacement of ERPs to unattended stimuli reported previously.

7. CONCLUSION AND PERSPECTIVES : AN ADAPTIVE FILTERING MODEL OF SELECTIVE ATTENTION

Although a clear demonstration of an effect of attention at the cochlea has yet to be confirmed, the data reviewed above indicate that: (i) selective attention can alter auditory processing at several levels of sensory analysis, including auditory cortex, the brainstem, and very probably the cochlea; (ii) higher attentional load induces earlier effects of attention (15,16,21,93,95); and (iii) attention to frequency-specific regions induce frequency-

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specific changes in perceptual processing at behavioral (53,117-119), central cortical (35), and peripheral (93,100,101) levels. Altogether, these findings fit with the hypothesis of a flexible, adaptive filtering mechanism for selective auditory attention. This band-pass filter mechanism could be dynamically tuned depending on the attentional demand in the task: higher attentional demand yields sharper and more efficient filter tuning as well as earlier filtering operations. In other words, the "location of the bottleneck" would be variable, adapting for the most efficient result at the lowest energetic cost. Peripheral effects of attention would occur only if the system is "obliged" to do so. (This was particularly evident in our study (93), since effects of attention in EOAEs dramatically depended on the precise adjustment of the task difficulty for each subject - a slightly too easy task led to no effect). This flexibility in the locus of the bottleneck makes sense in an "energetic" and efficiency perspective. In an easy, less energy-demanding task, the effects of attention will occur later, leaving more resources to process unattended stimuli. Conversely, a high selective attentional load (strongly focused attention) would require the whole attentional system to be sharply tuned and would activate already the earliest, most peripheral structures able to participate in the attentional selection, thereby making the filter more active and efficient.

A variable locus of the bottleneck had been previously proposed in psychological models of attention (e.g. (120-122)). The recent physiological findings reviewed here could bring new support to these models as well as a double implication. The first is that they would overrule the discrepancy between the *early-* and *late-selection* theories of the structural models. The second is that flexible, adaptive filtering mechanisms for auditory selective attention would reduce the gap between the structural theories and the energetic views of attention.

The above hypotheses would be strengthened by the following: (i) the confirmation of an effect of attention at the peripheral level of sensory pathways and a deeper understanding of the OCB control on the efferent system, (ii) a better knowledge of the active mechanisms of rejection of unattended inputs and their relationship with attentional load, and (iii) further investigation of the location, functional role, and operative mode of the frontal structures involved in attentional control.

8. ACKNOWLEDGMENTS

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