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Auditory Attention

Selective ATTENTION may be defined as a process by which the perception of certain stimuli in the environment is enhanced relative to other concurrent stimuli of lesser immediate priority. A classic auditory example of this phenomenon is the so-called cocktail party effect, wherein a person can selectively listen to one particular speaker while tuning out several other simultaneous conversations.

For many years, psychological theories of selective attention were traditionally divided between those advocating early levels of stimulus selection and those advocating late selection. Early selection theories held that there was an early filtering mechanism by which "channels" of irrelevant input could be attenuated or even rejected from further processing based on some simple physical attribute (BROADBENT 1970; Treisman 1969). In contrast, late selection theories held that all stimuli are processed to the same considerable detail, which generally meant through completion of perceptual analysis, before any selection due to attention took place (Deutsch and Deutsch 1963).

Various neurophysiological studies have attempted to shed light on both the validity of these theories and the neural mechanisms that underlie auditory attention. One possible neural mechanism for early stimulus selection would be the attenuation or gating of irrelevant input at the early levels of the sensory pathways by means of descending modulatory pathways (Hernandez-Peón, Scherrer, and Jouvet, 1956). For example, there is a descending pathway in the auditory system that parallels the ascending one all the way out to the cochlea (Brodal 1981), and direct electrical stimulation of this descending pathway at various levels, including auditory cortex, can inhibit the responses of the afferent auditory nerves to acoustic input. Other animal studies have indicated that stimulation of pathways from the frontal cortex and the mesencephalic reticular formation can modulate sensory transmission through the THALAMUS, thus providing another mechanism by which higher brain centers might modulate lower level processing during selective attention (Skinner and Yingling 1977). In addition, sensory processing activity in primary auditory CEREBRAL CORTEX or early auditory association cortices could conceivably be directly modulated by "descending" pathways from still higher cortical levels.

It has proven difficult, however, to demonstrate that any of these possible mechanisms for sensory modulation are actually used during auditory attention. Early animal studies purporting to show attenuation of irrelevant auditory input at the sensory periphery (Hernandez-Peón, Scherrer, and Jouvet 1956) were roundly criticized on methodological grounds (Worden 1966). Nevertheless, there have been animal studies providing evidence of some very early (i.e., brainstem-level) modulation of auditory processing as a function of attentional state or arousal (e.g., Oatman and Anderson 1977). In addition, Benson and Heinz (1978), studying single cells in monkey primary auditory cortex during a selective attention task (dichotic listening), reported relative enhancement of the responses to attended stimuli. Attending to sounds to perform sound localization vs. simple detection also has been shown to result in enhanced firing of units in auditory cortex (Benson, Heinz, and Goldstein 1981).

Auditory attention has been investigated extensively in humans using event-related potentials (ERPs) and event-related magnetic fields (ERFs). These recordings can noninvasively track with high temporal resolution the brain activity associated with different types of stimulus events. By analyzing changes in the ERPs or ERFs as a function of the direction of attention, one can make inferences about the timing, level of processing, and anatomical location of stimulus selection processes in the brain.

In an early seminal ERP study, Hillyard et al. (1973) implemented an experimental analog of the cocktail party effect and demonstrated differential processing of attended and unattended auditory stimuli at the level of the "N1" wave at ~100 msec poststimulus. More recent ERP studies furthering this approach have reported that focused auditory selective attention can affect stimulus processing as early as 20 msec poststimulus (the "P20-50" effect; Woldorff et al. 1987). Additional studies using ERPs (Woldorff and Hillyard 1991) and using ERFs and source-analysis modeling (Woldorff et al. 1993) indicated these electrophysiological attentional effects occurred in and around primary auditory cortex, had waveshapes that precisely took the form of an amplitude modulation of the early sensory-evoked components, and were colocalized with the sources of these sensory-evoked components. These results were interpreted as providing strong evidence for the existence of an attentionally modulated, sensory gain control of the auditory input channels at or before the initial stages of cortical processing, thereby providing strong support for early selection attentional theories that posit that stimulus input can be selected at levels considerably prior to the completion of perceptual analysis. Moreover, the very early onset latency of these attentional effects (20 ms) strongly suggests that this selection is probably accomplished by means of a top-down, preset biasing of the stimulus input channels.

On the other hand, reliable effects of attention on the earliest portion of the human auditory ERP reflecting auditory nerve and brainstem-level processing have generally not been found (Picton and Hillyard 1974), thus providing no evidence for peripheral filtering via the descending auditory pathway that terminates at the cochlea. Nevertheless, recent research measuring a different type of physiological response—otoacoustic cochlear emissions—has provided some evidence for such early filtering (Giard et al. 1991).

Additional evidence that attention can affect early auditory processing derives from studies of another ERP/ERF wave known as the mismatch negativity/mismatch field (MMN/MMF), which is elicited by deviant auditory stimuli in a series of identical stimuli. Because the MMN/MMF can be elicited in the absence of attention and by deviations in any of a number of auditory features, this wave was proposed to reflect a strong automaticity of the processing of

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auditory stimulus features (reviewed in Naatanen 1990 and 1992). Both the MMN (Woldorff et al. 1991) and the MMF (Woldorff et al. 1998), however, can also be modulated by attention, being greatly reduced when attention is strongly focused elsewhere, thus providing converging evidence that attention can influence early auditory sensory analysis. On the other hand, the elicitation of at least some MMN/MMF for many different feature deviations in a strongly ignored auditory channel has been interpreted as evidence that considerable feature analysis is still performed even for unattended auditory stimuli (Alho 1992). An intermediate view that may accommodate these findings is that various aspects of early auditory sensory processing and feature analysis may be "partially" or "weakly" automatic, occurring even in the absence of attention but still subject to top-down attentional modulation (Woldorff et al. 1991; Hackley 1993). Under this view, the very earliest stimulus processing (i.e., peripheral and brainstem levels) tends to be strongly automatic, but at the initial cortical levels there is a transition from strong to weak automaticity, wherein some amount of analysis is generally obligatory but is nevertheless modifiable by attention (reviewed in Hackley 1993).

There are also various slower-frequency, longer-latency ERP auditory attention effects that are not modulations of early sensory activity, but rather appear to reflect "endogenous," additional activations from both auditory and nonauditory association cortex (e.g., "processing negativity," target-related "N2b," "P300"). This type of activity occurs only or mainly for attended-channel stimuli or only for target stimuli within an attended channel and might reflect later selection, classification, or decision processes that also occur during auditory attention (reviewed in Alho 1992; Näätänen 1992). Attention to less discriminable features of auditory stimuli (Hansen and Hillyard 1983) or to a conjunction of auditory features (Woods et al. 1991) also produces longer-latency differential activation that may reflect later selection processes. In addition, there is a build-up of endogenous brain electrical activity (a "DC shift") as subjects begin to attend to a short stream of auditory stimuli (Hansen and Hillyard 1988), which could reflect some sort of initiation of the controlling executive function.

In contrast to electrophysiological studies, relatively few hemodynamically-based functional neuroimaging studies have been directed at studying auditory attention in humans. In a recent study using POSITRON EMISSION TOMOGRAPHY (PET), O'Leary et al. (1996) reported enhanced activity in the auditory cortex contralateral to the direction of attention during a dichotic listening task. PET studies have also shown that attention to different aspects of speech sounds (e.g., phonetics vs. pitch) can affect the relative activation of the two hemispheres (Zatorre, Evans, and Meyer 1992). In addition, functional MAGNETIC RESONANCE IMAGING has indicated that intermodal attention can modulate auditory cortical processing (Woodruff et al. 1996).

Most neurophysiological studies of auditory attention in humans have focused on the *effects* of attention on the processing of sounds in auditory cortical areas. Less work has been directed toward elucidating the neural structures and mechanisms that *control* auditory attention. Based on various hemodynamic imaging studies, the anterior cingulate is likely to be involved, as it is activated during a number of cognitive and/or executive functions (Posner et al. 1988). In addition, human lesion studies suggest the prefrontal cortex is important for modulating the activity in the ipsilateral auditory cortex during auditory attention (Knight et al. 1981). It may be that some of the slower-frequency, endogenous ERP auditory attention effects reflect the activation of these areas as they serve to modulate or otherwise control auditory processing. Whether these mechanisms actually employ thalamic gating, some other modulatory mechanism, or a combination, is not yet known.

See also ATTENTION IN THE ANIMAL BRAIN; ATTENTION IN THE HUMAN BRAIN; AUDITORY PHYSIOLOGY; AUDITORY PLASTICITY; ELECTROPHYSIOLOGY, ELECTRIC AND MAGNETIC EVOKED FIELDS; TOP-DOWN PROCESSING IN VISION

—*Marty G. Woldorff*

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Auditory Physiology

The two main functions of hearing lie in auditory communication and in the localization of sounds. Auditory physiology tries to understand the perception, storage, and recognition of various types of sounds for both purposes in terms of neural activity patterns in the auditory pathways. The following article will try to analyze what auditory representations may have in common with other sensory systems, such as the visual system (see VISUAL ANATOMY AND PHYSIOLOGY), and what may be special about them.

Since the days of HELMHOLTZ (1885) the auditory system has been considered to function primarily as a frequency analyzer. According to von Békésy's work (1960), which was awarded the Nobel Prize in 1961, sound reaching the tympanic membrane generates a traveling wave along the basilar membrane in the cochlea of the inner ear. Depending on the frequency of the sound, the traveling wave achieves maximum amplitude in different locations. Thus frequency gets translated into a place code, with high frequencies represented near the base and low frequencies near the apex of the cochlea. Although the traveling wave has a rather broad peak, various synergistic resonance mechanisms assure