

# The dynamics of the construction of auditory perceptual representations: MEG studies in humans

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**ABSTRACT.** This chapter concerns the processes through which auditory sensory information is converted into a perceptual representation relevant for behavior. We describe a series of experiments where subjects listened to faint tones appearing amidst background noise, and were instructed to respond as fast as possible when they detect the tonal objects. Simultaneous psychophysical and brain imaging (MEG) measures were employed to study the mechanisms by which auditory objects are detected and separated from their surroundings. The results demonstrate a striking incongruence between behavioral responses and pre-attentive brain responses, and therefore dissociation between higher level mechanisms related to conscious detection of tones amidst the noise and the lower level, pre-attentive cortical mechanisms that sub-serve the physical extraction of the tonal targets. The implications of these data for the processes that underlie the creation of perceptual representations are discussed. These findings may also provide a methodological tool to study the heuristics humans employ in the course of conscious decision making about events in the world.

## 1 Introduction

Sound sources within the environment produce an aggregate wave-form that enters each ear. To make sense of the world, a listener must separate this input into source-related components, localize them, recognize them, and react accordingly. This chapter concerns the processes by which auditory *sensory* information is converted into a *perceptual representation* relevant for behavior. These processes are mostly automatic and do not require explicit effort (e.g. [Goldstein 2005], [Wolfe et al. 2006]): We follow a conversation in a noisy restaurant, or close our eyes in the park and still perceive the birds on the tree, the dog barking in the corner and the children playing in the playground. ‘The essence of Perception’ has engaged human interest throughout scientific history. These processes have been studied through introspection (e.g. Aristotle’s *On the soul* in [Barnes 1984], [Schwartz 2004]) and later with psychophysics [Boring 1942], [Yost et al. 1993], [Moore 1997]. Careful behavioral experimentation is instrumental in penetrating the private nature of perception (which is, by definition an *internal* representation) and measuring *what* it is a listener perceives: What is the perceptual loudness of the stimulus [Green 1993]? What is its perceived pitch [Moore 1993]? Which parts of the stimulus are assigned to foreground and which ones are relegated to background [Brochard et al. 1999]? This is especially important since we know that

identical physical inputs may result in different percepts, depending on the state of the listener [Bregman 1990], [Chait et al. 2004], [Micheyl et al. 2005]. Psychophysical experimentation has also played an important role in formulating models of the underlying brain systems and computations leading to perception. For example, by measuring listeners' sensitivity to different sounds, researchers have put constraints on pitch processing mechanisms (e.g. [Oxenham et al. 2004]), the structure of the peripheral auditory system (e.g. masking experiments by [Fletcher 1940]), binaural processing mechanisms [Blauert 1997] and the features into which sounds are decomposed by the auditory system [Cusack & Carlyon, 2003]. Throughout the history of auditory research, advancements in the understanding of hearing have arisen from the close interaction between psychophysics and electrophysiology. Behavioral reaction time measures are often used as an indicator of processing demands and computational load (e.g. [Pouliot & Grondin 2005]). In this chapter we will argue that in some cases, subject's behavioral performance might lead to erroneous conclusions about the nature of the processing involved.

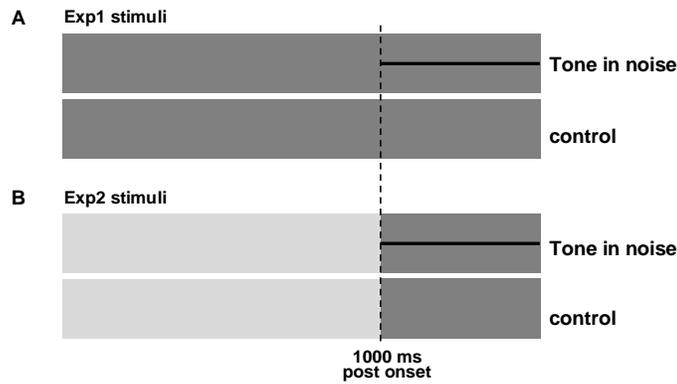
The major difficulty in trying to understand the computations that underlie the organization of sensory information is that perception is fast: perceivers are usually unaware of the stages of processing by which sensory information is converted into an internal image of the world. Arguably, Psychophysics, as it requires subjects' conscious participation, only taps the final representational stages. To study how perceptual representations are created from sensory input, we employ a combination of psychophysics and brain imaging (Magnetoencephalography; MEG). MEG, the magnetic counterpart of the more widely used EEG method, is a non-invasive neurophysiological technique that measures the magnetic fields generated by the neuronal activity of the cerebral cortex [Lu & Kaufman 2003]. Unlike fMRI or PET which are indirect measures of brain function reflecting brain metabolism, MEG is a direct measure of cortical activation and has a very high temporal resolution (events on the order of milliseconds can be resolved). Time-locked stimulus evoked cortical responses measured with MEG are characterized by increases in activation (peaks) at different latencies. Changes in this activation pattern (as a result of modifying the stimulus or the listener's attentional state) indicate changes within the neural mechanisms that these peaks reflect. Variations in latency can be interpreted as a slowing down or speeding up of a particular process, likewise changes in amplitude may reflect a difference in processing demands (e.g. [Friederici 2005]). At present, because the mechanisms that sub-serve the construction of auditory perceptual representations are not well understood, our hypotheses are mostly related to *time* (e.g. 'in the process of figure-ground segregation, computation A has to occur before computation B'). With its fine temporal resolution, MEG is especially suited for addressing questions related to the timing of brain activation. Reaction-time measurements are likewise well suited to measure the time course of behavioral responses. By studying how the dynamics of brain responses are related to behavior, we explore how behaviorally relevant representations arise from sensory input. This technique is particularly useful for dissociating bottom-up stimulus-driven processes from those that are affected by the perceptual state of the listener. In the visual system, these kinds of questions have been the focus of experimental research for quite a long time

(e.g. [Vecera et al. 2004],[Peterson 1999],[Robertson 2003],[Amano et al., 2005] ), but they are just beginning to attract attention in the field of auditory neuroscience [Kubovy & van Valkenburg 2001], [Carlyon 2004],[Griffiths & Warren 2004], [Nelken 2004], [Scott 2005]. Here, we present the results of a study where the simultaneous acquisition of MEG and behavioral data revealed a curious incongruence between behavior and electrophysiology. The dissociation between subjects' perception, as reflected by their behavior, from lower level brain responses reveals implicit (pre-attentive) brain function related to the construction of auditory perceptual representations.

The specific processes that will be discussed here are related to the extraction of objects from background noise. The division of the scene into a figure (onto which attention is focused) and background is an important concept in scene analysis [Carlyon 2004]. These are the processes that underlie listener's ability to follow a friend's voice in a noisy party or to detect (and hopefully avoid) an approaching car in a busy street. In order to study the properties of these neural mechanisms we use simpler signals - faint tonal objects in loud background noise - that are intended to model more complicated real-life situations. By measuring subjects' brain activity while performing a tone detection task, we attempt to elucidate the mechanisms that enable listeners to recognize the tonal signals amidst the background.

In the experiments described below, we recorded brain activity while subjects listened to 1500ms long wide-band noise stimuli. In half of the presentations, a faint 500ms tone, with variable frequency, appeared at 1000ms post onset (Figure 1). Subjects were instructed to press a button as fast as they can when they hear a tone popping out of the noise. The data reported here are a subset of the experimental data previously reported in [Chait et al. 2006]. Those experiments were designed to investigate the process by which information from the two ears is combined to create a single coherent percept. We compared the cortical and behavioral responses to Huggins Pitch (HP) [Cramer & Huggins 1958], a stimulus requiring binaural processing to elicit a pitch percept, with responses to tones embedded in noise (TN)—perceptually similar but physically very different signals. Here we focus only on a portion of the signals studied in the original experiments.

In Experiment 1 (Figure 1A) the background noise was interaurally correlated (same noise signals presented to the two ears). The stimuli sound like a loud noise source (perceptually somewhat like radio static) in the center of the head with a faint tone appearing at 1000ms post onset. In order to investigate the effect of changing background on tone extraction, the stimuli of Experiment 2 (Figure 1B) consisted of interaurally uncorrelated noise (different noise signals presented to the two ears) which changed into correlated noise at 1000ms post onset. These signals sound like a diffuse noise source that changes into a centered noise source. Half of the time, a faint tonal object appeared at the same time as the noise-change. The simultaneous recording of behavioral reaction times and MEG response latencies to these sounds enables the investigation of the dynamics of the process by which the physical signals are separated into a perceptual representation consisting of a figure (the tone) and a background (the noise) and the degree of correspondence between behavioral and electrophysiological measures.



**Fig. 1.** Schema of the stimuli used in the two experiments. (A) Stimuli for Exp1 consisted of 1500ms correlated wide-band noise (dark grey) with a 500ms faint tonal object (TN; black line) appearing at 1000ms post onset. Control stimuli were 1500ms long wide-band correlated noise. (B) Stimuli for Exp2 consisted of 1000ms of uncorrelated wide-band noise (light grey) followed by a 500ms long correlated noise segment which either contained a tonal object (target condition) or did not (control condition). Crucially, the last 500ms of the stimuli of Exp1 and Exp2 were identical

## 2 Methods

### 2.1 Subjects

Twenty subjects (mean age 24.6 years), took part in Experiment 1. Sixteen subjects (mean age 23.8) took part in Experiment 2. Twelve listeners participated in both experiments. All subjects were right handed [Oldfield 1971], reported normal hearing, and no history of neurological disorder. The experimental procedures were approved by the University of Maryland institutional review board and written informed consent was obtained from each participant. Subjects were paid for their participation.

### 2.2 Stimuli

The stimuli in Experiment 1 were 1500 ms long: 1000 ms of interaurally correlated white noise (diotic stimuli) followed by a 500 ms tonal-object (200, 400, 600 or 1000 Hz) embedded in noise or by 500ms of the same correlated noise (control condition). The tonal objects in noise were either: a pure tone (TN), or a perceptually similar di-

chotic-pitch signal (HP). As stated above, the data reported here will concern only the pure tones (TN stimuli). Full results are described in [Chait et al. 2006]. The stimuli of Experiment 2 were identical to those of Experiment 1 except that the initial noise was interaurally uncorrelated (statistically independent signals in each ear). In total each subject heard 100 presentations of each of the eight pitch conditions (HP 200, 400, 600, 1000 Hz; TN 200, 400, 600, 1000 Hz) and 800 (50% of all) presentations of the control stimulus. The order of presentations was randomized, with the inter-stimulus interval (ISI) semi-randomized between 500-2000 ms. The noises were created off-line by choosing 16000 pseudo-random (16 bit) numbers from a Gaussian normal distribution (sampling frequency 16 kHz), giving a broadband signal up to 8000 Hz. To reduce the chance that observed effects are due to a specific instance of the white noise signal, 4 different instantiations were used. The stimuli were gated on and off using 15 ms cosine-squared ramps, with no gating at 1000ms post onset.

### **2.3 Procedure**

The recording (~ 1.5 hours) consisted of two parts. First, subjects heard 200 repetitions of a 1 kHz (50 ms) sinusoidal tone (inter-stimulus interval randomized between 750-1550 ms) as a pre-experiment. Then subjects listened to the noise stimuli and performed a pitch detection task (50% of trials in Experiment 1 and 2) by pressing a button held in the right hand, as soon as they heard a faint tone pop out of the noise (tones appeared at 1000 ms post onset). Subjects were instructed to respond as quickly and as accurately as possible. The stimuli were presented in 10 blocks (approximately 8 minutes long) of 160 random stimuli.

### **2.4 Neuromagnetic recording and analysis**

The magnetic signals were recorded with a 160-channel, whole-head axial gradiometer system (KIT, Kanazawa, Japan). The pre-experiment data (1 kHz sampling rate) were filtered from 1 Hz and 58.8 Hz, baseline corrected to the 100 ms pre-onset interval and stored in 500 ms (100 ms pre-onset) stimulus-related epochs. The data for Experiments 1 and 2 (1 kHz sampling rate) were filtered between 1 and 200 Hz with a notch at 60 Hz, and stored for later analysis. Raw data were noise-reduced using the Continuously Adjusted Least-Squares Method [Adachi et al. 2001].

In the pre-experiment, auditory evoked responses to the onset of the pure tones were examined and the M100 response identified. The M100 is a prominent and robust (across listeners and stimuli) deflection at about 100 ms post onset, and has been the most investigated auditory MEG response (see [Roberts et al. 2000] for review). It was identified for each subject as a dipole-like pattern (i.e. a source/sink pair) in the magnetic field contour plots distributed over the temporal region of each hemisphere. In previous studies, under the same conditions, the resulting M100 current source localized to the upper banks of the superior temporal gyrus in both hemispheres [Lütkenhöner &

Steinsträter 1998]. For each subject, the 20 strongest channels at the peak of the M100 (5 in each sink and source, yielding 10 in each hemisphere) were considered to best reflect activity in the auditory cortex and thus chosen for the analysis of the experimental data.

In Experiments 1 and 2, 1500ms long epochs (50ms pre onset) were extracted for each condition Epochs with amplitudes larger than 3 pT were considered artifactual and discarded from further analysis, resulting in the rejection of ~ 10% of the trials. The rest were averaged, low-pass filtered at 20 Hz and base-line corrected to the full range of the epoch. In each hemisphere, the root mean square (RMS) of the field strength across the 10 channels, selected in the pre-experiment, was calculated for each sample point.

### 3 Results and discussion

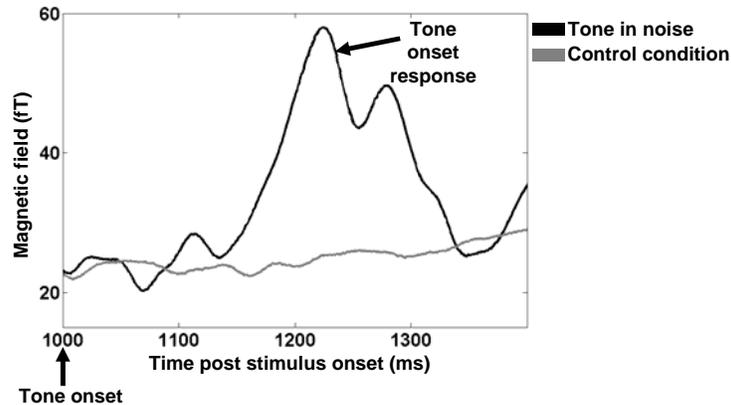
#### 3.1 MEG data

The stimuli of Experiment 1 (Fig. 1A) sound like a 1500 ms continuous noise located in the center of the head. In half of the trials, a faint tonal object appears amidst the noise at 1000 ms post onset. The initial portion of the stimuli of Experiment 2 sounds like a diffused noise (the binaural stimuli are not fused to a unitary auditory object). At 1000 ms the noise changes from diffused to centered, and at the same time, in half of the trials, a faint tonal object appears (Fig. 1B). Here we focus on the brain activity occurring after the appearance of the tonal object, at 1000 ms post stimulus onset.

In Experiment 1, we identified a cortical response, at approximately 160-200ms post tonal onset, evoked by the appearance of a tone in the noise. Figure 2 shows this response for the 200 Hz tone as an example. That this response is indeed related to the appearance of the tone is evident from the fact that it does not show in the control (no tone) condition and that it is affected by the frequency of the tonal object.<sup>1</sup> In Chait et al., (2006) we hypothesize that this increase in current is generated by the neural mechanisms that are responsible for the extraction of tonal objects from background noise. Alain et al. ([Alain et al. 2002], see also [Dyson & Alain 2004]), in EEG studies of concurrent sound segregation, reported that the perception of a mistuned harmonic as a separate sound is associated with a negative wave peaking at about 150 ms after sound onset. In their stimuli, the onset of mistuning coincides with that of the stimulus, so the response components of the two cannot be isolated but the properties of the wave (referred to as object-related-negativity) are very similar to those observed in the present study.

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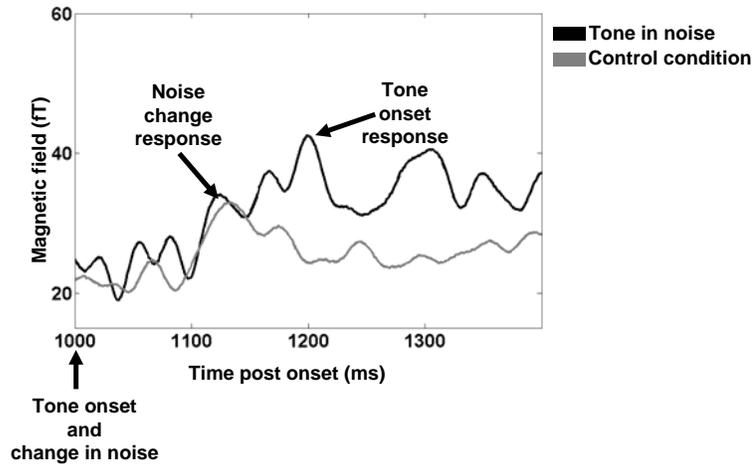
<sup>1</sup> Tones of different frequencies result in a response with a slightly different latency, such that low frequency tones evoke later responses than high frequency ones. See Figure 6 here and further discussion in Chait et al. [Chait et al. 2006]



**Fig. 2.** Electrophysiological data from Experiment 1. The group-RMS (RMS of individual subject RMSs) in the left hemisphere for the 200Hz tone condition, in black (all other conditions showed similar responses) and the control condition, in grey. The cortical response to the appearance of a tone amidst the noise was characterized by a magnetic deflection at about 160-200ms post tone onset. No such deflection appears in the control condition. To facilitate comparison between the two conditions, and to compensate for the fact that the control condition was averaged over many more (800 vs. 100) repetitions, the average amplitude (DC) of the control condition was adjusted (by 7 fT) to match that of the tone condition

The results of Experiment 2, are plotted in Figure 3 (as in Figure 2, we plot the 200Hz tone data as an example). The control stimuli of experiment 2 (Fig 1B) contained a change in the noise at 1000ms post onset. The neural response to this change is reflected in a peak at 1130ms (130ms post change), which is visible in the control condition data (grey line in Fig 3). As discussed above, the tonal conditions contained two simultaneous changes: a change in the interaural correlation of the noise, and the appearance of the tone. Remarkably, as can be seen from Figure 3, the responses to these changes happen at different times, and we observe two separate peaks that correspond to the change in the noise and to the onset of the tone, respectively.

Our ability to segregate the neural responses stems from their temporal separation (response to the onset of the tone is about 50-100ms later than the response to the change in the noise, depending on the specific frequency of the tone), the fact that the noise change peak is not modulated by the tonal frequency, and the fact that the two responses have different scalp distributions (the response to the onset of the tone is strongly left lateralized, whereas the response to the change in the noise is right lateralized), see Chait et al. [Chait et al. 2006] for more details. That the change in the noise and the appearance of the tone, though happening simultaneously in the signal, are processed separately, by different mechanisms (as indicated by the different scalp distributions of the responses) is consistent with [Nelken 2004] who hypothesizes that in auditory cortex, sound is not represented purely in terms of its physical features but rather in terms of auditory ‘objects’ – mental representations of the auditory sources that compose the input to the ear.



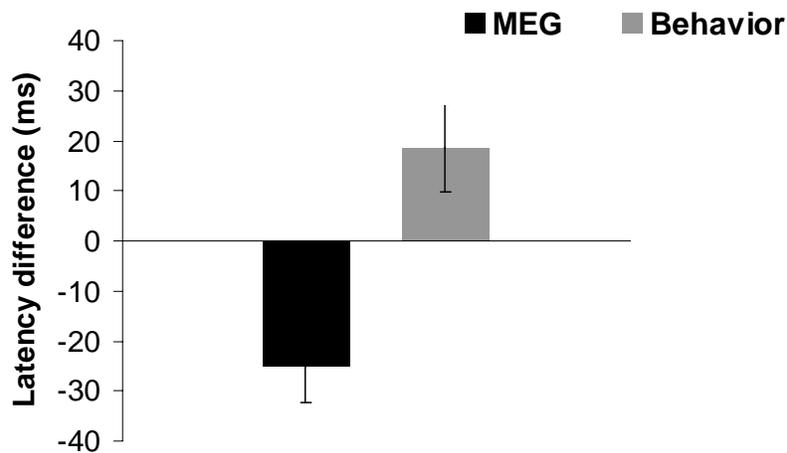
**Fig. 3.** Electrophysiological data from Experiment 2. The group-RMS (RMS of individual subject RMSs) in the left hemisphere for the 200Hz tone condition, in black (all other conditions showed similar responses) and the control condition, in grey. The response to the change in the noise (at 1000ms) is evident at ~1130ms in the control condition. In the tone condition, the response to the change in the noise and the response to the change in the tone are distinguishable. Thus, even though the appearance of the tone and change in the noise were simultaneous in the signal, these were processed at different times in cortex. To facilitate comparison between the two conditions, and to compensate for the fact that the control condition was averaged over many more (800 vs. 100) repetitions, the average amplitude (DC) of the control condition was adjusted (by 7 fT) to match that of the tone condition

### 3.2 Comparing behavioral and MEG data

Behaviorally, performance in Experiment 2 was worse than in Experiment 1. Those subjects that participated in both experiments (N=12) observed that Experiment 2 was more difficult. They reported that in addition to the change in the noise that occurred simultaneously with the appearance of pitch and hindered the detection, the quality of the noise (as two unfused objects at each ear) in the first 1000 ms of the stimulus made it harder to detect the tonal object. This difficulty was reflected in increased response times in experiment 2 relative to experiment 1 ( $p < 0.028$ ). On average, response times were about 20ms longer (see Figure 4). However, when comparing the latency of the brain responses to the onset of the tonal objects,<sup>2</sup> we observe the opposite pattern: The latency of the tone onset peak in Experiment 2 is *earlier* than in Experiment 1 for all

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<sup>2</sup> Electrophysiological response latencies are defined as the time at the peak of the response. For example, the latency of the tone onset response in Figure 1 is 1220 ms (220 ms post tone onset), whereas the latency of the tone onset response in Figure 2 is about 1200 ms (200 ms post tone onset).

tonal frequencies used ( $p < 0.01$ ). Thus behavioral and electrophysiological measures showed a fundamental incongruence (Figure 4): listeners *unconsciously* detected the tones in Experiment 2 faster than in Experiment 1, but *consciously* reported difficulties and detected the tones in Experiment 2 slower than in Experiment 1.

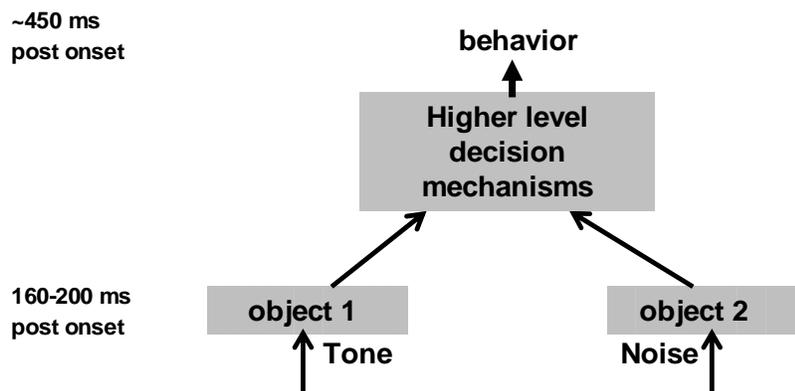


**Fig. 4.** Average response time differences (collapsed over frequencies) between Experiment 2 and Experiment 1 for the 12 subjects common to both experiments. Positive values indicate responses in Experiment 2 that were delayed relative to Experiment 1. Whereas behavioral responses (grey bar) were longer in Experiment 2 than in Experiment 1, electrophysiological responses to the same stimuli showed an opposite pattern and were earlier in Experiment 2 than Experiment 1

### 3.3 Implications for processing

The fact that the behavioral difficulty in Experiment 2 was not apparent in the brain responses we measured at  $\sim 150$ ms post tone onset suggests that behavior is affected by later processing stages. Figure 5 presents a schema of the hypothetical relationship between behavioral responses measured with psychophysics, and brain responses measured with MEG. In the lower level scene analysis stages, which correspond to the cortical responses we recorded, the change in the noise and the appearance of the tone are processed separately (bottom squares). These mechanisms receive information from earlier processing stages where the uncorrelated noise (in Experiment 2) aids the detec-

tion of the tonal objects.<sup>3</sup> The information from the tone and noise change-detectors is combined in a higher level, ‘conscious’ stage (top square) that makes the decision regarding whether a tone has actually appeared. This is the level that directly affects the initiation of behavior. A concurrent (irrelevant) change in the noise introduces an extra computational load at this stage and thus a slowing down is observed. This is in contrast to the neural detection task itself, which is not slowed down (and is in fact faster).

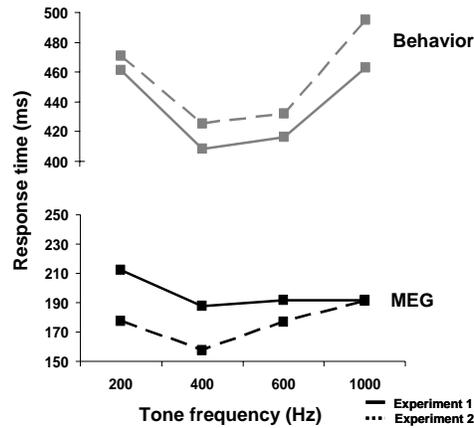


**Fig. 5.** A schema of the hypothetical relationship between behavioral responses measured with psychophysics, and brain responses measured with MEG. The MEG responses measured at 160-200ms post onset reflect a representation in which the information about the tone and about the noise are already segregated and processed by different mechanisms (bottom squares). The outputs of these computations are combined at a later stage that underlies subject’s conscious decision about the existence of the tone (top square). The uncorrelated leading noise in Experiment 2 causes a faster response (relative to Experiment 1) in the lower level ‘tone detecting’ stage (see [Chait et al. 2006] for details) and a slowing down (relative to Experiment 1) at the higher level decision mechanisms. This slowing down is a result of the additional computational load, caused by the task-irrelevant information about the change in the noise

Figure 6 presents further evidence for the indirect relationship between behavior and the MEG deflections we measured. When comparing the trends of the MEG responses in Experiment 1 and 2 (black solid and dashed lines) we find that they are not correlated: response latency difference varies with frequency. Moreover, when computing the correlation of response latencies across experiments for each frequency separately, we find that none showed a linear interaction between response latencies in Experiment

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<sup>3</sup> The change in the interaural configuration of the leading noise caused an *earlier* brain response to the appearance of the tone in Experiment 2 relative to Experiment 1. This response latency difference might originate as early as the Superior Olivary Complex (SOC) in the brain stem, where binaural processing begins. This is discussed in detail in [Chait et al. 2006].

1 and Experiment 2.<sup>4</sup> In the case of a linear relationship between behavior and the lower-level mechanisms reflected in the MEG responses, we would expect behavioral data to exhibit a similar pattern. However, behavioral responses in Experiment 1 and 2 (grey solid and dashed lines) are significantly correlated (Pearson's correlation coefficient  $\rho=0.961$   $p=0.039$ ), implying a similar latency shift for all frequencies. Additionally, when computing the degree of correlation between response latencies across experiments for each frequency separately, we find that all frequency conditions showed a strong linear relationship between the response times in Experiment 1 and Experiment 2 (200 Hz:  $\rho=0.826$   $p=0.001$ , 400 Hz:  $\rho=0.775$   $p=0.003$ ; 600 Hz:  $\rho=0.789$   $p=0.002$ ; 1000Hz:  $\rho=0.723$   $p=0.008$ ). Hence the difference between the stimuli of the two experiments had a non-linear effect on cortical response latencies, but a linear effect on behavioral response times.



**Fig. 6.** A comparison of behavioral response times (top) and MEG response latencies (bottom) for the 12 subjects common to both experiments. Experiment 1 data: solid lines; Experiment 2 data: dashed lines. MEG and behavioral responses in either experiment are not correlated. So is the relationship between the brain data of Experiment 1 and 2 (black solid and dashed lines). However, there is a strong correlation between behavioral responses in the two experiments (grey solid and dashed lines are parallel). Also visible in this figure are the increased behavioral response times and decreased MEG response latencies between Experiments 1 and 2

This pattern may be a result of a mechanism similar to the one described in Figure 5: the leading uncorrelated noise in Experiment 2 has effects on different levels of processing: (1) It affects low level (sub-cortical) mechanisms related to extracting the tone from the noise (see [Chait et al. 2006]), and thus may conceivably affect different frequencies in a different way. These mechanisms probably relay information to the cortical responses we observe ('object 1' block in Figure 5). (2) The change in the noise also

<sup>4</sup> This is possibly because the differing physical aspects of the stimuli in the two experiments differentially affected the processes underlying the tone extraction mechanisms.

activates the cortical noise-change detectors ('object 2' block in Figure 5). Even though the change in the noise is irrelevant to the subjects' task, we show that it influences their performance. The effect of the irrelevant noise change on the higher level decision mechanisms is a general increase in processing load (the information that the noise has changed is identically salient in all conditions) which results in a constant latency difference between Experiment 1 and Experiment 2.

### 3.4 Conclusions

In the case of the experiments presented here, behavior and electrophysiology, if studied separately, might lead to different conclusions about the nature of the processing involved. The simultaneous acquisition of both MEG and behavioral data puts stronger constraints on the interpretation, revealing a multi-staged process of the construction of perceptual representations. These findings contribute to our understanding of auditory scene analysis in several ways: They demonstrate that at approximately 150 ms post onset the change in the tone (figure) and the change in the noise (ground) are already processed separately. Additionally, they reveal at least two stages in the detection of auditory objects, and provide a time frame in which each of the stages operates. Behavioral response times in this study were about 450ms post tonal onset. Since it takes about 150ms to program a motor command (e.g. [Sereno & Rayner 2003]), we are faced with a 'missing 100 milliseconds' (from the peak of the cortical responses to when button-press motor commands are initiated). In order to study the nature of the computations that are executed between the subconscious detection of the tone and the conscious decision, we can manipulate the subject's task or the early cortical responses (by changing the properties of our stimuli) and examine the effect on reaction time. For example, a possible prediction is that even in the case of three concurrent changes in the stimulus, the low level stages should remain unaffected but behavioral responses should exhibit an even greater delay (more interference).

These findings are interesting from an auditory processing point of view because they reveal previously unobserved stages in the re-construction of the auditory scene from sensory information, and provide a methodological tool for a further, more rigorous, examination of how the different stages interact to affect behavior. These results may also be of interest to researchers of higher level human faculties, such as decision making and reasoning, because they reveal a method, possibly extendable to other modalities, by which one can measure the (pre-attentive) inputs into the decision system and how they affect its output (see also discussion in [Reddi & Carpenter 2000]). For instance, by manipulating the salience of auditory cues and parametrically affecting the outputs of the lower level cortical mechanisms (bottom squares in Figure 5) while at the same time measuring behavioral reaction times, one may be able to infer the kinds of reasoning rules and heuristics that subjects are employing in the process of making a response.

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