

Brain Mechanisms Mediating Auditory Attentional Capture in Humans

Susanne Watkins^{1,2}, Polly Dalton³, Nilli Lavie^{1,3} and Geraint Rees^{1,2}

¹Institute of Cognitive Neuroscience, University College London, London WC1N 3AR, UK, ²Wellcome Department of Imaging Neuroscience, University College London, London WC1N 3BG, UK and ³Department of Psychology, University College London, London WC1N OAP, UK

The ability to detect and preferentially process salient auditory stimuli, even when irrelevant to a current task, is often critical for adaptive behavior. This stimulus-driven allocation of processing resources is known as “attentional capture.” Here we used functional magnetic resonance imaging in humans to investigate brain activity and behavioral effects related to such auditory attentional capture. Participants searched a sequence of tones for a target tone that was shorter or longer than the nontarget tones. An irrelevant singleton feature in the tone sequence resulted in behavioral interference (attentional capture) and activation of parietal and prefrontal cortices only when the singleton was associated with a nontarget tone (nontarget singleton) and not when associated with a target tone (target singleton). In contrast, the presence (vs. absence) of a singleton feature in the sequence was associated with activation of frontal and temporal loci previously associated with auditory change detection. These results suggest that a ventral network involving superior temporal and inferior frontal cortices responds to acoustic variability, regardless of attentional significance, but a dorsal frontoparietal network responds only when a feature singleton captures attention.

Keywords: attention, auditory, fMRI

Introduction

In everyday life, people are often bombarded with different sensory signals, yet can usually focus on stimuli relevant for the task at hand. This can be achieved by using knowledge and expectations to focus attention on task relevant signals rather than competing irrelevant stimuli. Despite this top-down control, a unique stimulus can “capture attention,” even when task irrelevant. Although distracting subjects from their current task, such attentional capture may have a survival advantage, as a unique stimulus may often convey important information about the environment. In the visual modality, the effects of attentional capture have been extensively studied, using visual search tasks (Theeuwes 1992, 1994; Yantis 1993). These visual studies demonstrate that when a nontarget stimulus in the search array has a unique singleton feature, it will typically disrupt search performance. Such interruption of goal-driven attention can be found even when the nontarget object is a singleton on a dimension that is never relevant to the task, suggesting that attention was captured by the singleton rather than voluntarily allocated to it.

In the auditory domain, many previous studies concerning the neural response to deviant auditory stimuli have concentrated on the preattentive process of detection of such auditory deviants. Specifically, generation of the electrophysiological potential known as the mismatch negativity (MMN) is associated with the preattentive detection of deviant auditory stimuli

(Schroger 1994; Opitz, Mecklinger, Friederici, and von Cramon 1999; Opitz, Mecklinger, von Cramon, and Kruggel 1999; Wolff and Schroger 2001; Opitz and others 2002; Liebenthal and others 2003; Jaaskelainen and others 2004). Most previous studies of the MMN required subjects to passively listen to a stream of auditory stimuli with no measure of the effects of deviant auditory stimulus on behavior. Without a concurrent behavioral measure of the effects of such deviants on attention, such studies cannot distinguish neural responses associated with acoustic variability per se from those specific to attentional capture.

Recent studies have measured the electrophysiological potentials associated with a deviant auditory stimulus and related them to behavioral measures of distraction (Alho and others 1997; Escera and others 1998, 2001; Schroger and Wolff 1998; Schroger and others 2000; Roeber and others 2003; Rinne and others 2006). These revealed that the presence of a rare deviant auditory stimulus elicited MMN, N1, and P3a event-related potential components and slowed reaction times (RTs) to a subsequent auditory (Schroger and Wolff 1998; Schroger and others 2000; Roeber and others 2003; Rinne and others 2006) or visual target (Alho and others 1997; Escera and others 1998, 2001). However, as these previous studies have focused on the presence of rare sometimes novel stimuli (e.g., Escera and others 1998, 2001), the presence of a deviant stimulus was always associated with increased auditory variability. In contrast, the present study distinguishes neural activity associated with acoustic variability (and auditory change) in the stimulus from those specific to attentional capture. Therefore, we used a design that allowed us to compare neural activity between conditions that contain the same degree of auditory variability but vary in the extent to which this variability leads to attentional capture.

To this aim, we used functional magnetic resonance imaging (fMRI) in humans while they performed a behavioral paradigm that established an equivalent phenomenon of attentional capture in hearing as previously established in vision (Dalton and Lavie 2004). Participants searched a sequence of 5 rapidly presented tones for a target tone that differed in duration from the surrounding nontarget tones. Irrelevant variation in the frequency or intensity of one of the nontarget tones (nontarget singleton) increased RTs and error rates compared with the target-alone condition, suggesting that the irrelevant feature singleton captured attention. However, when the same irrelevant feature singleton was present in the target tone, it had no significant effect on RTs or error rates, compared with the target-alone condition. This is likely to be due to the target already being a singleton on another dimension (duration), and hence, the subjects were already able to focus their attention

onto the target without further auditory cues. Note that our behavioral design is different to previous MMN studies. Our tasks consisted of short sequences of rapidly presented sounds designed to be perceived as a single search array. There were often 2 deviant sounds in a 5-tone sequence compared with the low-frequency deviants typical of MMN studies. Thus, it is unlikely that these sounds would be treated as deviants in the same way as the odd rare sounds used in MMN studies. Importantly, our design allowed us to separate cortical responses that were related to increased auditory variation in the stimulus (i.e., the presence of an irrelevant feature singleton regardless of whether it was present in a target or a nontarget stimulus) from cortical responses that were specific to auditory attentional capture by a distracting nontarget singleton. Note that in such a paradigm, attentional capture does not depend simply on whether there is irrelevant variation in a stimulus but instead reflects the specific context (namely, target or distractor stimulus) in which that variability is present.

Methods

Participants

Twelve young adults (7 females, 18–30 years old, right handed) with normal hearing gave informed consent to participate in the study, which was approved by the Joint Ethics Committee of the Institute of Neurology and National Hospital for Neurology and Neurosurgery.

Stimuli

On each trial, 5 tones were presented sequentially with an intertone interval of 185 ms. Each tone comprised a sine wave of frequency 480 Hz and intensity 90 dB, with a ramp time of 5 ms at each end of the sound wave envelope. The reference for intensity was sound pressure level, measured using a sound meter (Radio Shack 33-2055). One tone was either shorter or longer than the rest and represented the target. The target tone was either 50 or 150 ms long, whereas nontarget tones were always 100 ms long. The target was always present in every trial type and was presented as the third or fourth tone in the sequence to enable participants to hear at least 2 standard length tones before the target. On two-thirds of the trials, additional auditory variation was present on an irrelevant dimension, defined by either frequency or intensity. This variation could be present in either a nontarget tone or a target tone. If present, the frequency singleton had the same duration and intensity as the other tones, but at a frequency of either 440 or 520 Hz. If present, the intensity singleton had identical duration and frequency as the other tones, but intensity was either 70 or 100 dB. On nontarget singleton trials, the singleton was positioned either directly before or after the target tone. There were thus 5 types of search trial: singleton absent, nontarget singleton present (either frequency or intensity), or target singleton present (either frequency or intensity).

Procedure

Stimuli were presented binaurally using electrostatic headphones (KOSS, Milwaukee, WI; Model: ESP 950 Medical) custom adapted for use in the scanner. Participants kept their eyes open and fixated a small cross projected centrally onto a screen mounted approximately 30 cm from their eyes and viewed by a mirror mounted on the head coil. Each experimental trial consisted of presentation of the 5 tones for 925 ms, followed by a 2500-ms response interval. Participants were required to make a speeded choice response indicating whether the duration of the acoustic target was long (150 ms) or short (50 ms), by pressing 1 of 2 response keys on a keypad held in their right hand. RTs were measured from the start of the target tone. One quarter of all trials were null trials, on which no sounds were presented. Each participant completed 4 blocks of 128 trials, divided equally between target singleton, nontarget singleton, singleton absent, and null trial types. Within separate scanning runs, the singleton dimension (intensity or frequency) was kept constant. Trials were pseudorandomly distributed to optimize the efficiency of estimating the fMRI response. Each participant performed

a half-hour practice session prior to entering the scanner in order to ensure they understood and were able to perform the task.

Eye Position Monitoring

During scanning, eye position was continually sampled at 60 Hz using long-range infrared video-oculography (ASL 504LRO Eye Tracking System, MA). The measures recorded were x and y coordinates of gaze direction (later combined to calculate the distance of eye position from the fixation point) and pupil diameter. Blinks and periods of signal loss were removed from the data, which was subsequently detrended to compensate for eye-tracker drift. The mean eye position was then computed for each trial and an analysis of variance (ANOVA) used to establish whether any statistically significant differences in eye position occurred in the different experimental conditions.

fMRI Scanning

A 3-T Siemens Allegra system was used to acquire both T_1 -weighted anatomical images and T_2 -weighted echo planar images (EPI) with blood oxygenation level-dependent contrast. Each EPI image volume comprised of forty 3-mm axial slices with an in-plane resolution of 3×3 mm positioned to cover the whole brain. Data were acquired in 4 runs, each consisting of 205 volumes. The first 5 volumes of each run were discarded to allow for T_1 equilibration effects. Volumes were acquired continuously with a time repetition of 2.6 seconds per volume.

Data Analysis

Functional imaging data were analyzed using Statistical Parametric Mapping software (SPM2, Wellcome Department of Imaging Neuroscience, University College London). All image volumes were realigned spatially to the first and temporally corrected for slice acquisition time (using the middle slice as a reference). Resulting volumes were spatially normalized to a standard EPI template volume based on the Montreal Neurological Institute reference brain in the space of Talairach and Tournoux (Talairach Tournoux 1988) and resampled to 2-mm isotropic voxels. The normalized image volumes were then smoothed with an isotropic 9-mm full-width half-maximum Gaussian kernel. These data were analyzed using an event-related random-effects model. Voxels that were activated in the experimental conditions were identified using a statistical model containing regressors that represented the transient responses evoked by the individual trials in each condition. The event-related changes in evoked activity were modeled by convolving an empirically derived hemodynamic impulse response function with trains of unitary events that were aligned on the trial onsets and lasted for the duration of the trial. A trial consisted of a 5-tone sequence followed by a response interval. Thus, each event-related regressor modeled the entire sequence of tones plus response interval. Each component of the model served as a regressor in a multiple regression analysis that included the 3 experimental conditions and the motion correction parameters (as effects of no interest). The data were high-pass filtered (cutoff frequency 0.0083 Hz) to remove low-frequency signal drifts, and global changes in activity were removed by proportional scaling. The resulting parameter estimates for each regressor at each voxel were then entered into a second-level analysis where each participant served as a random effect in a within-participants ANOVA. Appropriate corrections were made for nonsphericity (Friston and others 2002) and correlated repeated measures. The main effects and interactions between conditions were then specified by appropriately weighted linear contrasts and determined using the t -statistic on a voxel-by-voxel basis. An initial 2-factor ANOVA looking at the factors of singleton dimension (frequency or intensity) and singleton type (target singleton or nontarget singleton) showed no significant interaction between singleton type and singleton dimension ($P < 0.001$ uncorrected). In view of this result, we subsequently collapsed across the factor of singleton dimension and constructed a 1-factor ANOVA with 3 levels of singleton type (target singleton, nontarget singleton, and singleton absent). A t -test was used to identify cortical areas that showed a significant response to auditory attentional capture (nontarget singleton > target singleton). Cortical responses to the presence of additional auditory variability were determined by inclusively masking the statistical contrast of nontarget singleton versus singleton absent with the statistical contrast of target singleton versus singleton absent ($P < 0.0001$ uncorrected). This method was used to isolate cortical areas that were common to both comparisons. A statistical threshold of $P < 0.05$, FDR

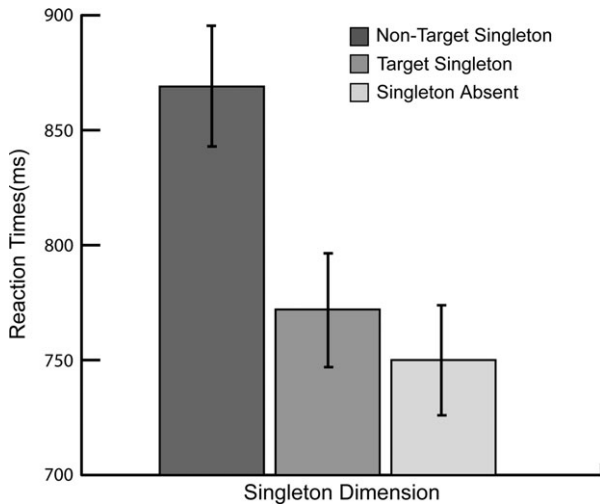


Figure 1. Behavioral results. Participants responded with a button press on each trial to indicate whether the target tone was longer or shorter than the surrounding tones. Mean RTs averaged across all participants ($n = 12$) are shown for the 3 different singleton types: nontarget singleton, target singleton, and singleton absent collapsed across singleton dimension (frequency or intensity). The error bars represent the standard error of the mean.

(Genovese and others 2002) corrected for multiple comparisons across the entire brain volume was used except for regions that were hypothesized a priori, where a threshold of $P < 0.001$, uncorrected for multiple comparisons was used.

Results

Behavior

We initially conducted a 2-way within-subjects ANOVA on the RT data. The factors were singleton dimension (frequency or intensity) and singleton type (target singleton, nontarget singleton, and singleton absent). We found a significant main effect of singleton type ($F_{1,11} = 15.6$, $P = 0.0004$) because RTs for nontarget singleton trials (M RT = 869 ms) were significantly longer than both target singleton trials (M RT = 772 ms; $t_{11} = 4.1$; $P = 0.002$) and singleton absent trials (M RT = 749 ms; $t_{11} = 4.3$; $P = 0.001$) (Fig. 1). There was no difference in RTs between target singleton and singleton absent trials ($t_{11} = 1.5$; $P = 0.2$). The main effect of singleton dimension was not significant ($F_{1,11} = 0.38$, $P = 0.6$). There was no significant interaction between singleton type and singleton dimension ($F_{2,22} = 2.4$, $P = 0.1$).

We also examined the error rates (incorrect target responses, not including missed responses) using a similar 2-way within-subjects ANOVA. We found a significant main effect of singleton type ($F_{1,11} = 28.5$, $P = 0.00001$) because error rates for nontarget singleton trials (M error rate [ER] = 18%) were significantly larger than both target singleton trials (M ER = 9%; $t_{11} = 5.8$; $P = 0.0001$) and singleton absent trials (M ER = 8%; $t_{11} = 7.5$; $P = 0.00001$). There was no difference in error rates between target singleton and singleton absent trials ($t_{11} = 2.0$; $P = 0.07$). The main effect of singleton dimension was not significant ($F_{1,11} = 0.6$, $P = 0.5$). There was no significant interaction between singleton type and singleton dimension ($F_{2,22} = 1.6$, $P = 0.2$).

In addition, we analyzed behavioral data to include separate trial types for nontarget singletons presented, before or after the target. Although numerical trends were for slower target responses with a nontarget singleton presented before (b) rather than after (a) the target, both for frequency singletons (M RTb =

900 ms, M RTa = 868 ms) and intensity singletons (M RTb = 873 ms, M RTa = 836 ms), these trends were not significant ($t_{11} = 1.8$, $P = 0.10$ for frequency singletons; $t_{11} = 1.1$, $P = 0.30$ for intensity singletons). Error rates showed similar trends: A greater number of errors were found when the singletons were presented before the target compared with after the target both for frequency singletons (M ERb = 23%, M ERa = 13%; $t_{11} = 2.89$, $P = 0.02$) and for intensity singletons, although the trend failed to reach significance in this case (M ERb = 22%, M ERa = 14%; $t_{11} = 1.8$, $P = 0.06$). We suggest that this may indicate that a singleton presented before the target can potentially interfere with more processes involved in target detection than a singleton presented after the target.

During scanning, eye position was monitored continually with long-range infrared oculography in 6 participants (see Methods for details). A repeated-measures ANOVA showed no significant differences in mean eye position comparing the different trial types across all participants ($F_{2,10} = 0.6$, $P = 0.5$).

The fMRI

Preliminary analysis of the functional imaging data confirmed, in agreement with the behavioral findings, that there were no significant ($P < 0.01$ uncorrected) differences between the effects of frequency and intensity singletons on brain activity (see Methods for further details). Therefore, for the subsequent analyses, we collapsed across the frequency and intensity singleton dimension.

Singleton Presence versus Absence

To identify cortical areas that showed a significant response to singleton presence (irrespective of whether the singleton was present in a target or nontarget tone), we compared all singleton present conditions with a singleton absent baseline, using a masking procedure (see Methods). The areas identified by this procedure responded to the presence (vs. absence) of a singleton, regardless of its type and its behavioral significance, and comprised left inferior frontal gyrus and bilateral superior temporal gyri (Fig. 2). The stereotactic locations and statistical values for these activated loci are shown in Table 1.

Nontarget Singleton versus Target Singleton

The presence of a nontarget singleton (compared with target singleton) was associated with activity in a restricted set of parietal and frontal loci: right superior parietal gyrus and intraparietal sulcus and left precentral gyrus (Fig. 3). The stereotactic loci and corresponding statistical values for each activated locus are shown in Table 2. There is no overlap between the cortical areas that showed activity related to singleton presence (vs. absence) compared with those whose activity was specifically related to nontarget singleton (vs. target) at the corrected threshold. A direct comparison of both contrasts at a liberal uncorrected threshold ($P < 0.001$ uncorrected) revealed a small area of overlap in the left inferior frontal gyrus. Areas that responded specifically to the presence of a nontarget singleton were located dorsally, whereas those areas that responded to any stimulus variability were located more ventrally. There were no significant differences in brain activity between nontarget singletons presented before or after the target ($t_{\max} = 4.19$; $P > 0.6$).

Discussion

The present study reveals the neural correlates of attentional capture by a distracting singleton in hearing. Our behavioral

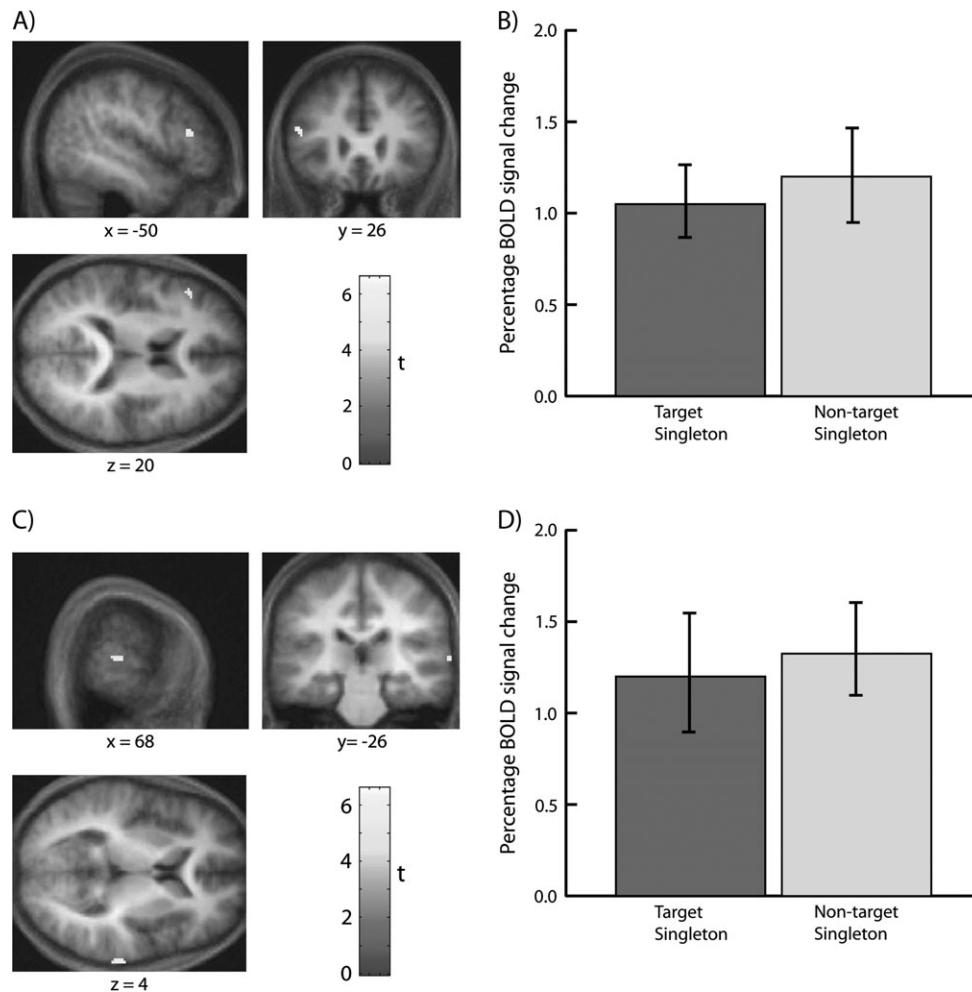


Figure 2. Cortical areas responding to auditory variability. Shown in the figure are cortical loci where event-related activity was significantly greater in both nontarget singleton trials compared with singleton absent trials and target singleton trials compared with singleton absent trials ($P < 0.05$, FDR corrected). Activated areas are shown projected onto the mean T_1 -weighted structural scan of the 12 individual participants. (A) Activated cortical loci in the left inferior frontal gyrus (see Table 1 for stereotactic coordinates and t -values). (B) Percentage blood oxygenation level-dependent (BOLD) signal in each condition relative to singleton absent baseline, averaged across participants, measured in the left inferior frontal gyrus. (C) Activated loci in the right superior temporal gyrus are shown (see Table 1 for stereotactic coordinates and t -values). (D) Percentage BOLD signal change in each condition relative to a singleton absent baseline, averaged across participants, measured at the right superior temporal gyrus. The error bars in both plots represent the standard error of the mean.

Table 1
Coordinates and t -values for event-related activation associated with acoustic variability

Anatomy	Coordinates (x y z)	Number of voxels in cluster	t -value
L inferior frontal gyrus	-44, 18, 24	7	6.58
L inferior frontal gyrus	-50, 26, 20	28	6.47
L superior temporal gyrus	-54, -4, -4	15	5.86
L superior temporal gyrus	-58, 4, -12	2	4.44
R superior temporal gyrus	68, -26, 4	80	6.41

Note: Shown in the table are loci where event-related activity was significantly greater for the comparison of singleton trials (either nontarget or target) compared with no singleton trials. Only the most significant peaks within each area of activation are reported in the table ($P < 0.05$, FDR corrected). L, left; R, right.

findings demonstrate that irrelevant variation in the frequency or intensity of the nontarget tones (nontarget singleton) increased RTs and error rates, suggesting that the irrelevant nontarget singleton captured attention. However, when the same irrelevant feature singleton was present in the target tone, it had no significant effect on performance, as expected given that the target was already a duration singleton and this was sufficient for attracting attention to the target.

Importantly, the contrast in the behavioral effects of physically identical nontarget singleton and target singleton tone sequences allowed us to distinguish between the cortical areas that responded to interference by an attention-capturing auditory singleton distractor from cortical areas that responded simply to an increase in the variability of the auditory sequence, irrespective of the effects on attention. Increased auditory variability was associated with enhanced activity in bilateral superior temporal gyri and left inferior frontal gyrus (Table 1 and Fig. 2). Note also, signal change in these areas is very similar when related separately to the singleton target or the singleton distractor (each compared with singleton absent conditions, Fig. 2 panels B,D), further suggesting the activity in these areas reflects the simple detection of greater sound variability. These findings are in line with previous findings of neural activity related to auditory change detection (Doeller and others 2003; Molholm and others 2005).

In contrast, activity specifically related to auditory attentional capture by a nontarget singleton (vs. target singleton) comprised a restricted set of cortical areas encompassing right

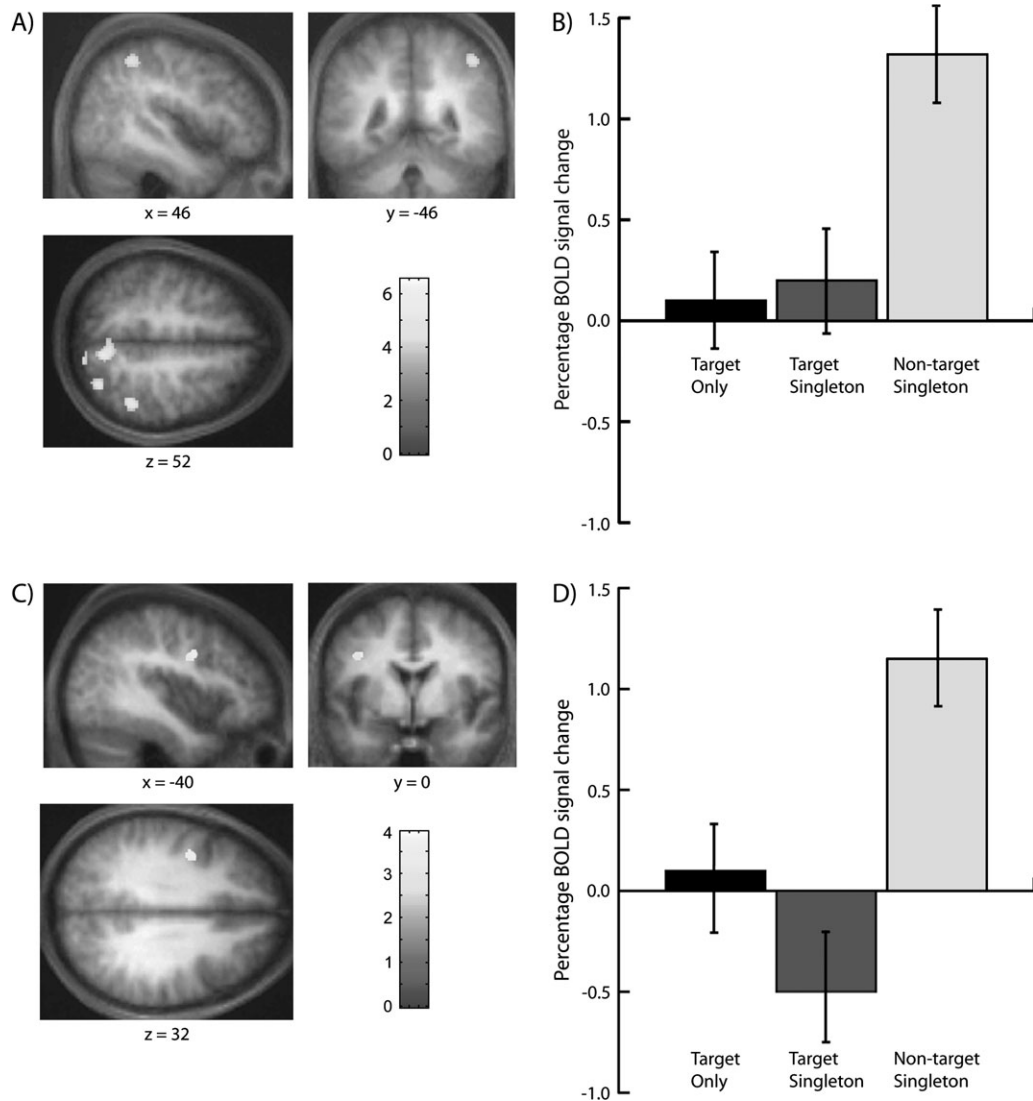


Figure 3. Cortical areas specific for auditory attentional capture. Shown in the figure are cortical loci where event-related activity was significantly greater during nontarget singleton trials compared with target singleton trials ($P < 0.05$ corrected). Activated areas are shown projected onto the mean T_1 -weighted structural scan of the 11 individual participants. (A) Activated cortical loci in the right superior parietal gyrus and right intraparietal sulcus (see Table 2 for stereotactic coordinates and t -values) (B) Percentage blood oxygenation level-dependent (BOLD) signal in each condition averaged across participants, measured in the right superior parietal gyrus. (C) Activated cortical loci in the left precentral gyrus (see Table 2 for stereotactic coordinates and t -values) projected onto an average T_1 -weighted structural scan. (D) Percentage BOLD signal in each condition averaged across participants, measured in the left precentral gyrus.

Table 2

Coordinates and t -values for event-related activation associated with auditory attentional capture

Location	Coordinates ($x\ y\ z$)	Number of voxels in cluster	t -value
R superior parietal gyrus	10, -68, 56	63	6.58
R intraparietal sulcus	46, -46, 52	15	5.64
R intraparietal sulcus	32, -70, 52	2	5.35
L precentral gyrus	-40, 0, 32	30	3.93

Note: Shown in the table are cortical loci where event-related activity was significantly greater during nontarget singleton trials compared with target singleton trials ($P < 0.05$, FDR corrected). Only the most significant peaks within each area of activation are reported in the table. L, left; R, right.

superior parietal gyrus, right intraparietal sulcus, and left precentral gyrus (Table 2 and Fig. 3). This activation of frontoparietal cortex cannot represent a response to stimulus variability per se, as the 2 singleton conditions were identical

with respect to their acoustic variability. Rather, it is the precise attentional significance (whether the feature singleton was associated with the search target or with a nontarget) that determined both whether behavioral interference occurred and whether associated frontoparietal activation was observed.

To further confirm the specificity of this activity to attentional capture by an irrelevant singleton nontarget, we also compared the effects of the target singleton and target-alone conditions. We postulated that when the additional irrelevant singleton was on the target, it was detected but did not cause any capture of attention because the subject's attention was already allocated to the target (because it was always a duration singleton). In line with this account, the contrast of target singleton with target alone revealed activation of a subset of the areas associated with deviance detection (only left inferior frontal gyrus $[-50\ 28\ 18]$ $t = 4.88$ significant at $P < 0.05$ corrected at cluster level, see Supplementary Fig. 1). Thus, whereas the

singleton nontarget produced attentional capture, as indicated both by behavioral interference effects and activity in the frontoparietal attention network, the same extra singleton when coinciding with the target (that was already a duration singleton in our design) did not appear to have any consequences on behavioral or neural indices of attention. Such divergence in the behavioral and neural consequences of an additional singleton as a function of whether it is added to a nontarget or a target (when the target already contains an attention-capturing singleton on another dimension) has previously been demonstrated in visual capture of attention (de Fockert and others 2004).

Voluntary allocation of auditory attention, typically in dichotic listening tasks, is associated in humans with activation in a network of superior frontal and parietal cortical areas (Pugh and others 1996; Tzourio and others 1997; Benedict and others 1998; Zatorre and others 1999; Lipschutz and others 2002). For example, voluntary nonspatial shifts of attention between auditory and visual streams are associated with activation of right superior parietal lobule, left inferior parietal lobule, and right frontal cortex (Shomstein and Yantis 2004). The present study goes beyond these earlier findings by establishing the cortical areas activated by capture of auditory attention by an irrelevant feature singleton. The overlap in activity related to voluntary allocation of attention and the involuntary capture of attention by a behaviorally interfering singleton distractor suggests these areas are involved in the allocation of attention regardless of whether attention was captured by an irrelevant singleton or voluntarily allocated to targets. Note, however, that the activation of frontoparietal cortex we observed could not be explained by changes in voluntary attention. In order to allocate more voluntary attention to nontarget singleton trials, subjects would need to know in advance the trial type. As trials were randomized this was not possible. It is also possible that subjects may have allocated more attentional resources to the temporal window containing the target (position 3 or 4 in the tone sequence). However, in half of the nontarget singleton trials, the nontarget singleton would have been presented in either position 3 or 4. Thus, overall subjects would not have benefited from this strategy.

The parietal and prefrontal networks associated with the voluntary (or here, involuntary) deployment of auditory attention and with nonspatial shifts of attention between vision and audition (Shomstein and Yantis 2004) is anatomically very similar to the network of areas proposed to fulfill a similar role in visual attention (for a review, see Corbetta and Shulman 2002). These findings suggest that the frontoparietal network may function as a supramodal attentional system. Consistent with such a hypothesis, our findings in auditory attentional capture strongly resemble those found associated with stimulus-driven visual attentional shifts. In a conceptually similar task, De Fockert and others (2004) found that capture of attention by an irrelevant visual feature singleton (characterized by an odd color) during performance of a search task based on the stimulus shapes (see Theeuwes 1992) was associated with activation in left prefrontal and bilateral superior parietal cortices. These loci are very close to those activated in the present study, consistent with a common supramodal network for stimulus-driven shifts of attention (Downar and others 2002). It is noteworthy that several previous studies have reported that stimulus-driven attentional shifts in vision are associated with activation of the right temporoparietal junction

(for a review, see Corbetta and Shulman 2002). In contrast, we did not see any such activation associated with stimulus-driven auditory attentional capture. However, recent visual studies have shown that activation of the right temporoparietal junction critically depends on the behavioral relevance of the particular object that captures attention (specifically, sharing a feature with the target of the search; Kincade and others 2005). In contrast, in the present study, the feature singleton was defined on a different dimension to the target and was thus not relevant to the search task. Consequently, activation of temporoparietal cortex was not anticipated. Consistent with this, temporoparietal activation is also not seen when an irrelevant visual singleton distractor (e.g., a nontarget with an odd color) captures attention during shape search task (de Fockert and others 2004).

In addition to establishing the neural substrates of auditory attentional capture, our results also shed light on how the brain responds to auditory stimulus variability, irrespective of its attentional role. Increased auditory stimulus variability (with the presence of singleton sounds) was associated with activity in left inferior frontal and bilateral superior temporal cortices (Fig. 2). These areas are similar to the network of areas that are proposed to mediate the generation of the MMN (Doeller and others 2003; Molholm and others 2005). Generation of the MMN has been consistently shown to involve bilateral superior temporal gyri (Giard and others 1990; Deacon and others 1998; Opitz, Mecklinger, von Cramon, and Kruggel 1999). However, recent studies have also demonstrated a role for the right (Opitz, Mecklinger, Friederici, and von Cramon 1999; Opitz and others 2002) and left (Doeller and others 2003; Molholm and others 2005) inferior frontal gyri. There is some debate about whether the cortical generators of the MMN vary as a function of the acoustic feature that changes. Several previous studies have suggested that the MMN network may differ depending on the acoustical dimension studied (Paavilainen and others 1991; Molholm and others 2005). In contrast, some studies find no difference (Sams and others 1991; Schairer and others 2001). In this study, we found no significant difference in cortical activity between frequency and intensity singleton dimensions.

Note, however, that the present experimental paradigm is rather different from those typically used to elicit the MMN. Typically, the MMN is evoked by rare deviant stimuli embedded in very long runs of auditory stimuli. In contrast, the present paradigm involved repeated auditory search in a short run of tones that frequently contained a deviant (either target or nontarget singletons). However, we did use the same standard tone throughout the experimental session therefore allowing subjects to build up a reliable trace of a standard tone against which a deviant tone could be detected. We did not measure electrophysiological brain responses in the present experiment, so cannot know whether MMN occurred to the singletons in the present data. Indeed, some authors (Näätänen and others 1993; Alho and others 1997; Opitz, Mecklinger, von Cramon, and Kruggel 1999; Liebenthal and others 2003) have proposed that the MMN is abolished if the deviants are frequent and the runs are short (though, for a contrary view, see Jaaskelainen and others 2004). Nevertheless, the striking similarity of the loci activated by singleton presence (vs. absence) in the present study with the putative MMN generators is consistent with the notion that this network represents a common cortical mechanism for the detection of acoustic variability (or salience).

Conclusion

Taken together, our findings suggest that a ventral network, involving bilateral superior temporal gyri and left inferior frontal gyri, responds to auditory variability regardless of its relevance to the behavioral task. In contrast, activation of a more dorsal network comprising of left precentral gyrus, right superior parietal gyrus, and right intraparietal sulcus responds specifically to capture of attention by a feature singleton. The ventral network is anatomically very similar to that previously described for automatic auditory change detection. In contrast, the more dorsal network is closely related to structures activated both in previous studies of visual attentional capture and during voluntary auditory shifts of attention.

Supplementary Material

Supplementary materials can be found at <http://www.cercor.oxfordjournals.org/>.

Notes

The Wellcome Trust supported this work. *Conflict of Interest:* None declared.

Address correspondence to Dr Susanne Watkins, Institute of Cognitive Neuroscience, University College London, 17 Queen Square, London WC1N 3AR, UK. Email: swatkins@fil.ion.ucl.ac.uk.

References

- Alho K, Escera C, Diaz R, Yago E, Serra JM. 1997. Effects of involuntary auditory attention on visual task performance and brain activity. *Neuroreport* 8(15):3233-3237.
- Benedict RH, Lockwood AH, Shucard JL, Shucard DW, Wack D, Murphy BW. 1998. Functional neuroimaging of attention in the auditory modality. *Neuroreport* 9(1):121-126.
- Corbetta M, Shulman GL. 2002. Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neuro Sci* 3(3):201-215.
- Dalton P, Lavie N. 2004. Auditory attentional capture: effects of singleton distractor sounds. *J Exp Psychol Hum Percept Perform* 30(1):180-193.
- de Fockert J, Rees G, Frith C, Lavie N. 2004. Neural correlates of attentional capture in visual search. *J Cogn Neurosci* 16(5):751-759.
- Deacon D, Nousak JM, Pilotti M, Ritter W, Yang CM. 1998. Automatic change detection: does the auditory system use representations of individual stimulus features or gestalts? *Psychophysiology* 35(4):413-419.
- Doeller CF, Opitz B, Mecklinger A, Krick C, Reith W, Schroger E. 2003. Prefrontal cortex involvement in preattentive auditory deviance detection: neuroimaging and electrophysiological evidence. *Neuroimage* 20(2):1270-1282.
- Downar J, Crawley AP, Mikulis DJ, Davis KD. 2002. A cortical network sensitive to stimulus salience in a neutral behavioral context across multiple sensory modalities. *J Neurophysiol* 87(1):615-620.
- Escera C, Alho K, Winkler I, Naatanen R. 1998. Neural mechanisms of involuntary attention to acoustic novelty and change. *J Cogn Neurosci* 10(5):590-604.
- Escera C, Yago E, Alho K. 2001. Electrical responses reveal the temporal dynamics of brain events during involuntary attention switching. *Eur J Neurosci* 14(5):877-883.
- Friston KJ, Penny W, Phillips C, Kiebel S, Hinton G, Ashburner J. 2002. Classical and Bayesian inference in neuroimaging: theory. *Neuroimage* 16(2):465-483.
- Genovese CR, Lazar NA, Nichols T. 2002. Thresholding of statistical maps in functional neuroimaging using the false discovery rate. *Neuroimage* 15(4):870-878.
- Giard MH, Perrin F, Pernier J, Bouchet P. 1990. Brain generators implicated in the processing of auditory stimulus deviance: a topographic event-related potential study. *Psychophysiology* 27(6):627-640.
- Jaaskelainen IP, Ahveninen J, Bonmassar G, Dale AM, Ilmoniemi RJ, Levanen S, Lin FH, May P, Melcher J, Stufflebeam S, and others. 2004. Human posterior auditory cortex gates novel sounds to consciousness. *Proc Natl Acad Sci USA* 101(17):6809-6814.
- Kincade JM, Abrams RA, Astafiev SV, Shulman GL, Corbetta M. 2005. An event-related functional magnetic resonance imaging study of voluntary and stimulus-driven orienting of attention. *J Neurosci* 25(18):4593-4604.
- Liebenthal E, Ellingson ML, Spanaki MV, Prieto TE, Ropella KM, Binder JR. 2003. Simultaneous ERP and fMRI of the auditory cortex in a passive oddball paradigm. *Neuroimage* 19(4):1395-1404.
- Lipschutz B, Kolinsky R, Damhaut P, Wikler D, Goldman S. 2002. Attention-dependent changes of activation and connectivity in dichotic listening. *Neuroimage* 17(2):643-656.
- Molholm S, Martinez A, Ritter W, Javitt DC, Foxe JJ. 2005. The neural circuitry of pre-attentive auditory change-detection: an fMRI study of pitch and duration mismatch negativity generators. *Cereb Cortex* 15(5):545-551.
- Naatanen R, Paavilainen P, Tiitinen H, Jiang D, Alho K. 1993. Attention and mismatch negativity. *Psychophysiology* 30(5):436-450.
- Opitz B, Mecklinger A, Friederici AD, von Cramon DY. 1999. The functional neuroanatomy of novelty processing: integrating ERP and fMRI results. *Cereb Cortex* 9(4):379-391.
- Opitz B, Mecklinger A, von Cramon DY, Kruggel F. 1999. Combining electrophysiological and hemodynamic measures of the auditory oddball. *Psychophysiology* 36(1):142-147.
- Opitz B, Rinne T, Mecklinger A, von Cramon DY, Schroger E. 2002. Differential contribution of frontal and temporal cortices to auditory change detection: fMRI and ERP results. *Neuroimage* 15(1):167-174.
- Paavilainen P, Alho K, Reinikainen K, Sams M, Naatanen R. 1991. Right hemisphere dominance of different mismatch negativities. *Electroencephalogr Clin Neurophysiol* 78(6):466-479.
- Pugh KR, offywitz BA, Shaywitz SE, Fulbright RK, Byrd D, Skudlarski P, Shankweiler DP, Katz L, Constable RT, Fletcher J, and others. 1996. Auditory selective attention: an fMRI investigation. *Neuroimage* 4(3 Pt 1):159-173.
- Rinne T, Sarkka A, Degerman A, Schroger E, Alho K. 2006. Two separate mechanisms underlie auditory change detection and involuntary control of attention. *Brain Res* 1077(1):135-143.
- Roeber U, Widmann A, Schroger E. 2003. Auditory distraction by duration and location deviants: a behavioral and event-related potential study. *Brain Res Cogn Brain Res* 17(2):347-357.
- Sams M, Kaukoranta E, Hamalainen M, Naatanen R. 1991. Cortical activity elicited by changes in auditory stimuli: different sources for the magnetic N100m and mismatch responses. *Psychophysiology* 28(1):21-29.
- Schäirer KS, Gould HJ, Pousson MA. 2001. Source generators of mismatch negativity to multiple deviant stimulus types. *Brain Topogr* 14(2):117-130.
- Schroger E. 1994. Automatic detection of frequency change is invariant over a large intensity range. *Neuroreport* 5(7):825-828.
- Schroger E, Giard MH, Wolff C. 2000. Auditory distraction: event-related potential and behavioral indices. *Clin Neurophysiol* 111(8):1450-1460.
- Schroger E, Wolff C. 1998. Behavioral and electrophysiological effects of task-irrelevant sound change: a new distraction paradigm. *Brain Res Cogn Brain Res* 7(1):71-87.
- Shomstein S, Yantis S. 2004. Control of attention shifts between vision and audition in human cortex. *J Neurosci* 24(47):10702-10706.
- Talairach J, Tournoux P. 1988. Co-planar stereotaxic atlas of the human brain. Stuttgart, Germany: Thieme.
- Theeuwes J. 1992. Perceptual selectivity for color and form. *Percept Psychophys* 51(6):599-606.
- Theeuwes J. 1994. Stimulus-driven capture and attentional set: selective search for color and visual abrupt onsets. *J Exp Psychol Hum Percept Perform* 20(4):799-806.
- Tzourio N, Massiou FE, Crivello F, Joliot M, Renault B, Mazoyer B. 1997. Functional anatomy of human auditory attention studied with PET. *Neuroimage* 5(1):63-77.
- Wolff C, Schroger E. 2001. Activation of the auditory pre-attentive change detection system by tone repetitions with fast stimulation rate. *Brain Res Cogn Brain Res* 10(3):323-327.
- Yantis S. 1993. Stimulus-driven attentional capture and attentional control settings. *J Exp Psychol Hum Percept Perform* 19(3):676-681.
- Zatorre RJ, Mondor TA, Evans AC. 1999. Auditory attention to space and frequency activates similar cerebral systems. *Neuroimage* 10(5):544-554.