Involvement of the Dorsal and Ventral Attention Networks in Oddball Stimulus Processing: A Meta-Analysis

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Abstract: The aim of this study was to provide the first, comprehensive meta-analysis of the neuroimaging literature regarding greater neural responses to a deviant stimulus in a stream of repeated, standard stimuli, termed here *oddball effects*. The meta-analysis of 75 independent studies included a comparison of auditory and visual oddball effects and task-relevant and task-irrelevant oddball effects. The results were interpreted with reference to the model in which a large-scale dorsal frontoparietal network embodies a mechanism for orienting attention to the environment, whereas a large-scale ventral frontoparietal network supports the detection of salient, environmental changes. The meta-analysis yielded three main sets of findings. First, ventral network regions were strongly associated with oddball effects and largely common to auditory and visual modalities, indicating a supramodal “alerting” system. Most ventral network components were more strongly associated with task-relevant than task-irrelevant oddball effects, indicating a dynamic interplay of stimulus saliency and internal goals in stimulus-driven engagement of the network. Second, the bilateral inferior frontal junction, an anterior core of the dorsal network, was strongly associated with oddball effects, suggesting a central role in top-down attentional control. However, other dorsal network regions showed no or only modest association with oddball effects, likely reflecting active engagement during both oddball and standard stimulus processing. Finally, prominent oddball effects outside the two networks included the sensory cortex regions, likely reflecting attentive and preattentive modulation of early sensory activity, and subcortical regions involving the putamen, thalamus, and other areas, likely reflecting subcortical involvement in alerting responses. *Hum Brain Mapp* 35:2265–2284, 2014. © 2013 Wiley Periodicals, Inc.

Key words: fMRI; attention; oddball; dorsal network; ventral network; meta-analysis

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INTRODUCTION

Aim of the Study

The ability to detect and orient attention toward salient, significant changes in the environment is critical to the survival of an organism. One of the most widely used experimental procedures to investigate this ability is commonly called an “oddball” paradigm, where participants are typically required to detect a target (oddball) presented infrequently (e.g., 5–15%) in a stream of frequent, standard stimuli. The relevant data analysis attempts to characterize enhanced neural responses to oddball stimuli relative to

standard stimuli, referred to here as *oddball effects*. Although early studies [Squires et al., 1975] have described several event-related potential oddball effects including the prominent P300 component, the advent of functional neuroimaging techniques such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) facilitated direct enquiry of the brain regions preferentially engaged in oddball stimulus processing. The goal of this study was to provide the first, comprehensive meta-analysis of the neuroimaging literature regarding oddball effects. This meta-analysis considered only activations (oddball > standard) and not deactivations (standard > oddball), restricting the data to those from healthy individuals. Deactivations were not considered owing to an extremely limited number of available reports.

Although there are large interstudy variations in specific findings, the presentation of oddball stimuli typically elicits its widespread brain activity involving diverse cortical and subcortical regions. For example, a large scale ($n = 100$) fMRI study of an auditory oddball task [Kiehl et al., 2005b] has implicated nearly 40 brain regions in oddball effects, including parts of frontal, parietal, temporal, occipital, deep gray, and cerebellar regions. An increasing body of evidence indicates that many activations observed in neuroimaging studies are not regions activated in isolation, but rather are components of intrinsic, large-scale networks that respond in concert [Bressler and Menon, 2010; Fox et al., 2005; Raichle et al., 2001]. This evidence compels cognitive neuroscience researchers to go beyond localizing complex cognitive functions onto individual brain areas and take a more principled, network-based approach to the interpretations of activations during cognition [Kim, 2010]. In line with this demand, the main goal of this meta-analysis was to evaluate to what extent regional distributions of oddball effects conform to an influential model proposed by Corbetta and Shulman [2002] of two attention networks.

Dorsal and Ventral Attention Networks

The two attention networks models [Corbetta and Shulman, 2002; Sestieri et al., 2012] suggest that a first, dorsal frontoparietal network, whose main components include the frontal eye field (FEF), inferior frontal junction (IFJ), located in the posterior extent of the inferior frontal sulcus, superior parietal lobule (SPL), medial intraparietal sulcus (IPS) and motion-sensitive middle temporal area (MT+), implements the mechanism for orienting of attention to the external environment by sending top-down biasing signals to a subset of sensory input. A second, ventral frontoparietal network, which comprises the temporoparietal junction (TPJ), a supramarginal area around the end of the Sylvian fissure, anterior insula (AI), and adjacent frontal operculum (FO) and anterior cingulate cortex (ACC), is involved in detecting salient changes in the environment and acting as an alerting mechanism or “circuit-breaker” for the first, dorsal system. One of the early, key observations to distinguish

the two networks involved the Posner spatial cueing paradigm [Corbetta et al., 2000], where the presentation of cues activated dorsal, but not ventral, network regions, likely reflecting attentional orienting or “attentional set” in anticipation of the target. In comparison, the presentation of targets, especially invalidly cued targets, recruited both ventral network regions, likely reflecting the detection of salient stimuli, and dorsal network regions, likely reflecting attentional reorienting to the salient stimuli.

One of the critical, recent developments is the confirmation of the two networks solely on the basis of spontaneous fluctuations in fMRI blood-oxygen-level-dependent (BOLD) signals during the awake, resting state [Fox et al., 2006; Vincent et al., 2008; Yeo et al., 2011]. Resting-state functional connectivity data [Fox et al., 2005; Fransson, 2005; Golland et al., 2008] also showed an anticorrelation between the dorsal attentive and the default-mode networks, likely reflecting spontaneous fluctuations between externally and internally focused attention. This validation based on intrinsic functional connectivity provides strong evidence against the generic criticism that “the idea of a ‘network’ can be little more than a metaphor for wide-spread brain activity” [Uttal, 2011, p.264]. Furthermore, a connectivity-based map is free of bias owing to the specific task used and likely provides a more complete picture of a network than a task-activation map. A recent resting-state functional connectivity study [Yeo et al., 2011] based on a large-scale sample ($n = 1,000$) and an extensive range of validation analysis (e.g., replication study) provides one of the best estimates of dorsal and ventral attention network boundaries. As shown in Figure 1, these estimates largely reproduce the spatial topography of the two networks on the basis of task-activation paradigms and additionally disclose more subtle members, for example, the anterior middle frontal gyrus (amFG) and supplementary motor area (SMA) of the ventral frontoparietal network. Based on the understanding that functional network boundaries may be dynamically organized rather than strictly defined, this study uses this map as a “flexible” template to constrain the interpretations of activation findings in this meta-analysis.

This study predicted a strong association of the ventral network but only a modest association of the dorsal network with oddball effects. The presentation of an oddball stimulus, which is salient by virtue of being rare, likely activates the ventral “alerting” network more strongly than does the presentation of a standard stimulus. As regards the dorsal network, participants maintain the same “attentional set” from the beginning to the end of the run, continuously searching for oddball stimuli. Thus, the dorsal network is likely strongly engaged during both oddball and standard stimulus processing, which should result in a relatively weak association of the network with oddball effects. Although attentional reorienting and stimulus-response mapping associated with the detection of targets (oddballs) may involve differential dorsal network activity, this may involve relatively circumscribed regions. Furthermore, a large majority of oddball studies have

Figure 1.

Yeo et al. [2011]'s seven-network parcellation of the human cerebral cortex based on 1,000 subjects. The parcellation was determined on the basis of a clustering algorithm performed on intrinsic fluctuations in fMRI BOLD signal during the passive resting state. The components of the green-and violet-colored networks closely reproduce those previously described to be engaged in goal-directed attention (the dorsal attention system) and stimulus-driven attention (the ventral attention system), respectively [Corbetta and Shulman, 2002]. The figures were adapted from Yeo et al. [2011, Figure 11] with permission of J Neurophysiol, 2011, 106, 1125–1165. ACC, anterior cingulate cortex; AI, anterior insula; aMFG, anterior middle frontal gyrus; FEF, frontal eye field; FO, frontal operculum; IFJ, inferior frontal junction; mIPS, medial intraparietal sulcus; MT+, motion-sensitive middle temporal area; SMA, supplementary motor area; SPL, superior parietal lobule; TPJ, temporoparietal junction. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

defined the oddball by a feature (e.g., pitch, color, form, etc.) that differs from the standard rather than by a different location. Nonspatial, feature-based attentional control may involve *less* extensive dorsal network regions relative to spatial attentional control [Giesbrecht et al., 2003; Slagter et al., 2007; Smith et al., 2010]. In agreement with these predictions, the oddball effects reported in prior studies have typically included core ventral network regions such as TPJ and AI [Bledowski et al., 2004; Brázdil et al., 2005; Clark et al., 2000; Fichtenholtz et al., 2004; Linden et al., 1999; Menon et al., 1997; Stevens et al., 2000]; however, the involvement of any dorsal network regions has been reported with much less frequency [Bledowski et al., 2004; Clark et al., 2000; Stevens et al., 2000].

Stimulus Modality and Task-Relevance Effects

In addition to the general meta-analysis involving all relevant oddball studies, this study includes more specific

meta-analysis that compares different types of oddball effects. In particular, the study investigates two variables of oddball stimuli: stimulus modality (auditory vs. visual) and task relevance (relevant vs. irrelevant). Choice of these two variables was guided by theoretical considerations as well as by sufficient studies to ensure a meaningful analysis.

First, oddball studies have historically used both auditory and visual tasks. To compare auditory and visual oddball effects, this study included separate meta-analysis of the two effects and their direct comparison. Both auditory [Brázdil et al., 2005; Linden et al., 1999; Menon et al., 1997] and visual [Bledowski et al., 2004; Clark et al., 2000; Fichtenholtz et al., 2004] oddball studies have commonly reported the involvement of core ventral network regions, supporting the hypothesis that the ventral frontoparietal network is a supramodal “alerting” system [Corbetta et al., 2008]. Thus, this meta-analysis predicted that many ventral network components would show both auditory and visual oddball effects. As regards the dorsal network, no extensive difference between auditory and visual oddball effects involving the network is expected, given the likely modest association of the network with oddball effects. However, some posterior portions of the dorsal network such as posterior IPS and MT+ may be more specific to visual oddball effects because they are adjacent to or part of the extrastriate visual cortex.

Second, prior oddball studies have used not only *task-relevant oddballs*, that is, rare stimuli that participants are required to detect, but also *task-irrelevant oddballs*, that is, rare stimuli that participants are not required to detect, typically in a three-stimulus paradigm (task-relevant oddball, task-irrelevant oddball, and standard). To compare task-relevant versus task-irrelevant oddball effects, this study included separate meta-analysis of the two effects and their direct comparison. Prior within-study comparisons of the two oddball effects have established more extensive brain regions associated with task-relevant oddballs [Bledowski et al., 2004; Clark et al., 2000; Gur et al., 2007b; Kiehl et al., 2001b; O’Connell et al. 2012; Stevens et al., 2007]. Furthermore, these regions have typically included one or more ventral network components, supporting the hypothesis that ventral network activity does not solely reflect stimulus saliency but a dynamic interplay of stimulus saliency and internal goals [Corbetta et al., 2008]. Thus, this meta-analysis predicted that many ventral network components would be more strongly activated by the presentation of task-relevant than task-irrelevant oddball stimuli. Although no extensive difference between task-relevant and task-irrelevant oddball effects involving the dorsal network is expected, any difference may be in the direction of a greater association with task-relevant than task-irrelevant effects, given the likely greater association of the ventral network with task-relevant oddball effects.

Finally, this meta-analysis also investigated oddball effects outside the dorsal and ventral attention networks. Sensory cortex and subcortical regions are two of the

broad regions that have been frequently associated with oddball effects in prior studies. Enhanced responses of sensory cortex to oddball stimuli have been attributed to attentive [Kruggel et al., 2001; Linden et al., 1999; Strange et al., 2000] and preattentive [Habermeyer et al., 2009; Molholm et al., 2005; Opitz et al., 1999a] modulation of early sensory processing. A critical piece of evidence for preattentive modulation is the finding that the mismatch negativity potential to deviant stimuli is elicited even when participants are not paying attention to the stimuli [Näätänen et al., 2007]. The presence of oddball effects in selective subcortical regions, including thalamus, basal ganglia, and cerebellum, has been one of the most robust findings in prior relevant studies [Braver et al., 2001; Clark et al., 2000; Kiehl et al., 2001a; Menon et al., 1997; Opitz et al., 1999a; Stevens et al., 2000; Yoshiura et al., 1999]. Although these subcortical effects remain poorly theorized, they might reflect subcortical alerting and other related responses to salient events, likely in association with the ventral attention network [Menon and Uddin, 2010; Seeley et al., 2007; Shulman et al., 2009; Zink et al., 2003].

MATERIALS AND METHODS

Study/Contrast Selection

Candidate studies for the meta-analysis were identified through a search of the PubMed database using the search terms “(PET OR fMRI) AND oddball.” on June 5, 2012. This search retrieved 271 studies. The search results were then screened to include only those studies that (i) included healthy participants, (ii) included an activation contrast between an oddball versus a standard condition, (iii) performed whole-brain analysis, and (iv) reported coordinate-based analyses of the data. This filtering yielded 70 studies. An additional five studies, not identified by the online database search, were obtained during the review process of these studies. Thus, the meta-analysis ultimately included a total of 75 studies that collectively involved 1,415 participants.

Selected contrasts were those that involved a comparison between an oddball versus a standard condition, or between an oddball condition versus an implicit (null) baseline. When more than one relevant contrast was reported in a study, if they involved different stimulus modalities or task-relevance conditions, each was selected for inclusion. However, if they involved both the same modality and the task-relevance condition, only one was selected to prevent these studies from influencing the results more than those containing only one contrast. Typically, the one that yielded the largest number of activation foci was selected for inclusion, the rationale for which was to increase sensitivity of this meta-analysis. Ultimately, a total of 93 contrasts met the inclusion criteria and provided 1,699 foci of peak activation. The Appendix lists the imaging modality, number of participants, stimulus

modality, task-relevance type, number of foci reported, and a brief description of oddball and standard stimuli for each of the included studies. Owing to insufficient descriptions, it was not always possible to definitely determine whether a given contrast compared the oddball to the standard or implicit baseline. However, approximately 55% of the selected contrasts compared the oddball to the standard. There are pros and cons for use of both the oddball–standard contrast and the oddball–baseline contrast [Friedman et al., 2009]. Yet, the two types of contrasts tend to yield relatively comparable results because a stream of frequent standard stimuli largely “saturates” the baseline [Stevens et al., 2006]. Thus, the two types of contrasts were considered together in this meta-analysis.

Contrast Groupings

The selected contrasts were grouped according to stimulus modality (auditory vs. visual) and task-relevance type (relevant vs. irrelevant). Few other dimensions were available to distinguish the selected contrasts and thereby ensure a meaningful meta-analysis. First, a classification by stimulus modality indicated 49 contrasts involving auditory stimuli, 42 involving visual stimuli, and 2 involving tactile stimuli. Second, task-relevance type was classified as “task-relevant” if the presentation of oddball stimuli required a different type of response from standard stimuli, most typically, a button pressing for oddball stimuli and no response for standard stimuli, and classified as “task-irrelevant” if the presentation of the oddball stimuli involved the same response type from standard stimuli, most typically, no response for both types of stimuli. Thus, the terms “task-relevant” and “task-irrelevant” are used here strictly to distinguish between the target and the nontarget oddball condition. This is emphasized because all stimuli, regardless of response demand, are “task-relevant” in some way. A classification by task-relevance type indicated 56 contrasts involving task-relevant oddball stimuli, 36 involving task-irrelevant oddball stimuli, and 1 involving a mixture of task-relevant and task-irrelevant oddball stimuli.

Table I summarizes a classification of oddball–standard pairs used in each subgroup of contrasts by stimulus types and response design. The most common oddball–standard stimulus type was (a) within the auditory–task-relevant subgroup, a type of pure tones–pure tones that differed only in sound frequency (e.g., 2 kHz tone–1 kHz tone); (b) within the auditory–task-irrelevant subgroup, a type of digital noises–pure tones; (c) within the visual–task-relevant subgroup, a type of geometric shapes–geometric shapes that differed in size, form, color, and so forth; and (d) within the visual–task-irrelevant subgroup, a type of geometric shapes–geometric shapes. The most common type of response design was (a) within the auditory–task-relevant subgroup, a single-response design (no response to the standard); (b) within the auditory–task-irrelevant

TABLE I. A classification of oddball–standard pairs according to stimulus type and response design

Oddball–standard		Contrast subgroup			
		Auditory– task-relevant (<i>n</i> = 30)	Auditory– task-irrelevant (<i>n</i> = 18)	Visual– task-relevant (<i>n</i> = 24)	Visual– task-irrelevant (<i>n</i> = 18)
Stimulus type	Pure tones–pure tones	29	3	0	0
	Digital noises–pure tones	0	7	0	0
	Environmental sounds–pure tones	0	3	0	0
	Auditory syllables–auditory syllables	0	3	0	0
	Geometric shapes–geometric shapes	0	0	14	9
	Letters/ words–letters/ words	0	0	6	6
	Other	1	2	4	3
Response design	Response–no response	28	0	15	0
	Response–response	2	2	9	10
	No response–no response	0	16	0	8

subgroup, a nonresponse design (no responses to both the oddball and the standard); (c) within the visual–task-relevant subgroup, a single-response design; and (d) within the visual–task-irrelevant subgroup, a dual-response design (responses to both the oddball and the standard). The response modality was manual in 78.3% of the relevant studies and silent counting in 18.8%. The responding hand was right in 72.3% of the relevant studies, left in 2.1%, and bimanual or counterbalanced between the two hands in 25.6%. Although variations in stimulus types and response design/modality are of potential interest, the small number of studies in most categories precluded their analyses in this study. Given the prevalent use of a single-response design in the task-relevant subgroups, task-relevant oddball effects measure not only the activations from detecting and orienting to the oddball, but also those from responding to the oddball. As such, the possible confounding effect of motor responses is considered in the interpretation of relevant meta-analytic findings.

Data Analyses

Three sets of meta-analysis were performed. The first meta-analysis analyzed all selected contrasts together (*n* = 93), with the aim of determining the regions generally associated with oddball effects. To investigate the modulation of oddball effects by stimulus modality, the second set of meta-analysis involved separate meta-analysis of the auditory subgroup (*n* = 49) and the visual subgroup (*n* = 42) and a direct comparison between the two subgroups. The proportion of contrasts involving task-relevant oddball stimuli was 61.2% in the auditory subgroup and 57.1% in the visual subgroup, indicating that a comparison between the two subgroups was largely unbiased with respect to task-relevance type. To address the modulation of oddball effects by task-relevance type, the third, final set of meta-analysis involved separate meta-analysis of the task-relevant subgroup (*n* = 56) and the task-irrelevant subgroup

(*n* = 36) and a direct comparison between the two subgroups. The proportion of contrasts involving auditory oddball stimuli was 53.6% in the task-relevant subgroup and 50.0% in the task-irrelevant subgroup, indicating a minimal bias owing to stimulus modality in the comparison between the two subgroups.

The present subgroup meta-analyses emphasized the main effects by collapsing across some subgroups. Alternatively, one could emphasize simple effects by performing separate meta-analysis of each of the four subgroups (auditory–task-relevant, auditory–task-irrelevant, visual–task-relevant, and visual–task-irrelevant) and a series of paired subtraction analyses in a cell-by-cell format. The author chose to emphasize the main effects because (i) the main effects of the stimulus modality were largely unbiased with respect to possible confounding effects of the task-relevance type and vice versa, as described above, (ii) testing of the main effects gave better statistical power to detect subgroup differences, and (iii) analyses of the main effects provided a more compact “picture” of subgroup differences than multiple simple-effects analyses did.

Meta-Analysis Techniques

All meta-analyses were performed using the revised activation likelihood estimation (ALE) algorithm as described by Eickhoff et al. [2009] and implemented in GingerALE 2.2 software (www.brainmap.org). The aim of the algorithm is to determine brain regions showing above-chance convergence of activations across different independent studies. To this end, the algorithm models activation foci reported by individual studies as centers for 3D Gaussian probability distributions that reflect the spatial uncertainty associated with each focus. One of the major changes from the previous ALE algorithm is that the revised one tests for above-chance convergence between studies (i.e., random effects) rather than above-chance convergence between foci (i.e., fixed effects), thus

enabling generalization of the results beyond the studies included in the meta-analysis. Another major change is that the width of the Gaussian probability distributions is modeled based on the empirical estimates for the between-subject and between-template variance of the stereotaxic locations of local maxima [Eickhoff et al., 2009] rather than manually specified by the user. In this study, the meta-analysis involving all selected contrasts had the full-width half-maximum median value of 9.50 mm, with the maximum and minimum values of 11.38 and 8.58 mm, respectively. In both the original and the revised ALE method, one of the major limitations is that it models the center of activations across studies, disregarding the extent of activations.

The ALE algorithm was applied to the current meta-analyses according to the following steps. First, the spatial normalization space was determined for each study and all activation foci reported in Montreal Neurological Institute coordinates were converted into Talairach coordinates [Talairach and Tournoux, 1988] using the Lancaster transformation [Laird et al., 2010; Lancaster et al., 2007]. Second, the reported foci were modeled as peaks of a 3D Gaussian probability distribution which captured the associated uncertainty in spatial location. Third, the probabilities of all foci found in a given contrast were combined and then summed across analyzed studies to create an ALE map that estimated the activation likelihood for each voxel across the entire set of studies. Finally, to determine the statistical significance of the ALE map, ALE scores were compared to that expected under the null distribution, assuming a random spatial association among studies.

A comparison analysis between the two ALE results (i.e., subtraction meta-analysis) was performed using the revised subtraction algorithm as described by Eickhoff et al. [2011]. The revised subtraction algorithm also involves a random effects analysis and is largely robust against unequally large sets of studies involved in a comparison. The subtraction ALE algorithm was applied to the current meta-analysis according to the following steps. First, the two groups of studies contributing to each ALE map were pooled, randomly split into two sets of studies that had the same size as the original two groups of studies, and the difference in ALE scores between the two sets was calculated. Second, this process was repeated 5,000 times to estimate the null distribution of a chance difference. Finally, the “observed” difference in ALE scores was then compared to the null distribution of a chance difference to determine the associated statistical significance.

All statistical tests were thresholded with a false discovery rate value of $P < 0.05$ [Genovese et al., 2002] and clusters of suprathreshold voxels exceeding 400 mm^3 . To visualize the meta-analytic results, the thresholded ALE maps were projected onto an inflated population average landmark surface (PALS) using CARET software [Van Essen, 2005]. The boundaries of the dorsal and ventral attention networks as estimated by Yeo et al. [2011] were also projected onto the PALS as a flexible guide to evaluate whether an activation is located within or outside

TABLE II. Summary of significant activations from an ALE meta-analysis of all included studies

Classification	Region	Left	Right
Ventral attention	TPJ	+	+
	AI	+	+
	aMFG	+	+
	ACC/SMA	+	+
Dorsal attention	IFJ	+	+
	Medial IPS/SPL	+	+
	MT+	+	+
Auditory/visual	Transverse gyrus	+	+
	Superior temporal gyrus	+	+
	Lateral occipital cortex	+	+
	Lingual gyrus	+	+
Subcortical	Amygdala	+	+
	Putamen	+	+
	Thalamus	+	+
	Cerebellum	+	+
Other	Precentral gyrus	+	+
	Postcentral gyrus	+	+
	Lateral IPS/IPPL	+	+
	Posterior cingulate cortex	+	+

For abbreviations, see Figure 1. For more detailed listing of the ALE results, see Supporting Information Table S1.

of the networks. The thresholded maps were also overlaid onto an International Consortium for Brain Mapping template using MANGO software (<http://ric.uthscsa.edu/mango>), mainly to observe subcortical activation clusters not visible on the PALS.

RESULTS

All Included Studies

Table II and Figure 2 show the results of an ALE meta-analysis of all included oddball contrasts (for more detailed listing of the ALE results, see Supporting Information Table S1). The main results were as follows. First, the activation of ventral network regions was extensive, involving the TPJ, AI, aMFG, and ACC/SMA regions bilaterally. Except for the TPJ clusters, which were more extensive on the right- than left-hand side, other clusters were bilaterally more equal. Second, except for the IFJ, which was strongly activated bilaterally, the recruitment of other dorsal network components was modest, involving small anterior and posterior segments of the medial IPS, a small left MT+ region and no cluster involving the FEF. Third, sensory cortex activations involved the transverse/superior temporal gyri bilaterally and the bilateral lingual and left lateral occipital regions. Fourth, subcortical activations were observed in the putamen, thalamus, and amygdala bilaterally and in the left cerebellum. Finally, other activations included regions within the bilateral precentral gyrus, left postcentral gyrus, bilateral lateral IPS, and posterior cingulate cortex. The lateral IPS cluster on

Figure 2.

Brain regions associated with oddball effects (oddball > standard) in an ALE meta-analysis of all included contrasts. Green- and violet-colored borderlines mark estimates of the dorsal and ventral attention networks. The boundaries were drawn from Yeo et al. [2011]'s seven-network parcellation data in Caret PALS surface space that can be downloaded from the Surface Management System Database (SumsDB, <http://sumsdb.wustl.edu/sums>). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

the right-hand side extended ventrally into the anterior portion of the inferior parietal lobule (IPL).

Stimulus Modality Effects

Table III and Figures 3 and 4 show the results of separate ALE meta-analyses of auditory oddball effects, visual oddball effects, and a direct comparison between the two effects (for more detailed listing of the ALE results, see Supporting Information Table S2). The meta-analysis of auditory oddball effects mainly indicated the following (Fig. 3A). First, ventral network recruitment was extensive, involving the TPJ, AI, aMFG, and ACC/SMA regions bilaterally. As observed in the analysis of all included contrasts, the activation of the TPJ was predominantly right-sided. Second, dorsal network involvement was modest, involving only the bilateral IFJ and a small anterior segment of the left SPL. Third, sensory cortex activations involved an extensive range of the auditory cortex

bilaterally and a small segment of the medial visual cortex bilaterally. Finally, subcortical activations were largely comparable to those observed in the analysis of all included contrasts.

The meta-analysis of visual oddball effects mainly indicated the following (Fig. 3B). First, ventral network recruitment involved the TPJ, AI, and ACC/SMA regions bilaterally. The activation of the TPJ was again predominantly right-sided. Second, dorsal network activations included the bilateral IFJ, small anterior and posterior segments of the bilateral medial IPS, and portions of the left MT+. Third, sensory cortex activations included a range of the lateral occipital cortex bilaterally but no auditory cortex regions. Finally, subcortical activations were observed in the left putamen and thalamus.

A direct comparison between auditory and visual oddball effects yielded three main sets of findings (Fig. 4). First, the most pronounced differences involved sensory cortex regions, reflecting a stronger association of bilateral auditory cortex regions with auditory than visual oddball effects and a stronger association of bilateral lateral visual cortex regions with visual than auditory oddball effects. Second, dorsal network regions involving a small posterior segment of the left medial IPS and portions of the left MT+ were more strongly associated with visual than auditory oddball effects. Third, ventral network regions involving portions of the left TPJ and AI were more strongly associated with auditory than visual oddball effects. Finally, subcortical regions involving the right putamen, thalamus, and amygdala were also more strongly associated with auditory than visual oddball effects. Thus, some differential trends between the thresholded maps shown in Figure 3A,B did not survive the direct statistical comparison shown in Figure 4.

Task-Relevance Effects

Table IV and Figures 5 and 6 show the results of separate ALE meta-analyses of task-relevant oddball effects, task-irrelevant oddball effects, and a direct comparison between the two effects (for more detailed listing of the ALE results, see Supporting Information Table S3). The meta-analysis of task-relevant oddball effects yielded results that were largely comparable to those observed in the meta-analysis of all included contrasts (compare Figs. 2 and 5A).

The meta-analysis of task-irrelevant oddball effects yielded relatively weak convergence across studies and mainly indicated the following (Fig. 5B). First, ventral network involvement included portions of the TPJ, AI, and ACC/SMA bilaterally. Second, dorsal network recruitment involved the bilateral IFJ and small posterior segments of the bilateral medial IPS. Third, sensory cortex activations included the bilateral transverse/superior temporal gyri and a small left lateral occipital region. Finally, subcortical activations were observed in the right thalamus, bilateral amygdala, and left cerebellum.

TABLE III. Summary of significant activations from separate ALE meta-analyses of auditory and visual oddball effects and a direct comparison of the two effects

Classification	Region	Auditory		Visual		Auditory > visual		Visual > auditory	
		Left	Right	Left	Right	Left	Right	Left	Right
Ventral attention	TPJ	+	+	+	+	+			
	AI	+	+	+	+	+			
	aMFG	+	+						
	ACC/SMA	+	+	+	+				
Doral attention	IFJ	+	+	+	+				
	Medial IPS/SPL	+		+	+			+	
	MT+			+				+	
Auditory/visual	Transverse gyrus	+	+			+	+		
	Superior temporal gyrus	+	+			+	+		
	Lateral occipital cortex			+	+			+	+
	Lingual gyrus	+	+						
Subcortical	Amygdala	+	+				+		
	Putamen		+	+			+		
	Thalamus	+	+	+			+		
	Cerebellum	+	+						
Other	Precentral gyrus	+	+	+					
	Postcentral gyrus	+		+					
	Lateral IPS/IPL	+	+	+	+				
	Posterior cingulate cortex	+	+				+		

For abbreviations, see Figure 1. For more detailed listing of the ALE results, see Supporting Information Table S2.

A direct comparison between task-relevant and task-irrelevant oddball effects mainly indicated the following (Fig. 6). First, a relatively wide range of regions were more strongly associated with task-relevant than task-irrelevant oddball effects, including ventral network regions involving the TPJ, AI, aMFG, and ACC/SMA bilaterally, a small left SPL region and subcortical regions involving the left putamen, bilateral thalamus, and right cerebellum. Second, regions associated more strongly with task-irrelevant than task-relevant oddball effects were comparatively sparse, including only two minor clusters, one in the left superior temporal gyrus and the other in the right lateral IPS. Thus, even with controlled statistical power used in the direct subtraction analysis, an overall convergence of activations across studies was greater for task-relevant than task-irrelevant oddball effects.

DISCUSSION

The meta-analysis yielded three main sets of findings. First, ventral network regions were strongly associated with oddball effects, consistent with the hypothesis that the network detects salient, environmental changes. Second, except for the IFJ, which showed consistent activation in all oddball conditions, other dorsal network components showed no or only modest association with oddball effects, likely reflecting active involvement in both oddball and standard stimulus processing. Finally, prominent oddball effects outside the two networks included sensory

cortex regions, likely reflecting attentive and preattentive modulation of sensory activity, and selective subcortical regions, likely reflecting subcortical involvement in alerting responses. These three sets of findings are discussed in separate sections below.

The Ventral Network

An extensive range of ventral network regions, including the TPJ, AI, aMFG, and ACC/SMA bilaterally, was associated with oddball effects and largely common to auditory and visual modalities, supporting the hypothesis that the network is a modality-independent “alerting” system [Corbetta et al., 2008; Macaluso, 2010]. This result extends relevant findings in prior within-study comparisons of auditory and visual oddball tasks [Kiehl et al., 2001a; Linden et al., 1999; Stevens et al., 2000; Yoshiura et al., 1999] by integrating results across a large number of studies and relating widespread activity to a large-scale intrinsic network. Evidence from other prior studies [Chen et al., 2010; Downar et al., 2000; Macaluso et al., 2002] associated core ventral network components such as the TPJ with tactile oddball effects, further validating a supramodal “alerting” system. Despite a large overlap of auditory and visual oddball effects in the ventral network, small segments of the left TPJ and AI were more strongly associated with auditory than visual oddball effects. This finding may be attributable primarily to the auditory and visual stimuli used in prior studies. Many of the auditory,

Figure 3.

Brain regions associated with auditory oddball effects (**A**) and visual oddball effects (**B**). For an explanation of green- and violet-colored borderlines, see Figure 2. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

but not visual, studies used the same type of oddball–standard pair (pure tones–pure tones; Table I), likely increasing the chance of convergent findings across studies.

Most ventral network regions were also common to both task-relevant and task-irrelevant oddball effects. However, the strength and scope of this association was much greater for task-relevant oddball effects in most constituent regions, including the TPJ, AI, aMFG, and ACC/SMA bilaterally. Along with relevant findings in prior within-study comparisons of task-relevant and task-irrelevant oddball effects [Bledowski et al., 2004; Brázdil et al., 2005; Clark et al., 2000; Fichtenholtz et al., 2004; Linden et al., 1999; Menon et al., 1997; Stevens et al., 2000], this result supports the hypothesis that ventral network activity does not solely reflect stimulus saliency but rather a dynamic interplay of stimulus saliency and internal goals [Corbetta et al., 2008]. Other types of attention studies have also indicated that task-relevance is a critical factor in stimulus-driven engagement of the ventral network [Fockert et al., 2004; Indovina and Macaluso, 2007; Kincade et al., 2005; Serences et al., 2005]. For example, Serences et al. [2005] showed that distractors that shared a critical feature with targets evoked a greater response in TPJ and AI regions than did distractors that did not share a critical feature with targets, a phenomenon termed “contingent attentional capture.” An interplay of stimulus-driven (exogenous) and voluntary (endogenous) factors in driving the ventral network may enable the

system to respond selectively to behaviorally important stimuli [Corbetta et al., 2008].

The involvement of the TPJ component in oddball effects was more extensive on the right- than left-hand side. Although activations in other ventral network components were bilaterally more balanced, a right-sided TPJ activation was observed in both auditory and visual modalities and both task-relevant and task-irrelevant conditions. Along with numerous prior relevant findings [Corbetta et al., 2000; Petit et al., 2007; Shulman et al., 2010; Stevens et al., 2005], this finding indicates that the ventral network is predominantly lateralized to the right hemisphere. As discussed previously by other authors [Corbetta and Shulman, 2011], predominant right-lateralization of the parietal and other ventral network components may be the neuroanatomical basis for the well-known clinical observation that hemineglect syndrome is more frequent and severe following right than left hemisphere lesions.

An inherent limitation of an oddball effect contrast (oddball > standard) is that neural responses to oddball stimuli are nonindependently estimated from those to standard stimuli. Thus, a significant oddball effect cannot, by itself, distinguish between activation to oddball stimuli versus deactivation to standard stimuli. In a visual search study that was designed to separately estimate search- and detection-related signals [Shulman et al., 2003, 2007b], participants required to search for infrequent targets (digits) among a rapid serial visual presentation (RSVP) stream of

Figure 4.

Differential brain regions in a direct comparison of auditory versus visual oddball effects. For an explanation of green- and violet-colored borderlines, see Figure 2. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

distractors (letters). A critical finding of this study was that the TPJ, AI, and other regions showed not only activation to the detection of targets but also sustained deactivation during search. The authors proposed that the deactivation during search may function to suppress involuntary stimulus-driven reorienting to distracting sensory stimuli. Irrespective of the functional specificity of the deactivation, their finding suggests that the present oddball effects involving the TPJ and other ventral network regions likely reflect deactivation during a stream of standard stimuli as well as activation to the detection of targets.

The Dorsal Network

The bilateral IFJ was associated with oddball effects in both auditory and visual modalities and both task-relevant and task-irrelevant conditions, indicating a central role in attentional control associated with the detection of targets (oddballs). This consistent IFJ involvement was in a sharp contrast to other dorsal network components, which showed no or only modest association with oddball effects (see below). Brass et al. [2005] noted that the “IFJ is located at the junction of three functional neuroanatomical

domains, namely the premotor domain, the language domain, and the working memory domain” [p.316]. Based on this observation and activation of the IFJ in a broad spectrum of cognitive control tasks [Derrfuss et al., 2005; Owen et al., 2005; Wager et al., 2004], they proposed that the IFJ is involved in the maintenance and manipulation of “task representations,” which roughly refer to abstract description of stimulus–response rules. An application of this hypothesis may attribute the IFJ oddball effects to greater activations of task representations during oddball than standard stimulus processing. Other researchers emphasized the role of the IFJ in the functional interaction between the dorsal and the ventral networks by showing significant correlations of spontaneous activity in the IFJ with both networks [Fox et al., 2006] and convergence of goal-directed and stimulus-driven attention in the IFJ [Asplund et al., 2010]. Thus, the IFJ involvement may also reflect greater functional interaction between the two networks during oddball than standard stimulus processing.

Unlike the IFJ, other dorsal network components showed no or only modest association with oddball effects. Auditory oddball effects were confined to a small left SPL cluster, visual oddball effects were observed only in a few small clusters involving anterior and posterior subregions of the medial IPS and a small left MT+ cluster, and no cluster involving the FEF was detected in any analysis. As noted in the **Introduction** section, both standard and oddball stimulus processing involve externally focused attention, which likely tax the dorsal mechanism for orienting attention to the environment. Thus, the weak association of the dorsal network with oddball effects likely reflects “subtracting out” owing to strong involvement in both standard and oddball stimulus processing. Supporting this hypothesis, the aforementioned RSVP study [Shulman et al., 2003] indicated both search- and detection-related signals in FEF and IPS regions. Furthermore, a recent independent component analysis (ICA) of fMRI data obtained with a visual oddball task [Mantini et al., 2009] indicated that an ICA component that best matched the ventral network was transiently modulated by the presentation of oddball stimuli, whereas an ICA component that best matched the dorsal network showed more sustained activity throughout the task.

The weak association of the dorsal network with oddball effects may also be related to the fact that a large majority of the analyzed studies have defined the oddball by a feature that differs from the standard rather than by a different location. Although dorsal network regions are involved in the control of both spatial and nonspatial, feature-based attention [Giesbrecht et al., 2003; Liu et al., 2003; Serences et al., 2004; Shomstein and Yantis, 2006; Slagter et al., 2007; Smith et al., 2010], feature-based attentional control may involve *less* extensive subregions of the dorsal network than space-based attentional control does. In line with this hypothesis, several studies have described retinotopically organized responses in a large portion of

TABLE IV. Summary of significant activations from separate ALE meta-analyses of task-relevant and task-irrelevant oddball effects and a direct comparison of the two effects

Classification	Region	Task-relevant		Task-irrelevant		Task-relevant > task-irrelevant		Task-irrelevant > task-relevant	
		Left	Right	Left	Right	Left	Right	Left	Right
Ventral attention	TPJ	+	+	+	+	+	+		
	AI	+	+	+	+	+	+		
	aMFG	+	+			+	+		
	ACC/SMA	+	+	+	+	+	+		
Doral attention	IFJ	+	+	+	+				
	Medial IPS/SPL	+	+	+	+	+			
	MT+								
Auditory/visual	Transverse gyrus	+	+	+	+				+
	Superior temporal gyrus	+	+	+	+				+
	Lateral occipital cortex			+					
	Lingual gyrus	+	+						
Subcortical	Amygdala	+	+	+	+				
	Putamen	+	+			+			
	Thalamus	+	+		+	+	+		
	Cerebellum	+	+	+			+		
	Precentral gyrus	+	+			+			
Other	Postcentral gyrus	+				+			
	Lateral IPS/IPL		+	+	+				+
	Posterior cingulate cortex	+	+	+	+	+	+		

For abbreviations, see Figure 1. For more detailed listing of the ALE results, see Supporting Information Table S3.

dorsal network regions [Silver and Kastner, 2009], including greater responses to contralateral than ipsilateral “shift” cue [Shulman et al., 2010]. Furthermore, a study that directly compared spatial (location) and nonspatial orienting (color) indicated subregions of the dorsal network that were more active during spatial than nonspatial orienting, but no subregions that were more active during nonspatial than spatial orienting [Giesbrecht et al., 2003]. Finally, different feature-based attentions, such as color-, shape-, and direction-based, may involve separate subregions within the dorsal network [Liu et al., 2003; Serences et al., 2004; Shomstein and Yantis, 2006], making it difficult to detect them in a meta-analysis unless a large number of procedurally similar studies are analyzed.

The subregions of the medial IPS, SPL, and MT+ which showed significant oddball effects may play a role in shifting feature-based attention. Some of these regions were also associated with significant effects of stimulus modality or task-relevance type. A posterior segment of left medial IPS and an MT+ region was more strongly associated with visual than auditory oddball effects, indicating that posterior margins of the dorsal network are mainly involved in control of visual attention. A subregion of the left SPL was more strongly associated with task-relevant than task-irrelevant oddball effects, indicating that this region is sensitive to a joint contribution of endogenous and stimulus-driven factors.

Other Regions

Prominent oddball effects outside the two attention networks were observed mainly in four broad areas: sensory cortex, subcortical regions, lateral IPS/IPL regions, and precentral and postcentral gyrus. First, oddball effects involving sensory cortex regions were largely modality specific, mainly involving portions of the bilateral transverse/superior temporal cortex in auditory tasks and parts of the bilateral lateral occipital cortex in visual tasks. These effects likely reflect attentive modulation of early sensory activity via the dorsal network [Bressler et al., 2008; Kastner and Ungerleider, 2000] as well as preattentive, automatic signals from sensory regions to deviant stimuli [Näätänen et al., 2007]. A segment of the left auditory cortex was more strongly associated with task-irrelevant than task-relevant oddball effects. This finding may be attributable primarily to the auditory oddball stimuli used in prior studies. Oddball stimuli may be differentiated based on whether they are categorically different from the standard (e.g., environmental sounds–pure tones) or fall into the same stimulus category (e.g., pure tones–pure tones). Auditory oddball stimuli that were categorically different from the standard were more frequently used in a task-irrelevant than a task-relevant condition (Table I), likely promoting greater modulation of auditory cortex activity by task-irrelevant oddball stimuli.

Figure 5.

Brain regions associated with task-relevant oddball effects **(A)** and task-irrelevant oddball effects **(B)**. For an explanation of green- and violet-colored borderlines, see Figure 2. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Second, subcortical oddball effects were observed in the putamen, thalamus, amygdala, and cerebellum. Each of these four regions was associated with oddball effects in at least three out of the four subgroup meta-analyses, indicating a relatively stable contribution. Several research groups [Menon and Uddin, 2010; Raz and Buhle, 2006; Seeley et al., 2007; Shulman et al., 2009; Zink et al., 2003] have highlighted the sensitivity of selective subcortical regions, including the stratum, thalamus, amygdala, cerebellum, and midbrain area, to salient events, indicating that an “extended” ventral alerting system may include selective subcortical regions. For example, Seeley et al. [2007] identified a “salience network” anchored by frontoinsula and anterior cingulate cortices with robust linkage to several subcortical and limbic structures. Although specific subcortical alerting functions remain largely uncertain, they are likely associated with, but not identical to, specific cortical alerting functions [Corbetta et al., 2008; Zink et al., 2003]. The putamen, thalamus, and cerebellum regions were also associated more strongly with task-relevant than task-irrelevant oddball effects, indicating that task-relevance modulates stimulus-driven engagement of these regions. Alternatively, the task-relevance effect may reflect a motor response (e.g., key pressing) associated with the detection of task-relevant, but not task-irrelevant, oddball stimuli.

Third, oddball effects involving the lateral IPS were observed in all subgroup analyses. Although many of these activations were not clearly demarcated from medial IPS activations, making it difficult to determine their

origin, some of them extended ventrally into the IPL, more clearly indicating an origin outside of the dorsal network. According to recent functional connectivity analyses [Vincent et al., 2008; Yeo et al., 2011], the lateral IPS/IPL region is a component of a frontoparietal “cognitive-control” network (Fig. 1, orange regions). Based on this finding and a likely assumption that participants in an oddball test expect to see standard items rather than oddball items, the oddball effects involving the lateral IPS/IPL may reflect control operations to countermand the expectation that items should be standard ones. Broadly consistent with this hypothesis, a recent study using a memory analog of the Posner precuing paradigm [O’Connor et al., 2010] indicated that an IPL region tracked “expectancy violation” (invalid cueing > valid cueing).

Finally, regions involving the pre- and postcentral gyrus were associated with oddball effects. These activations were more prominent on the left- than right-hand side and more strongly associated with task-relevant than task-irrelevant oddball effects, indicating that they largely relate to a right-handed motor response to task-relevant oddball stimuli. The activation of the postcentral gyrus likely reflects the somatosensory process of the motor response [Linden et al., 1999].

Other Attention Network Models

Although influential, Corbetta and Shulman’s model [2002] is certainly not the only available attention network

Figure 6.

Differential brain regions in a direct comparison of task-relevant versus task-irrelevant oddball effects. The inset shows an activation cluster located on the “inside” surface of the right TPJ. For an explanation of green- and violet-colored borderlines, see Figure 2. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

scheme. Thus, in this section, two other attention network schemes are considered in relation to the results of this meta-analysis. The first scheme originates from the seminal work of Posner and proposes three attention networks: alerting, orienting, and executive [Fan et al., 2005; Raz and Buhle, 2006]. Although there is no one-to-one direct correspondence, the alerting and orienting networks are relatively similar to the ventral and dorsal attention networks in terms of both anatomy and function. However, one of the major divergences involves the anterior cingulate cortex: in the three-networks scheme, the region is a central component of the executive network, mediating conflict detection/modulation, but in Corbetta and Shulman’s scheme, it is a member of the ventral alerting network. Thus, according to the three-networks view, the oddball effects in the region may reflect conflict-related factors than stimulus saliency per se. This alternative explanation is well worth investigating, given prominent activations of the region in conflict tasks such as the classic Stroop task [Carter and Van Veen, 2007; Laird et al., 2005].

The second scheme [Calhoun et al., 2006] results from a joint application of spatial ICA of fMRI data and temporal ICA of ERP data both obtained during an auditory oddball task. This study indicated six spatiotemporal components that jointly described oddball networks. The combined spatial topography of the six components was relatively similar to that observed in the auditory subgroup analysis of this study. However, the ICA decomposition suggested a different network scheme from Corbetta and Shulman’s model: for example, the early portion of the P300 component (P3a) was associated mainly with fMRI activity in thalamic and posterior SPL regions, whereas the late portion (P3b) was associated mainly with fMRI activity in TPJ, SMA, and cerebellar regions. This divergence is perhaps not surprising, given that the notion of “network independence” is not a core feature of Corbetta and Shulman’s model. Although not easy to reconcile with Corbetta and Shulman’s scheme, the ICA and other related results [Calhoun et al., 2008] highlight the fact that there is not one, but multiple ways of fractioning oddball networks.

CONCLUSIONS

This study provides the first, comprehensive meta-analysis of the neuroimaging literature regarding oddball effects, with special reference to the dorsal and ventral attention networks. An application of the two attention networks model to oddball paradigms predicts that the dorsal network is strongly involved in both standard and oddball stimulus processing, whereas the ventral network is more strongly involved in oddball than standard stimulus processing. Consistent with this prediction, the meta-analysis indicated a strong association of ventral network regions but no or only modest association of dorsal network regions with oddball effects. In terms of componential differentiation, the meta-analysis was most informative about the IFJ, an anterior core of the dorsal network. In a sharp contrast to other dorsal network components, the bilateral IFJ was associated with oddball effects in all four subgroup analyses, indicating a central role in top-down attentional control. Prominent oddball effects outside the two networks included the sensory cortex regions, likely reflecting attentive and preattentive modulation of early sensory activity, and selective subcortical regions involving the putamen, thalamus and other areas, likely reflecting subcortical involvement in alerting responses. Taken together, these and other related findings clarify the roles of the dorsal and ventral attention networks and other regions in detecting and orienting toward salient, environmental changes. More generally, the findings support the notion that many activations observed in neuroimaging studies are components of intrinsic, large-scale networks that respond in concert rather than regions activated in isolation.

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APPENDIX. Details of Individual Studies Included in the Meta-Analysis

References	Imaging modality	Subjects	Stimulus modality	Oddball type	Foci	Standard stimulus	Oddball stimulus
Allen et al. [2009]	fMRI	40	Visual	Task-relevant	54	A light-blinking green	A light-blinking red
Bhattacharyya et al. [2012]	fMRI	15	Visual	Task-irrelevant	21	Horizontal arrows	Slightly slanted arrows
Bledowski et al. [2004]	fMRI	13	Visual	Task-relevant	17	A 1.53° circle (or 1.36° square)	A 1.38° circle (or 1.21° square)
			Visual	Task-irrelevant	21	A 1.53° circle (or 1.36° square)	A 1.36° square (or 1.53° circle)
Braver et al. [2001]	fMRI	14	Visual	Task-relevant	9	The letter "X"	non-"X"
Brázdil et al. [2005]	fMRI	8	Auditory	Task-relevant	16	A 1-kHz tone	A 2-kHz tone
Brázdil et al. [2007]	fMRI	20	Visual	Task-relevant	25	A string of characters "OOOO"	A string of characters "XXXX"
Bryant et al. [2005]	fMRI	14	Auditory	Task-relevant	11	A 0.5-kHz tone	A 1-kHz tone
Bunzeck et al. [2007]	fMRI	21	Visual	Task-irrelevant	40	Face A/Scene A	Face B/Scene B
Chen et al. [2008]	fMRI	9	Tactile	Task-relevant	16	Stimuli delivered to the ulnar nerve	Stimuli delivered to the median nerve
Chen et al. [2010]	fMRI	13	Tactile	Task-relevant	13	Stimuli delivered to the ulnar nerve	Stimuli delivered to the median nerve
Clark et al. [2000]	fMRI	6	Visual	Task-relevant	11	The letter "T"	The letter "X"
Clark [2002]	fMRI	17	Visual	Task-relevant	44	The letter "I"	The letter "X"
			Visual	Task-irrelevant	23	The letter "I"	The letter "C"
Czisch et al. [2012]	fMRI	14	Auditory	Task-relevant	4	A 1-kHz tone	A 1.5-kHz tone
Dichter et al. [2009]	fMRI	15	Visual	Task-relevant	8	Neutral/sad images	A bullseye
Diukova et al. [2012]	fMRI	14	Auditory	Task-relevant	34	A 1-kHz tone	A 1.5-kHz tone
			Auditory	Task-irrelevant	14	A 1-kHz tone	Noises
Fichtenholtz et al. [2004]	fMRI	22	Visual	Task-relevant	8	Squares	Circles/aversive scenes
Friedman et al. [2009]	fMRI	15	Auditory	Task-relevant	35	A 0.5 (or 0.35) kHz tone	A 0.35 (or 0.5) kHz tone
			Auditory	Task-irrelevant	10	A 0.5 (or 0.35) kHz tone	Environmental sounds
Fukami et al. [2004]	fMRI	8	Visual	Task-relevant	17	A square	A triangle
Gur et al. [2007a]	fMRI	28	Visual	Task-relevant	22	An arrangement of red elements	An arrangement of green elements
			Visual	Task-irrelevant	16	An arrangement of red elements	Fractal images
Habermeyer et al. [2009]	fMRI	16	Auditory	Task-irrelevant	8	Five-tone melodies "ABCD"	Five-tone melodies "ABCD"
Holecova et al. [2008]	PET	10	Auditory	Task-irrelevant	13	A 0.8-kHz tone	Subject's own name
Horn et al. [2003]	fMRI	15	Auditory	Task-relevant	14	A 4-kHz tone	A 1-kHz tone
Horowitz et al. [2002]	fMRI	7	Auditory	Task-relevant	9	A 1-kHz tone	A 1.5-kHz tone
Huetzel et al. [2004]	fMRI	14	Visual	Task-relevant	12	A square	A circle
Juckel et al. [2012]	fMRI	32	Auditory	Task-relevant	11	A 0.8-kHz tone	A 1.3-kHz tone
Kang et al. [1999]	fMRI	14	Visual	Task-irrelevant	5	Normal verbal phrases	Anomalous verbal phrases
Khullar et al. [2011]	fMRI	28	Auditory	Task-relevant	12	A 0.5-kHz tone	A 1-kHz tone
Kiehl et al., 2001a	fMRI	10	Visual	Task-relevant	36	A large square	A small square
			Visual	Task-irrelevant	28	A large square	Geometric shapes

APPENDIX . Continued

References	Imaging modality	Subjects	Stimulus modality	Oddball type	Foci	Standard stimulus	Oddball stimulus
Kielhl et al. [2001b]	fMRI	10	Auditory	Task-relevant	35	A 1-kHz tone	A 1.5-kHz tone
Kiehl et al. [2005a]	fMRI	18	Auditory	Task-irrelevant	24	A 1-kHz tone	Digital noises
			Auditory	Task-relevant	38	A 0.5-kHz tone	A 1-kHz tone
			Auditory	Task-irrelevant	33	A 0.5-kHz tone	Digital noises
Kielhl et al. [2005b]	fMRI	100	Auditory	Task-relevant	38	A 1-kHz tone	A 1.5-kHz tone
			Auditory	Task-irrelevant	33	A 1-kHz tone	Digital noises
Krugger et al. [2001]	fMRI	12	Visual	Task-relevant	7	Non-Kaniza square images	A Kaniza square image
Lagopoulos et al. [2006]	fMRI	6	Auditory	Task-relevant	7	A 1-kHz tone	A 1.5-kHz tone
			Auditory	Task-irrelevant	6	A /deh/, /day/, or /teh/ sound	A /day/, /deh/, or /tay/ sound
Laurens et al. [2005]	fMRI	28	Auditory	Task-irrelevant	29	A 1-kHz tone	Digital noises
			Visual	Task-irrelevant	3	Horizontal arrows	Slightly slanted arrows
			Visual	Task-relevant	12	Landolt rings	A Landolt ring pointing to the left
Liddle et al. [2006]	fMRI	28	Auditory	Task-relevant	31	A 1-kHz tone	A 1.5-kHz tone
Linden et al. [1999]	fMRI	5	Auditory	Task-relevant	8	A 1-kHz tone	A 2-kHz tone
			Visual	Task-relevant	8	A large angle	A small angle
Mantini et al. [2009]	fMRI	13	Visual	Task-relevant	22	A yellow disk	A blue disk
Marois et al. [2000]	fMRI	14	Visual	Task-relevant	19	A "standard" object	Changes in object identity/location
Melcher and Gruber [2006]	fMRI	9	Visual	Task-irrelevant	16	Blue or yellow colored words	Red colored words
Melcher et al. [2011]	fMRI	14	Visual	Task-irrelevant	5	The word "ROUND"	Twelve different words
Menon et al. [1997]	fMRI	11	Auditory	Task-relevant	6	A 1-kHz tone	A 2-kHz tone
Milham et al. [2003]	fMRI	16	Visual	Task-irrelevant	16	Color unrelated words	Color or semantically related words
Mulert et al. [2004]	fMRI	9	Auditory	Task-relevant	17	A 0.8-kHz tone	A 1.3-kHz tone
Müller et al. [2003]	fMRI	16	Auditory	Task-relevant	45	A 1-kHz tone	A 0.5-kHz tone
Nagan et al. [2003]	fMRI	14	Auditory	Task-relevant	6	A 1-kHz tone	Speech sounds
			Visual	Task-relevant	8	A 3.5-cm diameter circle	A 4-cm diameter circle
O'Connell et al. [2012]	fMRI	29	Visual	Task-irrelevant	1	A 3.5-cm diameter circle	A black and white checkerboard
Opitz et al. [1999a]	fMRI	16	Auditory	Task-relevant	4	A tone	An "oddball" tone in the attended condition
			Auditory	Task-irrelevant	2	A tone	An "oddball" tone in the unattended condition
Opitz et al. [1999b]	fMRI	14	Auditory	Task-irrelevant	4	A pure tone	Environmental sounds
Opitz et al. [2005]	fMRI	16	Auditory	Task-irrelevant	4	A 0.33-kHz tone	A 0.30-kHz tone
			Auditory	Task-relevant	46	A 1-kHz tone	A 2-kHz tone delivered to the attended ear
Petit et al. [2007]	fMRI	8	Auditory	Task-irrelevant	24	A 1-kHz tone	A 2-kHz tone delivered to the unattended ear

APPENDIX . Continued

References	Imaging modality	Subjects	Stimulus modality	Oddball type	Foci	Standard stimulus	Oddball stimulus
Rubia et al. [2007]	fMRI	18	Visual	Task-irrelevant	5	Horizontal arrows	Slightly slanted arrows
Rubia et al. [2010]	fMRI	63	Visual	Task-irrelevant	8	Horizontal arrows	Slightly slanted arrows
Sabri et al. [in press]	fMRI	17	Auditory	Task-relevant	11	A 1-kHz tone	A frequency deviance from the standard
Schock et al. [2012]	fMRI	20	Auditory	Task-irrelevant	7	A /ba/ sound	A /pa/ or /ga/ sound
Schofield et al. [2009]	fMRI	37	Auditory	Task-relevant	9	A 0.5-kHz tone	A 1-kHz tone
Shityrov et al. [2008]	fMRI	11	Auditory	Task-irrelevant	6	CVC pseudowords	CVC words
Stevens et al. [2000]	fMRI	10	Auditory	Task-relevant	23	A 0.63-kHz tone	A 0.81-kHz tone
			Visual	Task-relevant	20	A string of characters "OOO"	A string of characters "XXX"
Stevens et al. [2006]	fMRI	20	Auditory	Task-relevant	34	A 1-kHz tone	A 1.5-kHz tone
Stevens et al. [2007]	fMRI	23	Auditory	Task-relevant	36	A 1-kHz tone	A 1.5-kHz tone
			Auditory	Task-irrelevant	24	A 1-kHz tone	Digital noises
Strange et al. [2000]	fMRI	12	Visual	Task-irrelevant	3	Neutral words	Deviant words
Strobel et al. [2008]	fMRI	14	Auditory	Mixed	41	A standard tone	Novel tone/environmental sounds
Tamm et al. [2006]	fMRI	12	Visual	Task-relevant	7	A circle	A triangle
Vossel et al. [2008]	fMRI	20	Visual	Task-irrelevant	8	A grating with a specific color and orientation	Gratings other than the standard
Warbrick et al. [2011]	fMRI	39	Visual	Task-relevant	37	A black and white checkerboard	A reversal of the checkerboard pattern
Warbrick et al. [2012]	fMRI	19	Visual	Task-relevant	7	A black and white checkerboard	A reversal of the checkerboard pattern
Wessell et al. [2012]	fMRI	19	Visual	Task-irrelevant	47	A triangle	Common objects
Williams et al. [2007]	fMRI	16	Auditory	Task-relevant	9	A 0.5-kHz tone	A 1-kHz tone
Winterer et al. [2007]	fMRI	47	Visual	Task-relevant	10	A black and white checkerboard	A reversal of the checkerboard pattern
Witt et al. [2010]	fMRI	31	Auditory	Task-relevant	28	A 1-kHz tone	A 1.5-kHz tone
			Auditory	Task-irrelevant	5	A 1-kHz tone	Digital noises
Wolf et al. [2008]	fMRI	21	Auditory	Task-relevant	27	A 1-kHz tone	A 2-kHz tone
			Auditory	Task-irrelevant	22	A 1-kHz tone	Environmental sounds
Yomogida et al. [2010]	fMRI	24	Visual	Task-irrelevant	27	A character jumping in one direction	A character jumping in the other direction
Yoshiura et al. [1999]	fMRI	13	Auditory	Task-relevant	28	A 1-kHz tone	A 2-kHz tone
			Visual	Task-relevant	28	A string of characters "OOO"	A string of characters "XXX"