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Modality-Specific Perceptual Expectations Selectively Modulate Baseline Activity in Auditory, Somatosensory, and Visual Cortices

Robert Langner[1,2,3], Thilo Kellermann[1,4], Frank Boers[3], Walter Sturm[2], Klaus Willmes[2] and Simon B. Eickhoff[1,3,4]

[1]Department of Psychiatry, Psychotherapy and Psychosomatics, and [2]Neuropsychology Section, Department of Neurology, Medical School, RWTH Aachen University, 52074 Aachen, Germany, [3]Institute of Neuroscience and Medicine (INM-2, INM-4), Research Centre Jülich, 52425 Jülich, Germany and [4]JARA - Translational Brain Medicine, Germany

Address correspondence to Dr Robert Langner, Klinik fuer Psychiatrie, Psychotherapie und Psychosomatik, Universitaetsklinikum Aachen, Pauwelsstrasse 30, 52074 Aachen, Germany. Email: robert.langner@rwth-aachen.de.

Valid expectations are known to improve target detection, but the preparatory attentional mechanisms underlying this perceptual facilitation remain an open issue. Using functional magnetic resonance imaging, we show here that expecting auditory, tactile, or visual targets, in the absence of stimulation, selectively increased baseline activity in corresponding sensory cortices and decreased activity in irrelevant ones. Regardless of sensory modality, expectancy activated bilateral premotor and posterior parietal areas, supplementary motor area as well as right anterior insula and right middle frontal gyrus. The bilateral putamen was sensitive to the modality specificity of expectations during the unexpected omission of targets. Thus, across modalities, detection improvement arising from selectively directing attention to a sensory modality appears mediated through transient changes in pretarget activity. This flexible advance modulation of baseline activity in sensory cortices resolves ambiguities among previous studies unable to discriminate modality-specific preparatory activity from attentional modulation of stimulus processing. Our results agree with predictive-coding models, which suggest that these expectancy-related changes reflect top-down biases—presumably originating from the observed supramodal frontoparietal network—that modulate signal-detection sensitivity by differentially modifying background activity (i.e., noise level) in different input channels. The putamen appears to code omission-related Bayesian "surprise" that depends on the specificity of predictions.

Keywords: fMRI, intermodal attention, multimodal stimulus anticipation, predictive coding, surprise

Introduction

Valid expectations improve performance in speeded reaction tasks, presumably by top-down modulation of perceptual, central, and motor processes starting before the target event occurs (Brunia and van Boxtel 2001; Hackley 2009; Rolke and Ulrich 2010). The preparatory facilitation of perceptual processing (Correa et al. 2005; Bausenhart et al. 2007) is hypothesized to result from supramodal attentional control signals that establish a bias in the competition between concurrent sensory inputs in favor of expected information (Desimone and Duncan 1995), either voluntarily (endogenously, "top-down") or automatically (exogenously, "bottom-up") (Beck and Kastner 2009). Apart from well-known beneficial effects of location-, time-, or feature-based attentional biases, performance gains have also been shown to arise from advance information on the relevant sensory channel (e.g., Spence and Driver 1997). Here, we investigated neural correlates of voluntary attentional biases toward the sensory modality of an expected target in the absence of stimulation.

Modality-selective attentional modulations of sensory processing have previously been investigated in tasks requiring the selection of one sensory modality versus another during multimodal stimulation (i.e., intersensory selective attention). For instance, electrophysiological recordings in monkeys revealed selective modulation of activity in areas V1, V2, and V4 while attending to visual stimuli and ignoring auditory ones (Mehta et al. 2000). In a pioneering positron emission tomography (PET) study in humans, Roland (1982) showed that during simultaneous auditory, tactile, and visual stimulation, attention to one modality selectively enhanced activity in sensory areas that process stimuli of the to-be-attended modality, with the exception of somatosensory cortex. Later neuroimaging studies, using bimodal visuoauditory or visuotactile stimulation, corroborated these early findings but also found attentional modulations in somatosensory areas (Kawashima et al. 1999; Macaluso et al. 2002; Shomstein and Yantis 2004). Analogously, studies using electroencephalography (EEG) reported modality-selective attentional modulation of sustained steady-state responses (Saupe et al. 2009) and of early perceptual components of electrocortical activity (Eimer and Schröger 1998; Teder-Sälejärvi et al. 1999; Foxe and Simpson 2005; Karns and Knight 2009).

Attention-induced modulations of brain activity during stimulus processing, however, only provide indirect evidence for the neural basis of attentional biases in perception. In particular, these modulations (i.e., the difference between attended and nonattended stimulus processing) may be driven by unknown overadditive or underadditive interactions between attention- and stimulation-related signals, making it hard to isolate purely attentional effects. More direct evidence for neural correlates of attentional biasing comes from studies investigating attention-induced increases in baseline activity in the absence of actual sensory stimulation (cf. Beck and Kastner 2009). For instance, single-cell recordings in monkeys during visual attention revealed significantly increased spontaneous (baseline) firing rates for neurons in ventral-stream areas V2v and V4 when the animal covertly attended to a location within the neuron's receptive field before stimulus presentation (Luck et al. 1997). A similar effect was shown in the lateral intraparietal sulcus (IPS) as part of the dorsal visual stream (Colby et al. 1996). Moreover, several studies using functional magnetic resonance imaging (fMRI) in humans showed that within-modality allocation of attention to the location or a specific feature of a visual stimulus induces increased baseline activity in relevant areas of visual cortex (Chawla et al. 1999;

Kastner et al. 1999; Giesbrecht et al. 2006; Sylvester et al. 2007; Smith et al. 2010). Analogous results have been reported for auditory spatial attention (Wu et al. 2007; Smith et al. 2010). Findings from the tactile domain are equivocal: an early PET study on neural correlates of anticipating touch only found reduced blood flow in somatosensory areas representing nontarget body zones (Drevets et al. 1995), whereas a later fMRI study reported both increased activity in task-relevant somatosensory areas and decreased activity in task-irrelevant ones (Carlsson et al. 2000).

In contrast to preparatory within-modality attention, there is a surprising dearth of evidence for the neural correlates of preparatory between-modality attention, that is, directing attention to a specific sensory channel in the absence of stimulation. Using EEG, Brunia and van Boxtel (2004) reported selectively enhanced preparatory activity (as indicated by an increased slow cortical negativity prior to stimulus onset) over frontal or occipital areas when anticipating auditory or visual feedback stimuli, respectively. Another EEG study (Foxe et al. 2005), using trial-by-trial cueing of the upcoming target modality, demonstrated a larger negativity over left frontocentral regions when expecting auditory targets and a larger positivity over right parietooccipital regions when expecting visual targets. In a pioneering fMRI study on the endogenous orienting of visual and tactile spatial attention, Macaluso et al. (2003) found spatially selective but no modality-selective transient preparatory increases in baseline activity. According to the authors' reasoning, the blocked presentation of stimuli of a given modality might have prevented the establishment of transient modality-specific increases in baseline activity over persistent sustained modulations. A more recent event-related fMRI study using auditory and visual targets (Mozolic et al. 2008) reported deactivations in irrelevant sensory cortices but did not find increased baseline activity in relevant cortices when attention was directed to either modality. This lack of baseline increases is at odds with the above-mentioned baseline increases during within-modality expectations in human and nonhuman primates as well as with the results of human EEG studies on between-modality preparatory attention.

In light of these sparse and inconsistent findings on the neural mechanisms underlying modality-specific perceptual expectations, we aimed to answer the following questions:

1. Does modality-selective preparatory attention transiently increase baseline activity in task-relevant sensory cortices, decrease activity in task-irrelevant ones, or both? And, is there a consistent pattern to be found across different modalities?
2. Which areas are activated supramodally (i.e., across modalities) during modality-specific expectations, potentially controlling top-down attention and motor preparation?
3. Are differential neural "surprise" responses induced by the absence of stimulation under specific versus nonspecific expectancy conditions? If so, are they represented in the basal ganglia (cf. den Ouden et al. 2009)?

These questions were tackled using event-related fMRI to measure changes in baseline activity evoked by cue-induced expectations of auditory, vibrotactile, or visual targets in a speeded detection task. To isolate pure expectancy effects, analysis of brain activity was restricted to those trials where the modality cue was not followed by any target ("cue-only trials").

Materials and Methods

Participants

Twenty-four (10 females) healthy right-handed volunteers (mean age = 24.1 years, standard deviation = 3.5) were recruited via advertisements and paid for their participation in the experiment. The study was approved by the ethics committee of the RWTH Aachen University Hospital, and all participants gave written informed consent before entering the study.

Task and Stimuli

In all experimental conditions, the task was to respond as fast as possible to an auditory, tactile, or visual imperative stimulus by a button press with the right-hand index finger. Using a simple reaction-time (RT) task prevented potential confounds from differential response-preparation processes (cf. Hahn et al. 2006). Modality-specific expectancies were evoked by announcing the upcoming target's modality via a symbolic visual cue. The cueing stimulus consisted of a centrally presented white grid (width 5.42° × height 5.73° visual angle) with a left and right column, each containing 3 rows (Fig. 1). These rows were associated with an eye, hand, or ear symbol, respectively, whose appearance indicated the corresponding modality of the upcoming target. The cue indicated either 1, 2, or all 3 modalities at a time, thus being either highly, moderately, or not predictive for target modality. This report, however, is only concerned with the highly predictable and completely unpredictable (i.e., uninformative) conditions. The validity of predictive cues was 75% (i.e., 25% predicted the wrong modality).

The 2 grid columns (left and right), in which the modality symbols appeared, indicated the upcoming stimulus presentation side. This explicit spatial cueing was specifically introduced to actively control the participants' engagement in endogenous spatial orienting. This way we sought to equate the allocation of top-down spatial attention across modalities, which might otherwise be uncontrollably influenced by differential modality-specific tendencies to use the expected locus of stimulus presentation (ear, hand, eye) as an implicit spatial cue. Symbols could appear in either column or both simultaneously, thus creating predictable (left or right) and unpredictable (i.e., uninformative) conditions with respect to the upcoming target's laterality. Left and right spatial cues were always valid.

The auditory imperative stimulus was a 1000-Hz sine tone (70 dB), presented via noise-shielded headphones to either the left or right ear. The tactile imperative stimulus was a vibration generated by the repeated 1-mm extension of 8 blunt plastic rods (each generating a force of about 5 mN) from piezoelectric Braille stimulators strapped to the inner side of the upper phalanx of either ring finger. The visual imperative stimulus consisted of a white square (5.73° visual angle),

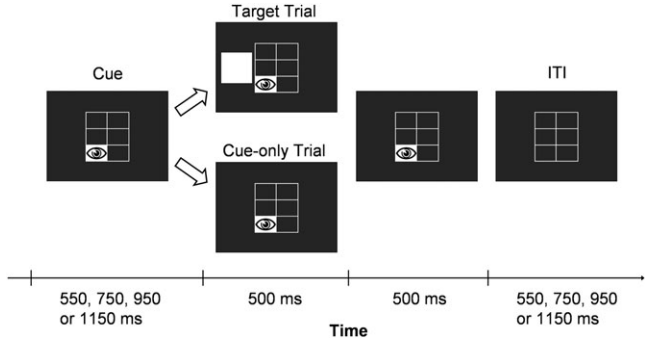

Figure 1. Temporal trial structure. The majority of trials (ca. 70%) contained targets ("target trials"), the remaining trials did not ("cue-only trials"). The example shows the course of a target and a cue-only trial with predictive cue (the eye symbol) for a visual target (the white square). Expectations of tactile or auditory targets were evoked via hand or ear symbols, respectively. All targets were to be responded to as fast as possible via a button press with the right index finger. Both the cue–target onset asynchrony and the ITI ranged between 550 and 1150 ms, such that the total length of trial plus ITI always was 2700 ms.

presented via MRI-compatible goggles to the left or right of the central cueing stimulus (distance between the cue's and either square's center: 7.63° visual angle). Since by their nature, vibrotactile stimuli can only be presented in a cyclic on/off fashion, all imperative stimuli were presented for 500 ms with a frequency of 10 Hz (five 50-ms-on/50-ms-off cycles each) to maximize comparability among modalities.

Procedure and Design

The experiment was run on a standard PC using Presentation 10.0 (Neurobehavioral Systems, Inc.). The structure and timing of a trial is shown in Figure 1. Target onset followed cue onset with a variable, equiprobable delay of 550, 750, 950, or 1150 ms. This temporal unpredictability required participants to continuously pay attention to stimulus modality and location while anticipating the target. The cue remained present during the imperative stimulus and for another 500 ms afterward. It disappeared, with only the empty grid remaining, during the subsequent intertrial interval (ITI), which varied in length from 550 to 1150 ms such that the total trial-plus-ITI duration always was 2700 ms.

The task was presented in 7 separate 4.7-min runs, each containing 72 experimental trials and 36 null-event trials (i.e., baseline periods with only the grid present). Of the 72 experimental trials per run, 21 (i.e., about 30%) were cue-only trials, in which no target was presented after the cue. In each run, the modality cue was highly predictive (i.e., unimodal) on 33 trials, moderately predictive (i.e., bimodal) on 30 trials, and uninformative (i.e., trimodal) on 9 trials. Within the first 2 categories, the 3 modalities were cued equally often. Thus, in each run, there were 3 cue-only trials per modality with highly predictive cues and 3 cue-only trials with uninformative cues. On invalid or uninformative target trials, target modality was distributed equally. Left, right, and uninformative spatial cues were equally distributed among all experimental trials. The order of trial types was pseudorandomized within each run.

Participants were instructed to pay attention to the cue and use it to prepare themselves, even when the cue sometimes was misleading (i.e., in trials with invalidly cued modality) or not followed by a target at all (i.e., in cue-only trials). After instruction, participants were familiarized with the task during a practice block.

fMRI Data Acquisition

Brain imaging data were obtained with a 3-T MRI scanner (Philips Achieva, Philips Medical Systems) with a SENSE head coil. Participants lay supine in the scanner, their heads immobilized with cushions to minimize movements. Blood oxygenation level–dependent signals were acquired using echo-planar imaging (EPI) covering the whole brain in 28 transverse slices parallel to the AC/PC line (echo time = 32 ms, repetition time = 2.0 s, flip angle = 80°, SENSE factor = 1.3, matrix size = 64 × 74, field of view = 192 × 228 mm^2, voxel size = 3 × 3 × 3.6 mm^3, 0.8-mm gap between slices, interleaved slice acquisition). During each run, 133 volumes were acquired, preceded by 7 dummy scans.

fMRI Data Analysis

Data were analyzed with SPM5 (Wellcome Department of Imaging Neuroscience) implemented in Matlab 7.2 (The MathWorks, Inc.). After discarding the dummy scans, EPI images were corrected for head movement by affine registration using a 2-pass procedure by which images were initially realigned to the first image and subsequently to the mean of the realigned images. Spatial normalization into standard stereotaxic Montreal Neurological Institute (MNI) space was achieved by applying the "unified segmentation" procedure (Ashburner and Friston 2005) to each participant's mean EPI image. This approach combines the segmentation of the mean EPI image of each participant with a nonlinear spatial normalization into the space of the priors used for this segmentation (i.e., the MNI tissue probability maps). The resulting parameters of a discrete cosine transformation, which define the deformation field necessary to move the participant's data into the space of the MNI tissue probability maps, were combined with a second deformation field that describes the optimal transformation between the MNI tissue probability maps and the MNI single-subject template (Holmes et al. 1998). The ensuing combined deformation was subsequently applied to all individual EPI volumes, which were hereby transformed into the MNI single-subject space and resampled at 2 × 2 × 2-mm^3 voxel size. Normalized images were spatially smoothed with a Gaussian filter of 8mm full-width at half-maximum to accommodate assumptions of random-field theory as well as residual interindividual variation.

The expected hemodynamic response for each trial was modeled by convolving trial onsets and durations with a canonical hemodynamic response function (HRF; Friston et al. 1998) and its first-order temporal derivative to create predictors in a general linear model. Trials were averaged across all cue–target delays and spatial-cue types. The analysis included the following 10 regressors of interest: 3 regressors for auditory, tactile, and visual cue-only trials; the same for validly cued target trials with highly predictive (unimodal) modality cues; the same for target trials with uninformative (trimodal) modality cues; one regressor for cue-only trials with uninformative modality cues. Additionally, we included nuisance regressors for the remaining conditions (trials with invalid or bimodal modality cues) and for 6 head-motion parameters (translation and rotation movements). Low-frequency signal drifts were filtered using a cutoff period of 128 s. After correction of the time series for dependent observations according to an autoregressive first-order correlation structure, parameter estimates of the HRF regressors were calculated from the least-mean-squares fit of the model to the time series.

Group analyses were done by entering parameter estimates of the regressors of interest into a random-effects repeated-measures analysis of variance (ANOVA), allowing for unequal variances among conditions and participants, as implemented in SPM5. By restricting the analysis of expectancy effects to cue-only trials, we excluded trivial differences based on processing different sensory input as well as confounding effects of stimulus-driven orienting and attentional modulations of target processing. Additionally, we report supplementary analyses that included both cue-plus-target and cue-only trials. Activity differences were considered significant when surviving a single-voxel threshold of $P < 0.001$ and a cluster-level threshold of $P < 0.05$, familywise error (FWE) corrected for multiple comparisons across the whole brain (Worsley et al. 1996).

Results

Behavioral Data

To examine the effectiveness of our expectancy manipulation, we analyzed the behavioral effects of cueing stimulus modality in target trials (i.e., in those trials in which the cue was actually followed by a target). Because of the saliency of the imperative stimuli, detection performance was at ceiling: errors of omission and false alarms were very rare (0.42% and 0.27%, respectively, on average) and not further analyzed. Cueing effects on individual median RT were tested by a 3 × 3 repeated-measures ANOVA with factors target modality (auditory, tactile, visual) and cue validity (valid, uninformative, invalid). Whenever necessary, the Greenhouse–Geisser correction was employed to compensate for violations of sphericity. Group-averaged RT data for each condition are shown in Figure 2.

The ANOVA on RT revealed a main effect for both target modality ($F_{2,46} = 20.66$, $P < 0.001$, $\eta_p^2 = 0.47$) and cue validity ($F_{2,46} = 58.47$, $P < 0.001$, $\eta_p^2 = 0.72$). Simple contrasts revealed that responses to tactile stimuli were significantly faster than responses to auditory ($F_{1,23} = 19.65$, $P < 0.001$, $\eta_p^2 = 0.46$) or visual ($F_{1,23} = 30.94$, $P < 0.001$, $\eta_p^2 = 0.57$) stimuli, with the latter 2 not being significantly different from each other ($F_{1,23} = 1.70$, $P > 0.2$). The analysis further showed that, across modalities, responses to validly cued targets were faster than responses to uninformatively cued ones ($F_{1,23} = 38.03$,

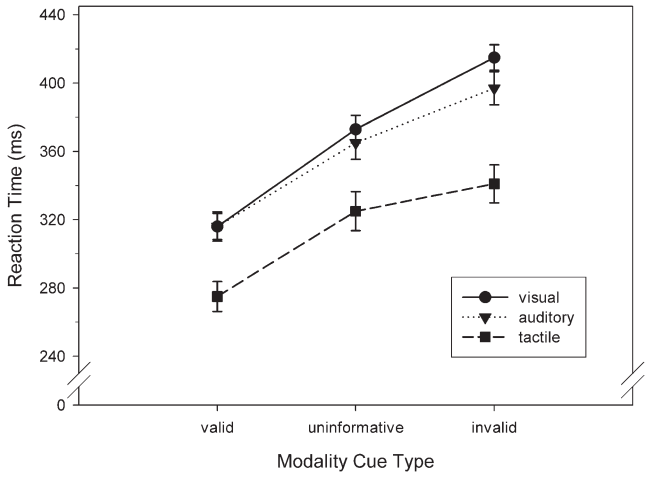

Figure 2. Group-averaged RT for responses to visual, auditory, and tactile targets after valid, uninformative, and invalid cues.

$P < 0.001$, $\eta_p^2 = 0.62$), which were, in turn, faster than responses to invalidly cued targets ($F_{1,23} = 36.77$, $P < 0.001$, $\eta_p^2 = 0.62$). There was also a significant target-modality × cue-validity interaction ($F_{4,92} = 3.84$, $P = 0.014$, $\eta_p^2 = 0.14$), which was driven by a stronger validity effect in the visual modality, as compared with the tactile or auditory one. Nevertheless, since this interaction was ordinal, that is, cue validity affected all 3 modalities in the same direction (and vice versa), the validity main effect can be interpreted globally. Thus, across modalities, performance depended on the validity of the cue in a similar manner, which corroborates the effectiveness of our modality-cueing manipulation.

Imaging Data

Modality-Selective Baseline Increases

Activation driven by top-down attention to a given sensory modality was analyzed by calculating balanced contrasts between cue-only trials for one modality and those for the remaining 2. The outcome was restricted to true task-related (positive) activations by means of a conjunction analysis across the difference of interest and its minuend (i.e., the main effect of the condition of interest), the latter being assessed relative to resting baseline as provided by the randomly interspersed null-event trials. That is, we, for example, assessed where auditory attention significantly modulated baseline activity and did so more strongly than visual or tactile attention. The conjunction approach (based on the minimum *t*-statistic; Nichols et al. 2005) was preferred over an inclusive masking procedure, since the former constitutes a more rigorous test. In particular, only a conjunction combines the *t*-maps of all contrasts involved to make a joint statistical inference. The results of these analyses, including anatomical localization based on cytoarchitectonic probability maps (Eickhoff et al. 2005), are reported in Table 1 and Figure 3. Over all conditions, modality-specific cue-driven activity was predominantly found in areas specialized in processing input of the respective sensory channel: Comparing auditory attention (AA) with tactile (TA) and visual (VA) attention [(2 × AA – (TA + VA)) ∩ AA] revealed stronger bilateral activity in Heschl's gyrus as well as in posterior and middle aspects of the superior and middle temporal gyri (for cytoarchitectonic assignments, see Table 1). These areas correspond to primary and higher order auditory cortices. Further bilateral activity was found in the supramarginal gyrus and precuneus. Contrasting tactile against auditory and visual attention [(2 × TA – (AA + VA)) ∩ TA] resulted in stronger bilateral activity in the postcentral and

Table 1
Modality-specific activations during preparatory attention to a given sensory modality (cue-only trials)

Cluster/macroanatomical structure	*x*, *y*, *z*	Histological assignment	*t*-Score
Auditory attention			
Cluster 1 ($k = 2417$, $P < 0.001$)			
R posterior STG	44, −36, 12	—	6.7
R supramarginal gyrus	48, −40, 26	PFm	6.0
R posterior MTG	64, −44, 8	—	5.6
R middle STG	52, −18, −2	—	4.9
R middle STG	46, −24, 2	TE 1.1	4.7
R middle STG	66, −20, 10	TE 3	4.4
R supramarginal gyrus	50, −36, 22	PFcm	3.9
R Heschl's gyrus	54, −22, 10	TE 1.0	3.6
R Rolandic operculum	44, −31, 16	OP 1	3.4
Cluster 2 ($k = 2278$, $P < 0.001$)			
L posterior STG	−50, −32, 10	—	6.6
L middle STG	−48, −18, −2	—	6.0
L Heschl's gyrus	−48, −24, 6	TE 1.0	5.7
L Rolandic operculum	−36, −32, 16	TE 1.1	5.6
L posterior STG	−40, −36, 16	PFcm	5.6
L posterior STG	−62, −32, 9	TE 3	5.1
L Rolandic operculum	−43, −26, 16	OP 1	4.3
L supramarginal gyrus	−54, −46, 30	PFm	4.2
L supramarginal gyrus	−50, −40, 28	PFcm	4.0
L middle STG	−53, −10, 0	TE 1.2	4.0
Cluster 3 ($k = 134$, $P = 0.047$)			
R precuneus	4, −66, 40	7M	4.2
L precuneus	−4, −68, 40	7A	4.1
L/R precuneus	0, −70, 42	7P	4.0
Tactile attention			
Cluster 1 ($k = 371$, $P < 0.001$)			
L postcentral gyrus	−50, −20, 30	PFt	5.0
L supramarginal gyrus	−60, −26, 30	PFop	3.8
L IPL	−52, −30, 44	Area 2	3.3
Cluster 2 ($k = 138$, $P = 0.043$)			
R supramarginal gyrus	40, −36, 44	Area 2	4.8
R postcentral gyrus	32, −42, 66	PFt	4.2
Visual attention			
Cluster 1 ($k = 2528$, $P < 0.001$)			
R superior occipital gyrus	28, −82, 22	—	7.2
R IPS	26, −56, 44	hIP3	6.3
R lingual gyrus	14, −90, −6	Area 18	6.0
R fusiform gyrus	28, −78, −8	hOC3v (V3v)	5.8
R middle occipital gyrus	30, −70, 34	—	5.3
R lingual gyrus	10, −84, −14	Area 17	4.4
R/L pericalcarine cortex	−2, −94, −4	Area 17	4.3
R fusiform gyrus	32, −68, −12	hOC4v (V4)	4.3
R SPL	18, −62, 60	7A	3.9
R precuneus	12, −62, 62	7A	3.7
R middle occipital gyrus	26, −94, 10	Area 18	3.4
Cluster 2 ($k = 1478$, $P < 0.001$)			
L middle occipital gyrus	−32, −78, 20	—	8.7
L SPL	−16, −64, 60	7A	4.7
L IPS	−26, −54, 44	hIP3	4.2
L superior occipital gyrus	−16, −98, 12	Area 18	3.9
L precuneus	−13, −66, 56	7A	3.5
Cluster 3 ($k = 277$, $P = 0.002$)			
L fusiform gyrus	−38, −70, −14	—	4.1
L lingual gyrus	−14, −86, −14	hOC3v (V3v)	4.0
L lingual gyrus	−12, −84, −16	Area 18	4.0
L fusiform gyrus	−26, −76, −12	hOC4v (V4)	3.5

Notes: Coordinates *x*, *y*, *z* of local maxima refer to MNI space; k = number of voxels in cluster; P = cluster-level error probability corrected for multiple comparisons. L = left; R = right; STG = superior temporal gyrus; MTG = middle temporal gyrus. References for histological assignments: 7A, 7M, 7P: Scheperjans et al. (2008); Area 2: Grefkes et al. (2001); Areas 17, 18: Amunts et al. (2000); hIP3: Scheperjans et al. (2008); hOC3v, hOC4v: Rottschy et al. (2007); OP 1: Eickhoff et al. (2006); PFm, PFcm, PFt, PFop: Caspers et al. (2006); TE 1.0, TE 1.1, TE 1.2: Morosan et al. (2001); TE 3: Morosan et al. (2005).

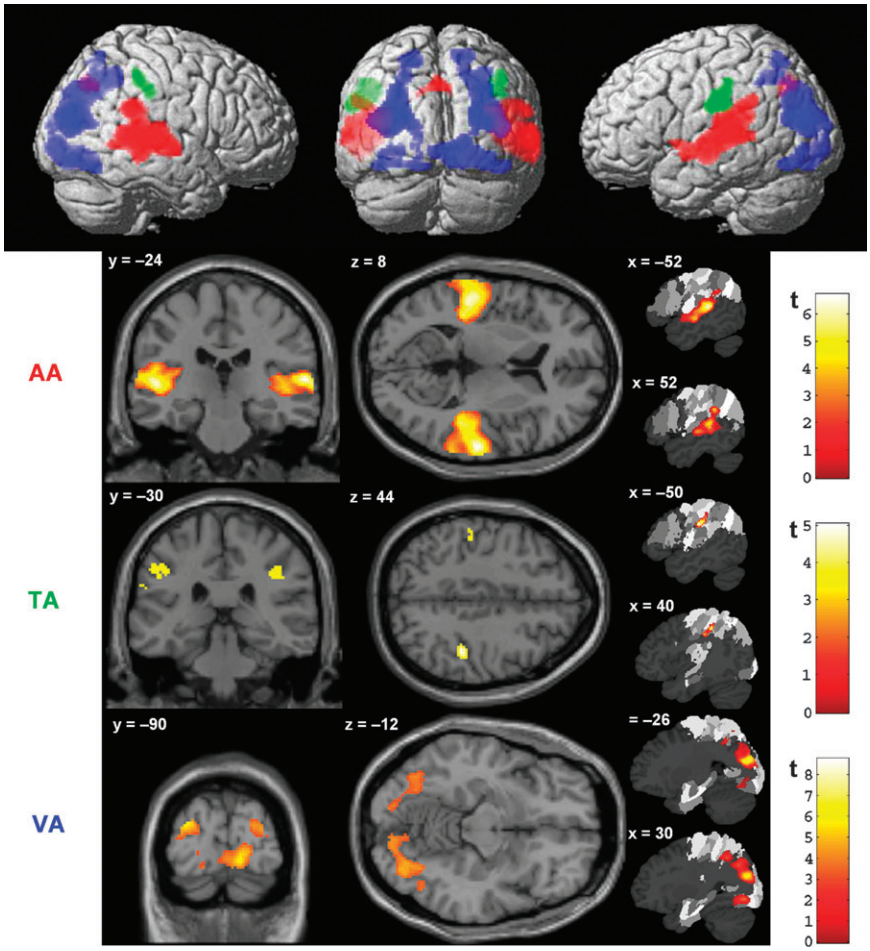

Figure 3. Modality-selective increases in cortical baseline activity while expecting auditory (red, AA), tactile (green, TA), or visual (blue, VA) targets (for overlap between baseline increases and activations related to actual stimulus detection, see Supplementary Fig. S1). Coordinates refer to MNI space; activations are significant at $P < 0.05$ (familywise error corrected at cluster level; voxelwise cluster-forming threshold $P < 0.001$).

supramarginal gyri and parietal operculum (for cytoarchitectonic assignments, see Table 1). These regions correspond to primary (S1) and secondary (S2) somatosensory cortices and somatosensory association areas. Finally, comparing visual with auditory and tactile attention [(2 × VA – (AA + TA)) ∩ VA] revealed stronger bilateral activity in superior and middle occipital gyri, pericalcarine cortex, fusiform and lingual gyri, caudal superior parietal lobule (SPL), and precuneus (for cytoarchitectonic assignments, see Table 1). These regions correspond to primary (V1), secondary (V2), and higher order visual areas of the dorsal and ventral processing streams. Across modalities, the time course of expectancy-induced baseline shifts in relevant sensory cortices was similar, with a slightly less sustained shift in visual areas (see Supplementary Fig. S3).

In a supplementary analysis, we tested for regions commonly active during both expectation and actual stimulus detection. To this end, target trials were analyzed in the same way as was just described for cue-only trials but additionally in conjunction with modality-specific baseline increases. For example, we assessed where auditory attention significantly modulated auditory stimulus detection and did so more strongly than visual or tactile attention during visual or tactile stimulus detection, in conjunction with those areas where auditory attention modulated baseline activity more strongly than did tactile or visual attention. For all 3 modalities, these conjunction analyses largely yielded the same clusters as expectation alone (see Supplementary Fig. S1), showing that expectancy affects baseline activity in brain regions that also subserve actual target detection.

Modality-Selective Baseline Decreases

Deactivation driven by top-down attention to a given sensory modality was analyzed by reversing the balanced contrasts for activations as described above. Results were restricted to true deactivations (relative to baseline) via conjunction across the difference of interest and the negative main effect of its subtrahend. Again, these contrasts were exclusively based on cue-only trials. Auditory attention [(–2 × AA + TA + VA) ∩ –AA] was specifically related to activity decreases in right fusiform and lingual gyri (hOC3v; hOC4v; Area 18 [for references regarding histologically defined areas, see Table 1]; MNI coordinates and *t*-score of local maxima: 24/–72/–10, $t = 4.6$; 32/–50/–12, $t = 4.3$; and 20/–78/–8, $t = 4.2$). Testing our hypothesis at a more liberal threshold ($P < 0.001$, uncorrected; cluster-extent threshold $k = 30$) yielded 2 additional foci of deactivation in the left anterior fusiform gyrus (–36/–50/–14, $t = 4.1$) and left anterior middle temporal gyrus (–42/8/–30, $t = 4.0$) (Fig. 4). The deactivated areas correspond to higher order visual areas presumably subserving object recognition.

During tactile attention [(–2 × TA + AA + VA) ∩ – TA], specific deactivations were found in bilateral pericalcarine cortex, cuneus, and lingual gyrus (Area 17; Area 18; –2/–68/12, t = 5.2; –4/–96/18, t = 4.8; 2/–68/2, t = 4.8), corresponding to V1 and V2. A more lenient cluster threshold (k = 30) did not yield any further deactivation foci (Fig. 4). Finally, visual attention [(–2 × VA + AA + TA) ∩ – VA] was specifically associated with right-lateralized perisylvian activity decreases in Heschl's gyrus, superior temporal gyrus, and the parietal operculum (TE1.0; TE1.2; OP4; 56/–10/8, t = 4.4; 58/–2/4, t = 3.7; 56/–14/12, t = 3.6], corresponding to primary auditory cortex and auditory-belt regions as well as S2. At a more liberal threshold (k = 30), additional clusters of deactivation were found in S1 (Fig. 4): 1) right postcentral gyrus (Area 2; 26/–40/56, t = 3.9); 2) left postcentral gyrus and SPL (Areas 1 [Geyer et al. 1999] and 7A; –32/–42/64, t = 3.6; –26/–50/68, t = 3.5); and 3) left postcentral gyrus (Areas 1 and 2; –50/–20/44, t = 3.6; –50/–22/48, t = 3.4). At this threshold, 2 additional clusters were found in right supplementary motor area (SMA; 2/–18/52, t = 3.6) and right precuneus (18/–42/8, t = 4.0).

Supramodal Activity during Modality-Specific Expectations

Activation driven by top-down attention to a given sensory modality regardless of the specific channel was analyzed via a conjunction across the 3 modality main effects relative to rest (AA ∩ TA ∩ VA), again exclusively based on cue-only trials. The

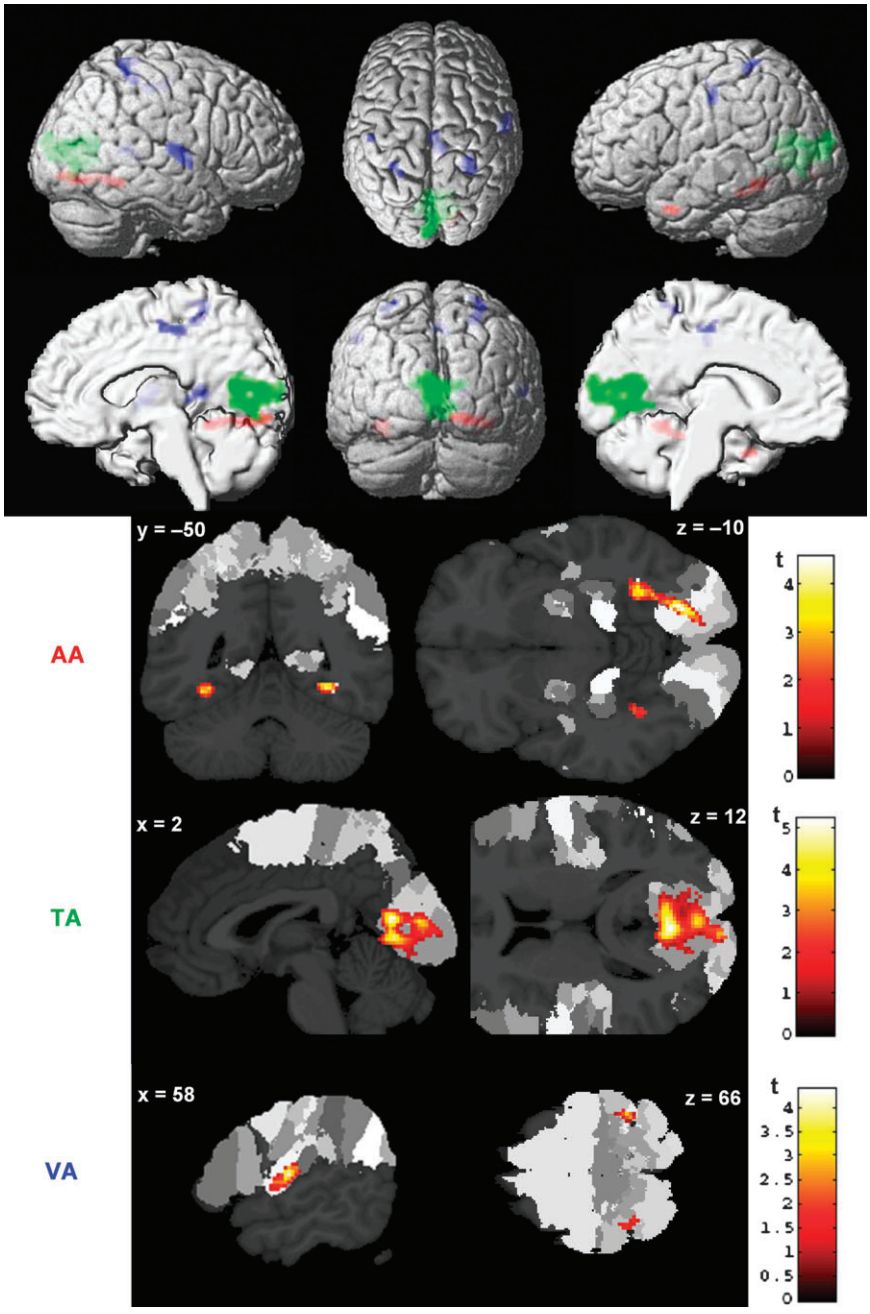

Figure 4. Modality-selective decreases in cortical baseline activity while expecting auditory (red, AA), tactile (green, TA), or visual (blue, VA) targets. Coordinates refer to MNI space; activations are significant at voxel-level $P < 0.001$ (uncorrected; cluster-extent threshold $k = 30$).

Table 2

Supramodal brain activity during preparatory attention to a given sensory modality (conjunction across cue-only trials of all 3 modalities)

Cluster/macroanatomical structure	*x*, *y*, *z*	Histological assignment	*t*-Score
Cluster 1 (k = 1645, $P < 0.001$)			
L SPL	−22, −64, 56	7A	5.9
L IPS	−34, −50, 44	hIP3	5.8
L IPS	−36, −48, 46	hIP1	5.8
L SPL	−20, −74, 48	7P	4.9
L IPL	−28, −64, 44	PGa	4.6
L IPS	−50, −42, 50	hIP2	3.9
L SPL	−30, −52, 52	7PC	3.6
Cluster 2 (k = 1195, $P < 0.001$)			
R SPL	22, −66, 54	7P	6.3
R SPL	28, −66, 54	7A	4.9
R angular gyrus	30, −52, 44	hIP3	4.4
R IPS	34, −62, 50	hIP3	4.3
R angular gyrus	38, −56, 52	PGa	3.9
L SPL	28, −44, 42	7PC	3.5
L IPL	32, −72, 48	PGp	3.5
L IPS	40, −54, 44	hIP1	3.2
L IPS	40, −48, 50	hIP2	3.1
Cluster 3 (k = 791, $P < 0.001$)			
R precentral gyrus	42, −4, 50	—	6.1
R precentral gyrus	38, −4, 48	Area 6	6.1
R IFG (pars triangularis)	46, 26, 30	—	4.8
R MFG	44, 20, 32	—	4.3
Cluster 4 (k = 757, $P < 0.001$)			
R middle occipital gyrus	34, −86, 8	—	6.4
R middle occipital gyrus	26, −92, 8	hOC3Ad (V3A)	5.2
R middle occipital gyrus	26, −94, 4	hOC3v (V3v)	5.1
R superior occipital gyrus	20, −98, 6	Area 18	5.1
R pericalcarine cortex	18, −100, 2	Area 17	4.6
R inferior occipital gyrus	38, −84, −6	hOC4v (V4)	3.6
Cluster 5 (k = 463, $P < 0.001$)			
L middle occipital gyrus	−28, −90, 8	—	4.9
L inferior occipital gyrus	−40, −80, −12	hOC4v (V4)	4.9
L inferior temporal gyrus	−46, −60, −24	—	4.7
L middle occipital gyrus	−28, −92, 12	hOC3Ad (V3A)	3.8
L middle occipital gyrus	−24, −96, 10	hOC3d (V3d)	3.4
L middle occipital gyrus	−22, −97, 8	Area 18	3.2
Cluster 6 (k = 444, $P < 0.001$)			
L precentral gyrus	−38, −44, 8	—	6.8
L precentral gyrus	−36, −8, 46	Area 6	5.2
L precentral gyrus	−46, −2, 44	Area 6	3.5
Cluster 7 (k = 274, P = 0.002)			
R posterior SFG (SMA)	4, 2, 54	Area 6	4.7
L posterior SFG (SMA)	−4, 6, 48	Area 6	4.4
R posterior SFG (pre-SMA)	6, 14, 50	Area 6	4.0
R/L dorsal midcingulate cortex	−2, 8, 44	—	3.3
Cluster 8 (k = 172, P = 0.018)			
R anterior insula	34, 24, −2	—	5.0
R IFG (pars triangularis)	46, 18, 5	Area 45	3.3

Notes: Coordinates *x*, *y*, *z* of local maxima refer to MNI space; k = number of voxels in cluster; P = cluster-level error probability corrected for multiple comparisons. L = left; R = right; IFG/SFG = inferior/superior frontal gyrus. References for histological assignments: 7A, 7P, 7PC: Scheperjans et al. (2008); Area 6: Geyer (2004); Areas 17, 18: Amunts et al. (2000); Area 45: Amunts et al. (1999); hIP1, hIP2: Choi et al. (2006); hIP3: Scheperjans et al. (2008); hOC3Ad, hOC3d: Kujovic et al. (2007); hOC3v, hOC4v: Rottschy et al. (2007); PGa, PGp: Caspers et al. (2006).

analysis yielded activity in a widespread frontoparietal network (Table 2 and Fig. 5) including bilateral IPS and adjacent areas in superior and inferior parietal lobules (IPL), bilateral dorsal premotor cortex (dPMC) including the frontal eye fields (FEFs) as well as bilateral SMA extending into dorsal midcingulate cortex. Additional right-lateralized activations were found in pre-SMA, middle frontal gyrus (MFG), and anterior insula. Furthermore, we observed increased modality-independent activity in bilateral middle and inferior occipital gyri, presumably reflecting the processing of the symbolic cueing stimulus, which was present across conditions (cf. Hopfinger et al. 2000). Supramodal activity decreases were restricted to bilateral inferior precuneus (6/−58/18, t = 4.5; −8/−54/12, t = 4.2).

To control for potential effects of cue-driven spatial orienting, a supplementary analysis examined supramodal activations in a model exclusively based on those (cue-only) trials that contained spatially uninformative cues. Since the power of this model, relative to the main analyses, was substantially reduced by small trial numbers, we did not apply a strict cluster-level correction but used a minimum cluster extent of k = 30 voxels. At this threshold, all but 2 of the original nodes of the observed supramodal network (right middle/inferior frontal gyrus and right anterior insula) showed significant activation in the conjunction analysis (see Supplementary Fig. S2). The 2 missing areas, however, also showed activity at lower thresholds (P < 0.05). These results demonstrate that the supramodal network's activity does not substantially depend on any endogenous spatial cue–driven orienting of attention.

Activity Related to Violations of Specific Versus Nonspecific Expectations

Our experimental design also lent itself to studying stimulus-independent brain responses to expectancy violations arising from the unexpected absence of targets in cue-only trials. Specifically, we hypothesized that omission-related responses under more specific expectations should be stronger than responses under less specific expectations. Therefore, we compared activity between cue-only trials with predictive (indicating a specific modality) and with uninformative (indicating all 3 modalities) cues, in conjunction with the main effect of predictively cued trials averaged across modalities. Since we expected differential activity in basal-ganglia structures (cf. O'Doherty et al. 2004; den Ouden et al. 2009), we employed a small-volume correction for these regions of interest, comprising caudate, putamen, and pallidum as defined

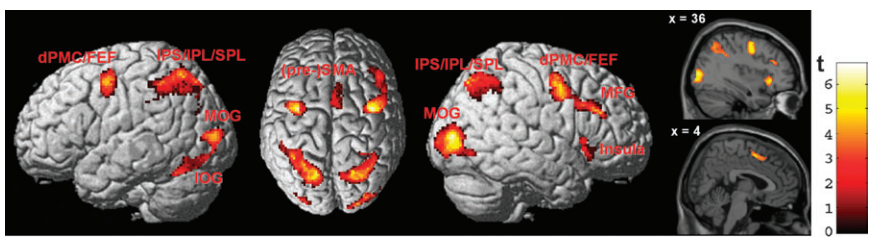

Figure 5. Supramodal activity while expecting auditory, tactile, or visual targets (conjunction across main effects of all 3 modality-specific expectancy conditions relative to resting baseline). Coordinates refer to MNI space; activations are significant at $P < 0.05$ (familywise error corrected at cluster level; voxelwise cluster-forming threshold $P < 0.001$). Abbreviation: IOG/MOG = inferior/middle occipital gyrus.

with 50% probability by the Harvard–Oxford anatomical atlas (distributed with the FSL software package; http://fsl.fmrib.ox.ac.uk/fsl). Averaged across modalities, absence of targets after predictive modality cues was associated with stronger activation in bilateral ventral striatum (anterior [–20/14/–4, t = 4.5; 24/14/–4, t = 3.6] and posterior [–28/–8/0, t = 3.8; 30/–14/4, t = 3.8] putamen) (Fig. 6; for a color version, see Supplementary Fig. S4).

Discussion

This study examined the neural correlates of voluntarily directing attention to a given sensory modality in the absence of stimulation, induced by explicit modality-specific expectations for upcoming auditory, tactile, or visual targets. Since the main analyses were restricted to trials without target presentation (cue-only trials), their results should reflect pure effects of allocating attention (cf. Beck and Kastner 2009). Modality-specific preparatory attention was associated with significant increases and decreases in baseline activity of relevant and irrelevant sensory cortices, respectively. Supplementary analyses revealed that these baseline changes occurred in areas that were also selectively activated during actual stimulus detection. Faster responses in target trials with valid versus uninformative or invalid modality cues indicated that the expectancy-driven preparatory changes in brain activity most likely reflect a processing bias in favor of the cued modality. In all cue-only trials, the sensory input was identical across modalities (except for the slight difference in the cueing symbols) and should have canceled each other out in direct comparison. Thus, modality-specific baseline changes exclusively reflect effects of directed (top-down) attention.

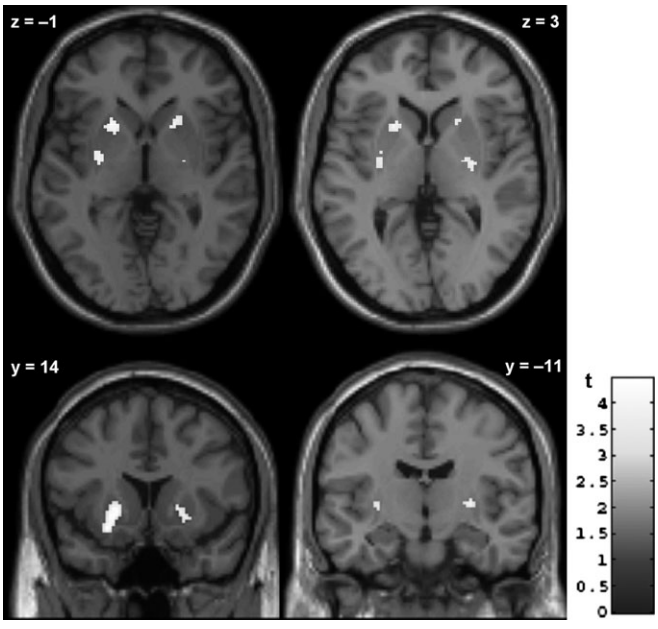

Figure 6. Activity in bilateral anterior and posterior putamen related to violating specific (cue-only trials with predictive cues) versus nonspecific (cue-only trials with uninformative cues) expectations, presumably reflecting stronger surprise at the unexpected omission of predictively cued sensory input. Coordinates refer to MNI space; left hemisphere shown on the left; activations are significant at $P < 0.05$ (small-volume familywise error corrected for the basal ganglia at cluster level; voxelwise cluster-forming threshold $P < 0.001$). For a color version, see Supplementary Figure S4.

Attention-Related Changes in Baseline Activity of Sensory Cortices

The results of our study bridge 2 as-yet isolated literatures on attentional mechanisms in the human brain: they connect previous evidence on the modulation of stimulus processing by intersensory selective attention during multimodal stimulation (Roland 1982; Kawashima et al. 1999; Mehta et al. 2000; Macaluso et al. 2002; Shomstein and Yantis 2004; Saupe et al. 2009) with findings of preparatory changes in baseline activity during attention to some stimulus feature within a given modality (Colby et al. 1996; Chawla et al. 1999; Kastner et al. 1999; Carlsson et al. 2000; Hopfinger et al. 2000; Giesbrecht et al. 2006; Wu et al. 2007; Smith et al. 2010). To our knowledge, we show here for the first time with fMRI that brain activity can be flexibly tuned in advance, on a trial-by-trial basis, not only according to space- or object-selective expectations but also according to more basic expectations about stimulus modality. This resolves ambiguities among previous studies which either could not discriminate modality-specific preparatory activity from attentional modulation of stimulus processing (e.g., Macaluso et al. 2002; Langner et al. 2011) or could not isolate cue-driven modality-selective increases in baseline activity, presumably due to prevailing sustained selection biases (Macaluso et al. 2003).

Despite these differences, our results substantially overlap with modality-specific attentional modulation of stimulus-driven activity: We found the same cortical areas selectively preactivated by attention that 1) are devoted to processing input of the cued modality and 2) showed activity modulation by attention in previous studies. This overlap suggests that the mechanisms underlying attentional modulation of baseline activity and those underlying attentional facilitation of stimulus processing are closely related. A recent study (Sylvester et al. 2009) provided direct evidence for this assumption with respect to visuospatial attention. Similarly, Esterman and Yantis (2010) found support for a substantial congruence between regions recruited by visual anticipation and subsequent perception in a cued category judgment task. Based on our results, we conjecture that the congruence between expectancy- and processing-related modulations might generalize across modalities and, moreover, to selective attention to a particular sensory channel.

Further, we found specific decreases in baseline activity of sensory areas that were rendered irrelevant by the modality cue. These deactivations might reflect an inhibitory mechanism of the brain to reduce the impact of irrelevant input that is complementary to enhancing activity in relevant areas (Mozolic et al. 2008). Such anticipatory suppression has also been reported during unimodal spatial attention with regard to irrelevant locations (Sylvester et al. 2008) or body parts (Drevets et al. 1995). Our results are also consistent with reports of modality-selective decreases in brain activity when directing attention away from a given sensory modality during bimodal stimulation (Kawashima et al. 1995; Sokolov et al. 2004). Taken together, these decreases corroborate the assumption of an active filtering of unwanted information in the unattended modality, which appears to be implemented not only during stimulus processing but already during modality-specific expectations.

Our results are consistent with biased-competition models of attention, according to which expected sensory input is

favored by selectively prioritizing its processing through top-down modulations (Desimone and Duncan 1995; Beck and Kastner 2009). We clearly show that this advance bias also covers the sensory modality of the upcoming stimulus. Behaviorally, this was evidenced by performance gains from valid modality cues and performance losses from invalid ones, relative to uninformative cues, respectively. Neurally, this effect was reflected by anticipatory activity increases in primary and higher order sensory cortices, suggesting a rather pervasive effect of preparatory modulations across the sensory processing hierarchy. In light of previous reports on locally more restricted changes in baseline activity during space- or object-based preparatory attention, this supports the notion of modality-based attention as a more abstract category of attention with broad impact on sensory processing.

Functional Significance of Preparatory Activity

Previous studies showed that baseline changes induced by visual attention are positively related to subsequent performance (Ress et al. 2000; Giesbrecht et al. 2006; Sylvester et al. 2007). Similarly, spontaneous trial-to-trial fluctuations in pretarget activity of sensory cortices were also found to predict performance in auditory (Sadaghiani et al. 2009), tactile (Boly et al. 2007), and visual (Hesselmann et al. 2008) perceptual tasks. This raises the question of how increased baseline activity levels translate into perceptual facilitation and behavioral advantage. Evidence-accumulation models (Smith and Ratcliff 2004) argue that cortical activity reflects sensory evidence whose accumulation is biased by preparatory increases in baseline activity such that perceptual inference that leads to the detection of the expected stimulus is achieved faster (i.e., requiring less bottom-up sensory evidence). In contrast, predictive-coding models (Rao and Ballard 1999; Friston 2005) maintain that cortical activity reflects top-down predictions and bottom-up prediction errors that are accumulated and used to optimize predictions. In this latter framework, increased baseline activity in sensory cortex would reflect a suppression of sensory noise. Noise suppression, in turn, amplifies prediction errors and, hence, gives more weight to bottom-up sensory evidence relative to top-down predictions (cf. Hesselmann et al. 2010).

Thus, accumulation models suggest that preparatory baseline increases bias toward stimulus detection (since the sensory evidence for expected stimuli gets a "head start" and reaches the decision criterion earlier), whereas predictive-coding models suggest that such increases bias toward correct inference (i.e., enhance signal-detection sensitivity). A recent study (Hesselmann et al. 2010) provided evidence for the latter account regarding the relationship between spontaneous pretarget activity fluctuations and perceptual performance. In our study, we observed an increase in response speed after valid modality cues, compared with uninformative ones, whereas false-alarm rate remained at very low levels. This lack of a speed–accuracy criterion shift under directed attention again provides some support for the notion of a preparatory sensitivity increase as suggested by models of predictive coding. Within this framework, Friston (2009, p. 299) recently proposed that the attentional "selection" of a sensory channel is an emergent property of prediction-driven (i.e., modality-specific) reduction in sensory noise; the channel with the lowest noise and, hence, highest impact prediction errors will enjoy the greatest sensory gain. The assumption of noise suppression additionally gains physiological plausibility from single-cell recordings in monkeys that demonstrated increased synchronization of neuronal firing (i.e., the opposite of random noise) to attended stimuli in the respective sensory cortices (e.g., Fries et al. 2001). Nevertheless, several questions remain for future research, such as 1) whether modulations of baseline activity in primary versus higher order sensory cortices have the same functional meaning across the processing hierarchy, 2) whether such modulations constitute necessary and/or sufficient conditions for detection benefits, and 3) whether these neural mechanisms similarly apply to different tasks requiring preparatory attention to modality, ranging from simple detection to mental imagery in search tasks (cf. Bartolomeo 2002; Esterman and Yantis 2010).

Supramodal Activity during Expectancy: Directing Attention and Preparing the Response

In contrast to sensory cortices, a set of frontoparietal areas was commonly upregulated by directing attention to any modality. This supramodal network included bilateral parietal areas around the IPS, bilateral dPMC/FEF, and SMA as well as right pre-SMA, MFG, and anterior insula. The consistent modality-independent activity of this network suggests that it might be the source of the attentional biasing signals that led to modality-selective changes in sensory-cortex baseline activity. This view is in line with previous studies relating top-down attentional control to activity in IPS, dPMC/FEF, and MFG (Corbetta and Shulman 2002). Moreover, these areas were also found active during unimodal location- or object-based attention in the absence of stimulation (Kastner et al. 1999; Hopfinger et al. 2000; Macaluso et al. 2003; Giesbrecht et al. 2006; Smith et al. 2010). Recently, studies using transcranial magnetic stimulation (TMS) concurrent with fMRI (Ruff et al. 2008) or EEG (Capotosto et al. 2009) confirmed the causal influence of this frontoparietal network on activity in visual cortex by showing that stimulating or disrupting IPS or FEF elicits distinct changes in visual cortex activity during visual attention. Similar conclusions were drawn from Granger causality analyses of activity in IPS, FEF/dPMC, and visual cortex during preparatory visuospatial attention (Bressler et al. 2008).

Since attention was explicitly cued to 1 of 2 stimulus locations in two-thirds of the trials (see Materials and Methods), the question may arise as to what degree the observed supramodal network might be driven by demands for the spatial orienting of attention. A supplementary analysis showed that the network commonly activated across modalities was reproducible also in the absence of explicit spatial orienting (i.e., in trials with spatially uninformative cues). This result suggests that modality-selective preparatory activity may not be dominated by spatial orienting as has been reported for feature-selective preparatory attention (McMains et al. 2007). Our finding is in line with evidence for behavioral benefits resulting from attention to target modality occurring independently of spatial attentional orienting (Spence and Driver 1997).

Nevertheless, even in trials with spatially uninformative cues, attention might have been partially allocated based on spatial information implicitly provided by the nature of the 3 different modalities, which entailed presenting stimuli at 3 different locations (ears, hands, eyes). We would thus like to emphasize that one cannot conclude from our study that the observed supramodal network is exclusively devoted to directing attention to stimulus modality. We may, however, look at this

seeming drawback from the opposite direction: in exchange for the remaining ambiguity regarding pure attention-to-modality effects, we gain further evidence for the modality independence of the network controlling spatial attention (cf. Eimer and Van Velzen 2002; Krumbholz et al. 2009; Smith et al. 2010). Moreover, since modality- and location-based attention are usually interwoven in real life, our finding of a supramodal core network that may subserve both attentional functions has higher ecological validity than results from previous studies on attention toward single stimulus dimensions.

Apart from preparatory attention to sensory input, our task also induced motor preparation. Indeed, we found supramodal preparatory activity in dPMC, SMA, and pre-SMA, which have been previously found involved in preparatory motor processes. For instance, a TMS study revealed dPMC involvement in using cue information for the preparatory scaling of grip force (Chouinard et al. 2005). Dorsal PMC was also found to process information from spatial cues to direct movements, regardless of the cue's sensory modality (Weinrich and Wise 1982). Hoshi and Tanji (2007) argued that dPMC integrates sensory and memory information to establish action intentions and develop associated motor programs (see also Cieslik et al. 2010). Our data are consistent with this notion of dPMC function, which might include the preparatory activation of the currently expected stimulus–response mapping (Jakobs et al. 2009). SMA and pre-SMA were also shown to be involved in movement preparation (Matsuzaka and Tanji 1996; Hoshi and Tanji 2004; Cunnington et al. 2005). Since in simple RT paradigms like ours the motor response can be fully prepared in advance, our findings agree well with the assumption that dPMC, SMA, pre-SMA, and midcingulate cortex subserve the establishment of a preparatory set for the expected movement, independent of the response signal's modality.

Finally, the anterior insula is known to be involved in representing bodily states (Craig 2002), including arousal induced by mental or physical stressors (Critchley et al. 2000; Pollatos et al. 2007). Thus, cue-induced insula activity may reflect the general alerting property of the cue. This way the insula might code the behavioral relevance of the cue and establish an appropriate level of alertness to ready body and brain for an efficient response to the impending imperative signal (Sterzer and Kleinschmidt 2010; Langner et al. 2011). Additionally, the anterior insula might contribute to (re)activating the general task set following the cue (Dosenbach et al. 2006).

Taken together, our results show that in simple RT tasks top-down control of attention and mechanisms of response preparation, which in the current design could not be separated, operate mainly independently of the modality of expected response signals. This underlines the importance of using various sensory input channels in studies on "central" processes such as preparation, in order to arrive at generalizable conclusions. Otherwise, input-specific and input-independent effects might be hard to disentangle. For instance, our results suggest that earlier findings of increases in firing rate of monkey lateral IPS during anticipation (Colby et al. 1996) might not be specific to visual attention but rather supramodal.

Activity Related to the Unexpected Omission of Response Signals

Apart from preparatory activity, expectancy effects should also manifest themselves when expectations are not met, that is, in the brain response to the omission of an expected response signal. As predicted, this response was stronger, across modalities, in the anterior and posterior putamen after disconfirming more precise expectations (in cue-only trials with predictive cues) compared with less precise ones (in cue-only trials with uninformative cues). This differential omission-related response provides independent support for the view that predictive cues were used indeed to develop selective expectations leading to perceptual facilitation.

We suggest that increased activity in the anterior putamen reflects enhanced prediction-error responses to target omissions after predictive versus uninformative cues. This assumption is corroborated by other studies that found activity in this area to covary with prediction errors (McClure et al. 2003; O'Doherty et al. 2004), including error responses to the unexpected absence of input (den Ouden et al. 2009). Importantly, our results indicate that such omission-related responses may not simply be equated with information-theoretic (Shannon) surprise, which denotes the improbability of a given event (here: the target omission in any cue-only trial; cf. Strange et al. 2005). Rather, we found omission-related response differences between specific and nonspecific expectations, although the event of interest, that is, the omission of sensory input, was similarly improbable under both specific and nonspecific expectancy conditions (27.3% and 33.3% cue-only trials in conditions with predictive and uninformative cues, respectively). This similarity argues against a simple dependence of event-bound putaminal surprise responses on the event's occurrence probability. Instead, finding substantial differences despite highly similar occurrence probabilities agrees more with recent notions that surprise is captured best in a relative manner related to subjective expectations of the observer (Itti and Baldi 2009). Based on this premise, event-bound surprise has been defined in a Bayesian framework as the degree to which prior expectations are violated and, thus, changed ("updated") by the occurrence of an event (Baldi 2005; see also Maguire et al. 2011). Within this framework, omission-related responses in the anterior putamen might index the omission-induced degree of adjustment of the prior expectation rather than information-theoretic surprise.

Our finding that putaminal responses to omissions of expected input are stronger when expectations are specific fits very well with the predictive-coding approach alluded to above, which argues that modality-specific expectations selectively reduce noise in relevant sensory cortices (cf. Friston 2009). In a Bayesian perspective, this reduces prior variance, hereby enhancing the weight of bottom-up input for perceptual inference on a given sensory channel. If, as in cue-only trials, the expected input does not arrive, a prediction error is generated. When predictions are specific, such as after predictive cues, the error's impact and the associated striatal response are enhanced compared with nonspecific predictions, such as after uninformative cues. This reasoning is in line with the view that the perceived level of surprise at a given event be associated with the difficulty of integrating the event (here: the stimulus omission) with an existing representation (Maguire et al. 2011). That is, when the integration even of low-probability events is made easy, for instance by nonspecific (as compared with highly specific) expectations, only little surprise is evoked, since the existing representation is not changed much by the event's integration. In sum, this effect demonstrates that information-theoretic (Shannon) surprise, which was highly similar for both trial types, and Bayesian

surprise, which depends on the specificity of prior beliefs, are dissociably represented in the human brain.

The response in the posterior putamen might be specifically related to predictive coding in the motor domain (cf. Kilner et al. 2007; Jakobs et al. 2009): predictive cues are thought to elicit enhanced motor preparation (Koski et al. 1999; Bestmann et al. 2008), contributing to shorter RT. This interpretation corresponds to previous findings on the role of the posterior putamen in skeletomotor control and movement initiation (Alexander and Crutcher 1990; Boussaoud and Kermadi 1997). The functional differentiation between posterior and anterior putaminal activity accords with the finding that learning sequential finger movements versus overlearned responding activated anterior as opposed to posterior putamen and vice versa (Jueptner and Weiller 1998).

Conclusions

We have shown that voluntarily directing attention to various sensory channels in a flexible, trial-by-trial manner leads to improved detection performance and transient changes in baseline activity of sensory cortices, with increased activity in relevant cortices and decreased activity in irrelevant ones. These expectancy-related changes occur for attention to auditory, tactile, and visual channels alike, attesting to the generality of the mechanism. Modulations of sensory cortices appear to be controlled via a common supramodal frontoparietal network, which may emit biasing top-down signals that influence competition between sensory inputs in favor of the most relevant (i.e., expected) information. It remains to be examined whether attention-induced increases in baseline activity reflect increased synchrony (i.e., reduced noise) in sensory cortices, as suggested previously for spontaneous pretarget fluctuations, or whether these increases (also) reflect the "replacement" of sensory data with top-down expectations to facilitate target detection by speeding up evidence accumulation. Finally, activity in the anterior putamen related to unexpected input omissions may reflect a prediction-error signal that is sensitive to the specificity of expectations and represents (Bayesian) surprise.

Supplementary Material

Supplementary material can be found at: http://www.cercor.oxfordjournals.org/

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Notes

Conflict of Interest: None declared.

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