COGNITIVE NEUROSCIENCE

Task-dependent uncertainty modulation of perceptual decisions in the human brain

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Abstract

Perceptual judgments are frequently made during uncertain situations. Previous human brain imaging studies have revealed multiple cortical and subcortical areas that are activated when decision uncertainty is linked to outcome probability. However, the neural mechanisms of uncertainty modulation in different perceptual decision tasks have not been systematically investigated. Uncertainty of perceptual decision can originate either from highly similar object categories (e.g. tasks based on criterion comparison) or from noise being added to visual stimuli (e.g. tasks based on signal detection). In this study, we used functional magnetic resonance imaging (fMRI) to investigate the neural mechanisms of task-dependent modulation of uncertainty in the human brain during perceptual judgements. We observed correlations between uncertainty levels and fMRI activity in a network of areas responsible for performance monitoring and sensory evidence comparison in both tasks. These areas are associated with late stages of perceptual decision, and include the posterior medial frontal cortex, dorsal lateral prefrontal cortex, and intraparietal sulcus. When the modulation of uncertainty on the two tasks was compared, dissociable cortical networks were identified. Uncertainty in the criterion comparison task modulated activity in the left lateral prefrontal cortex related to rule retrieval. In the signal detection task, uncertainty modulated activity in higher visual processing areas thought to be sensory information 'accumulators' that are active during early stages of perceptual decision. These findings offer insights into the mechanism of information processing during perceptual decision-making.

Introduction

Our sensory systems frequently encounter situations in which decisions need to be made under imperfect perceptual conditions (Gold & Shadlen, 2007; Heekeren *et al.*, 2008). Perceptual uncertainty can arise during a task based on criterion comparison in which decisions on category membership must be made about perceptually similar objects. Perceptual uncertainty may also arise during a task based on signal detection in which objects must be identified in a noisy background before they can be accurately classified. Being able to cope with these perceptually ambiguous conditions is critical for our daily life.

Investigators have attempted to understand how decision uncertainty is represented in the human brain through a number of behavioral (Kahneman & Tversky, 1982; Barthelme & Mamassian, 2009; Wei & Kording, 2010), electrophysiological (Kepecs *et al.*, 2008; Kiani & Shadlen, 2009) and neuroimaging (Barch *et al.*, 2001; Critchley *et al.*, 2001; Paulus *et al.*, 2001; Volz *et al.*, 2003, 2004; Hsu *et al.*, 2005; Huettel *et al.*, 2005; Grinband *et al.*, 2006; Yoshida & Ishii, 2006; Stern *et al.*, 2010; Daniel *et al.*, 2011) experiments. A majority of the human neuroimaging studies have suggested that the

performance-monitoring area [the posterior medial frontal cortex (pMFC)] plays a central role in mediating decision uncertainty (Ridderinkhof *et al.*, 2004). However, uncertainty-induced changes in brain activity vary significantly across task and experiment (Critchley *et al.*, 2001; Paulus *et al.*, 2001; Volz *et al.*, 2004; Hsu *et al.*, 2005; Huettel *et al.*, 2005; Grinband *et al.*, 2006; Yoshida & Ishii, 2006; Stern *et al.*, 2010; Daniel *et al.*, 2011). The aim of this study was to determine whether perceptual decision processes are modulated by task-dependent uncertainty in the human brain.

Previous research has identified the involvement of distinct functional networks in perceptual decision-making. These networks include sensory information 'accumulator' areas involved in early stages of perceptual decision-making (Mazurek *et al.*, 2003; Ploran *et al.*, 2007) and sensory information 'comparator' areas (Heekeren *et al.*, 2004, 2006; Romo *et al.*, 2004; Hare *et al.*, 2011) associated with late stages of perceptual decision-making. However, the effect of task-dependent uncertainty modulation on these early-stage and late-stage perceptual decision areas has yet to be determined. In this study, we generated two sets of parameterized Glass pattern stimuli for the criterion comparison and signal detection tasks. We then compared functional magnetic resonance imaging (fMRI) activity related to decision uncertainty on the two tasks. Our results demonstrate the task-dependent uncertainty modulation of perceptual decision-making in the human brain.

Materials and methods

Observers

Twenty observers (seven males; mean age, 22.05 years) with normal or corrected-to-normal vision participated in the experiment. All observers were from Peking University, and gave written informed consent. The study was approved by the Human Subjects Review Committee of Peking University. All participants were paid equally, regardless of their task performance.

Stimuli

The stimuli were Glass patterns (Glass, 1969; Glass & Perez, 1973) defined by white dot dipoles displayed within a square aperture (7.3° × 7.3°) on a black background. The dot density of the stimuli was 3%, and the Glass shift (i.e. the distance between the two dots in a dipole) was 15.4 arc min. Each white dot occupied one pixel on the screen. These parameters were chosen on the basis of previous studies (Li *et al.*, 2009, 2012; Mayhew *et al.*, 2010) showing that coherent form patterns are reliably perceived under these conditions. For each dot dipole, the spiral angle was defined as the angle between the hidden line linking the two dots of the dipole and the radius from the center of the stimulus aperture to the center of the dipole. The proportion of dipoles aligned according to a specified spiral angle was defined as the signal level for each stimulus. For noise dipoles, the spiral angles were randomly assigned. In each stimulus, a white fixation square (8.8×8.8 arc min^2) was positioned at the center of the aperture.

By manipulating different parameters of the Glass patterns, two stimuli sets were generated (Fig. 1). For the criterion comparison task, stimuli were generated between radial and concentric patterns by parametrically varying the spiral angles from 0° (radial pattern) to 90° (concentric pattern). All stimuli were presented at 100% signal level. Observers were trained by using a categorical boundary at a 45° spiral angle. As stimuli approached this boundary, uncertainty (and therefore the difficulty in making the proper decision) increased. In the signal detection task, perceptual uncertainty was created by manipulating the signal-to-noise ratio. Thus, stimuli were presented at either 0° (radial pattern) or 90° (concentric pattern) spiral angles, but the signal level ranged from 0 to 100%. In this task, uncertainty (and therefore the decision difficulty) increased as the proportion of task-relevant signal decreased.

Design

Each observer successively participated in a psychophysical training session and an fMRI scanning session on separate days. In the psychophysical training session, the observer was trained on both the criterion comparison task and the signal detection task. Observer's perceptual thresholds for both tasks were estimated in a post-training test. Stimuli presented during the fMRI session were matched in task difficulty between observers and tasks.

Psychophysical training

Perceptual decision tasks on categorization

In both the criterion comparison and signal detection tasks, observers were asked to categorize the stimuli as either radial or concentric. Observers were familiarized with both sets of stimuli during a short practice run. After the practice run, observers completed four runs of self-paced psychophysical training on categorization tasks. This training consisted of two criterion comparison task runs and two signal detection task runs. The run order was randomized. Each training run was composed of 120 trials with a categorical boundary of spiral angle 45°. For the criterion comparison task, observers were presented with 100% signal Glass patterns at 20°, 30°, 40°, 50°, 60° and 70° spiral angles. For the signal detection task, observers were presented with 0° and 90° Glass patterns at 10, 20, 30, 40 and 50% signal levels. Each trial started with a 200-ms stimulus presentation, and this was followed by a maximum 1.8-s response interval, during which observers were instructed to indicate which category the stimulus belonged to by pressing one of two buttons. Observers received auditory feedback following incorrect choices.
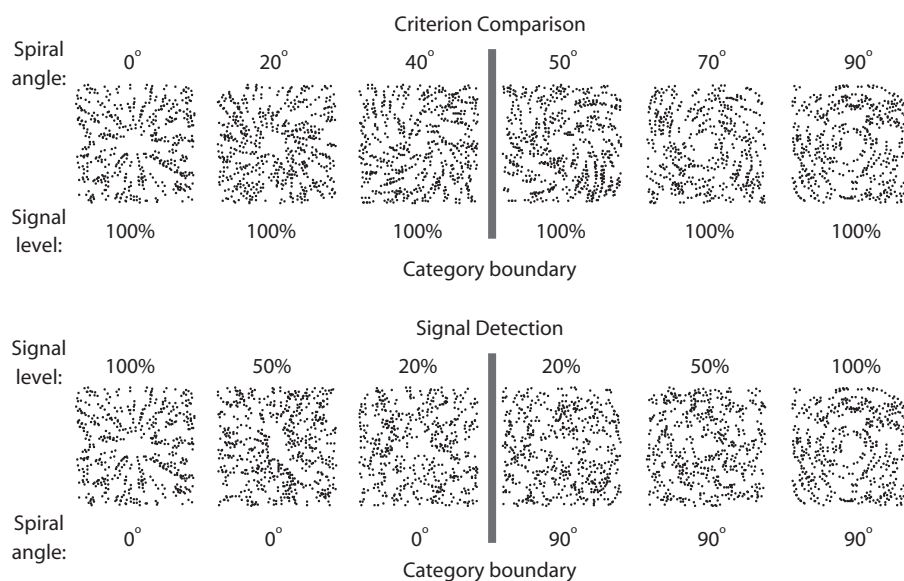

FIG. 1. Stimulus sets for two tasks. For the criterion comparison task, the signal level of the stimuli was set to 100% and the spiral angles varied from 0° to 90°. The categorical boundary for this task was 45° spiral angle. For the signal detection task, Glass patterns of 0° (radial) and 90° (concentric) spiral angle were presented, and the signal level was varied between 0 and 100%.

Following training, observers performed four post-training test runs to estimate their perceptual thresholds for both tasks. The post-training test consisted of two criterion comparison task runs and two signal detection task runs. The run order was randomized. Each test run comprised 120 trials. For the criterion comparison task, observers were presented with 100% signal Glass patterns at different spiral angles (0°, 25°, 35°, 40°, 42°, 44°, 46°, 48°, 50°, 55°, 65°, and 90°). For the signal detection task, observers were presented with 0° and 90° spiral angle Glass patterns at different signal levels (5, 9, 15, 35, 55, and 100%). Each trial started with a 200-ms stimulus presentation, and this was followed by a maximum 1.8-s blank screen for response. No auditory feedback was given during the post-training test.

Control task on letter identification

After the post-training test, observers performed one run (160 trials) of self-paced psychophysical training on a control task of letter identification. Observers were presented with 100% signal and 0° and 90° spiral angle Glass patterns. Each stimulus was presented for 200 ms, and followed by the maximum 1.8-s blank response screen. During the stimulus presentation, three letters (in a $0.5° \times 0.5°$ area) were sequentially presented at the center of the pattern. Observers were instructed to indicate whether the letter 'T' was presented by pressing one of the two buttons (presence or absence). Observers received auditory feedback for incorrect choices.

fMRI measurement

Observers participated in a single scanning session during which they performed two perceptual decision categorization task runs and two letter identification control task runs. Observers were asked to perform the tasks as accurately as possible. The run order was randomized. A blocked fMRI design of 20 trials per block was used, with each block lasting 40 s. Each fMRI run comprised eight blocks with two blocks for each condition. Fixation periods of 12 s were inserted between neighboring blocks and at the start and end of each run. Each trial started with a 0–500-ms jittered onset delay, and this was followed by the 200-ms stimulus presentation. For each categorization task, a white fixation square was positioned at the center of the stimulus. In the letter identification task, the fixation square was replaced by a sequence of three letters during the stimulus presentation period. Following stimulus presentation, observers were required to press one of two buttons to indicate the stimulus category (radial or concentric) on the categorization tasks or the presence of the letter 'T' (presence or absence) on the letter identification task.

For each observer, the same sets of Glass pattern stimuli were presented for the categorization and letter identification tasks. Glass pattern stimuli for each observer were chosen on the basis of the threshold estimations from each observer's post-training test. Psychometric (proportion concentric) data from the post-training test of the categorization tasks were fitted with cumulative Gaussian functions with a procedure that implements a maximum-likelihood method (Wichmann & Hill, 2001). Thresholds for spiral angle (for the criterion comparison task) and signal level (for the signal detection task) were estimated between 87.5 and 92.5% correct for the easy condition, and between 57.5 and 62.5% correct for the difficult condition. This procedure resulted in four stimulus conditions with matched task difficulty between observers and categorization tasks: criterion comparison easy, criterion comparison difficult, signal detection easy, and signal detection difficult.

Data acquisition

Echo planar imaging and T1-weighted anatomical $(1 \times 1 \times 1 \text{ mm}^3)$ data were collected from a Siemens Trio 3T scanner with a 12-channel phase-array coil. echo planar imaging data were acquired from 33 axial slices (whole brain coverage; repetition time, 2000 ms; echo time, 30 ms, flip-angle, 90°; resolution, $3 \times 3 \times 3 \text{ mm}^3$).

fMRI data analysis

Pre-processing

The fMRI data were processed with BRAINVOYAGER QX (Brain Innovations, Maastricht, The Netherlands). Pre-processing of the functional data included slice scan time correction, three-dimensional head motion correction, temporal high-pass filtering (three cycles), and linear trends removal. Spatial smoothing (Gaussian filter; full-width at half maximum, 8 mm) was performed for the group random effects general linear model (GLM) analysis but not for the multi-voxel pattern analysis (MVPA). The functional images were co-registered to anatomical data, and then transformed into Talairach space.

GLM analysis

To identify brain areas modulated by uncertainty, we generated two uncertainty regressors: one for the criterion comparison task, and one for the signal detection task. For each regressor, uncertainty level and reaction time were explicitly modeled with millisecond resolution. Each trial was modeled from stimulus onset to the observer's response (Grinband et al., 2008). The uncertainty level, u, of a block was defined as $u = 1 - \text{abs}(r - 0.5) \times 2$, where r is the behavioral accuracy of that block. The amplitudes of the trials in a block were set to the uncertainty level of the block. A separate unmodulated regressor was generated to model general cognitive processes shared by both tasks (Grinband et al., 2006). For this unmodulated regressor, a trial was modeled from stimulus onset until the observer's response, and the amplitude was set to 1. Another regressor was generated to model the fixation periods. All regressors were collected with millisecond resolution, and then convolved with a canonical double-gamma hemodynamic response function and downsampled to the scanning resolution (repetition time, 2 s). These downsampled regressors were used to form a GLM along with six other regressors derived from the motion correction parameters. Serial correlations between neighboring scans in fMRI data were removed with a first-order autoregressive model (Bullmore et al., 1996). The resulting maps were corrected for cluster size threshold with an iterative Monte Carlo-based simulation procedure (Forman et al., 1995; Goebel et al., 2006).

MVPA analysis

Searchlight-based MVPA analysis (Kriegeskorte et al., 2006) was performed to identify brain areas showing significantly different activation between the two categorization tasks. For this analysis, a 9-mm-radius sphere was defined and moved through the brain voxel by voxel. A linear support vector machine and leave-two-block-out cross-validation procedure were used to perform a beta-value-based pattern classification. At each cross-validation, one block from each class was excluded from training the classifier. A GLM was constructed to estimate beta-values pertaining to each of the eight blocks per run. For each block, trials were modeled from stimulus onsets to the observer's response, with all amplitudes set to 1. The spatial patterns of the estimated beta-values across voxels in a

sphere were fed into the classifier together with the label of its corresponding block (criterion comparison vs. signal detection). Across observers, a second-level permutation-based random effect analysis with nonparametric mapping was performed to identify voxels that showed significantly higher than chance level accuracy (Nichols & Holmes, 2002). The resulting maps were corrected for cluster size threshold with an iterative Monte Carlo-based simulation procedure (Forman *et al.*, 1995; Goebel *et al.*, 2006).

Results

Behavioral results

Observers were trained to categorize radial and concentric Glass pattern stimuli. We estimated the thresholds of spiral angle (for the criterion comparison task) and signal level (for the signal detection task) for the easy condition (between 87.5 and 92.5% correct) and the difficult condition (between 57.5 and 62.5% correct). Stimuli corresponding to these two task difficulty levels were used in the fMRI session.

The observers' behavioral performance during the fMRI session is shown in Fig. 2A. A repeated measures ANOVA (categorization task × difficulty level) showed that, for the categorization tasks, observers were significantly more accurate ($F_{1,19} = 185.44$, $P < 0.001$) and faster ($F_{1,19} = 40.27$, $P < 0.001$) during the easy condition than during the difficult condition. There were no significant differences in accuracy ($F_{1,19} = 0.17$, $P = 0.69$) and reaction

time ($F_{1,19} = 1.04$, $P = 0.32$) between the two categorization tasks. There was also no significant interaction between categorization task and task difficulty level for either accuracy ($F_{1,19} = 3.94$, $P = 0.06$) or reaction time ($F_{1,19} = 0.05$, $P = 0.82$). For the letter identification task, a repeated measures ANOVA (stimulus set × difficulty level, as determined by stimulus parameters on the categorization task) showed that there was no significant main effect on difficulty level (accuracy, $F_{1,19} = 0.40$, $P = 0.54$; reaction time, $F_{1,19} = 0.43$, $P = 0.52$) or stimulus set (accuracy, $F_{1,19} = 0.44$, $P = 0.51$; reaction time, $F_{1,19} = 0.13$, $P = 0.73$). In addition, there was no interaction between difficulty and stimulus set (accuracy, $F_{1,19} = 0.08$, $P = 0.78$; reaction time, $F_{1,19} = 2.75$, $P = 0.11$). These results demonstrate that our manipulation of uncertainty levels was successful, and that the two categorization tasks were matched in task difficulty. Additionally, we observed a certain amount of variability in uncertainty levels for both the easy and difficult task conditions, as shown in Fig. 2B. That is, observers' performance varied across blocks for the same experimental condition. To better account for this variability in uncertainty level, we employed a parametric GLM for the following fMRI analysis of uncertainty modulation.

fMRI results

Uncertainty modulation in perceptual decision

We identified brain areas modulated by uncertainty with a parametric GLM for the criterion comparison and signal detection tasks. A
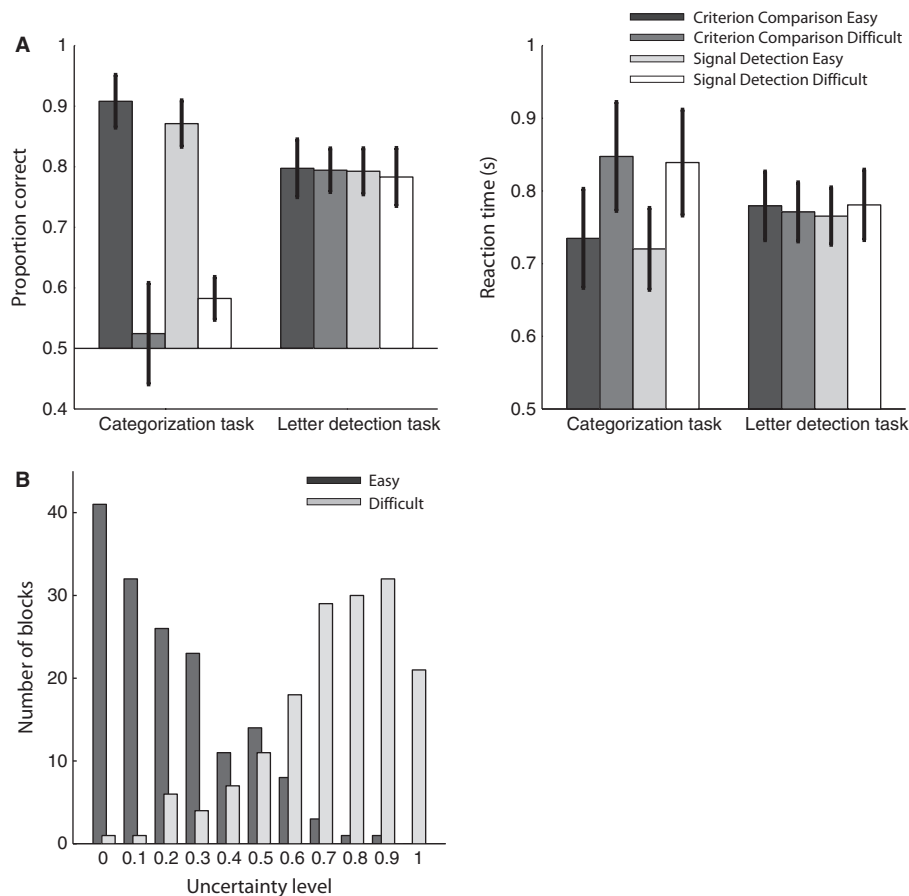

FIG. 2. Behavioral data. (A) Behavioral accuracy and reaction times on the categorization task and letter identification task during the fMRI session. The data are grouped by stimulus condition. Error bars indicate standard error of the mean across observers. (B) Distribution of uncertainty level for the easy and difficult conditions across two categorization tasks.
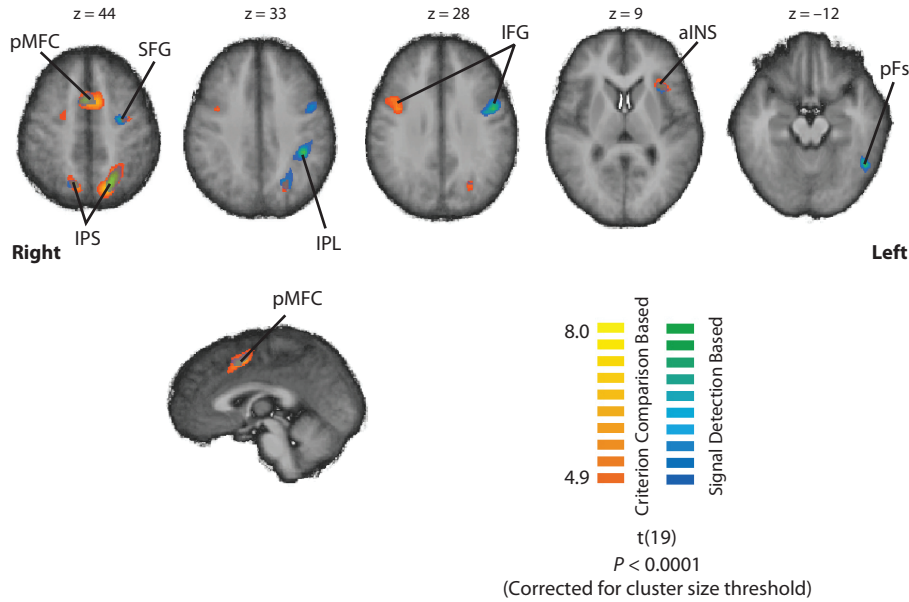
FIG. 3. fMRI result: uncertainty modulation. Random effects GLM analysis showed significant modulation of decision uncertainty (*P* < 0.0001, corrected for cluster size threshold) for the criterion comparison task and the signal detection task, respectively (see Table 1 for Talairach coordinates).

random effects analysis across observers revealed significant modulation of uncertainty (*P* < 0.0001, corrected for cluster size threshold) in multiple brain areas (Fig. 3; see Table 1 for Talaraich coordinates).

Specifically, brain activity modulated by uncertainty on both tasks was observed in the pMFC, left dorsal lateral prefrontal cortex [DLPFC, i.e. superior frontal gyrus (SFG)], left anterior insular (aINS), and bilateral intraparietal sulcus (IPS). Previous studies have suggested that DLPFC activation is associated with the representation of decision variables (Heekeren *et al.*, 2004; Boettiger & D'Esposito, 2005; Muhammad *et al.*, 2006; Li *et al.*, 2007) and therefore exhibits the characteristics of a 'comparator' during late stages of perceptual decision-making (Romo *et al.*, 2004; Heekeren *et al.*, 2006). Other studies have suggested that activity in the aINS represents decision uncertainty (Critchley *et al.*, 2001; Volz *et al.*, 2004; Huettel *et al.*, 2005; Grinband *et al.*, 2006; Daniel *et al.*, 2011) and a more general error-based learning about subjective feeling states (Singer *et al.*, 2009).

In the criterion comparison task, uncertainty modulation was observed in the right DLPFC and the right ventral lateral prefrontal cortex [VLPFC, i.e. inferior frontal gyrus (IFG)]. The right VLPFC is activated by criterion-based (or rule-based) tasks, and plays a role in retrieving newly learned rules (Patalano *et al.*, 2001; Grossman *et al.*, 2003; Bunge, 2004). In the signal detection task, fMRI signals in the left VLPFC, left inferior parietal lobule (IPL), and left posterior fusiform (pFs) were modulated by uncertainty. It has been suggested that the left VLPFC is associated with verbal working memory (Smith & Jonides, 1997; D'Esposito *et al.*, 1998), and is activated in various categorization tasks when the category labels can be verbally expressed (Grossman *et al.*, 2002a,b; Koenig *et al.*, 2005). The pFs is the anterior portion of the lateral occipital complex, which is an important cortical region for visual object processing (Grill-Spector *et al.*, 2001). The IPL has been associated with stimulus-driven attention (Tootell *et al.*, 1998; Corbetta *et al.*, 2000), and is modulated by the DLPFC during sensory information processing (DiQuattro & Geng, 2011). These higher visual areas may serve as sensory accumulators for perceptual judgements made during earlier stages of visual processing, especially those involving perceptual judgements of noisy visual inputs (Ploran *et al.*, 2007).

To eliminate the possibility that the observed uncertainty modulation in higher visual areas resulted from stimulus signal level and not perceptual decision processes, we performed a GLM on the letter identification task data. This analysis compared the fMRI signals corresponding to high and low signal levels in the letter identification task. No significant activations in the above-mentioned areas were observed. This result affirms that the activations in the pFs and IPL are related to decision uncertainty.
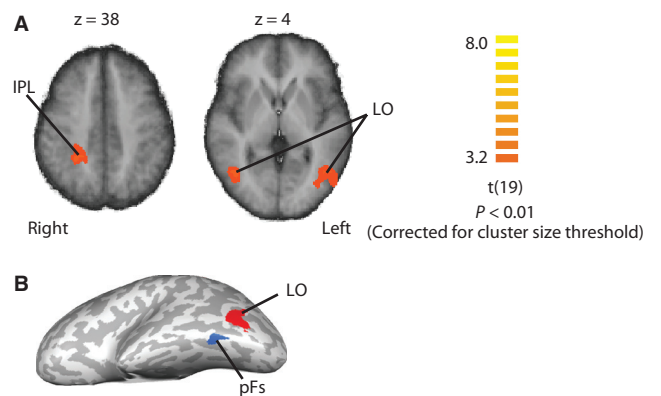

FIG. 4. fMRI result: searchlight analysis. (A) Multivariate searchlight analysis was performed to directly compare the fMRI-measured brain activity present during both categorization tasks. A second-level analysis (permutation *t*-test for observer accuracy) was performed to identify voxels showing significantly higher accuracy than chance (*P* < 0.01, corrected for cluster size threshold). The bilateral LO (Talairach coordinates: left hemisphere, *x* = −37, *y* = −61, *z* = 0; right hemisphere, *x* = 39, *y* = −57, *z* = 5) and the right IPL (Talairach coordinates: *x* = 26, *y* = −44, *z* = 38) showed significantly different activation patterns between the two tasks. (B) Illustration of the locations of the LO and pFs. The two areas are overlaid on an inflated left hemisphere cortical surface.

TABLE 1. Talairach coordinates for all regions of interest (ROIs) that are significantly modulated by uncertainty

ROI	Left hemisphere			Right hemisphere		
	x	y	z	x	y	z
(A) Criterion comparison task						
pMFC				2	7	44
IPS	−15	−67	44	10	−65	48
SFG	−18	−4	54	19	−5	55
aINS	−30	20	8			
IFG				39	5	26
(B) Signal detection task						
pMFC				4	6	45
IPS	−19	−59	41	13	−63	45
SFG	−27	−10	43			
aINS	−31	18	8			
IFG	−43	2	28			
IPL	−36	−36	32			
pFs	−46	−49	−12			

Searchlight results

To rule out the possibility of uncertainty being modulated by general brain activation differences, we performed a GLM analysis directly comparing the fMRI signals during the two categorization tasks. Reaction times for each trial were modeled in the GLM. We found no significant task differences. To validate this result, we employed a more sensitive multivariate searchlight analysis (Kriegeskorte *et al.*, 2006) to identify brain areas that were differentially activated by the two categorization tasks. The whole brain searchlight analysis has the potential to discover information in unexpected brain areas (Kriegeskorte & Bandettini, 2007). Interestingly, we observed bilateral activations in the lateral occipital (LO), an area of the posterior lateral occipital complex that may represent global patterns (Ostwald *et al.*, 2008; Zhang *et al.*, 2010). We also observed activity in the right IPL. Both areas showed significant differential multi-voxel activations between the two tasks ($P < 0.01$, permutation-based random effect analysis, corrected for cluster size threshold; Fig. 4A). Outside of the LO and IPL, no other areas showed significant univariate or multivariate activations in this analysis.

Control analysis on letter identification task

Next, we performed a multivariate searchlight analysis to identify brain activations induced by the two physically dissimilar stimulus sets. The results showed no significantly different activations, further demonstrating that the LO activation was related to the categorization task. In other words, passive exposure to physically dissimilar stimuli does not contribute to this effect.

Discussion

Previous studies of decision uncertainty have focused on outcome probability (Critchley *et al.*, 2001; Paulus *et al.*, 2001; Volz *et al.*, 2003, 2004; Hsu *et al.*, 2005; Huettel *et al.*, 2005; Yoshida & Ishii, 2006; Stern *et al.*, 2010). In the present study, we focused on the neural mechanisms underlying modulation of perceptual uncertainty (Grinband *et al.*, 2006; Daniel *et al.*, 2011). Specifically, we investigated the task-dependent modulation of uncertainty in perceptual decision tasks based on criterion comparison and signal detection. Our results identified brain regions that correlate with uncertainty on both tasks. We also identified brain regions that correlate with uncertainty in a task-dependent manner. These findings advance our

understanding of adaptive perceptual decision-making in the human brain in several ways.

First, our study complements previous knowledge of the brain networks that are modulated by decision uncertainty. Converging evidence suggests that the pMFC plays an important role in monitoring behavioral performance. In addition, the activity of this area is correlated with the degree of decision uncertainty (Barch *et al.*, 2001; Critchley *et al.*, 2001; Volz *et al.*, 2003, 2004; Grinband *et al.*, 2006; Stern *et al.*, 2010; Daniel *et al.*, 2011). It has been suggested that the pMFC is involved in monitoring response conflict (Botvinick *et al.*, 2001). Response conflict is created when tasks require competition between candidate responses (Ridderinkhof *et al.*, 2004). The pMFC may also interact with the central executive control systems (e.g. the DLPFC) by delivering monitoring signals to these areas (Garavan *et al.*, 2002; Kerns *et al.*, 2004). Our results are in agreement with this proposal, in that fMRI signals in the pMFC are significantly modulated by perceptual uncertainty. This uncertainty is independent of the perceptual decision task being performed. In addition, we found that fMRI activity in both the DLPFC and the IPS is modulated by uncertainty on both tasks. These areas are part of the classical fronto-parietal loop, which is critical for top-down attentional processing and executive control (Culham & Kanwisher, 2001; Miller & Cohen, 2001; Grefkes & Fink, 2005). In addition to response conflict, increased attentional demand can occur when uncertain choices are faced. The modulation of uncertainty observed in the DLPFC and the IPS probably reflects the increased attentional resources triggered by a monitoring signal from the pMFC and allocated by the central executive system (Huettel *et al.*, 2005; Daniel *et al.*, 2011). Our results provide novel evidence that this fronto-parietal pathway underlies a general performance-monitoring mechanism that exists in different types of perceptual decision tasks.

Second, brain areas that are commonly modulated by uncertainty (e.g. the pMFC, DLPFC, and IPS) fit the criteria for 'comparator' areas identified in decision-making experiments (Heekeren *et al.*, 2006; Wunderlich *et al.*, 2009; Hare *et al.*, 2011). In particular, Hare *et al.* (2011) showed that the pMFC and IPS perform value comparisons based on the signals received from areas that encode stimulus values (i.e. the ventral medial prefrontal cortex). In our study, the values of stimuli were not explicitly manipulated. Instead, candidate perceptual evidence was compared by the central performance monitoring system before a final decision action was executed. Together with the previous findings, our results suggest that evidence comparison is a key performance-monitoring process in perceptual decision-making, and that this process is modulated by decision uncertainty.

Third, our results provide new insights into the neural mechanisms underlying perceptual decision tasks based on criterion comparison or signal detection. Our experimental design manipulated uncertainty levels in the criterion comparison task by morphing between two prototype patterns (radial and concentric). The task can be solved with a one-dimensional rule-based (i.e. the spiral angle) category decision (Ashby & Maddox, 2005). Previous studies have linked the right dorsal lateral prefrontal cortex with the retrieval of newly learned rules (Patalano *et al.*, 2001; Grossman *et al.*, 2003; Bunge, 2004). Our findings agree with this proposal, suggesting that uncertainty modulates fMRI signals in the right VLPFC and DLPFC in the criterion comparison task. Adding noise to visual stimuli increases processing demands related to the extraction and integration of visual features, thus increasing uncertainty. Accordingly, the results of the signal detection task show modulation of uncertainty in higher visual area (pFs) and stimulus-driven attention areas (IPL).

These areas are known as the early-stage perceptual information 'accumulators' (Ploran *et al.*, 2007; Donner *et al.*, 2009). Our study is the first to reveal task-dependent modulation of uncertainty at different stages of perceptual decision-making. In our study, the uncertainty created in both the criterion comparison and signal detection tasks modulated the cortical regions associated with late stages of perceptual decision-making, whereas only the uncertainty in the signal detection task modulated brain activity in the visual areas related to the early stages of perceptual processing. These findings support the theory that the human brain implements adaptive strategies to optimally represent task-relevant perceptual information (Duncan, 2001; Miller & Cohen, 2001).

Finally, our results provide novel evidence that the anterior and posterior portions of higher occipitotemporal areas play different roles in perceptual processing. Our parametric GLM revealed that stimulus-driven attention areas, including the IPL and the anterior portion of the higher occipitotemporal area (pFs), are modulated by decision uncertainty created when noise is added to visual stimuli. Our MVPA analysis also showed that activation differences on the two perceptual decision tasks in the posterior portion of the higher occipitotemporal area (LO) could be explained by sensory processing differences related to the two stimulus sets. Previous studies have shown that the brain activity measured by fMRI in the pFs represents more abstract information and correlates better with observers' perceptual states than activity in the LO (Grill-Spector *et al.*, 1999; Lerner *et al.*, 2001; Kourtzi *et al.*, 2003; Haushofer *et al.*, 2008). In our signal detection task, the fMRI-measured brain activity in the pFs was correlated with the increased perceptual uncertainty created by the degradation of Glass pattern stimulus signal coherence. Changes in brain activity in the LO, however, probably reflect differences in low-level sensory processing of the two different stimulus sets. These results support the proposal that the neural activity in the pFs is associated with the observers' perceptual states (i.e. uncertainty level), and that activity in the LO represents task-relevant stimulus differences.

Acknowledgements

Abbreviations

aINS, left anterior insular; DLPFC, left dorsal lateral prefrontal cortex; fMRI, functional magnetic resonance imaging; GLM, general linear model; IFG, inferior frontal gyrus; IPL, inferior parietal lobule; IPS, bilateral intraparietal sulcus; LO, lateral occipital; MVPA, multi-voxel pattern analysis; pFs, posterior fusiform; pMFC, posterior medial frontal cortex; SFG, superior frontal gyrus; VLPFC, ventral lateral prefrontal cortex.

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