

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.

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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 ($7.3^\circ \times 7.3^\circ$) 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

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 $0.5^\circ \times 0.5^\circ$ 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

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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

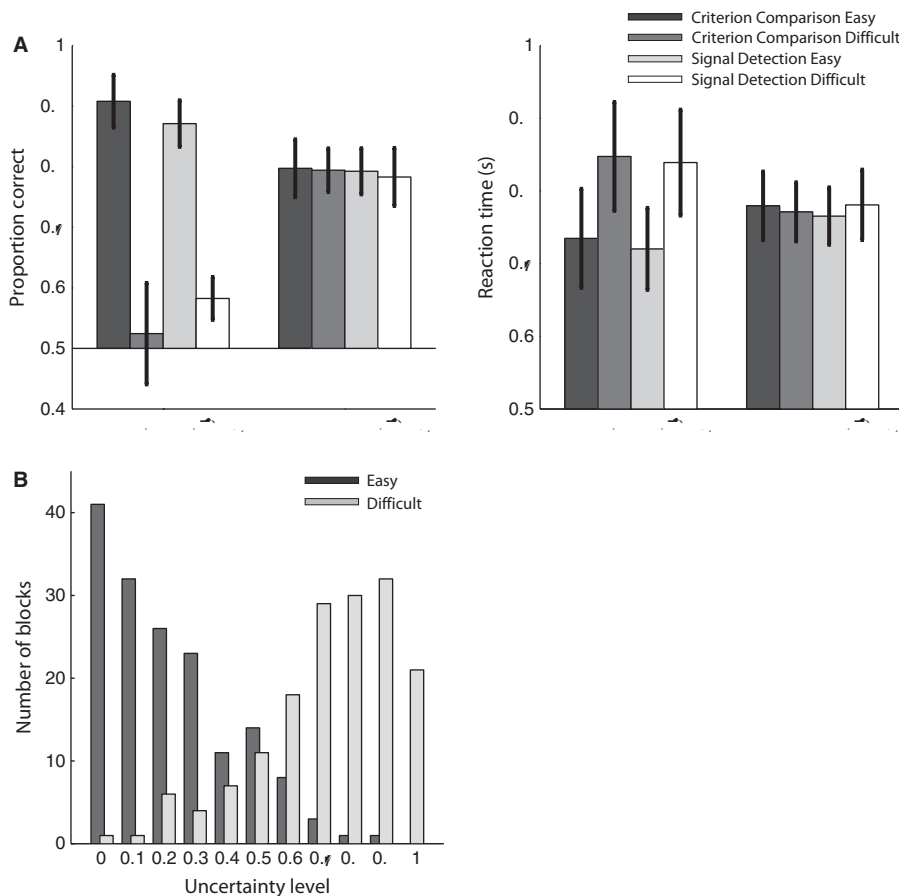


FIG. 2. Behavioral data. (A) Behavioral accuracy and reaction times on the categorization task and letter identification task during the fMRI session. The data are grouped by stimulus condition. Error bars indicate standard error of the mean across observers. (B) Distribution of uncertainty level for the easy and difficult conditions across two categorization tasks.

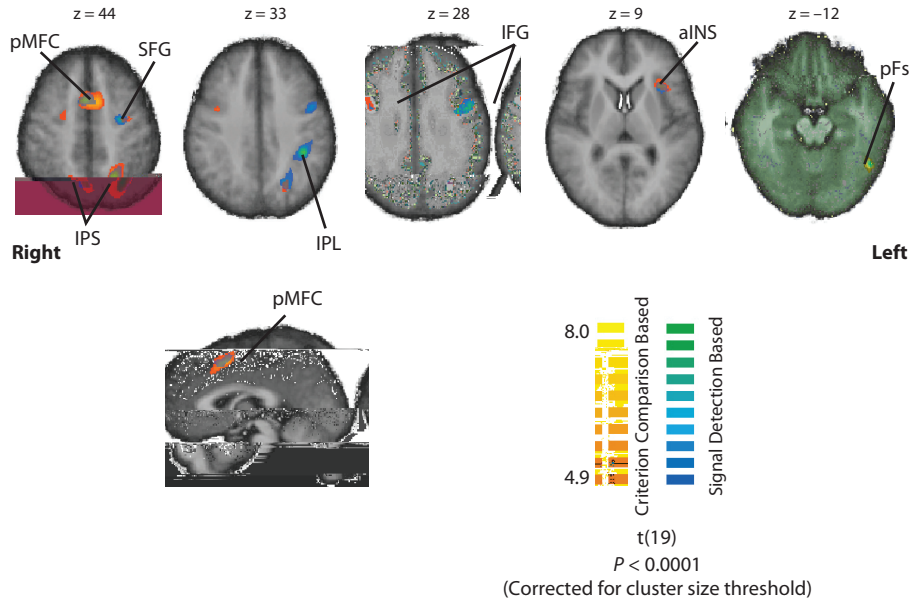


FIG. 3. fMRI result: uncertainty modulation. Random effects GLM analysis showed significant modulation of decision uncertainty ($P < 0.0001$, corrected for cluster size threshold) for the criterion comparison task and the signal detection task, respectively (see Table 1 for Talairach coordinates).

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 Talairach 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.

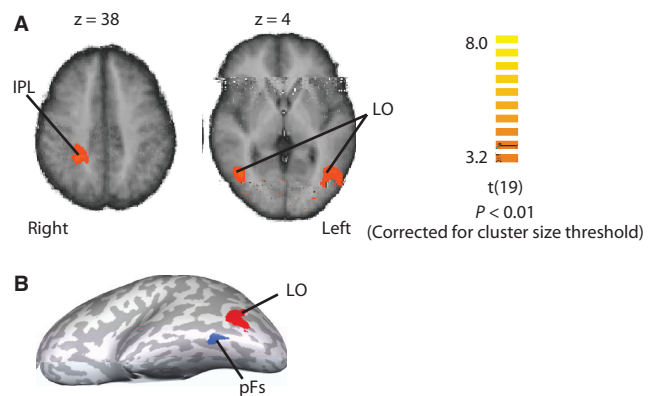


FIG. 4. fMRI result: searchlight analysis. (A) Multivariate searchlight analysis was performed to directly compare the fMRI-measured brain activity present during both categorization tasks. A second-level analysis (permutation t-test for observer accuracy) was performed to identify voxels showing significantly higher accuracy than chance ($P < 0.01$, corrected for cluster size

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.

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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.

References

- Ashby, F.G. & Maddox, W.T. (2005) Human category learning. *Annu. Rev. Psychol.*, **56**, 149–178.
- Barch, D.M., Braver, T.S., Akbudak, E., Conturo, T., Ollinger, J. & Snyder, A. (2001) Anterior cingulate cortex and response conflict: effects of response modality and processing domain. *Cereb. Cortex*, **11**, 837–848.
- Barthelme, S. & Mamassian, P. (2009) Evaluation of objective uncertainty in the visual system. *PLoS Comput. Biol.*, **5**, e1000504.

- Boettiger, C.A. & D’Esposito, M. (2005) Frontal networks for learning and executing arbitrary stimulus–response associations. *J. Neurosci.*, **25**, 2723–2732.
- Botvinick, M.M., Braver, T.S., Barch, D.M., Carter, C.S. & Cohen, J.D. (2001) Conflict monitoring and cognitive control. *Psychol. Rev.*, **108**, 624–652.
- Bullmore, E., Brammer, M., Williams, S.C., Rabe-Hesketh, S., Janot, N., David, A., Mellers, J., Howard, R. & Sham, P. (1996) Statistical methods of estimation and inference for functional MR image analysis. *Magn. Reson. Med.*, **35**, 261–277.
- Bunge, S.A. (2004) How we use rules to select actions: a review of evidence from cognitive neuroscience. *Cogn. Affect. Behav. Neurosci.*, **4**, 564–579.
- Corbetta, M., Kincade, J.M., Ollinger, J.M., McAvoy, M.P. & Shulman, G. L. (2000) Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nat. Neurosci.*, **3**, 292–297.
- Critchley, H.D., Mathias, C.J. & Dolan, R.J. (2001) Neural activity in the human brain relating to uncertainty and arousal during anticipation. *Neuron*, **29**, 537–545.
- Culham, J.C. & Kanwisher, N.G. (2001) Neuroimaging of cognitive functions in human parietal cortex. *Curr. Opin. Neurobiol.*, **11**, 157–163.
- Daniel, R., Wagner, G., Koch, K., Reichenbach, J.R., Sauer, H. & Schlosser, R.G. (2011) Assessing the neural basis of uncertainty in perceptual category learning through varying levels of distortion. *J. Cogn. Neurosci.*, **23**, 1781–1793.
- D’Esposito, M., Aguirre, G.K., Zarahn, E., Ballard, D., Shin, R.K. & Lease, J. (1998) Functional MRI studies of spatial and nonspatial working memory. *Brain. Res. Cogn. Brain. Res.*, **7**, 1–13.
- DiQuattro, N.E. & Geng, J.J. (2011) Contextual knowledge configures attentional control networks. *J. Neurosci.*, **31**, 18026–18035.
- Donner, T.H., Siegel, M., Fries, P. & Engel, A.K. (2009) Buildup of choice-predictive activity in human motor cortex during perceptual decision making. *Curr. Biol.*, **19**, 1581–1585.
- Duncan, J. (2001) An adaptive coding model of neural function in prefrontal cortex. *Nat. Rev.*, **2**, 820–829.
- Forman, S.D., Cohen, J.D., Fitzgerald, M., Eddy, W.F., Mintun, M.A. & Noll, D.C. (1995) Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): use of a cluster-size threshold. *Magn. Reson. Med.*, **33**, 636–647.
- Garavan, H., Ross, T.J., Murphy, K., Roche, R.A. & Stein, E.A. (2002) Dissociable executive functions in the dynamic control of behavior: inhibition, error detection, and correction. *Neuroimage*, **17**, 1820–1829.
- Glass, L. (1969) Moire effect from random dots. *Nature*, **223**, 578–580.
- Glass, L. & Perez, R. (1973) Perception of random dot interference patterns. *Nature*, **246**, 360–362.
- Goebel, R., Esposito, F. & Formisano, E. (2006) Analysis of functional image analysis contest (FIAC) data with brainvoyager QX: from single-subject tn19.(0activath5ea7fvior:)

- Haushofer, J., Livingstone, M.S. & Kanwisher, N. (2008) Multivariate patterns in object-selective cortex dissociate perceptual and physical shape similarity. *PLoS Biol.*, **6**, e187.
- Heekeren, H.R., Marrett, S., Bandettini, P.A. & Ungerleider, L.G. (2004) A general mechanism for perceptual decision-making in the human brain. *Nature*, **431**, 859–862.
- Heekeren, H.R., Marrett, S., Ruff, D.A., Bandettini, P.A. & Ungerleider, L.G. (2006) Involvement of human left dorsolateral prefrontal cortex in perceptual decision making is independent of response modality. *Proc. Natl. Acad. Sci. USA*, **103**, 10023–10028.
- Heekeren, H.R., Marrett, S. & Ungerleider, L.G. (2008) The neural systems that mediate human perceptual decision making. *Nat. Rev.*, **9**, 467–479.
- Hsu, M., Bhatt, M., Adolphs, R., Tranel, D. & Camerer, C.F. (2005) Neural systems responding to degrees of uncertainty in human decision-making. *Science*, **310**, 1680–1683.
- Huettel, S.A., Song, A.W. & McCarthy, G. (2005) Decisions under uncertainty: probabilistic context influences activation of prefrontal and parietal cortices. *J. Neurosci.*, **25**, 3304–3311.
- Kahneman, D. & Tversky, A. (1982) Variants of uncertainty. *Cognition*, **11**, 143–157.
- Kepecs, A., Uchida, N., Zariwala, H.A. & Mainen, Z.F. (2008) Neural correlates, computation and behavioural impact of decision confidence. *Nature*, **455**, 227–255.
- Kerns, J.G., Cohen, J.D., MacDonald, A.W. III, Cho, R.Y., Stenger, V.A. & Carter, C.S. (2004) Anterior cingulate conflict monitoring and adjustments in control. *Science*, **303**, 1023–1026.
- Kiani, R. & Shadlen, M.N. (2009) Representation of confidence associated with a decision by neurons in the parietal cortex. *Science*, **324**, 759–764.
- Koenig, P., Smith, E.E., Glosser, G., DeVita, C., Moore, P., McMillan, C., Gee, J. & Grossman, M. (2005) The neural basis for novel semantic categorization. *Neuroimage*, **24**, 369–383.
- Kourtzi, Z., Erb, M., Grodd, W. & Bulthoff, H.H. (2003) Representation of the perceived 3-D object shape in the human lateral occipital complex. *Cereb. Cortex*, **13**, 911–920.
- Kriegeskorte, N. & Bandettini, P. (2007) Analyzing for information, not activation, to exploit high-resolution fMRI. *Neuroimage*, **38**, 649–662.
- Kriegeskorte, N., Goebel, R. & Bandettini, P. (2006) Information-based functional brain mapping. *Proc. Natl. Acad. Sci. USA*, **103**, 3863–3868.
- Lerner, Y., Hendler, T., Ben-Bashat, D., Harel, M. & Malach, R. (2001) A hierarchical axis of object processing stages in the human visual cortex. *Cereb. Cortex*, **11**, 287–297.
- Li, S., Ostwald, D., Giese, M. & Kourtzi, Z. (2007) Flexible coding for categorical decisions in the human brain. *J. Neurosci.*, **27**, 12321–12330.
- Li, S., Mayhew, S.D. & Kourtzi, Z. (2009) Learning shapes the representation of behavioral choice in the human brain. *Neuron*, **62**, 441–452.
- Li, S., Mayhew, S.D. & Kourtzi, Z. (2012) Learning shapes spatiotemporal brain patterns for flexible categorical decisions. *Cereb. Cortex*, **22**, 2322–2335.
- Mayhew, S.D., Li, S., Storrar, J.K., Tsvetanov, K.A. & Kourtzi, Z. (2010) Learning shapes the representation of visual categories in the aging human brain. *J. Cogn. Neurosci.*, **22**, 2899–2912.
- Mazurek, M.E., Roitman, J.D., Ditterich, J. & Shadlen, M.N. (2003) A role for neural integrators in perceptual decision making. *Cereb. Cortex*, **13**, 1257–1269.
- Miller, E.K. & Cohen, J.D. (2001) An integrative theory of prefrontal cortex function. *Annu. Rev. Neurosci.*, **24**, 167–202.
- Muhammad, R., Wallis, J.D. & Miller, E.K. (2006) A comparison of abstract rules in the prefrontal cortex, premotor cortex, inferior temporal cortex, and striatum. *J. Cogn. Neurosci.*, **18**, 974–989.
- Nichols, T.E. & Holmes, A.P. (2002) Nonparametric permutation tests for functional neuroimaging: a primer with examples. *Hum. Brain Mapp.*, **15**, 1–25.
- Ostwald, D., Lam, J.M., Li, S. & Kourtzi, Z. (2008) Neural coding of global form in the human visual cortex. *J. Neurophysiol.*, **99**, 2456–2469.
- Patalano, A.L., Smith, E.E., Jonides, J. & Koeppel, R.A. (2001) PET evidence for multiple strategies of categorization. *Cogn. Affect. Behav. Neurosci.*, **1**, 360–370.
- Paulus, M.P., Hozack, N., Zauscher, B., McDowell, J.E., Frank, L., Brown, G.G. & Braff, D.L. (2001) Prefrontal, parietal, and temporal cortex networks underlie decision-making in the presence of uncertainty. *Neuroimage*, **13**, 91–100.
- Ploran, E.J., Nelson, S.M., Velanova, K., Donaldson, D.I., Petersen, S.E. & Wheeler, M.E. (2007) Evidence accumulation and the moment of recognition: dissociating perceptual recognition processes using fMRI. *J. Neurosci.*, **27**, 11912–11924.
- Ridderinkhof, K.R., Ullsperger, M., Crone, E.A. & Nieuwenhuis, S. (2004) The role of the medial frontal cortex in cognitive control. *Science*, **306**, 443–447.
- Romo, R., Hernandez, A. & Zainos, A. (2004) Neuronal correlates of a perceptual decision in ventral premotor cortex. *Neuron*, **41**, 165–173.
- Singer, T., Critchley, H.D. & Preusschoff, K. (2009) A common role of insula in feelings, empathy and uncertainty. *Trends Cogn. Sci.*, **13**, 334–340.
- Smith, E.E. & Jonides, J. (1997) Working memory: a view from neuroimaging. *Cogn. Psychol.*, **33**, 5–42.
- Stern, E.R., Gonzalez, R., Welsh, R.C. & Taylor, S.F. (2010) Updating beliefs for a decision: neural correlates of uncertainty and underconfidence.