TITLE: Predictions shape confidence in right inferior frontal gyrus

ABBREVIATED TITLE: Predictions shape confidence in rIFG

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Abstract

1   It is clear that prior expectations shape perceptual decision-making, yet their

2   contribution to the construction of subjective decision confidence remains largely

3   unexplored. We recorded fMRI data while participants made perceptual decisions

4   and confidence judgements, controlling for potential confounds of attention. We

5   recorded fMRI data while participants made perceptual decisions accompanied by

6   confidence judgements, controlling for potential confounds of attention. Results show

7   that subjective confidence increases as perceptual prior expectations increasingly

8   support the decision, and that this relationship is associated with BOLD activity in

9   right inferior frontal gyrus (rIFG). Specifically, rIFG is sensitive to the discrepancy

10 between expectation and decision (mismatch), and, crucially, higher mismatch

11 responses are associated with lower decision confidence. Connectivity analyses

12 revealed the source of the expectancy information to be bilateral orbitofrontal cortex

13 (OFC) and the source of sensory signals to be intracalcarine sulcus. Altogether, our

14 results indicate that predictive information is integrated into subjective confidence in

15 rIFG, and reveal an occipital-frontal network that constructs confidence from top-

16 down and bottom-up signals. This interpretation was further supported by exploratory

17 findings that the white matter density of intracalcarine sulcus and OFC negatively

18 predicted their respective contributions to the construction of confidence. Our

19 findings advance our understanding of the neural basis of subjective perceptual

20 processes by revealing an occipito-frontal functional network that integrates prior

21 beliefs into the construction of confidence.

22

1   **Significance statement**

2   Perceptual decision-making is typically conceived as an integration of bottom-up and

3   top-down influences. However, perceptual decisions are accompanied by a sense of

4   confidence. Confidence is an important facet of perceptual consciousness, yet

5   remains poorly understood. Here we implicate right inferior frontal gyrus (rIFG) in

6   constructing confidence from the discrepancy between perceptual judgement and its

7   prior probability. Furthermore, we place rIFG within an occipito-frontal network,

8   consisting of orbitofrontal cortex and intracalcarine sulcus, which represents and

9   communicates relevant top-down and bottom-up signals. Together, our data reveal a

10   role of frontal regions in the top-down processes enabling perceptual decisions to

11   become available for conscious report.

1 Perception is increasingly being seen as an active process, in which current or future

2 sensory states are inferred from predictive information (Engel et al., 2001; Lee, 2002;

3 Bar, 2007; Beck and Kastner, 2009; Fiser et al., 2010; Gilbert and Li, 2013). These

4 predictions can be modelled in Bayesian terms as prior beliefs, which bias

5 perceptual inference towards solutions that are *a priori* more likely in a given context

6 (Bülthoff et al., 1998; Seriès and Seitz, 2013; Trapp and Bar, 2015). Predictions, or

7 priors, can have striking effects on perception, especially under high sensory

8 uncertainty. For example, ambiguous rotational motion can be subjectively

9 disambiguated by prior exposure to rotation direction, such that a mean rotation

10 direction is perceived despite none existing in the physical stimulus (Maloney et al.,

11 2005). In laboratory conditions, such behavioural effects of prediction are typically

12 accompanied by increases in BOLD and ERP amplitude, as well as evoked gamma

13 power, over sensory (Kouider et al. 2015; Egner et al. 2010; Saaltink et al. 2015; Kok

14 et al. 2011; Jiang et al. 2013; Wacongne et al. 2011; Bauer et al. 2014) and decision-

15 related (Bubic et al., 2009) brain regions - a 'prediction error' response profile that

16 reflects the discrepancy between internal templates and perceptual content.

17 The perceptual content that forms the basis of our visual experience is accompanied

18 by a degree of subjective confidence. Confidence reflects the estimated success of a

19 perceptual choice, and can be seen as a gate for post-perceptual processes, such

20 as learning and belief-updating (Nassar et al., 2010; Yeung and Summerfield, 2012).

21 The communication of decision confidence can also facilitate group decision-making

22 (Bahrami et al., 2010). Yet, while subjective confidence is an integral part of

23 perceptual experience that can be easily probed in human subjects (Seth et al.,

24 2008; Sandberg et al., 2010; Overgaard and Sandberg, 2012; Fleming and Lau,

3

1 2014; Wierzchoń et al., 2014), the construction of confidence remains poorly

2 understood.

3 It is clear that confidence increases with evidence in support of the decision (Yeung

4 and Summerfield, 2012; Hebart et al., 2014; Fetsch et al., 2015; Gherman and

5 Philiastides, 2015). Decision and confidence are thought to evolve together until the

6 first-order, objective decision has been made (Ratcliff and Starns, 2009; Kepecs and

7 Mainen, 2012), and accordingly, there exists strong evidence for a common sensory

8 signal underlying both types of report (Kiani and Shadlen, 2009; Fetsch et al., 2014;

9 Kiani et al., 2014). Surprisingly, there has been much less research that considers

10 the role of prior expectations on subjective confidence. There is converging

11 behavioural evidence for subjective confidence increasing with prior evidence in

12 favour of the associated choice (Aitchison et al., 2015; Meyniel et al., 2015a;

13 Sherman et al., 2015), but the neural substrates of this have remained unexplored.

14 Here we aimed to identify brain regions in which prior perceptual expectations are

15 integrated into confidence judgements. Based on previous work, we reasoned that

16 confidence should be high when decisions are supported by prior knowledge, that is,

17 when the discrepancy between expectation and perceptual decision is low. We

18 therefore sought to identify brain regions that, first, are sensitive to both prediction

19 error and confidence, and second, in which confidence is negatively associated with

20 prediction error. In such a region, confidence would be associated with the mismatch

21 between internal templates and perceptual report.

22 We further hypothesised that regions found to integrate prior expectations into

23 confidence judgements (as described above) should be functionally connected with

24 two information sources: one that represents the decision evidence, or sensory

1   information; and one that represents the prior expectation. As confidence

2   increasingly depends on prior expectations, functional connectivity with the source of

3   the priors should increase. Similarly, when confidence is less dependent on priors,

4   functional connectivity with the sensory region should increase.

5

6   **Materials and Methods**

7   **Participants**

8   The study was approved by the Brighton and Sussex Medical School Research

9   Governance and Ethics Committee. Twenty-four healthy, English speaking and right-

10 handed subjects were tested. Data from five participants were excluded: two whose

11 thresholding failed (see section 'Staircases', Gabor hit rate = 2%, visual search d' = -

12 0.1); one for revealing abnormal vision only after scanning (and whose estimated

13 contrast thresholds were accordingly > 2SD from the mean); one for excessive head

14 movement in the scanner such that their T1 scan was unusable; and one for failing

15 to respond on 33% of trials (relative to a mean of 3%). This left 19 participants with

16 normal or corrected-to-normal vision for analysis. All participants gave informed,

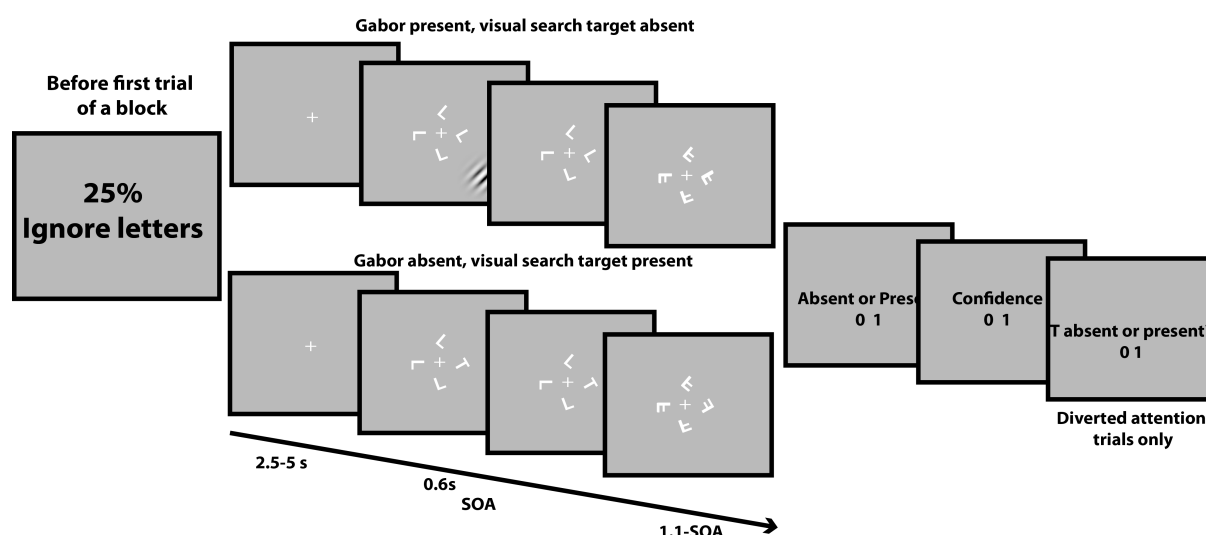17 written consent and were reimbursed £50 for their time.

Figure 1. Trial sequence. Blocks began with instructions signalling the expectation and attention condition. On each trial a visual search target T was either absent (top) or present (bottom) with 50% probability. On each trial a target Gabor was either present (top) or absent (bottom) with probability determined according to condition. Response cues followed the offset of the stimuli. Staircase trials were identical, except there was no condition-specific instruction at the beginning and only task-relevant response cues were presented.

Procedure

The experiment was conducted over three sessions at least 2 hours apart (no participant completed all three on a single day). In session one informed consent was obtained. Participants were trained on all tasks before scanning, which consisted of on-screen instructions, followed by a minimum of 10 practice trials of each task. Participants were encouraged to continue training until the task was well understood and response mappings learned.

To equate performance accuracy across conditions and subjects, participants subsequently completed three staircase procedures in the scanner but without acquiring echoplanar images (EPIs). Next, two 17 minute runs of experimental trials were completed while EPI scans were acquired.

1   Session two did not include a training component but was otherwise identical to

2   session one. Session three consisted of: 10 minutes for T1 acquisition; 15 minutes of

3   retinotopy (data from which is not used in this paper); and, time permitting, one more

4   experimental run.

5   After three sessions participants were compensated for their time and debriefed.

6   **Experimental design**

7   The paradigm used in the present study is adapted from a previously reported

8   design(Sherman et al., 2015). The visual display was identical in all sections of the

9   experiment (training, staircase and experimental). It consisted of a central visual

10   search array and the presence or absence of a to-be-detected, Gabor patch in the

11   periphery (see figure 1 and subsection 'Trial Sequence').

12   In experimental trials, the principal task was Gabor detection and two factors were

13   orthogonally manipulated: prior expectations of Gabor presence and attention to

14   Gabor detection. Expectations were manipulated block-wise, by changing the

15   probability of target Gabor presentation ($\mathbb{P}$ (Gabor present) = .25, .50 or .75). The

16   $\mathbb{P}$(Gabor present) = .25 condition induced an expectation of Gabor absence, whereas

17   the $\mathbb{P}$ (Gabor present) = .75 condition induced an expectation of Gabor presence.

18   The $\mathbb{P}$ (Gabor present) = .50 condition acted as a control (flat prior). Attention was

19   manipulated by instructing participants to either perform or ignore a visual search

20   task presented concurrently to the Gabor target. This task consisted of detecting

21   target 'T's amongst an array of distracter 'L's. Performing both tasks concurrently

22   diverted attention from the Gabor detection task, allowing us to separate effects of

23   expectation from those of attention.

1   These conditions were manipulated block-wise, in groups of 12 trials. Each condition

2   occurred once per scanning run in fully counter-balanced order. Before each

3   experimental block began participants were informed of both the expectation and

4   attention condition via the presentation of an instruction screen presented for 10

5   seconds (see figure 1). Participants were instructed to always maintain fixation at a

6   central cross.

7   **Trial sequence**

8   The trial sequence was identical for training, staircasing and experimental trials and

9   is shown in figure 1. Only instructions varied (see 'Experimental design'). Trials

10 began with a white fixation cross of random duration between 2.5 and 5 seconds.

11 Next, a visual search array appeared, which consisted of seven letters: either all

12 white, capital 'L's (50% chance), or a white, capital 'T' replacing an 'L' (50% chance).

13 All letters were equidistant from fixation and took an independently random

14 orientation. These were subsequently masked by a matching array of 'F's to increase

15 task difficulty. In total the visual search array was present for 1.1 seconds. The

16 stimulus onset asynchrony (SOA) between target and masking arrays was titrated for

17 each participant such that accuracy was at 78% (see Staircases).

18 On some trials a near-threshold (see section Staircases) peripheral Gabor patch

19 (orientation = 135°, phase 45° on 50% of trials, 225° on 50% of trials, sf = 2c/°,

20 Gaussian SD = 30) was additionally presented. On these trials the stimulus

21 appeared at the same time as the visual search array. To minimise attentional

22 capture it was presented over 0.6 seconds in a Gaussian time envelope so that it

23 had a gradual onset and offset. Stimulus contrast was titrated to equate performance

24 across levels of attention and participants at 78% accuracy (see Staircases).

1   The interval between offset of the masking array and onset of response prompts was

2   jittered during scanning only (i.e. experimental trials) to minimise motor cortex

3   activity reflecting response anticipation. Jitter was randomly selected from the

4   discrete values 1.3s:0.3s:3.1s.

5   Response prompts were presented at the end of the trial. The first prompt referred to

6   the Gabor detection task. 'Absent' responses were recorded by pressing the outer

7   left key and 'present' responses, the outer right key. This prompt was presented on

8   all trials except those of the visual search staircase procedure (only visual search

9   performed). The second prompt asked whether participants guessed (inner left) or

10   were confident (inner right) in their Gabor detection response (not presented on

11   staircasing trials). The third prompt was only presented on trials where participants

12   performed the Gabor detection task and the visual search task together (dual-task

13   trials). This asked whether the visual search target 'T' was absent (outer left) or

14   present (outer right). Response prompts remained onscreen for 2 seconds and

15   responses were coded as missed trials if no response was given within the allowed

16   time.

17   **Staircases**

18   Prior to each experimental session, three separate adaptive 1-up-3-down

19   psychophysical staircase procedures (9 reversals) were completed in the scanner.

20   Trials were identical to those in staircase trials (see Trial structure) except: there was

21   no manipulation of attention or expectation; the Gabor was always present, but

22   randomly oriented either 45° to the left or to the right; the Gabor task was 2AFC

23   orientation discrimination instead of target detection; confidence ratings were not

24   requested.

1   Staircase 1 titrated Gabor contrast to achieve 78% accuracy under full attention.

2   Initial contrast was 1.5%. The visual search array was masked after 0.5 seconds.

3   Participants were instructed to ignore the visual search array but still fixate centrally.

4   Staircase 2 titrated the SOA between the visual search array and masking array to

5   set performance at 78% (in the visual search task). Initial SOA was 500ms.

6   Participants ignored the 2AFC task and performed the visual search task. Here, the

7   ignored Gabor was presented at the contrast acquired in staircase 1.

8   Staircase 3 titrated Gabor contrast to achieve 78% accuracy (in Gabor detection)

9   under diverted attention. Initial contrast was set at that obtained in staircase 1 and

10   visual search SOA was set at the value obtained by staircase 2. Here, participants

11   performed both the Gabor and the visual search tasks. The visual search SOA was

12   set at the value obtained in the previous staircase and initial contrast was set at that

13   obtained in the first and titrated over the course of the staircase to obtain the diverted

14   attention contrast level.

15   **Statistical analyses**

16   Gabor detection sensitivity and decision threshold were quantified by computing type

17   1 signal detection theoretic (SDT) measures d' and c respectively. These are

18   computed by classifying trials as hits (h), misses (m), false alarms (fa) or correct

19   rejections (cr). Then,

20
$$HR = \frac{\sum h}{\sum h + \sum m} \text{ and } FAR = \frac{\sum fa}{\sum fa + \sum cr}$$

21   so that

22
$$d' = Z(HR) - Z(FAR) \text{ and } c = \frac{-(Z(HR) + Z(FAR))}{2},$$

10

1   where Z is the inverse cdf of the normal distribution.

2   To obtain a measure of confidence threshold (i.e. bias towards reporting 'confident'

3   or 'guess'), which we denote as C, we used type 2 SDT. Here trials are classified as

4   type 2 hits, misses, false alarms or correct rejections (Evans and Azzopardi, 2007).

5   While in the type 1 case these are given by comparing stimulus class and response,

6   in the type 2 case these are given by comparing decisional accuracy and confidence

7   report. For example, a type 2 hit is a confident and correct response, whereas a type

8   2 false alarm is a confident but incorrect response. C is then defined analogously to

9   c, but using type 2 hit rate and type 2 false alarm rate. This method allows us to

10   quantify confidence relative to decision accuracy.

11   Behavioural and follow-up statistical tests were run on JASP (Love, J., Selker, R.,

12   Marsman, M., Jamil, T., Dropmann, D., Verhagen, A. J., Ly, A., Gronau, Q. F.,

13   Smira, M., Epskamp, S., Matzke, D., Wild, A., Rouder, J. N., Morey, R. D. &

14   Wagenmakers, 2015). When the null hypothesis was predicted, Bayesian t-tests and

15   repeated-measures ANOVAs implemented the JASP default Cauchy prior of 0.7

16   HWHM. All results presented were robust to reasonable adjustments of this value.

17   Bayes factors greater than 1/3/10/100 are respectively interpreted as showing

18   insensitive/moderate/strong/very strong evidence for the alternative hypothesis(Kass

19   and Raftery, 1995). Bayes factors less than the reciprocal of these values are given

20   the same labels, but refer to the null hypothesis.

21   Unless otherwise stated, all repeated-measures ANOVA results met the assumption

22   of sphericity. Where sphericity was violated, corrected degrees of freedom and p-

23   values are presented. The Greenhouse-Geisser correction is used for small

24   violations ($\varepsilon < .75$) and the Huynh-Feldt correction for large violations ($\varepsilon > .75$).

1 **MRI acquisition and pre-processing**

2 Functional T2* sensitive echoplanar images (EPIs) were acquired on a Siemens

3 Avanto 1.5T scanner. Axial slices were tilted to minimise signal dropout from frontal

4 and occipital cortices. 34 2mm slices with 1mm gaps were acquired (TR = 2863ms,

5 TE = 50ms, FOV = 192mm x 192mm, Matrix = 64 x 64, Flip angle = 90°). Full brain

6 T1-weighted structural scans were acquired on the same scanner and were

7 composed of 176 1mm thick sagittal slices (TR = 2730ms, TE = 3.57ms, FOV =

8 224mm x 256mm, Matrix = 224 x 256, Flip angle = 7°) using the MPRAGE protocol.

9 Functional runs, each lasting 17 minutes, were collected per scanning session.

10 Images were processed using SPM8 software

11 (http://www.fil.ion.ucl.ac.uk/spm/software/spm8/). The first four functional volumes of

12 each run were treated as dummy scans and discarded. Images were pre-processed

13 using standard procedures: anatomical and functional images were reoriented to the

14 anterior commissure; images were slice-time corrected with the middle slice used as

15 the reference; EPIs were aligned to each other and co-registered to the structural

16 scan by minimising normalised mutual information. Next, EPIs were spatially

17 normalised to MNI space using parameters obtained from the segmentation of T1

18 images into grey and white matter. Finally, spatially normalised images were

19 smoothed with a Gaussian smoothing kernel of 8mm FWHM.

20 **fMRI statistical analysis**

21 At the participant level BOLD responses were time-locked to the onset of the visual

22 search array (which appeared at the same time as the Gabor, if present), enabling

23 us to examine BOLD responses to both target present and target absent trials.

24 BOLD responses were modelled in a GLM with regressors and their corresponding

12

1 temporal derivatives for each combination of the following factors: Attention (full,

2 diverted), Expectation (25%, 50%, and 75%), Stimulus (target present, target

3 absent), Report (yes, no) and Confidence (confident, guess). If a certain combination

4 of factors had no associated trials for a particular participant, that regressor was

5 removed from the participant's first level model and contrast weights rescaled.

6 The reliability of the regression weights was maximised by entering data from all

7 runs and sessions together, increasing the trial count per regressor. To avoid

8 smearing artefacts, no band-pass filter was applied. Instead, low-frequency drifts

9 were regressed out by entering white matter drift (averaged over the brain) as a

10 nuisance regressor (Law et al., 2005). Nuisance regressors representing the

11 experimental run and six head motion parameters were also included.

12 Comparisons of interest were tested by running one-sample t-tests against zero at

13 the participant level, then running group-level paired t-tests on the one-sample maps.

14 Unless otherwise stated, all contrasts at the group level were run with peak

15 thresholds of $p < .001$ (uncorrected) and corrected for multiple comparisons at the

16 cluster level using the FDR method.

17 We wanted to control for possible confounds between reaction speed and

18 confidence (which correlate (Petrusic and Baranski, 2003; Grinband et al., 2006),

19 and between individual or condition-wise differences in Gabor contrast and

20 confidence (which correlate, Rahnev et al., 2011). To do this, a control GLM was

21 computed. Here, each regressor was parametrically modulated by both Gabor

22 contrast and reaction time. By design, in this model confidence was independent of

23 reaction time and BOLD amplitude was independent of individual and condition-wise

24 differences in stimulus contrast. The Results section reports analyses on our main

13

1 model, i.e. that which does not model Gabor contrast and reaction speed. We did

2 this because the control model has a four-fold increase in number of regressors,

3 reducing statistical power. Nonetheless, all GLM analyses were replicated under our

4 control model when using a peak threshold of $p < .005$. Crucially, all results under

5 rIFG were also replicated when using a peak threshold of $p < .001$.

6 Functional ROIs were defined using the MarsBaR 0.42 toolbox

7 (http://marsbar.sourceforge.net/download.html). Anatomical areas showing

8 significant differences in BOLD were identified using the SPM Anatomy toolbox

9 (Eickhoff et al., 2005) and Brodmann areas were identified using MRIcro (Rorden

10 and Brett, 2000). Results of whole-brain analyses were plotted onto glass brains

11 using MATcro (http://www.mccauslandcenter.sc.edu/CRNL/tools/surface-rendering-

12 with-matlab).

Psychophysiological interaction (PPI) analysis

14 The psychophysiological interaction analysis (PPI) was performed using the CONN

15 functional connectivity toolbox (http://web.mit.edu/swg/software.htm). The GLM

16 comprised regressors for attention condition (full/diverted), confidence

17 (confident/guess) and expectation-response congruence

18 (congruent/neutral/incongruent). Nuisance regressors were identical to those used in

19 the GLM on BOLD. Again, the signal was not band-pass filtered but instead the

20 mean WM drift was entered as a nuisance regressor. The data were denoised by

21 regressing out signal from white matter, CSF and each individual condition, plus

22 signal associated with all nuisance regressors. The PPI was run on univariate

23 regression weights to identify effective connectivity between a functionally defined

24 seed and remaining voxels. These weights were examined in a second level model

1 which used an uncorrected peak threshold of $p < .005$ and FWE cluster corrected

2 threshold of $p < .05$.

3 **Voxel-based morphometry (VBM)**

4 T1-weighted structural scans were reoriented to the anterior commissure and

5 segmented into grey matter (GM), white matter (WM) and CSF. These were

6 normalised to MNI space using DARTEL with SPM defaults and a Gaussian

7 smoothing kernel of 8mm FWHM (Ashburner and Friston, 2000). White matter and

8 grey matter images were separately compared across participants in a multiple

9 regression with age and total intracranial volume (GM + WM + CSF) as nuisance

10 regressors. Including gender resulted in multicollinearity (older participants were

11 more likely to be male) so gender was not modelled. Unless reported otherwise,

12 clusters reported as significantly correlating with behaviour survived voxel-wise FWE

13 correction.

14 <center>**Results**</center>

15 **Expectations liberalise decisions and attention increases contrast sensitivity**

16 Our first analyses confirmed the efficacy of our paradigm. To equate difficulty across

17 attention conditions and participants, adaptive psychophysical staircases identified

18 the stimulus contrast required for 78% accuracy on the Gabor detection task (see

19 Methods subsection Staircases). Comparing the acquired contrasts in the full ($M =$

20 4.34%, $SD = 3.50\%$) and diverted ($M = 5.69\%$, $SD = 3.79\%$) attention conditions

21 revealed that contrast thresholds were significantly lower under full than diverted

22 attention, $t(19) = 2.95$, $p = .014$, 95%CI [0.50%, 2.31%], $d_z = 0.70$ (fig. 2A). Thus, our

23 paradigm successfully manipulated attention.

1   To ensure that our staircase procedure successfully equated detection sensitivity *d'*

2   across conditions we ran a within-subjects Attention (full, diverted) $\times$ Expectation

3   (25%, 50%, 75%) ANOVA. This revealed no significant difference between *d'* under

4   full (M = 1.06, SE = 0.14) and diverted (M = 1.21, SE = 0.20) attention conditions,

5    $F(1,18) = 0.34$, *p* = .569, η_p^2 = .02 (fig. 2B), and was corroborated by a Bayesian

6   repeated-measures ANOVA of the same design that revealed moderate evidence for

7   the null hypothesis (BF = 0.240). There was also no significant effect of Expectation

8   on *d'*, $F(2,36) = 0.70$, *p* = .505, η_p^2 = .04, BF = 0.07 (strong evidence for the null) and

9   no significant interaction term $F(2,36) = 0.76$, *p* = .476, η_p^2 = .04, BF = 0.016 (strong

10   evidence for the null). Our staircases therefore successfully equated *d'*.

11   To determine whether we had successfully manipulated priors, we compared signal

12   detection theoretic decision thresholds (*c,* see Methods) across expectation

13   conditions (de Lange et al., 2013; Morales et al., 2015; Sherman et al., 2015). As the

14   expectation of Gabor presence over absence increases, decision threshold should

15   become increasingly biased towards 'yes' responses (i.e. liberalised, shown by

16   smaller values of *c*). This was confirmed in a within-subjects Attention (full, diverted)

17    $\times$ Expectation (25%, 50%, 75%) ANOVA, $F(1.65, 29.72) = 18.10$, *p* < .001, η_p^2 = .50.

18   LSD post-hoc tests revealed a greater bias towards reporting 'yes' in the 50%

19   (neutral) than the 25% (expect absent) condition, *p* = .010, d_z = 1.15, and greater still

20   in the 75% (expect present) than the 50% (neutral) condition, *p* < .001, d_z = 1.39 (fig.

21   2C). We found no evidence for attentional effects on decision threshold, $F(1, 18) =$

22   3.38, *p* = .083, η_p^2 = .16, and no Expectation $\times$ Attention interaction, $F(2, 36) = 0.37$,

23   *p* = .693, η_p^2 = .020. Summarising these results, our design successfully

24   independently manipulated attention and expectation, while keeping detection
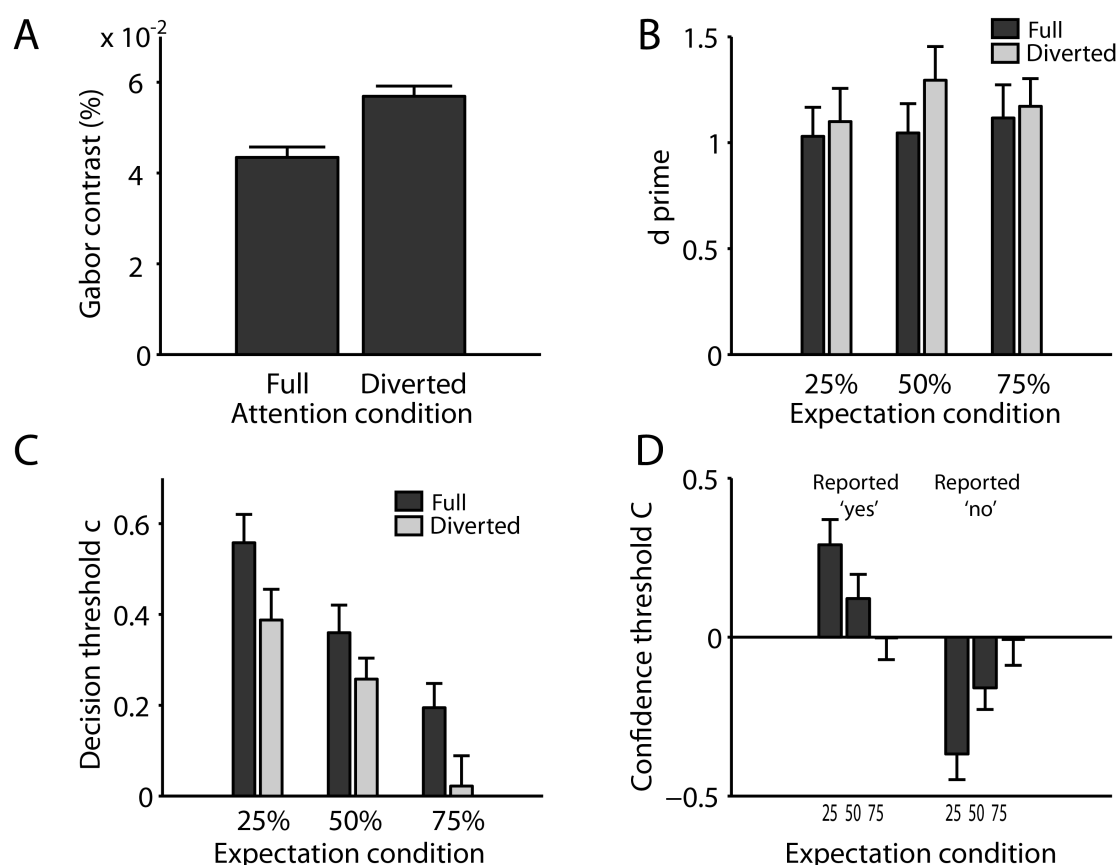
25   sensitivity constant across conditions.

Figure 2. Behavioural effects of expectation and attention on objective and subjective decision-making. **A.** Stimulus contrast as a function of attention condition. To achieve 78% correct on the Gabor detection task contrast had to be higher under diverted than full attention. **B.** Detection sensitivity d' as a function of expectation and attention condition. No significant differences were found. **C.** Decision threshold *c* as a function of expectation and attention condition. Independently of attention, bias towards reporting 'yes' (lower values of *c*) increases with the prior probability of Gabor presence **D.** Confidence threshold *C* as a function of expectation and perceptual report. Confidence for 'yes' responses increases (lower values of *C*) with increasing prior probability of target presence. Confidence for 'no' increases with increasing prior probability of target absence. Effect of expectation on type 2 C (confidence threshold). Therefore, confidence increases with expectation-response congruency. Error bars represent within-subjects SEM.

1 **Expectations liberalise confidence judgements**

2 We have previously shown that subjective confidence increases when perceptual

3 decisions are congruent with prior expectations (Sherman et al., 2015), and on this

1 basis hypothesised that confidence would relate to prediction error signals. To

2 determine whether we had replicated this behavioural result, we compared

3 confidence for perceptual decisions that were congruent with expectations against

4 those that were incongruent. Congruent responses are 'yes' reports in the 75%

5 (expect present) condition and 'no reports in the 25% (expect absent) condition. The

6 reverse applies for incongruent responses. Confidence was analysed using type 2

7 SDT (see Methods for details). Broadly, while decision threshold c quantifies the

8 extent to which perceptual decisions are biased towards 'no' reports, confidence

9 threshold C quantifies bias towards reporting 'guess' over 'confident'. An Attention $\times$

10 Expectation $\times$ Report ANOVA on confidence threshold C revealed that we replicated

11 our previous finding. There was a significant Expectation $\times$ Report interaction,

12 $F(2,38) = 22.78$, $p < .001$, $\eta_p^2 = .555$, such that when participants reported 'yes',

13 participants became more likely to report decisions with confidence as the prior

14 probability of target presence increased, $F(1,18) = 17.00$, $p = .001$, $\eta^2 = .486$.

15 Similarly, when participants reported 'no', high confidence became more likely as the

16 prior probability of target absence increased, $F(1,18) = 15.51$, $p = .001$, $\eta^2 = .463$

17 (figure 2D).

18 **Two forms of congruency**

19 To unravel the neural correlates of predictive influences on confidence, we first

20 needed to identify brain regions sensitive to perceptual expectations. We predicted,

21 based on previous work, that areas sensitive to perceptual expectations would

22 exhibit an increased BOLD amplitude for trials on which expectations were violated

23 (Egner et al., 2010; Kok et al., 2011; Jiang et al., 2013; John-saaltink et al., 2015;

24 Kouider et al., 2015). There are two possible ways to define expectancy violations

25 here. Because the experimental design used near-threshold stimuli, leading to

18

1   potential dissociations between percept and physical stimulus presentation,

2   violations could occur with respect to either physical stimulus presentation, or

3   perceptual report. We term the neural correlates of these types of incongruence

4    $PE_{STIMULUS}$ and PE_{REPORT} respectively. The former reflects the BOLD response to

5   discrepancy between internal templates and stimulus presentation, whereas the

6   latter reflects the BOLD response to discrepancy between internal templates and

7   participants' reported percept. $PE_{STIMULUS}$ is most often observed at lower levels of

8   the perceptual hierarchy[15–20], whereas the decision-related PE_{REPORT} signals are

9   often reported in higher-level, decision-related areas (Bubic et al., 2009), though they

10   can be observed in visual cortex as well (Pajani et al., 2015).

11   **Representation of $PE_{STIMULUS}$ in visual cortex**

12   In our first analysis, we searched for regions that are sensitive to discrepancies

13   between expectation and stimulus presentation ($PE_{STIMULUS}$) over whole brain. To do

14   this, we computed the contrast unexpected stimulus presentation > expected

15   stimulus presentation. Target presence is expected in the 75% condition but

16   unexpected in the 25% condition. Target absence is expected in the 25% condition

17   but unexpected in the 75% condition. Our analysis identified one $PE_{STIMULUS}$-

18   sensitive area in contralateral occipital cortex (V1 to V3, BA18, peak MNI x = -12, y =

19   -80, z = 22, Z_{peak} = 4.09, 0.66cm^3, cluster p_{FDR} = .350, p_{uncorr} = .023) and one on the

20   ipsilateral side (V1 to V3, BA18, peak MNI x = 8, y = -80, z = 18, Z_{peak} = 3.99,

21   1.01cm^3, cluster p_{FDR} = .205, p_{uncorr} = .007). Neither of these clusters survived

22   cluster-level correction, so they will not be considered beyond this point. They are

23   presented to simply to show consistency with previous studies, in which statistical

24   power was improved by constraining the analysis with functional localisers (Smith

19

1   and Muckli, 2010; Kok et al., 2011, 2012; Larsson and Smith, 2012; Jiang et al.,

2   2013) .

3   The whole-brain contrast $PE_{STIMULUS,\ attended} > PE_{STIMULUS,\ unattended}$ yielded no

4   significant or marginally significant clusters, indicating no evidence for a $PE_{STIMULUS}$

5     $\times$ attention interaction.

6   Using a peak threshold of $p < .005$ both of these analyses were replicated under our

7   control model, which included reaction speed and Gabor contrast as parametric

8   modulators (unexpected > expected, contralateral: $p_{FDR} = .446$, $p_{uncorr} = .014$,

9   ipsilateral: $p_{FDR} = .446$, $p_{uncorr} = .011$).

10   **Regions representing PE_{REPORT}**
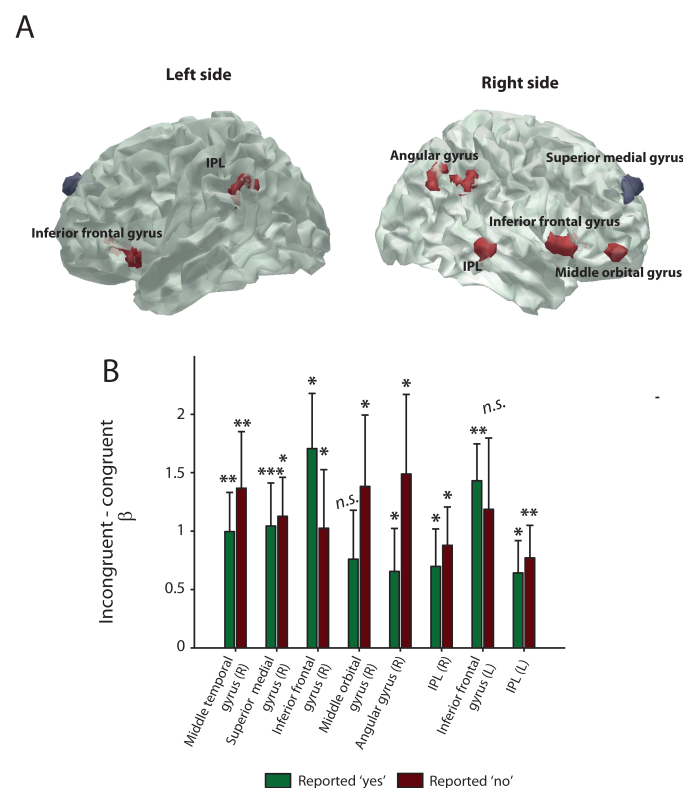
Figure 3. Report prediction error. **A.** Results of contrast incongruent response > congruent response over whole brain. Only clusters surviving FDR cluster-correction

are shown. **B.** PE_{REPORT} (incongruent – congruent), by region and perceptual report. BOLD has been averaged over levels of attention. Stars represent whether PE_{REPORT} is significantly different from zero. Error bars represent SEM * *p < .05,* ** *p* < .01,   *** *p* < .001

1   Next, we searched for regions whose BOLD response reflects the discrepancy

2   between expectation and perceptual report (PE_{REPORT}). Expectation-congruent

3   reports are 'yes' responses in the 75% (expect present) condition and 'no' responses

4   in the 25% (expect absent) condition. The reverse applies for expectation-

5   incongruent reports. These definitions differ from those in the previous analysis,

6   because they consider perceptual report instead of stimulus presence or absence.

7   The contrast expectation-incongruent report > expectation-congruent report was

8   computed over whole-brain. This revealed eight significant clusters reflecting

9   PE_{REPORT}, distributed throughout cortex (figure 3A and table 1). Our control analysis

10 revealed that this effect was not driven by differences in Gabor contrast or reaction

11 speed. We found no significant clusters for the reverse contrast, even with a more

12 liberal peak threshold of *p* < .005 uncorrected.

Table 1. Results of whole-brain analysis expectation-incongruent report > expectation-congruent report

Region	BA	Side	Volume (cm^3)	Peak z-value	p_{FDR}	Peak MNI		
						X	y	z
Middle temporal gyrus	21	R	2.29	4.78	.007	54	-30	-2
Superior medial gyrus	9/10	R	4.15	4.54	< .001	12	58	32
Inferior frontal gyrus	**47/48**	**R**	**2.70**	**4.45**	**.004**	**56**	**12**	**-2**
Middle orbital gyrus	47/46	R	2.08	4.33	.009	40	50	-6

Angular gyrus	39	R	1.21	3.95	.044	46	-64	36
Inferior parietal lobule	40	R	1.21	3.91	.044	58	-40	40
Inferior frontal gyrus	47	L	1.90	3.79	.012	-38	26	-4
Inferior parietal lobule	40/48	L	1.60	3.75	.021	-54	-46	34

1 Regions exhibiting a PE_{REPORT} pattern should show heightened BOLD for

2 incongruent responses irrespective of whether that response was a 'yes' or a 'no'

3 (Kok et al., 2011). To test this in the above ROIs, median regression coefficients

4 were extracted as a function of attention, expectation and report, and subjected to

5 separate repeated-measures ANOVAs. Results are depicted in figure 3B and

6 statistics are presented in table 2. All regions exhibited a significant PE_{REPORT}

7 response for both 'yes' and 'no' judgements, except middle orbital gyrus and left

8 inferior frontal gyrus. As a result these are not considered regions representing

9 PE_{REPORT}.

10 All significant results here were replicated (at least at marginal significance) under

11 our control model (for rIFG, our critical region, p_{FDR} = .044). Results were fully

12 replicated when using a peak threshold of $p < .005$.

13 We have therefore identified six regions signalling PE_{REPORT}: Right middle temporal

14 gyrus (rMTG); right superior medial gyrus (rSMG), right inferior frontal gyrus (rIFG);

15 right angular gyrus (rAG); and bilateral inferior parietal lobule (IPL). These results

16 implicate this set of regions as having sensitivity to the discrepancy between

17 perceptual expectations and perceptual choice.

18

Table 2. Effect of expectation, separately for 'yes' and 'no' reports. Both effects should be significant for the region to be deemed a PE_{REPORT} region

Region	Reported 'no'			Reported 'yes'			PE_{REPORT} represented
	F	p	η^2	F	p	η^2	
Middle temporal gyrus	8.82	.008	3.29	5.83	.006	.245	Yes
Superior medial gyrus	8.10	.001	.310	4.46	.014	.213	Yes
Inferior frontal gyrus (R)	**4.70**	**.015**	**.207**	**3.45**	**.041**	**.162**	**Yes**
Middle orbital gyrus	1.95	.157	.098	3.42	.044	.160	No
Angular gyrus	3.52	.040	.164	4.07	.025	.185	Yes
Inferior parietal lobule (R)	4.71	.044	.207	7.17	.015	.285	Yes
Inferior frontal gyrus (L)	5.62	.008	.238	2.87	.070	.137	No
Inferior parietal lobule (L)	5.39	.032	.230	6.04	.005	.251	Yes

1

2   **High confidence is associated with an attenuated PE_{REPORT} response in right**

3   **IFG**

4   Our main hypothesis was that high confidence would be associated with low

5   PE_{REPORT}. However, confidence can be also influenced by attention (Rahnev et al.,

6   2011) and tracks accuracy (Dienes, 2008; Pleskac and Busemeyer, 2011). To test

7   whether any PE_{REPORT} region represented confidence after controlling for these

8   potential confounds, median regression weights from each PE_{REPORT} region were

9   extracted as a function of confidence, attention and decision accuracy. These

10   regression coefficients were then subjected to separate Bayesian repeated-

11   measures ANOVAs. We were looking for regions whose BOLD response (in these

12   regions, representing PE_{REPORT}) differs with confidence. Note that we could not test

13   for a $PE_{REPORT} \times$ Confidence interaction because the participant has signalled low

1 confidence yes/no decisions as unreliable, that is, their perception of Gabor

2 presence or absent does not necessarily correspond to their report.

3 Only one region demonstrated a BOLD response (i.e. PE_{REPORT} amplitude) that

4 differed as a function of subjective confidence: rIFG. Here, supporting our

5 hypothesis, BOLD amplitude was higher for guess than confident reports (figure 4A).

6 Crucially, the analysis revealed substantially more evidence for modelling rIFG

7 BOLD as a function of confidence alone (BF = 13.620) than as a function of just

8 accuracy (BF = 0.877), just attention (BF = 0.711), or as a combination of confidence

9 and any other factors (BF = 0.003 - 2.069, see table 3 for summary of results from all

10 ROIs). A frequentist ANOVA gave the same result: a significantly higher BOLD

11 amplitude for guess than confident responses, $F(1,18) = 6.04$, $p = .024$, $\eta^2 = .251$,

12 95% CI [0.10, 1.28]. These results are depicted in figure 4B.

13 Next, we wanted to confirm that the effect of confidence on rIFG BOLD indeed

14 reflects changes in PE_{REPORT}. To do this, we restricted our analysis to confident

15 responses and asked whether PE_{REPORT} decreases as expectations exert stronger

16 influences on behavioural confidence. This would show that high confidence is

17 associated with low PE_{REPORT} amplitude (i.e. a low expectation-report mismatch

18 response). Furthermore, it would show that our behavioral effect of expectation on

19 confidence is reflected in rIFG BOLD.

20 To test this, we calculated ΔC = incongruent type 2 C - congruent type 2 C. The

21 group-level mean of ΔC is reflected in the slopes of figure 2D. This quantity reflects

22 the extent to which confidence judgements are influenced (or weighted) by

23 expectations. Next, we computed the BOLD difference between incongruent and

24 congruent reports (PE_{REPORT}), restricted to confident responses. Results showed that

1   these quantities were negatively correlated, ρ = -.607, *p* = .007 (fig. 4C), confirming

2   our finding that high confidence is associated with low PE_{REPORT} in rIFG: the more

3   expectation increased confidence behaviourally, the more confidence was

4   associated with low rIFG PE_{REPORT}.

5   To ensure that these differences were not driven by differences in reaction speed or

6   Gabor contrast, we extracted data from the cluster revealed by our control GLM. This

7   revealed that even after controlling for these possible confounds, rIFG BOLD was

8   significantly higher for guess that confident responses $t(18) = 2.21$, *p* = .041, d_z =

9   0.44. The significant brain-behaviour correlation was also replicated, rho = -.575, *p* =

10   .014.

11   Together, these analyses reveal that subjective confidence is reliably associated with

12   PE_{REPORT} in right IFG, even after controlling for attention, Gabor contrast, decision

13   accuracy and reaction speed.

14
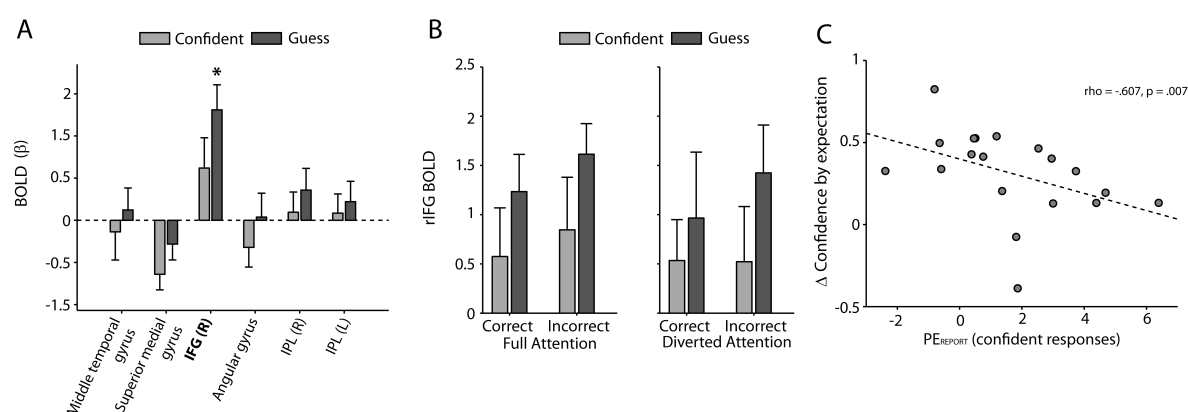
Figure 4. The relationship between confidence and report prediction error. **A**. BOLD as a function of confidence in each PE$_{REPORT}$ region. BOLD is higher for guess than confident responses in rIFG only. **B.** rIFG BOLD is higher for guess than confident responses independently of attention and decision accuracy **C.** Brain-behaviour correlation. The higher the PE$_{REPORT}$ response (confident reports only), the less that expectations increased confidence. Error bars represent +/- SEM. * $p < .05$, ** $p < .01$ *** $p < .001$

Table 3. Results of Bayesian Confidence x Accuracy x Attention repeated-measures ANOVAS. Bayes factors correspond to the evidence for the listed model relative to the evidence for all other models

Region	Bayes factors				
	Confidence	Accuracy	Attention	Confidence + others	Null
Middle temporal gyrus	0.137	0.681	4.961	0.012-2.255	1.000
Superior medial gyrus	0.850	1.793	1.958	0.025-2.666	1.11
Inferior frontal gyrus (R)	**13.620**	**0.877**	**0.711**	**0.003-2.069**	**3.958**
Angular gyrus	1.351	9.830	0.527	0.005-3.417	3.467
Inferior parietal lobule (R)	2.635	0.844	2.419	0.003-1.130	10.065
Inferior parietal lobule (L)	1.741	5.517	1.841	0.002-1.170	10.22

1

2 **Sources of priors and sensory signals for confidence.**

3 We have shown that rIFG activity associates response prediction error with

4 confidence. Assuming a model in which decision confidence is a weighted function of

5 top-down expectations and 'bottom-up' sensory signals (or decision evidence), we

6 asked whether we could identify sources of these variables. To do this we ran a

7 seed-to-voxel psychophysiological interaction analysis (PPI), with rIFG as a

8 functionally defined seed.

9 We were interested in regions communicating predictive information, and therefore

10 regions of interest would demonstrate functional connectivity with rIFG that differs for

11 congruent and incongruent reports. We reasoned that while confidence should be a

26

1   function of both sensory signals and expectations, there would be individual

2   differences in how each component would be weighted, reflecting, for example, how

3   reliable the expectation information is thought to be. Capitalising on these individual

4   differences, we reasoned that rIFG would show stronger functional connectivity with

5   the expectation region in participants whose confidence was weighted more by

6   expectation. By contrast, rIFG would show stronger functional connectivity with the

7   source of sensory signals in participants whose confidence was only weakly shaped

8   by expectation.

9   To test this hypothesis we used a behavioural covariate of interest – the influence of

10   expectations on confidence. This weighting function was assumed to be a function of

11   the aforementioned behavioural variable $\Delta C = C_{\text{Incongruent}} - C_{\text{Congruent}}$. , where C

12   denotes confidence thresholds. This quantity is the same as the behavioural variable

13   in figure 4B. Higher values signify that expectations exerted a stronger influence on

14   confidence.

15   Sources of predictive information for confidence were identified by computing the

16   contrast incongruent ≠ congruent, with ΔC as a between-subjects covariate of

17   interest.

18   As shown in figure 5 (A-C), the PPI analysis revealed three significant clusters. The

19   more expectations shaped confidence (higher ΔC), the more that congruence was

20   associated with functional connectivity (FC) between rIFG and left orbitofrontal

21   cortex (ΔC x congruent > incongruent; peak MNI $x = -34$, $y = 36$, $z = 20$, 2.82cm^3,

22   cluster $P_{\text{FDR}} = .020$) and right orbitofrontal cortex (ΔC x congruent > incongruent;

23   peak MNI $x = 10$, $y = 26$, $z = -18$, 2.16cm^3, cluster $P_{\text{FDR}} = .036$). On the other hand,

24   the less expectations shaped confidence the more that congruence was associated

27

1. with FC between rIFG and intracalcarine sulcus (ΔC x congruent > incongruent: peak

2. MNI x = 6, y = -58, z = 12, 2.92cm^3, cluster P_{FDR} = .025). Thus, intracalcarine sulcus

3. and bilateral orbitofrontal cortices (OFC) exhibited a push-pull relationship, with the

4. dominant region predicted by ΔC.

5. Although the *balance* of FC between these regions was determined by ΔC, FC

6. between these rIFG and these regions was present independently of ΔC.

7. Specifically, FC between rIFG and OFC was significantly stronger on congruent than

8. incongruent trials (lOFC p = .009, rOFC p = .043), whereas intracalcarine sulcus-

9. rIFG FC was marginally stronger on incongruent than congruent trials (p = .078).

10. Because bilateral OFC was primarily associated with congruent responses, we

11. reasoned that functional connectivity with these regions might reflect the

12. communication of perceptual priors. Consistent with this, we found a main effect of

13. expectation condition on lOFC BOLD F(2,36) = 3.61, p = .037, η_p^2 = .167, such that

28
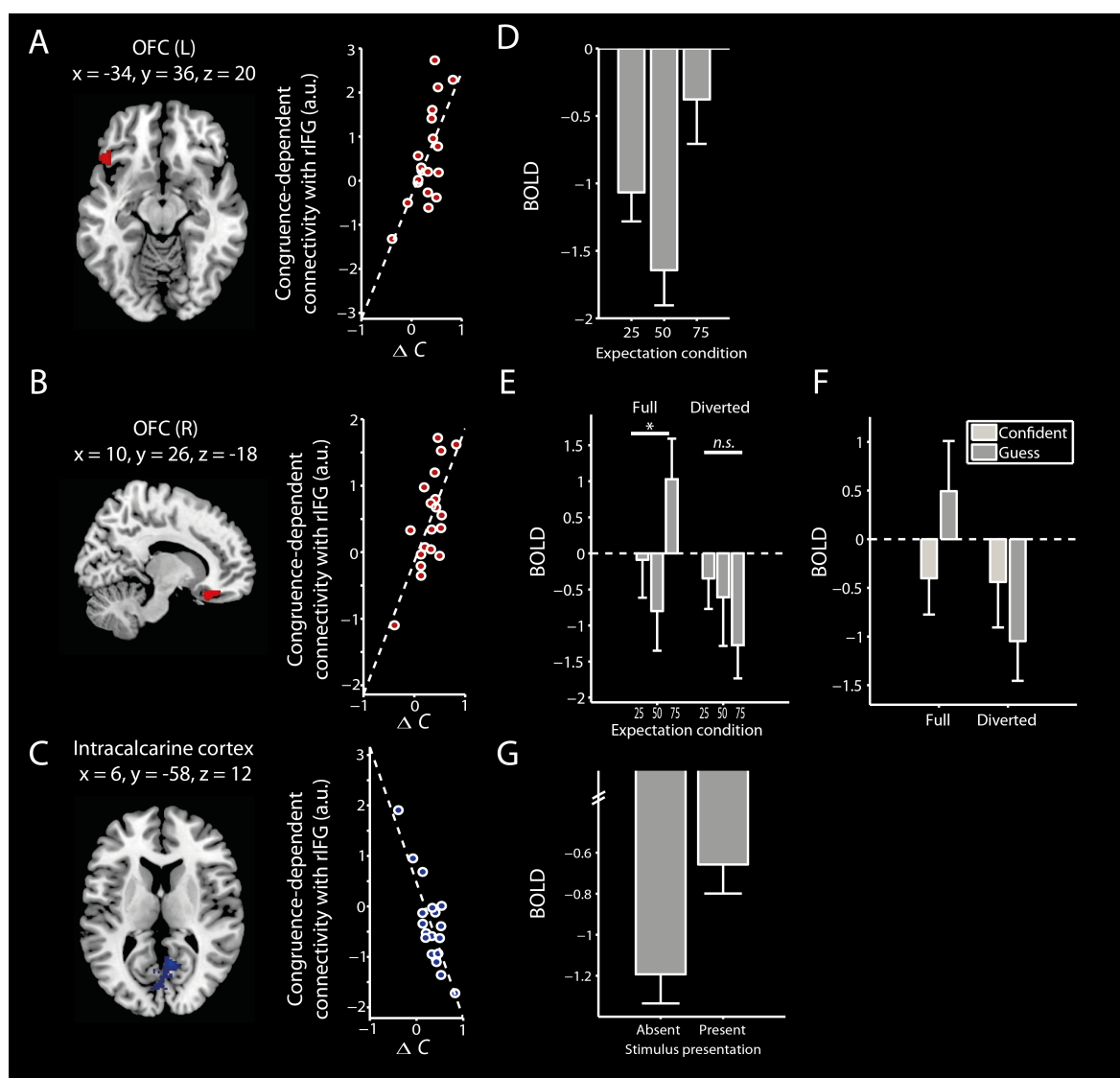
*Figure 5.*Results of PPI analysis, depicting functional connectivity with rIFG that differs for congruent and incongruent reports and scales with ΔC. Higher values of ΔC were associated with greater congruency-dependent connectivity with left **(A)** and right **(B)** orbitofrontal cortex, and less congruency-dependent connectivity with intracalcarine sulcus **(C)**. Scatterplots to the left of each cluster depict the correlation between ΔC and congruence-dependent functional connectivity. Panels **D-F** depict results from follow-up analyses in these regions. **(D)** Left OFC BOLD as a function of expectation. (**E**) Right OFC BOLD as a function of expectation and attention. **(F)** Right OFC BOLD as a function of confidence and attention. **(F)** Intracalcarine sulcus BOLD as a Gabor presence and absence. This difference is only marginally significant. Error bars represent within-subjects SEM.

1   the expectation and BOLD were related by a 'U' shape function (fig. 5D),

2   characteristic of the representation of prior information. This 'U' represents prior

29

1   information because BOLD is higher when there is an informative prior (the 25% and

2   75% conditions) than when the prior is flat, or neutral (the 50% condition). In rOFC,

3   this pattern was exhibited under full ($F(2,36) = 3.51$, $p = .040$, $\eta_p^2 = .163$, but not

4   diverted, $F(2,36) = 1.04$, $p = .363$, $\eta_p^2 = 0.55$, attention (interaction $p = .030$, fig. 5E).

5   Interestingly, in rOFC there was also a significant attention by confidence interaction,

6   $F(1,18) = 7.87$, $p = .012$, $\eta_p^2 = .304$ (fig. 5F), such that attention reversed the BOLD

7   response to confident versus guess responses.

8   These results are consistent with the interpretation of bilateral OFC communicating

9   prior information. While lOFC represented prior information independently of

10 attention, rOFC did this only under full attention. Moreover, the attention by

11 confidence interaction under rOFC BOLD suggests that this region may additionally

12 represent the degree of (reverse) uncertainty associated with attentional state.

13 We next asked whether intracalcarine sulcus represented prediction error signals.

14 Response prediction error is demonstrated in an expectation by report interaction,

15 whereas stimulus prediction error is demonstrated in an expectation by stimulus

16 interaction. However, neither analysis was significant (both $p > .441$). Rather, the

17 BOLD response here was marginally higher for stimulus present than absent trials,

18 $F(1,18) = 3.53$, $p = .077$, $\eta_p^2 = .164$ (fig. 5G).

19 One might wonder whether bilateral OFC directly signals priors to intracalcarine

20 sulcus, or vice versa for sensory signals. This was not the case. Re-running the PPI

21 analysis in the same way, but with each OFC cluster as our seed revealed no

22 significant or marginally significant connectivity with intracalcarine sulcus. Similarly,

23 running the analysis setting each intracalcarine sulcus as the seed revealed no

24 significant or marginally significant connectivity with either OFC cluster.

1 Taken together, these results suggest that the predictive information signalled to (or

2 from) rIFG is a balance of priors and sensory signals. Moreover, they suggest that

3 expectation-induced biases in subjective confidence are associated with increased

4 rIFG-OFC functional connectivity, relative to sensory regions.

5 **The contribution of visual regions and OFC to confidence is predicted by white**

6 **matter density**

7 Our connectivity analyses revealed that OFC and intracalcarine sulcus represent

8 priors and sensory signals respectively, and that the balance of rIFG connectivity

9 with these regions differed across individuals. The presence of these individual

10 differences motivated an exploratory follow-up analysis that asked whether they are

11 reflected in brain structure. More specifically, we considered whether the weighting

12 of top-down predictions and bottom-up prediction errors was a function of white or

13 grey matter (WM and GM respectively) density of the source regions (i.e. OFC and

14 intracalcarine sulcus).

15 The BOLD response of our cluster in OFC reflected an effect of perceptual

16 expectations on objective decision. The behavioural correlate of this is therefore Δc

17 $= c_{25\%} - c_{75\%}$, - the extent to which perceptual expectations bias (yes/no) decision.

18 We performed a whole-brain multiple regression analysis on WM density, with total

19 intracranial volume and participant age as nuisance covariates, and with Δc as the

20 regressor of interest. This analysis revealed that propensity to incorporate low-level

21 priors into decision-making, as measured by Δc, was negatively correlated with

22 rOFC white matter density (fig 6A and B, peak MNI $x = 23$, $y = 30$, $z = -14$, 11.51cm^3,

23 $P_{peak-FWE} = .030$, $Z = 5.08$). The same analysis for GM yielded no significant results.
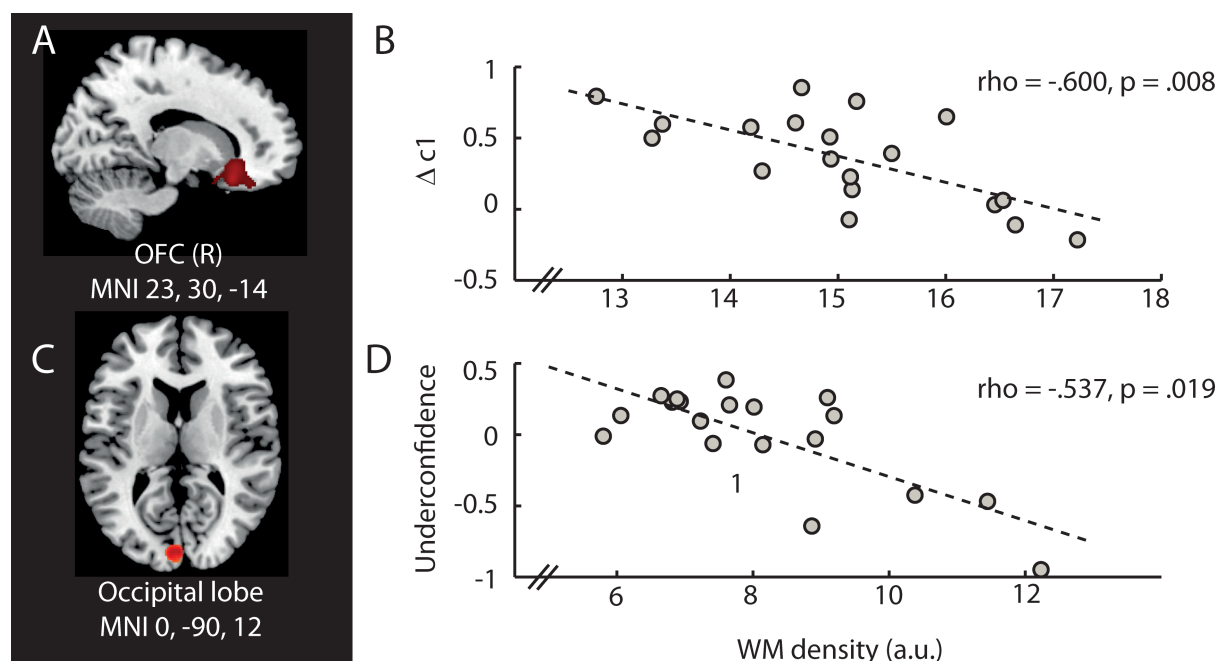
Figure 6. VBM results. **A, B.** White matter density in right orbitofrontal cortex negatively predicts the effect of expectation on perceptual decision. **C,D.** White matter density in contralateral occipital pole is negatively correlated with underconfidence bias (mean confidence threshold).

1 Given that both rOFC and rIFG BOLD predicted confidence we performed the same

2 analysis, but this time with mean confidence threshold as the regressor of interest.

3 Confidence threshold represents one's overall belief in their perceptual performance,

4 such that lower values as associated with higher confidence in decision-making

5 ability. This revealed a significant cluster in contralateral occipital lobe. Here,

6 increasing WM density significantly predicted more liberal confidence thresholds at

7 the cluster, but not the peak level (figure 6C and D peak MNI x = 0, y = -90, z = 12,

8 6.31cm^3, $P_{peak-FWE}$ = .879, P_{FDR} = .031).

9 Together these results suggest that the dependence of confidence on functional

10 connectivity with source regions is reflected in anatomical indications of that

11 connectivity: WM density in OFC was negatively predicted by its functional correlate;

1 and increasing occipital pole WM density was associated with mean confidence, that

2 is, beliefs of better perceptual performance.

3 **Discussion**

4 In the present paper we have shown that behavioural confidence in perceptual

5 decision increases when decisions are supported by (or congruent with) prior

6 expectations. Crucially, we show that this predictive information is, at least in part,

7 integrated into confidence in right inferior frontal gyrus (rIFG).

8 We have shown that unexpected percepts, taken with respect to the decision or

9 report, are associated with a heightened BOLD response (termed here PE_{REPORT}) in

10 a distributed set of frontal, parietal and temporal decision-related regions.

11 Interestingly, this expectation-sensitive set resembles those implicated in other forms

12 of 'top-down' processing such as modality-independent sensory change detection

13 (Downar et al., 2000), response inhibition (Verbruggen and Logan, 2008; Criaud and

14 Boulinguez, 2013), and detection of behavioural salience (Downar et al., 2002).

15 Our crucial result was that the contribution of top-down expectations to subjective

16 confidence judgements was reflected in fMRI BOLD, specifically in right inferior

17 frontal gyrus (rIFG). Here, high confidence was associated with a lower prediction

18 error response profile. Furthermore, the more that confidence was shaped by

19 expectation behaviourally, the more that confidence was associated with low

20 prediction error signals in this area. Our results therefore indicate a central role for

21 rIFG in perceptual decision making in which the 'match' between internal templates

22 and perceptual content is integrated into subjective confidence judgements.

33

1   Under an alternative account, the sensitivity of rIFG to confidence would be an

2   indirect effect of sensitivity to task difficulty. For example, rIFG may infer task

3   difficulty from the degree to which the percept is surprising. However, this

4   interpretation was ruled out by control analyses, which showed that the PE_{REPORT}-

5   confidence relationship was not driven by choice accuracy. These control analyses

6   additionally excluded attention, stimulus contrast, and reaction speed as driving the

7   observed relationship between PE_{REPORT} and confidence in rIFG.

8   This process of relating predictive information into confidence judgements recruited

9   both intracalcarine sulcus, primarily when incongruent reports were made, and

10   bilateral orbitofrontal cortices, primarily when congruent reports were made. The

11   former region showed a marginally significant BOLD response to the stimulus. We

12   assume that this effect was weak because the effect was localised to a large cluster,

13   while reflecting the neural response to a small stimulus in retinotopically-organised

14   space. We interpret the functional connectivity with intracalcarine sulcus as the

15   communication of sensory signals. Broadly in this region, white matter density

16   predicted participants' overall level of confidence (confidence threshold), implicating

17   this perceptual region in shaping beliefs in one's perceptual performance. By

18   contrast, we found that both right and left orbitofrontal cortex represented prior

19   information, consistent with previous work (Schoenbaum and Roesch, 2005; Wallis,

20   2007; Trapp and Bar, 2015). Interestingly, the representation of attentional state was

21   lateralized in these areas: left OFC represented prior information independently of

22   attention, whereas right OFC was sensitive to attentional state. Here, representation

23   of the prior required attention, and furthermore, the BOLD response to decision

24   confidence reversed with attention. Under full attention rOFC BOLD was higher for

25   guess responses than confident responses, as is usually found (Fleming et al., 2012;

34

1   Hilgenstock et al., 2014). However, under diverted attention this pattern reversed,

2   possibly indicating that rOFC represents the uncertainty associated with attentional

3   state: high under full attention, but low under diverted attention. Increasing white

4   matter density in rOFC was associated with the behavioural effect of expectations on

5   decision, supporting our interpretation of its role in representing the prior.

6   Altogether, we interpret these results as showing that subjective confidence is

7   represented in rIFG as a combination of both stimulus-driven signals, communicated

8   from intracalcarine sulcus, and shaped by top-down perceptual expectations,

9   communicated from bilateral OFC. OFC has been repeatedly been shown to reflect

10   reward expectations and beliefs (Kepecs et al., 2008; Kim et al., 2011; De Martino et

11   al., 2013; Lebreton et al., 2015), however here we place OFC belief representations

12   within a larger hierarchical structure for perceptual processing, generating

13   predictions (Stalnaker et al., 2015; Trapp and Bar, 2015) that constrain subjective

14   confidence judgements in perceptual decision. Importantly, our PPI analysis cannot

15   determine the directionality of functional connections in this network. One possibility

16   is that rIFG is involved in constructing confidence from an integration of PE_{REPORT}

17   signals and top-down expectations. Here, both intracalcarine sulcus and OFC would

18   be sending signals to rIFG. However, another possibility is that PE_{REPORT} signals are

19   passed from occipital lobe to rIFG, and an initial transformation of PE_{REPORT} into

20   confidence is signalled to rOFC. Under such an account, the role of rOFC here may

21   be one which transforms the confidence estimate represented in rIFG into a

22   reportable judgement, based on the mismatch between the estimate, expectations,

23   and potentially, attentional state (Lebreton et al., 2015). Further studies will be

24   needed to disambiguate these possibilities.

1 Our results are readily interpretable from Bayesian brain perspectives (Lee, 2002;

2 Yuille and Kersten, 2006; Friston, 2009; Clark, 2013). These propose that perceptual

3 inference is a weighted integration of sensory evidence and prior beliefs about the

4 cause of the sensation, such that the perceptual report corresponds to the belief with

5 the greatest posterior probability. The posterior probability increases as the

6 correspondence between prior and sensory signal increases. Therefore, inference is

7 deemed 'successful', and so should be associated with high confidence, when we

8 see a low 'prediction error' response, as we saw here (Meyniel et al., 2015b).

9 Neuronal representations of prediction errors are well-established in the reward

10 domain (Nakahara et al., 2004; Bayer and Glimcher, 2005), but in the perceptual

11 domain evidence remains restricted to BOLD correlates such as PE_{REPORT}. Under

12 such a Bayesian brain account, our connectivity results suggest that intracalcarine

13 sulcus passes sensory signals to rIFG, and rOFC passing top-down predictions. In

14 this view, the finding that PE_{REPORT} amplitude in rIFG was lower for confident

15 responses is consistent with the representation or construction of the posterior belief

16 in this region. This in turn is in line with empirical evidence for rIFG encoding of the

17 decision variable, either in Bayesian form (the posterior; d'Acremont et al. 2013) or

18 as decision evidence (Hebart et al., 2014), which are mathematically equivalent,

19 Bitzer et al. 2014).

20 Previous work has separately implicated rIFG in the representation of both the

21 decision variable (Bubic et al., 2009; d'Acremont et al., 2013) and expectation

22 violation in a range of modalities, from speech perception (Clos et al., 2014) to

23 auditory deviance detection (Garrido et al., 2009) and visual perception (Bubic et al.,

24 2009). Previous work has also implicated rIFG in the representation of subjective

25 uncertainty (Fleck et al., 2006; Fleming and Dolan, 2012). However, to our

36

1   knowledge these variables had not been related to each other before. rIFG has also

2   been implicated in a wide range of related executive processes, such novelty

3   detection (Hampshire et al., 2010), change detection (Beck et al., 2001), and

4   behavioural relevance (Hampshire et al., 2010), including, crucially, detecting or

5   resolving response conflict (Casey et al., 2000; Hampshire et al., 2010), and as a

6   key component of the response inhibition network (Verbruggen and Logan, 2008;

7   Criaud and Boulinguez, 2013). This raises the intriguing possibility of a functional

8   overlap between resolution of response conflict and the formation of confidence.

9   These roles could be unified by considering rIFG as the region in which the posterior

10   is computed, because the posterior belief on sensory causes affords a hypothesis

11   space for adaptive, plausible actions (Mansouri et al., 2009). Such a view is

12   consistent with evidence for rIFG in appropriately acting on perceptual choices

13   (Suzuki and Gottlieb, 2013), computing behavioural significance (Sakagami and Pan,

14   2007) , computing action-outcome likelihoods that modulate motor cortex (Morris et

15   al., 2014), and representing the posterior (d'Acremont et al., 2013). It has even been

16   shown that the rIFG BOLD response to decision errors is associated with both the

17   valence of the decision outcome, and the optimism of the participant ('self-belief';

18   Sharot et al. 2011), consistent with a view of rIFG in which high-level, abstracted

19   posteriors are computed from beliefs and errors. Anatomical considerations support

20   such a view, since the rIFG is directly connected with regions relevant for both

21   cognitive and motor control (Petrides and Pandya, 2002). We leave open for future

22   research the question of whether and how rIFG relates perceptual confidence to

23   action outcomes.

24   **Summary**

1   In summary, we have shown that top-down expectations are integrated into decision

2   confidence, and have shown that this occurs in a functional network consisting of

3   rIFG, bilateral OFC and intracalcarine sulcus. Here, top-down perceptual

4   expectations and bottom-up sensory inputs are integrated into a subjective sense of

5   perceptual confidence. Together, our data reveal a crucial role of top-down

6   influences in the mechanism by which perceptual decisions become available for

7   conscious report.

8

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