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RESEARCH ARTICLE

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fMRI response to automatic and purposeful familiar-face processing in perceptual and nonperceptual cortical regions

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Abstract

Viewing the faces of familiar people selectively activates a distributed network of brain regions implicated in both the perceptual and nonperceptual processing of conspecifics. In this functional magnetic resonance imaging (fMRI) study, we investigate the influence of depth of famous-face processing on this network, comparing a passive incidental face processing to a task that required the extraction of identity and biographic information. We observed that the precuneus, ventromedial prefrontal cortex (vmPFC), anterior temporal face patch (ATFP), and the amygdala exhibit a selective response even during incidental face processing. At the same time, face selectivity was enhanced in the lateral anterior temporal lobe (latATL) and the posterior superior temporal sulcus (pSTS) when identity and information extraction was required. In addition, goal-directed identity and information extraction was associated with a recruitment of inferior frontal gyrus (IFG), whereas this region was deactivated during passive viewing. Collectively, these results show that: *1*) in addition to active information extraction, the extended system is recruited by the passive retrieval of person-related knowledge and *2*) active access to such knowledge modulates activity in latATL and pSTS, potentially mediated via control circuits in the IFG.

NEW & NOTEWORTHY Information is extracted from familiar faces in both automatic and active modes. Using functional MRI, we show: *1*) that automatic access results in the selective activation of nonperceptual brain regions, the precuneus, ventromedial prefrontal cortex, and the anterior face patch and amygdala, demonstrating the automaticity of access to information in these regions; *2*) selective increases in the activation of the lateral anterior temporal lobe and posterior superior temporal gyrus when biographic information is actively extracted.

cortical networks; face perception

INTRODUCTION

Perceiving and knowing about others is key for human interaction and is fundamental to our daily lives. Effective interpersonal interaction involves not only the perceptual processing of faces but also nonperceptual cognitive processes related to emotional states, social processing, identity, and semantic information.

Person-related perceptual and nonperceptual processes are served by a well-characterized brain network divided into core and extended systems (1–3). The core system is closely linked to the visual perception of the invariant facial features that allow the perceptual processes that lead to the identification of individuals, as well as the perception of the changeable aspects of faces that allow recognition of facial expression. This core system includes, ventrally, the occipital face area (OFA) and fusiform face area (FFA) and, dorsally, the posterior superior temporal sulcus (pSTS) (3, 4). The nonperceptual extended system includes the anterior temporal cortex (ATL), the precuneus, ventromedial prefrontal cortex (vmPFC), the inferior frontal gyrus (IFG), and the amygdala.

Components of the extended system are believed to be responsible for a broad range of cognitive processes related to other people: identity representation (ATL, ATFP), semantic knowledge (ATL, IFG, precuneus), social knowledge and personality traits (precuneus, vmPFC, ATL, amygdala), emotional processing (amygdala, vmPFC), and naming (ATL, IFG), as well as executive control processes, such as working memory (IFG; 2, 5–12). The extended system is more active

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when viewing familiar individuals, which has been attributed to the spontaneous retrieval of nonperceptual information (2). However, experiments that have reported activation in the extended system by familiar faces generally employ tasks requiring some form of judgement to be made about the face stimulus (e.g., identity matching, superordinate categorization, semantic access; 8, 13, 14), and it is known that the directed retrieval of different forms of knowledge about others—social, nominal, semantic, physical, or episodic memories–differentially modulates activation within components of the extended system (15). On the other hand, when viewing a familiar face, we effortlessly and involuntary process the individual's sex, age, identity, emotional state, and a range of other characteristics. In this way, there are two modes in which we can access our knowledge about other people when we see their faces: the automatic information we reflexively access, as well as additional information that depends on the current goals. The degree to which recruitment of components of the nonperceptual extended system depends on current needs and goals remains uncertain.

This work investigates the degree to which recruitment of the extended system is contingent on the need to purposefully extract famous face identity to retrieve semantic information about the individual. We compare two tasks. In the incidental-processing task, participants performed a low-level perceptual judgment where they detected a salient contrast-change of the face stimulus. In the information-extraction task, participants were required to retrieve the nationality of the famous person, a task that necessitates both identification of the individual and the subsequent retrieval of semantic information.

Here we ask two questions, *1*) which regions continue to show a face-selective response during incidental face processing and *2*) which, if any, are modulated when semantic biographical information must be accessed. We predict that regions reflecting reflexive, automatic, person processing will continue to show a face-selective response in the incidental-processing task, and that regions involved in the goal-directed processing of faces will show enhanced face-selectivity when identity and information extraction are required.

MATERIALS AND METHODS

Participants

Thirty-three healthy volunteers (mean age 23.7 yr, 16 males) participated in the incidental-processing study. A separate sample of 32 healthy volunteers (mean age 23.9 yr, 10 males) participated in the information-extraction task. All participants were right-handed native Italian speakers. Participants had no history of neurological disorders and had normal or corrected-to-normal vision. All participants gave written informed consent to take part in the study and were reimbursed for their time. Procedures were approved by the Ethical Committee of the University of Trento.

Stimuli

Stimuli were 54 famous people and 45 famous monuments in the incidental-processing study and 49 famous people and 49 famous monuments in the information-extraction study. Stimuli were presented inside an oval shape superimposed on a phase-scrambled background. The faces were all in frontal view with a neutral expression, and all the stimuli were matched for luminance and dimension on the screen. For the control condition, we used 24 phase-scrambled images. Stimuli (600 × 800 pixels) were presented with Psychtoolbox (16, 17) running on MATLAB (MathWorks).

Experimental Paradigm

For both studies the experiment was split into four functional MRI (fMRI) runs. Each run was composed of 12 blocks of famous-face stimuli, 12 blocks of famous-place stimuli, and four blocks of scrambled images in a pseudorandomized order (Fig. 1). Stimuli were presented at 12 different interstimulus intervals (ISIs) (one ISI per block), ranging from 100 to 1,200 ms in 100 ms steps in the incidental-processing study and from 300 to 2,500 ms in 200 ms steps in the information-extraction study. Different ISIs were used to reflect the different time required to perform the two tasks. Critically, all reported analyses comparing experiments use the five ISIs that were present in both (300, 500, 700, 900, and 1,100 ms). Face and place stimuli were presented for half the ISI followed by the phase-scrambled background alone for the other half. Scrambled images appeared every seventh randomized block and had a fixed ISI of 1 s. Each block lasted 12 s, and blocks were separated by a 2-s fixation cross.

In the incidental-processing study, participants had to press a button whenever they saw a high-contrast face or place (see Fig. 1 for an example). In the information-extraction study, participants were required to press a button whenever they saw a non-Italian individual (for face stimuli) or a monument built before 500 C.E. (for place stimuli). Targets occurred, on average, 1.5 times per block. After the scanning session, participants were asked which famous people they had recognized and which they had seen for the first time. All the participants considered in the analysis had a recognition accuracy of above 95%.

fMRI Data Acquisition

Functional and structural data were collected with a Bruker BioSpin MedSpec 4-T scanner (Bruker BioSpin GmbH, Rheinstetten, Germany) while participants lay in the scanner and viewed the visual stimuli through a mirror system. Data collection was conducted at the Center for Mind/Brain Sciences (CIMeC), University of Trento, using a USA Instruments 8-channel phased-array head coil. Functional images were acquired using echo planar (EPI) T2*-weighted scans. Acquisition parameters were: repetition time (TR) of 2 s, an echo time (TE) of 33 ms, a flip angle (FA) of 73°, a field of view (FoV) of 192 mm, and a matrix size of 64 × 64. Total functional acquisition consisted of 796 volumes, over four runs, each of 34 axial slices (which covered the whole brain) with a thickness of 3 mm and a gap of 33% (1 mm). High-resolution (1 × 1 × 1 mm) T1-weighted MPRAGE sequences were also collected (sagittal slice orientation, centric phase encoding, image matrix = 256 × 224, field of view = 256 × 224 mm, 176 slices with 1-mm thickness, GRAPPA acquisition with

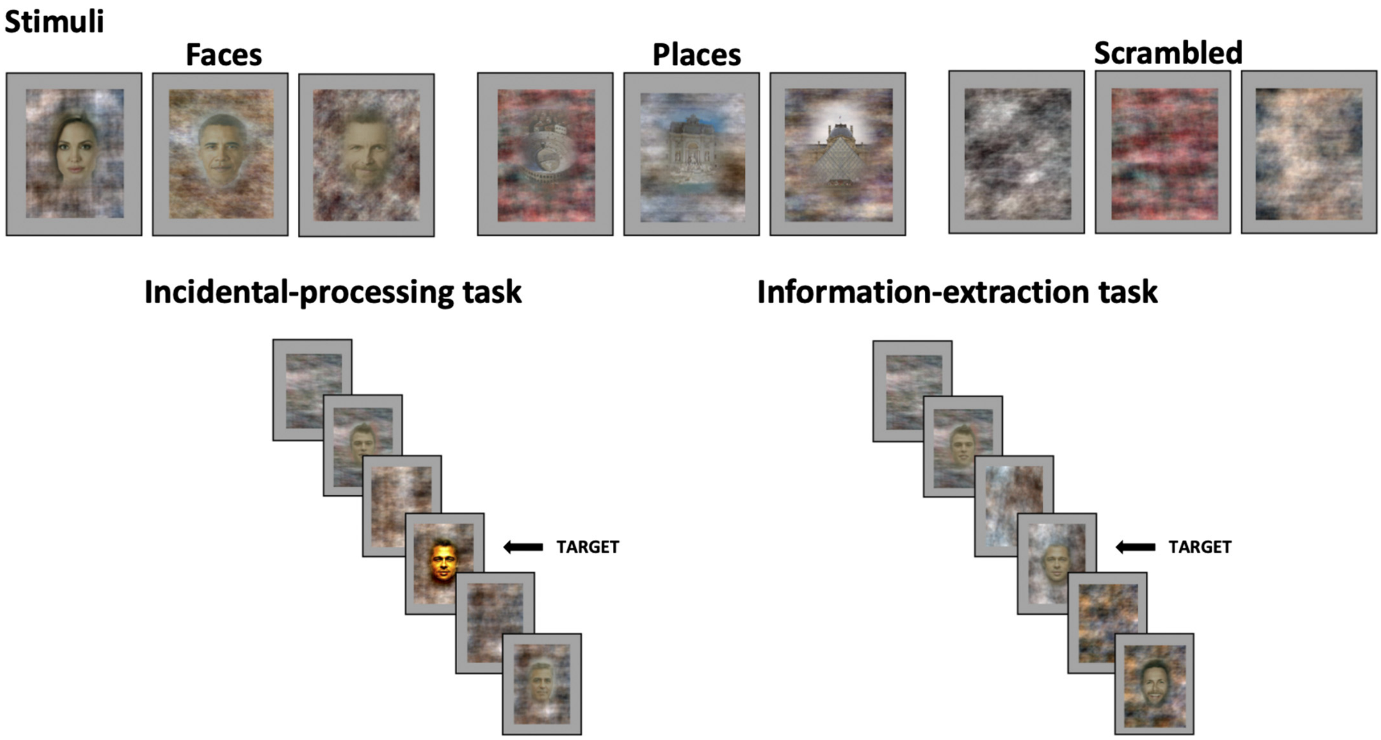

Figure 1. Stimuli and experimental paradigms. Stimuli were presented in 12-s blocks of faces, places, or scrambled images (baseline). In the incidental-processing task, participants were required to detect the presence of an occasional, salient, high-contrast face. In the information-extraction task, participants had to indicate if a non-Italian famous face or a building constructed prior to 500 C.E. was presented.

acceleration factor = 2, duration = 5.36 min, repetition time = 2,700, echo time = 4.18, TI = 1,020 ms, 7° flip angle).

fMRI Analysis

For the information-extraction study, data from 28 participants were included in this analysis. Data from four subjects were rejected due to within-run head motion exceeding 2 mm. For the incidental-processing study, data from 28 participants were included in this analysis. Data from three subjects were rejected due to within-run head motion exceeding 2 mm. One subject was removed due to low target-detection scores (2.5 SD below the mean). Data from one participant were deleted due to medical considerations.

For both studies, data were analyzed and preprocessed with SPM12 (http://www.fil.ion.ucl.ac.uk/spm/). The first four volumes of each run were discarded. All images were corrected for head movement. Subject-specific parameter estimates (β weights) for each of the 24 conditions (faces and places for each ISI) were derived through a general linear model (GLM), and a more lenient implicit mask for inclusion in the GLM (0.1 instead of the SPM default of 0.8) was coupled with an explicit gray-matter mask to maximize sensitivity in susceptibility-sensitive regions on our 4-T scanner. The control condition with scrambled images formed the implicit baseline. The six head-motion parameters were included as additional regressors of no interest.

ROI Selection

In both studies, regions of interest (ROIs) were defined using an independent group of subjects (n = 35) who performed a one-back identity-matching task on a rapid presentation of faces and places (ISI: 100–1,200 ms). Participants responded when they saw the mirrored repetition of the same image (average one per block, ± 1). Data from an independent set of participants were used to define ROIs. This avoids circularity or any form of bias in the ROIs selection across tasks. ROIs were defined by a sphere of 6-mm radius around the group coordinates (Table 1) masked by contrast face > places (face-selective ROIs) or places > faces (place-selection ROIs) for the independent data set, thresholded at $P < 0.001$. The center of ROIs is indicated in Fig. 2. To directly compare the differences between different levels of information retrieval, data were averaged across the five ISIs which matched in the two tasks (300, 500, 700, 900, and 1,100 ms).

RESULTS

Behavioral

Accuracy was average over the matched ISIs used in the main fMRI analyses and a mixed-measures ANOVA performed [factors: task (between), category (within)]. As expected, the main effect of task [$F_{(1,54)}$ = 63.7, $P < 0.001$] reflected higher accuracies in the incidental-processing task (93.4%; 93.1% faces, 93.7% places) than the information-extraction task (70.6%; 73.1% faces, 68.0% places). There was no main effect of stimulus category [$F_{(1,54)}$ = 1.1, P = 0.31]. Importantly for the interpretation of the reported fMRI results, there was no task-by-category interaction [$F_{(1,54)}$ = 1.7, P = 0.197], indicating that reported fMRI results are not influenced by differences in accuracy.

As expected, reaction times (RTs) were faster in the incidental-processing task compared with the information-

Table 1. *Spherical center of independent ROIs*

Region	Hemisphere					
	Left			Right		
OFA	−39	−82	−10	39	−79	−10
FFA	−42	−49	−22	42	−55	−19
pSTS	−51	−61	14	48	−61	11
IFG	−39	20	20	42	20	20
latATL	51	−13	−13	−51	−13	−13
ATFP	33	−7	−37	−33	−10	−37
Amygdala	21	−4	−16	−21	−7	−16
	Medial					
vmPFC	3	47	−22			
Precuenus	3	−55	29			

ATFP, anterior temporal face patch; FFA, fusiform face area; IFG, inferior frontal gyrus; latATL, lateral anterior temporal lobe; OFA, occipital face area; ROI, region of interest; pSTS, posterior superior temporal sulcus; vmPFC, ventromedial prefrontal cortex.

extraction task [$F_{(1,54)}$ = 83.6, $P < 0.001$; 594 ms, incidental-processing, 769 ms, information-extraction]. Although RT did not differ as a function of category [$F_{(1,54)}$ = 0.1], a task by category interaction was present [$F_{(1,54)}$ = 10.3, P = 0.002]. This effect was driven by faster responses for faces than places in the incidental-processing condition [faces: 571 ms, places: 617 ms, $t_{(27)}$ = 5.6, $P < 0.0001$], whereas descriptively faster response for places than faces in the information-extraction task did not reach significance [faces: 787 ms, places: 750 ms, $t_{(27)}$ = 1.5, P = 0.14].

Category Selectivity: Whole Brain Analysis

To assess the category-selective response in both experiments, in a preliminary analysis we contrasted faces with places, collapsing across all 12 ISIs (Fig. 2 and Table 2). In both experiments, face-selective responses (faces > places) were evident in core-system regions: bilateral OFA, FFA, and pSTS, as well as the precuneus. Additional face-selective responses were seen in the information-extraction task in the vmPFC, right lateral ATL, and bilateral amygdalae (Fig. 2*B*). The contrast places versus faces showed bilateral parahippocampal place areas (PPA), bilateral transverse occipital sulcus (TOS), and bilateral retrosplenial complex (RSC) in both experiments.

No Evidence for Differential Tuning Patterns between Incidental-Processing and Information-Extraction Tasks

Stimuli were presented across a range of ISIs (see MATERIALS AND METHODS) to assess differential patterns in temporal tuning (the relationship between presentation rate and fMR amplitude) between incidental-processing and information-extraction tasks. We did not observe systematic dissociations in these patterns between the two tasks, and the absence of modulation by ISI in some regions left the validity of regional comparisons uncertain. These null results are presented in Supplemental Data (https://doi.org/10.6084/m9.figshare.12789917).

Region of Interest Comparison between Tasks: Face-Selective Regions

Our design allowed us to directly compare regional responses between the two tasks by considering the averaged response to the shared ISIs (300, 500, 700, 900, 1,100). To assess the effects of task within brain regions specialized for face processing, we employ alterations in face selectivity (faces vs. places) as the dependent measure to better control for global differences across tasks. As there were no

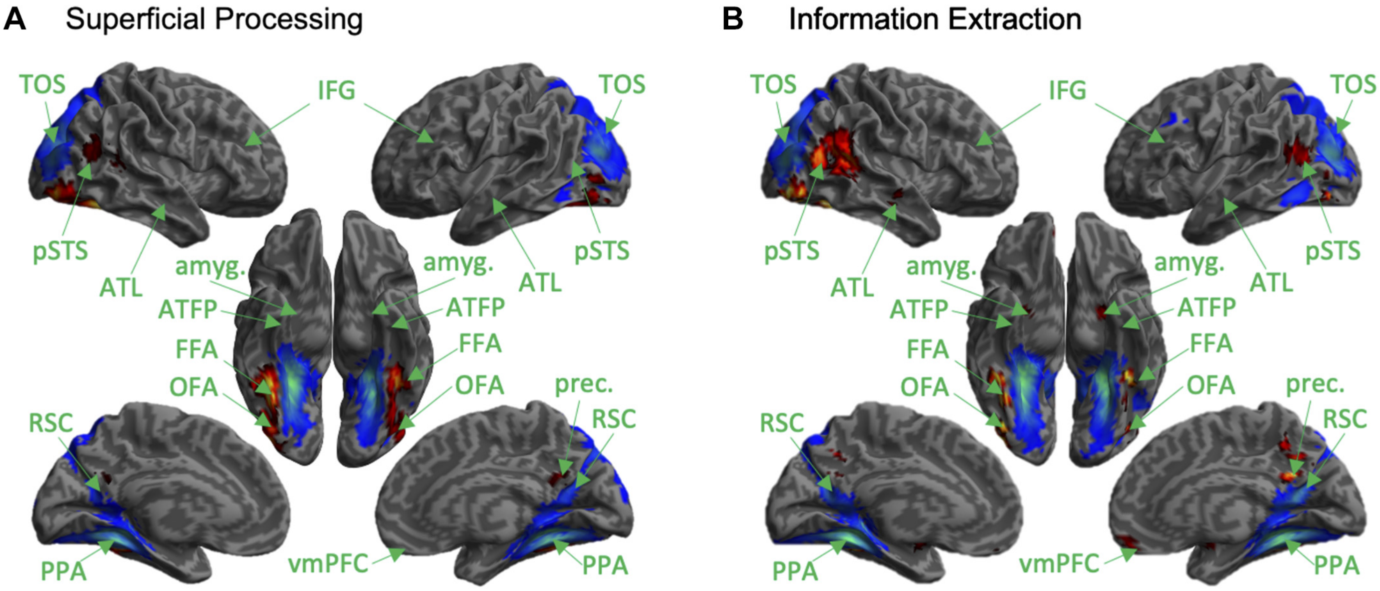

Figure 2. Whole brain analysis of face- (red) and place-selective (blue) responses in incidental-processing (*A*) and information-extraction (*B*) experiments. Face-selective responses are evident in core regions as well as the precuneus in both experiments and additionally, the lateral ATL, vmPFC, and amygdala in the information-extraction experiment. Classic place-selective regions, PPA, TOS, and RSC, are present in both experiments. See Table 2 for supporting statistical and location information. Maps are thresholded at $P < 0.001$, cluster extent 25 voxels. Arrows shown in *B* indicate the location of the independent ROIs used to formally interrogate results in both experiments. Amyg., amygdala; ATFP, anterior temporal face patch; ATL, anterior temporal lobe; FFA, fusiform face area; IFG, inferior frontal gyrus; OFA, occipital face area; PPA, parahippocampal place areas; prec., precuneus; pSTS, posterior superior temporal sulcus; RSC, retrosplenial complex; TOS, transverse occipital sulcus; vmPFC, ventromedial prefrontal cortex.

Table 2. *Significance, extent of face- and person-selective clusters in incidental-processing and information-extraction tasks, and location and t value of within-cluster peaks*

	Cluster		Peak	
Face-Selective Response	**$P_{(FWE\text{-}Corr)}$**	**Voxels**	***t***	***x, y, z* (mm)**
Incidental processing				
Right				
FFA	<0.001	504	17.0	42, −52, −19
OFA			11.8	39, −82, −10
pSTS	<0.001	209	6.0	51, −43, 11
Left				
FFA	<0.001	408	13.0	−39, −46, −19
OFA			7.8	−48, −79, −4
pSTS	0.308	26	3.6	−51, −61, 26
Medial				
Precuneus	<0.001	134	5.9	0, −55, 29
Information extraction				
Right				
FFA	<0.001	258	8.1	42, −49, −19
OFA			8.0	42, −79, −10
pSTS	<0.001	726	6.5	48, −43, 14
latATL	0.080	49	4.8	54, −13, −13
Amygdala	0.222	33	4.4	24, −4, −16
Left				
FFA	0.023	70	7.6	−39, −43, −22
OFA	<0.001	314	6.1	−39, −79, −10
pSTS			5.0	−48, −61, 17
Amygdala	0.086	48	4.7	−24, −4, −16
Medial				
Precuneus	<0.001	220	7.6	3, −55, 32
vmPFC	0.053	56	4.7	3, 53, −16
dmPFC	0.372	25	4.3	6, 59, 26
Mid-cingulate	0.288	29	4.1	6, −19, 44
Place-selective response				
Incidental processing				
Right				
PPA	<0.001	5089	28.1	27, −46, −7
TOS			19.4	33, −82, 23
RSC			11.4	21, −55, 20
Left				
PPA			26.4	−27, −46, −7
TOS			19.7	−33, −82, 23
RSC			8.6	−18, −52, 8
Information extraction				
Right				
PPA	<0.001	5342	22.2	30, −49, −7
TOS			15.1	−36, −82, 14
RSC			14.1	18, −55, 17
Left				
PPA			23.1	−27, −46, −7
TOS			15.8	33, −79, 14
RSC			11.2	−18, −58, 14
dlPFC	0.142	40	3.8	−48, 23, 38

Amyg., amygdala; ATFP, anterior temporal face patch; ATL, anterior temporal lobe; dlPFC, dorsolateral prefrontal cortex; dmPFC, dorsomedial prefrontal cortex; FFA, fusiform face area; IFG, inferior frontal gyrus; latATL, lateral anterior temporal lobe; OFA, occipital face area; PPA, parahippocampal place areas; pSTS, posterior superior temporal sulcus; RSC, retrosplenial complex; TOS, transverse occipital sulcus; vmPFC, ventromedial prefrontal cortex.

hemisphere-by-task-by-category interactions (all F values $<$ 1.8, all P values $>$ 0.40), we collapsed across hemisphere. Independently defined (see MATERIALS AND METHODS) ROI data showing the averaged fMR response across ISI for people and place stimuli in both tasks are presented in Fig. 3. A face-selective response was seen in all regions in the information-extraction task (IFG, $P = 0.042$; all other regions, $P <$ 0.001). In the incidental-processing task, face selectivity was evident in OFA, FFA, the precuneus, and the amygdala ($P <$ 0.001), vmPFC ($P = 0.002$), ATFP ($P = 0.004$), and pSTS ($P =$ 0.047) but not in the IFG ($P = 0.51$) or lateral ATL ($P = 0.12$).

The effect of task on the face-selective response was assessed through a mixed-measures ANOVA. A region-by-category-by-task ANOVA indicated that the effect of task on the category-selective response differed across regions [$F_{(8,432)} = 2.21$, $P = 0.021$], which were assessed through task-by-category interactions within individual regions. Task led to a selective increase in regional response in the lateral ATL [$F_{(1,54)} = 4.87$, $P = 0.032$], which was driven by the strong selective response in the information-extraction task [$t_{(27)} =$ 3.98, $P = 0.0004$] compared with the nonsignificant effect in the incidental-processing task [$t_{(27)} = 1.57$, $P = 0.12$]. Although a significant hemisphere-by-category effect was not present, closer inspection suggests this effect was driven by the absence of a selective response in the left lateral ATL in the incidental-processing task. In this unplanned analysis, we observed that, while a face-selective response was absent in the left lateral ATL [$t_{(27)} = 0.07$, $P = 0.94$], a response was evident in the right lateral ATL [$t_{(27)} = 2.62$, $P = 0.014$]. By contrast, in the information-extraction task, selective responses were evident both in left [$t_{(27)} = 2.99$, $P = 0.006$] and right [$t_{(27)} = 3.82$, $P = 0.0007$] lateral ATL. A task-by-category effect was also present in pSTS [$F_{(1,54)} = 5.61$, $P = 0.021$] and was driven by a stronger selective response in the information-extraction task [$t_{(27)} = 4.85$, $P = < 0.00005$] compared with a weak but still significant selective response in the incidental-processing task [$t_{(27)} = 2.08$, $P = 0.047$]. These region-of-interest results are broadly consistent with the descriptive differences seen in the whole brain analyses comparing face-selective responses within each task (Fig. 2). Specifically, pSTS activation can be seen to be more prominent in the information-extraction task and presence of the right ATL in information-extraction but not incidental-processing task.

An unanticipated but prominent feature evident in Fig. 3 is the negative response in the IFG during the incidental-processing task. Here, the response to both face and place stimulus was below baseline and strongly different from the response during the information-extraction task. This difference was statistically confirmed via an unplanned main effect of task [$F_{(1,27)} = 20.5$, $P = 0.0001$].

Significant task-by-category effects were evident in pSTS and latATL but not in the precuneus ATFP, vmPFC, or amygdalae. However, the nonsignificance of effects in these latter regions does not indicate the absence of such effects. To assess the relative support of the null hypothesis, Bayes factors were calculated for the effect of task on face selectivity (18). While evidence favored the null in all regions—precuneus (2.0), ATFP (2.2), vmPFC (1.4), amygdalae (1.2)—support at this level can only be considered anecdotal. For this reason, caution should be taken in the interpretation of these null effects, and it is possible that future studies with higher statistical power would detect influences of information extraction in additional regions of the extended system.

There was a significant interaction between category and task in reaction times, which may influence the response pattern observed in the pSTS, latATL, and IFG. To assess

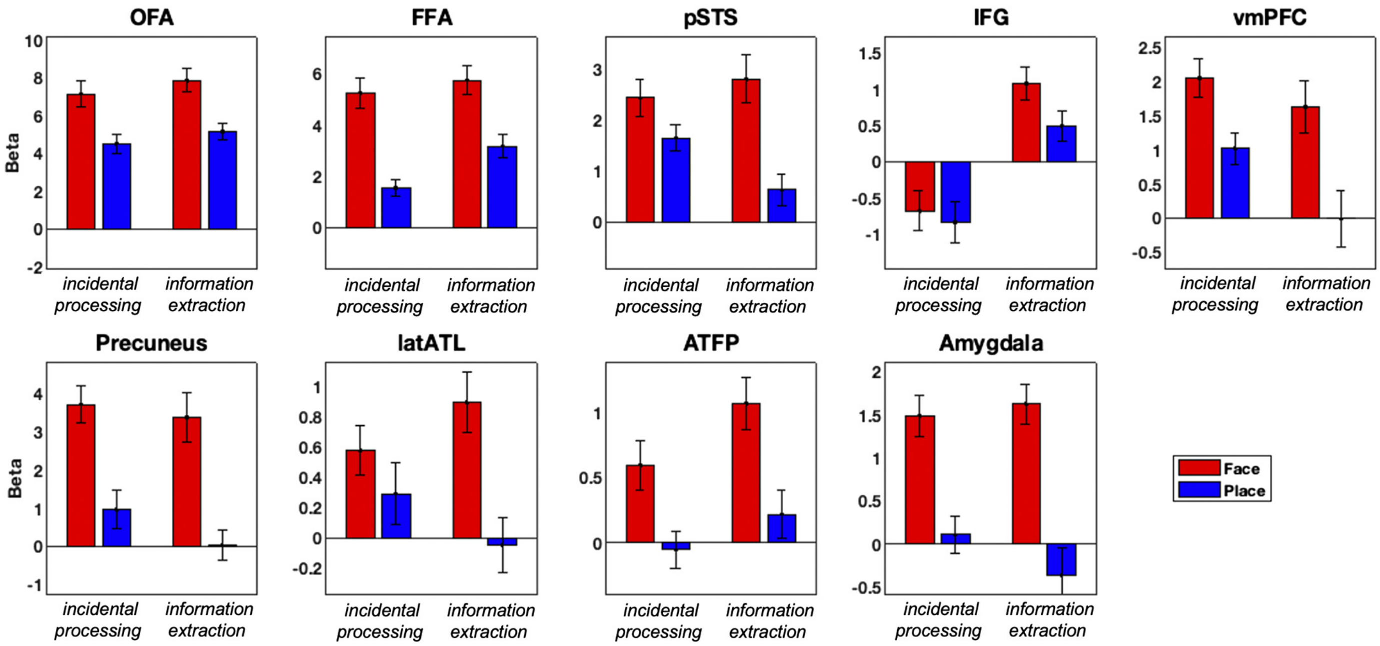

Figure 3. Signal plots of the response to face and place stimuli as a function of task in face-selective ROIs. Bars indicate the mean ROI response and error bars indicate 1 standard error. ATFP, anterior temporal face patch; FFA, fusiform face area; IFG, inferior frontal gyrus; OFA, occipital face area; latATL, lateral anterior temporal lobe; pSTS, posterior superior temporal sulcus; ROI, region of interest; vmPFC, ventromedial prefrontal cortex.

whether increases in reaction time were influencing the responses to faces in these regions, the correlation between RT and the response to faces was calculated across participants. In the incidental-processing task, such a relationship was not seen, with nonsignificant trends toward decreased activations with longer reaction times (pSTS: $r = -0.11$, $P = 0.59$; latATL: $r = -0.03$, $P = 0.88$; IFG: $r = -0.02$, $P = 0.91$). In the information-extraction task, pSTS did show a numeric trend toward an increase in responsivity with RT, but this was weak and did not approach significance ($r = 0.003$; $P = 0.99$). The opposite, nonsignificant, trend was seen in latATL and IFG (latATL: $r = -0.06$, $P = 0.75$; IFG: $r = -0.28$, $P = 0.15$). Collectively, these results suggest that reaction time differences do not influence responsivity in these regions.

Region-of-Interest Task Comparison: Place-Selective Regions

To assess whether incidental-processing and information-extraction tasks generalize to other object categories, we performed the complementary ROI analysis in place-selective regions. A robust place-selective effect was observed across all independently defined ROIs in both tasks ($P < 0.001$; see Fig. 4). A region-by-category-by-task ANOVA indicated that the effect of task on the category-selective response differed across regions [$F_{(2,110)} = 75.9$, $P < 0.001$]. Within-region task × category ANOVAs revealed significant differences between tasks in the selective response in PPA [$F_{(1,54)} = 5.14$, $P = 0.027$], driven by a larger selective response in the information-extraction task [$t_{(27)} = 13.5$, $P < 0.001$] compared with the incidental-processing task [$t_{(27)} = 12.3$, $P < 0.001$]. A significant interaction was also evident in the RSC [$F_{(1,54)} = 15.2$, $P = 0.0003$], which was likewise driven by a larger selective response in the information-extraction task [$t_{(27)} = 8.89$, $P < 0.001$] compared with the incidental-processing task [$t_{(27)} = 5.0$, $P < 0.001$]. In contrast, no effect of task was seen on the category-selective response in TOS [$F_{(1,54)} = 1.67$, $P = 0.20$].

Whole Brain Task Comparison

We complemented the primary ROI analyses with a whole brain analysis on the effect of task on the category-selective response (Fig. 5 and Table 3). The sole region to show a significant task-by-category interaction that was not evident in the ROI analysis was a section of the right lateral fusiform gyrus. This region exhibited increased category selectivity during the incidental-processing task, which is consistent with a trend evident in the ROI analysis (Fig. 3). The cluster was located 6 mm posteriorly and laterally to the center of the independent right FFA ROI, with which it shared no overlapping voxels.

Other regions identified in this analysis correspond to bilateral place-selective RSC and right PPA evident in the ROI analysis (Fig. 4).

DISCUSSION

In this work, we sought to determine the influence of the depth of face processing in core and extended elements of the distributed cortical network for perceiving and knowing about others. Using famous-face stimuli, we compared superficial, automatic face processing during an incidental-processing task to face processing that required the extraction of identity and semantic information in an information-extraction task. In our ROI analysis, we observed face-selective responses across regions of the core system in both tasks. Within the extended system, the precuneus, vmPFC, ATFP, and amygdala exhibited a profile consistent with the automatic

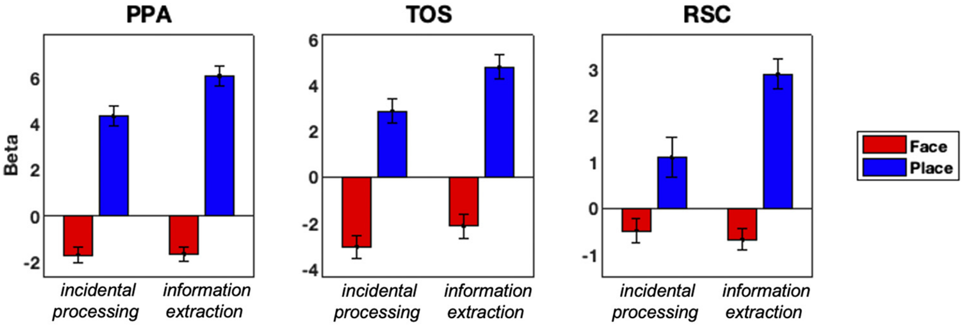

Figure 4. Signal plots of the response to face and place stimuli as a function of task in place-selective ROIs. Bars indicate the mean ROI response and error bars indicate 1 standard error. PPA, parahippocampal place areas; ROI, region of interest; RSC, retrosplenial complex; TOS, transverse occipital sulcus.

processing of conspecifics, with face-selective responses being present in both tasks. In contrast, lateral ATL and IFG exhibited a face-selective response only in the information-extraction task. Moreover, we observed that increased depth of processing led to increases in selectivity in the pSTS and lateral ATL, consistent with a role in the active extraction of person-related information.

Persistent Recruitment of the Precuneus, vmPFC, ATFP and Amygdala in Incidental Face Processing

Our independent ROI analysis revealed the presence of face-selective responses in the precuneus, vmPFC, ATFP, and amygdala during the incidental-processing of faces. The recruitment of these regions during a low-level contrast-

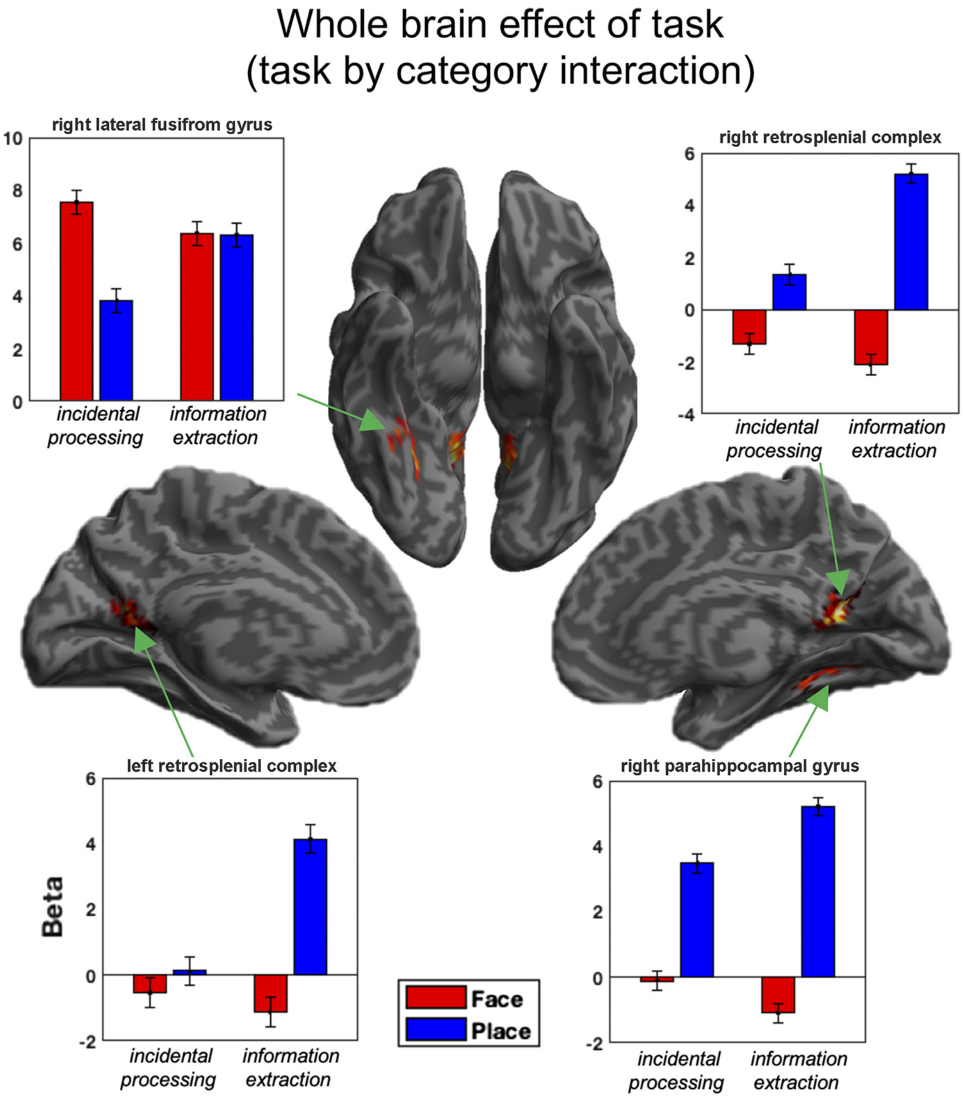

Figure 5. Whole brain analysis of the effect of task on the category-selective response (task-by-category interaction). Effects were driven by relative increases in place selectivity in bilateral retrosplenial cortex and the right parahippocampal gyrus in the information-extraction task. See Table 2 for supporting statistical and location information. Conversely, voxels in the right lateral fusiform gyrus show increased face selectivity in the incidental-processing task. Effects sizes and error bars (±1SE) are only descriptive in nature due to the high circularity in ROI definition and interrogation and should only be used to inform the nature of the effect driving the interaction.

Table 3. *Significance and extent of whole brain task-by-category interaction clusters and location and F value of within-cluster peaks*

Task × Category Interaction		Cluster		Peak	
		$P_{(\text{FWE-Corr})}$	Voxels	*F*	*x, y, z* (mm)
Left	RSC	0.006	88	5.9	−9, −58, 11
Right	RSC	0.002	70	5.1	15, −55, 14
	Parahipp.	0.026	51	4.5	33, −43, −13
	Lat. FG			3.8	36, −49, −22

latFG, lateral fusiform gyrus; Parahipp, parahippocampus; RSC, retrosplenial complex.

detection task that did not necessitate the processing of the faces can provide insight into the automaticity of the involvement of these regions in face and person perception.

The precuneus and vmPFC are part of the internalized default mode system and are removed from sensory and perceptual circuity (19, 20). These regions show highly similar cognitive response profiles across access to different forms of person knowledge (15) and are implicated in high-level cognitive functions, such as the retrieval of episodic, biographical and autobiographical memories, and aspects of social cognition, such as personality traits and emotional processing (8, 21–25). This present work demonstrates the automaticity with which high-level, nonperceptual cognitive processes are recruited when viewing familiar members of our species and provides a putative source for the diverse social and semantic information that allows our effective interaction with others.

Unlike the precuneus and vmPFC, the ATFP is structurally and functionally connected to ventral perceptual regions including OFA and FFA (26, 27). This region has been implicated in the representation of identity information about faces and contains viewpoint-independent representation of individuals (28, 29). The persistence of a response in this region during incidental face perception is consistent with the automatic extraction of face identity in the absence of explicit task demand. The amygdala is similarly connected to regions of the core system (1, 30). Its involvement in face processing is known to be modulated by the emotional expression of the observed face (31, 32), even when face stimuli are presented below the threshold of perceptual awareness (33). This response profile predicts the involvement of the amygdala during incidental face processing.

Information Extraction Enhances Selectivity in the pSTS and Lateral ATL

The region-of-interest analysis revealed that the requirement to extract identity and biographical information from famous-face stimuli increased selectivity in the pSTS and latATL. The pSTS is classically designated as an element of the perceptual "core" system, an attribution which would suggest that increased selectivity reflects an increasing perceptual demand associated with the identification of faces. It is true that, although the incidental-processing task did not necessitate processing of shape information or facial features, face identification (and the processing of facial features) was a necessary step in the information-extraction task. However, the pSTS is not strongly implicated in identity processing. The role of the pSTS in face perception is typically attributed to the changeable aspects of faces, such as eye gaze or emotional expression (3, 34) or the dynamic processing of faces (4), factors that did not vary across these tasks.

An alternate explanation for the increased role of the pSTS in the information-extraction task is the region's role in nonperceptual processes. The pSTS and neighboring elements of the temporal parietal junction (TPJ) are implicated in social cognition, such as inferring the mental states of others (2, 35), name knowledge (36) and the retrieval of person-related semantic information (22). Moreover, pSTS is adjacent to the angular gyrus, a region that is implicated in general semantic processing (37). It is possible that the role of pSTS in information extraction results from computational properties shared with these neighboring regions.

The question of whether increased selectivity in the pSTS reflects perceptual or nonperceptual processes cannot be definitively answered by the present data. However, the dissociation between the pSTS and other elements of the perceptual core system, the paucity of existing evidence to suggest that the pSTS plays a role in the identity processing of faces, and the well-documented role of this region in the representation of social and semantic knowledge about other people, support a nonperceptual role in information extraction. Lateral ATL exhibited a face-selective response during information extraction but not incidental face processing. This differential response indicates the involvement of this region in purposeful, task-relevant processing of conspecifics. The ATL has long been implicated in the representation of knowledge about unique entities (e.g., specific people or places) (38–41) and exhibits response selectivity during the active retrieval of knowledge about person-related concepts (22). Moreover, this region is believed to play a critical role in general semantic representation and was an early candidate for a semantic hub that links together semantic representations distributed across the cortex (42, 43). The relative role of the lateral ATL in person-related knowledge or general semantic knowledge, particularly relating to unique entities, is a topic of active debate (11, 24). The interaction between task and stimulus category in the present study supports the importance of social knowledge in the function of the lateral ATL.

The results in pSTS and latATL indicate that selectivity for faces increases in these face-specialized regions. It is noteworthy that this is influenced by an attenuation in the response for the nonpreferred category. This suggests a complex pattern that may result either from the relative suppression of the region when information is being extracted from place stimuli, a switch in the role of the region from a more generalized function in the incidental-processing task to a more specialized role in the information extraction task, other uncontrolled differences between these two tasks (such as cognitive load), or a combination of these factors.

A complementary whole brain analysis indicates that task-induced modulations in category selectivity were not strongly present outside the investigated ROIs. The exception was an aspect of the right lateral fusiform gyrus that showed enhanced category selectivity during the incidental-processing task. This runs counter to the general trend of increased category selectivity during information extraction and suggests that this region plays a particular role in the processing of low-level visual aspects of faces and argues against a general disengagement during the incidental-processing task.

Enhancements in selectivity observed in the pSTS and latATL were mirrored in the place-selective network, suggesting that the information-extraction related enhancement of category selectivity extends to object domains other than people. In this study, we saw in both the ROI and whole brain analyses, that PPA and RSC, but not the TOS, showed an increase in place selectivity during information extraction when compared with incidental place processing. This is consistent with the role of these regions not only in the perception of places (44, 45) but also in higher-level spatial representations, such as the location of a building with its broader geographical context (46) and the retrieval of geographic information about nonplace objects, such as the origin of well-known food dishes (47).

IFG Activation is Contingent on Information Extraction

The IFG has long been identified as a region of the extended system, although the nature of its role remains uncertain. The role of the IFG in face processing has been attributed both to the top-down control of perception (6, 7, 48), as well as access to semantic and nominal knowledge (5, 15, 34). The IFG represents the only region of the semantic system that is part of the executive control circuitry (37). Its involvement in selecting between multiple competing semantic responses and in making infrequent semantic associations has led to its function being attributed to semantic control and the guided retrieval of goal-relevant semantic information (49–51).

The attenuation of the response in the incidental-processing condition and its recruitment during information extraction (both for faces and places) may provide insight into its role. This pattern is consistent with its role in the guided identification and extraction of person-related information. The presence or absence of IFG activation does not appear to influence the face-selective responses in OFA and FFA, which argues against a direct role in top-down modulation of ventral face processing regions. Rather, the increased response in IFG accompanies the increases in face selectivity in the lateral ATl and pSTS, which suggests that executive control circuitry is required for access to information present in these regions. Conversely, these results suggest that access to information represented in other regions, such as the precuneus and vmPFC, is not contingent on an IFG response and that access to the knowledge in these regions can proceed automatically without the need for executive control mechanisms.

In this work, we investigated the role of task demand on activation within the core and extended systems for face perception. We observed that elements of the extended system, the precuneus, vmPFC, amygdala, and ATFP, continue to show a selective response during the superficial, surface-based processing of faces. Notably, this occurred in the absence of a response in IFG, a region implicated in active semantic control. The need to extract identity and biographical information produced a selective response in the IFG and was accompanied by enhanced selectivity in the ATL and pSTS, providing a potential modulatory neural mechanism for active access to stored knowledge. Collectively, these results provide insight into the diverse factors that drive recruitment and representation in the extended system and the automatic and purposeful neural systems that allow effective interaction with conspecifics.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

S.U. and S.L.F. conceived and designed research; S.U. performed experiments; S.U. and S.L.F. analyzed data; S.L.F. interpreted results of experiments; S.U. and S.L.F. prepared figures; S.U. and S.L.F. drafted manuscript; S.L.F. edited and revised manuscript; S.U. and S.L.F. approved final version of manuscript.

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