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The Influence of Perceptual and Knowledge-based Familiarity on the Neural Substrates of Face Perception

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Abstract

This study examined the neural substrates of facial familiarity and person-knowledge. Based on current neural models of face perception, it was hypothesized that distinct extended networks of brain regions differentiate the perception of (a) novel faces, (b) novel faces associated with person-knowledge, (c) perceptually familiar faces and (d) familiar faces for which person-knowledge was learned. To test this hypothesis, we conducted an event-related fMRI experiment during which participants viewed faces experimentally manipulated to represent these different levels of familiarity. Results confirmed that distinct networks of brain regions, particularly the medial prefrontal cortex (MPFC), underlie the perception of faces for which person-knowledge is available.

The Neural Substrates of Face Perception

Imaging research has revealed a network of brain areas that support the processing of various facial dimensions. Indeed, multiple brain areas are recruited when people perceive faces (Haxby, Gobbini, & Montgomery, 2004), particularly the fusiform gyrus (Grill-Spector, Knouf, & Kanwisher, 2004; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Kanwisher, McDermott, & Chun, 1997; Sergent, Ohta, & MacDonald, 1992). In addition, brain regions such as the superior temporal sulcus (STS), the amygdala, and the medial prefrontal cortex (MPFC) are activated when people examine faces in order to process eye gaze information (Cloutier, Turk, & Macrae, 2008; Hoffman & Haxby, 2000; Hooker et al., 2003; Pelphrey, Singerman, Allison, & McCarthy, 2003; Puce, Allison, Bentin, Gore, & McCarthy, 1998), race (Golby, Gabrieli, Chiao, & Eberhardt, 2001; Hart et al., 2000; Phelps et al., 2000), emotional expression (Adolphs, 2002; Davis & Whalen, 2001; Whalen et al., 2004) or familiarity (Gobbini, Leibenluft, Santiago, & Haxby, 2004; Gorno-Tempini & Price, 2001; Leibenluft, Gobbini, Harrison, & Haxby, 2004). These studies have led to extensive and comprehensive models of the neural systems supporting face processing (Adolphs, 2009; Gobbini & Haxby, 2007).

Many brain regions preferentially recruited when perceivers are presented with familiar faces have been implicated in social cognition (Adolph, 2009; Amodio & Frith, 2008). When more social knowledge about a social target is available, perceivers can create more complex impressions about them and consequently tend to construe them less superficially. Supporting this interpretation, social cognitive research on person-perception has

distinguished between the implementation of superficial initial impressions of social targets, generally based on social categorical information, and the implementation of individuated impressions based on specific information about social targets (Cloutier, Mason, & Macrae, 2004; Devine, 1989; Fiske & Neuberg, 2000; Macrae et al., 1999). Both at the behavioral and the neural levels of analysis, processes supporting person construal may differ based on the use of person-knowledge (i.e., descriptive information about a social target's biography, personality or intentions). When forming impressions of unknown social targets for which no relevant information is available, perceivers will rely on the perceptual information available as cues to form their impression. However, when person-knowledge is available, more individuated impressions, depending less on these physical cues, can be formed.

Similarly, the effects of familiarity on face perception can be divided into two broad categories: perceptual-based familiarity and knowledge-based familiarity. Faces that are *perceptually familiar* are those that perceivers have previously been exposed to, often repeatedly, but that are not associated with individuating information (i.e., person-knowledge). That is, the perceiver does not have access to person-knowledge describing these social targets. Viewing perceptually familiar faces has been associated with increased activity primarily in the posterior cingulate/precuneus and decreased activity in the fusiform gyrus and amygdala (Gobbini & Haxby, 2006; Kosaka et al., 2003). Due to their distinctiveness and social relevance, novel faces are believed to evoke stronger responses than perceptually familiar faces in many brain areas. Furthermore, when processing perceptually familiar faces, facilitated access to visual representations may be enacted by repetition-related reductions of neural activity in brain areas like the fusiform gyrus (Grill-Spector, Henson, & Martin, 2006).

In contrast to perceptually familiar faces, familiar faces for which person-knowledge is available often recruit an extended network of brain areas implicated in the inference of mental states and the processing of emotional stimuli (Gobbini & Haxby, 2007). The perception of personally familiar faces has been shown to preferentially activate the MPFC, the posterior STS, the precuneus and anterior temporal areas (Gobbini et al., 2004; Leibenluft et al., 2004; Pierce, Haist, Sedaghat, & Courchesne, 2004). Furthermore, even minimal previous exposure to person-knowledge about a social target evokes activity in these brain areas during face perception (Todorov, Gobbini, Evans, & Haxby, 2007).

Although studies have investigated facial familiarity using pictures of either famous individuals or personally familiar individuals (Gobbini et al., 2004; Leibenluft et al., 2004), no study to date has experimentally controlled for familiarity in order to compare perceptual and knowledge-based familiarity. The current study aims to investigate such questions and to further explore the influence of person-knowledge on the perception of novel faces. Particular emphasis is put on the potential role of the MPFC in supporting the representation or access of person-knowledge describing social targets.

To systematically distinguish the effects of perceptual and knowledge-based familiarity on the neural substrates supporting person perception, perceivers took part in multiple event-related fMRI sessions while viewing (a) novel faces without person-knowledge, (b) novel faces described by person-knowledge (i.e., faces preceded by descriptive sentences), (c) perceptually familiar faces (i.e., faces for which subjects are trained without prior person-knowledge) and (d) familiar faces with acquired person-knowledge (i.e., faces previously paired with person-knowledge during training sessions). Accordingly, this experiment examines the effects of person-knowledge on the perception of novel faces, the effects of perceptual familiarity on face perception, and the effects of familiarity from the availability of person-knowledge (Gobbini, & Haxby, 2006, 2007).

METHOD

In this study, participants took part in three fMRI sessions, with four behavioral training sessions in between the second and third scanning sessions. During the first fMRI session, participants were asked to form impressions of novel faces presented without person-knowledge. During the second fMRI session, they were asked to form impressions of a different group of novel faces preceded by descriptive person-knowledge. In the week following these first two fMRI sessions, participants were given four sessions of training on the previously presented faces to experimentally create perceptually familiar faces (without person knowledge) and familiar faces for which person-knowledge was acquired. In the final fMRI session, participants were asked to again form impressions of the now familiar faces. Importantly, the faces previously presented during the second scanning session were once again paired with the same descriptive information. Subjects participated in four one-hour training sessions taking place on different days (Somerville et al., 2006). During this third fMRI session, participants were once again asked to form impressions of the now familiar faces presented in sessions one and two.

Participants

Twenty-four female participants between the ages of 18 and 28 were recruited from the local Dartmouth College community. Five participants were excluded from analyses due to excessive movement in the scanner or presence of artifacts in the acquired data. The remaining 19 subjects (mean age of 18.9 years old) were included in analyses for all three fMRI sessions. Subjects reported no abnormal neurological history, had normal or corrected-to-normal visual acuity, and were strongly right-handed as measured by the Edinburgh Handedness Inventory (Oldfield, 1971; Raczkowski et al., 1974). Subjects received course credit or were paid for their participation and gave informed consent in accordance with the guidelines set by the Committee for the Protection of Human Subjects at Dartmouth College.

Material and design

Faces and sentences—Face stimuli consisted of 96 unfamiliar, non-nameable male faces used in a previous study (Cloutier et al., 2008) further supplemented with unfamiliar faces compiled from the media. The faces were cropped below the chin line and around the outer hairline, were scaled to center a 13.33 × 13.33 cm black canvas and displayed direct eye gaze. Faces were equated on nameability, attractiveness and emotional expressions (depicting either a neutral expression or a slight smile). The presentation of each face was counterbalanced across participants in the first two fMRI sessions.

The sentences, meant to experimentally ascribe person-knowledge to the social targets, described various characteristics of the target, including his personality, hygiene, social status or sexual attitude, and were previously judged to be attractive (i.e., he is adventurous), neutral (i.e., winter is his favorite season), or unattractive (i.e., he is boring to talk to). The sentences used were counterbalanced across conditions and scanning sessions.

Task Procedures

Brain imaging sessions: During each scanning session, subjects were instructed to form impressions of male faces based on their immediate reactions to them. More specifically, participants were asked to base their impressions of the social targets on their “gut reaction” following the presentation of the faces. During the first session, 24 faces were presented three times each without any information about the person shown for a total of 72 trials. The faces were presented for 1000 ms and were followed by a centrally presented fixation crosshair for 1000 ms. Face trials were pseudorandomly interspersed with fixation trials

consisting of a fixation crosshair presented for 2000 ms to introduce jitter into the fMRI time series (Ollinger et al., 2001). This resulted in a mean ITI of 3000 ms (range = 1000 ms to 5000 ms). Subjects responded to each face presentation by pressing a button with each index finger via a four-button fiber optic key press to indicate having formed their impression of the target.

During the second fMRI session, which occurred immediately following the first imaging session, subjects were presented with descriptive sentences that were sometimes followed by faces of the opposite sex. In this second session, 72 novel faces were presented three times preceded by unique descriptive sentences (consisting of information that was unattractive, neutral, or attractive) for a total of 216 trials. Participants were once again instructed to form impressions of the faces based on their immediate reactions but were also asked to consider the descriptive sentences that preceded the faces when forming their impressions. Furthermore, 87 additional sentences were presented as “catch-trials” (partial trials during which a sentence was not followed by a face). Participants were told that they should simply ignore the “catch-trial” sentences. Partial trials were included so that unique estimates of the hemodynamic response function could be computed for each subcomponent of the trial (Ollinger et al., 2001). Trial types, including partial trials, were pseudorandomly presented with each run and sentences attributed to each condition were counterbalanced across participants. It should be noted that the 72 faces in session two were not presented during the first fMRI session.

During the second imaging session, sentences were presented for 3500 ms and were followed by a centrally presented fixation crosshair for 500 ms. Sentences and faces were pseudorandomly interspersed with fixation trials consisting of a fixation crosshair presented for 2000 ms to introduce jitter into the fMRI time series (Ollinger et al., 2001). This resulted in a mean ISI of 2500 ms (range = 500 ms to 4500 ms). Faces were presented for 1000 ms and were followed by a centrally presented fixation crosshair for 1000 ms. Trials were pseudorandomly interspersed with fixation trials consisting of a fixation crosshair presented for 2000 ms to introduce jitter into the fMRI time series (Ollinger et al., 2001). This resulted in a mean ITI of 3000 ms (range = 1000 ms to 5000 ms). Subjects once again responded to each face presentation to indicate having performed their impression of the target.

During the third scanning session, which occurred either one or two days after the last behavioral training session (see below), subjects were once again presented with the faces shown in the previous two imaging sessions (which were also shown in the behavioral training sessions). Participants were asked to form impressions of the faces based on their immediate reactions. During this third imaging session, 96 faces were presented 3 times for a total of 288 trials. These faces were of two types. The first, used to assess perceptual familiarity, were composed of the faces presented in the first session for which there was no person-knowledge information provided during training. The second, used to assess the effects of person-knowledge, were composed of the faces previously paired with information during the initial scanning session and the behavioral training. As in the first session, the faces were presented for 1000 ms and were followed by a centrally presented fixation crosshair for 1000 ms. Once again, jitter was introduced, resulting in a mean ITI of 3000 ms (range = 1000 ms to 5000 ms). As in the previous sessions, subjects responded to each face presentation to indicate having performed their impression of the target.

Behavioral training sessions: During the behavioral training sessions, participants consolidated the impressions they formed during the first two imaging sessions. Each of the four training sessions was held on a separate day and consisted of two phases: an encoding phase and a test phase.

During the encoding phase, all faces from the first two fMRI sessions were shown three times. Faces from the first session were once again presented without any information (i.e., perceptual familiarity condition), whereas faces from the second session were preceded by the corresponding unique sentences describing putative characteristics of the person portrayed (i.e., person-knowledge condition). This created a total of 288 trials. Before these training sessions, participants were told that, for encoding runs, each face would be presented 3 times either with or without detailed descriptions.

Faces from the first session were shown in the center of the screen without sentences whereas faces from the second session were preceded by sentences describing characteristics. All trials ended when participants pressed the space bar and were followed by a centrally presented fixation crosshair for 500 ms. In the person-knowledge condition, the faces were presented with 3 sentences that were prejudged to be unattractive, neutral, or attractive information about individuals (the characteristics were consistent with respect to category for each face). Importantly, participants were also told that they would subsequently be tested on their memory for the type of information (attractive; neutral; unattractive; no information) paired with each face. During each training session, participants went through two runs of this encoding task.

Next, in the test phase, participants were asked to recall the type of information that was paired with each face (attractive; neutral; unattractive; no information). A trial consisted of a face being presented in the center of the computer screen until the subject responded using a number key on the keyboard (1 = attractive; 2 = neutral; 3 = unattractive; 4 = no information). Following the subjects' responses, they were shown the correct response. Subjects were instructed to be as accurate as possible in their response and to use the feedback in order to solidify their knowledge about the social targets. During this testing phase, all faces presented during the encoding phase were presented once.

Functional Imaging

For each of the 3 scanning sessions, anatomical and functional whole-brain imaging was performed on a 3-T Philips Intera Achieva Scanner (Phillips Medical Systems, Bothell, WA) equipped with a SENSE (SENSEitivity Encoding) head coil. An Apple Powerbook computer running Cedrus Superlab 4.0.2 (San Pedro, CA) was used for stimulus display and interfaced with a Lumina Response box. Stimuli were projected to subjects with an Epson (model ELP-7000) LCD projector onto a screen positioned at the head of the bore. Subjects viewed the screen through a mirror mounted on the head coil. Cushions were used to minimize head movement.

Anatomical images were acquired using a high-resolution 3-D magnetization-prepared rapid gradient echo sequence (MPRAGE; 160 sagittal slices, TE = 4.6 msec, TR = 9.9 msec, flip angle = 8°, voxel size = 1 × 1 × 1 mm). Functional images were collected using T2* fast field echo, echo planar functional images (EPIs) sensitive to BOLD contrast (TR = 2000 msec, TE = 35 msec, flip angle = 90°, 3 × 3 mm in-plane resolution, sense factor of 2). The first fMRI session consisted of one run comprised of 160 sets of images, the second fMRI session consisted of five runs comprised of 278 sets of images and the third fMRI session consisted of four runs comprised of 153 sets of images. Slices were acquired axially allowing whole brain coverage (36 slices; 3.5-mm slice thickness, 0.5 mm skip between slices).

Data Analysis

Functional MRI data were analyzed using the general linear model for event-related designs in SPM2 (Wellcome Department of Cognitive Neurology, London, UK; Friston et al., 1995).

For each functional run, data were preprocessed to remove sources of noise and artifact. Functional data were corrected for differences in acquisition time between slices for each whole-brain volume, realigned within and across runs to correct for head movement, and coregistered with each participant's anatomical data. Functional data were then transformed into a standard anatomical space (3-mm isotropic voxels) based on the ICBM 152 brain template (Montreal Neurological Institute) that approximates Talairach and Tournoux's atlas space (Talairach & Tournoux, 1988). Normalized data were then spatially smoothed (6-mm full width at half maximum) using a Gaussian kernel.

The first series of analyses were performed to identify brain regions preferentially responsive to novel faces without person-knowledge, novel faces with person-knowledge, perceptually familiar faces and familiar faces with person-knowledge. For each participant, a general linear model, incorporating all task effects (modeled with a canonical hemodynamic response function; Friston, Fletcher, et al., 1998) and covariates of no interest (a session mean, a linear trend, and six movement parameters derived from realignment corrections) were used to compute parameter estimates (β) and t-contrast images (containing weighted parameter estimates) for each comparison at each voxel. These individual contrast images were then submitted to a second-level random-effects analysis to create mean t-images (thresholded at $p < 0.001$ at the voxel-level with cluster size = 5 voxels, furthermore only activations surviving a cluster-level correction for multiple comparison of $p < 0.05$ were reported).

To further examine the effects of familiarity and person-knowledge on MPFC activity in an unbiased manner, a region of interest (ROI) was defined based on the peak activation in MPFC from a study by Leibenluft and colleagues (2004) which obtained preferential MPFC activation to personally familiar others (i.e., a mother's own child). A spherical ROI (6mm) was generated based on this peak activation in MPFC [8, 58, 26]. Signal intensity values for each trial type of interest were then extracted from each ROI and the parameter estimates were submitted to a 2 (familiarity: novel, familiar) \times 2 (person-knowledge: unavailable, available) ANOVA with repeated measures.

RESULTS

Behavioral Results

Behavioral sessions—Inspection of figure 1 shows that on average, participants reached the performance criterion of 90% for each condition by the end of the fourth training session. Furthermore, by the end of the last training session, every participant was able to attribute correct information type (i.e., attractive, neutral or unattractive) to the presented faces more than 85% of the time (chance performance would have been 25 %).

fMRI Results

A region of interest analysis was performed to identify the effects of person-knowledge and familiarity on MPFC activation. Additional analyses were performed to identify brain regions modulated by familiarity and the availability of person-knowledge during the formation of impression from faces. These analyses allowed the identification of the networks of brain regions preferentially responsive to: (a) novel faces without person-knowledge, (b) novel faces described by person-knowledge (i.e., faces preceded by descriptive sentences), (c) perceptually familiar faces (i.e., faces for which subjects are trained without prior person-knowledge) and (d) familiar faces with person-knowledge (i.e., faces previously paired with person-knowledge during training sessions).

ROI analysis of MPFC activation—For each subject, signal intensities for the MPFC ROI were calculated separately for each condition and examined statistically using a 2 (familiarity: novel, familiar) \times 2 (person-knowledge: unavailable, available) repeated measures ANOVA.

These analyses revealed that MPFC preferentially responded to both novel faces and faces for which person-knowledge is available (see figure 2). This region showed a main effect of familiarity, ($F[1,18] = 12.87, p = .002$); a main effect of person-knowledge, ($F[1,18] = 12.18, p = .003$); and no significant interaction between familiarity and person-knowledge ($F[1,18] = 3.82, p = .066$). Additional statistical analyses confirmed that novel faces paired with person-knowledge evoked more MPFC activation than novel faces not paired with person-knowledge ($t[18] = 2.89, p < .01$) and that familiar faces previously paired with person-knowledge evoked more MPFC activation than familiar faces not paired with person-knowledge ($t[18] = 2.16, p < .05$). This ROI analysis confirms that the MPFC is preferentially activated by person-knowledge, even when controlling for the perceptual familiarity of the faces.

First impressions of novel faces with or without person-knowledge—To identify brain areas recruited during the impression formation of novel faces with or without person-knowledge, images acquired from the first fMRI session (i.e., novel faces without descriptive sentences) and the second fMRI session (i.e., novel faces with descriptive sentences) were contrasted. Of particular interest was the impact of person-knowledge on the neural substrates underlying the perception of novel faces. Indeed, the involvement of brain regions previously shown to support social cognition (i.e., MPFC) was expected when more elaborate person construal, based on person-knowledge, was possible (Mitchell, Heatherton, & Macrae, 2002; Todorov et al., 2007).

Forming impressions of novel faces with person-knowledge: As expected, a number of brain regions showed increased activity when forming initial impressions of novel faces paired with person-knowledge (Table 1). Notably, activations were observed in the regions of the medial prefrontal cortex (MPFC, BA9: 0, 48, 31) (see Figure 3), the ventral lateral prefrontal cortex bilaterally (right VLPFC, BA47: 45, 26, -14; left VLPFC, BA47: -39, 37, -12), the precuneus/posterior cingulate gyrus (BA7/BA23: -6, -53, 39), and the right insula (45, -17, 12). In addition to the involvement of the MPFC, a region consistently involved in social cognitive tasks, a number of brain areas often ascribed to the “social brain” (Adolph, 2009; Amodio & Frith, 2008) were found to be preferentially recruited when perceivers viewed faces preceded by person-knowledge.

The results also revealed a number of brain regions displaying increased activity when forming initial impressions of novel faces that were not paired with person-knowledge (see Table 1).

Contrasting perceptually familiar faces to novel faces without person-knowledge—To identify brain areas underlying the impression formed of perceptually familiar faces, images acquired from the first fMRI session (i.e., novel faces without descriptive sentences) and part of the third fMRI session (i.e., faces viewed after familiarity training without descriptive sentences) were contrasted. Of particular interest was identifying the neural substrates underlying the perception of perceptually familiar faces never paired with person-knowledge. The interest was two-fold: first, to directly compare brain regions supporting the perception of novel faces to the brain regions supporting the same faces once perceptually familiar; second, to verify if brain regions believed to be specifically recruited when person-knowledge is available (i.e., MPFC) are also recruited by perceptually familiar targets.

Forming impressions of perceptually familiar faces: In agreement with previous studies of perceptual familiarity, results revealed that the precuneus/posterior cingulate (BA31: -15, -57, 25) were preferentially recruited by perceptually familiar faces compared to novel faces (see Table 2). These results confirm a hypothesized role in perceptual familiarity for the precuneus and suggest that the MPFC does not generally support familiarity without person-knowledge.

Forming impressions of novel faces compared to perceptually familiar faces: As expected, many brain regions showed increased activity when forming impressions of novel faces compared to perceptually familiar faces (see Table 2). These brain regions are most likely indicative of the increased processing requirements associated with the presentation of distinctive novel faces. Furthermore, in agreement with the expected reduction of activity in face specific regions when presented with perceptually familiar faces, preferential activation to novel faces was observed in the right fusiform/inferior temporal gyrus (BA 19/37: 50, -67, -9).

Contrasting perceptually familiar faces to familiar faces with person-knowledge—To identify brain areas recruited during the impression formation of the now familiar faces with or without person-knowledge, images acquired during the third fMRI session (i.e., familiar faces without descriptive sentences and familiar faces with descriptive sentences) were contrasted. Once again, of particular interest was the impact of person-knowledge on the neural substrates underlying face perception. Notably, this contrast aimed to confirm the preferential recruitment of MPFC by faces for which person-knowledge was learned rather than presented during the scanning session. By controlling for perceptual familiarity (e.g., comparisons with faces seen equally often in the absence of descriptive information), these analyses further ensured that the involvement of MPFC was associated with person-knowledge, not the repeated exposure to faces.

Forming impressions of familiar faces paired with person-knowledge: A number of brain regions showed increased activation when familiar faces previously paired with person-knowledge were presented (Table 3) (see Figure 4). Notably, activations were once again observed in brain regions associated with social cognition; such as the medial prefrontal cortex (MPFC, BA9: -6, 42, 12), the precuneus (BA31: 3, -65, 36), the left VLPFC (BA47: -48, 24 -6) and the posterior STS (BA22: -50, 60, 22). This contrast confirmed the role of the MPFC in construing familiar faces for which person-knowledge is available.

Forming impressions of perceptually familiar faces compared to familiar faces with person-knowledge: Finally, brain regions displayed increased activation when perceptually familiar faces were compared to faces previously paired with person-knowledge (Table 3). Notably, activations were observed in the right fusiform gyrus (rBA37: 42, -56, -10). This brain region might play a role in establishing impressions of social targets based on perceptual information alone.

DISCUSSION

The type of experiences perceivers have with social targets strongly affects which brain areas support the perception of these targets' faces. In the current study, perceptual familiarity and the availability of person-knowledge were shown to modulate the brain regions recruited when forming impressions of social targets. Of particular interest, the availability of person-knowledge was shown to preferentially recruit multiple regions of the so-called "social brain". Among these brain regions, activation of the MPFC appeared to be sensitive to the availability of person-knowledge, even when controlling for the perceptual

familiarity of the faces. The involvement of the MPFC in many social cognitive tasks suggests that its functions might be key to understanding how the brain instantiates person perception processes (Haxby, Hoffman, & Gobbini, 2002; Todorov et al., 2007). Indeed, theory of mind (Frith, 2007), forming impressions of others (Mitchell, Macrae, & Banaji, 2006) and self-referential processing (Kelley, Macrae, Wyland, Caglar, Inati, & Heatherton, 2002; Moran, Macrae, Heatherton, Wyland, & Kelley, 2006) are among the many important social cognitive abilities recruiting regions of the MPFC. The current results suggest that, as part of its role in social cognition, the MPFC might also support the representation or retrieval of person-knowledge (Mitchell et al., 2002; Todorov et al., 2007).

Involvement of precuneus in perceptual familiarity

The current study confirmed the involvement of the precuneus in perceptual familiarity. Indeed, perceptually familiar faces compared to novel faces were found to elicit stronger activity of the posterior cingulate/precuneus (Gobbini, & Haxby, 2006; Kosaka et al. 2003). The precuneus has been implicated in a variety of functions compatible with its role in supporting perceptual familiarity (Cavanna & Trimble, 2006). This region has been shown to be preferentially active to other types of familiar stimuli (Gobbini et al., 2004; Nakamura et al., 2001; Shah et al., 2001), it is recruited during episodic memory (Fletcher et al., 1995; Henson, Rugg, Shallice, Josephs, & Dolan, 1999; Shallice et al., 1994) and it has been shown to be involved in mental imagery (Ishai, Ungerleider, & Haxby, 2000; Knauff, Fangmeier, Ruff, & Johnson-Laird, 2003; Malouin, Richards, Jackson, Dumas, & Doyon, 2003). Conceivably, this region could participate in retrieving elaborated perceptual representations about familiar social targets. Alternatively, this brain region might also support the subjective feeling associated with perceiving faces that became self-relevant through familiarity (Cavanna & Trimble, 2006). Although the MPFC has been found to be preferentially responsive to familiar faces (Gobbini et al., 2004; Leibenluft et al., 2004), the current results show that perceptually familiar faces do not evoke more activation in this region than novel faces. This demonstrates that simple visual familiarity with faces does not elicit preferential MPFC activity. To the contrary, ROIs analyses and inspection of figure 5 suggests that novel faces, particularly those paired with person-knowledge, elicit stronger MPFC activity than familiar faces. This might be a consequence of the fact that perceivers have to form novel impression of the unfamiliar targets, which presumably requires increased involvement of the MPFC, but can access pre-existent representations when forming impressions of the novel faces. Supporting this explanation, a study investigating mentalizing operations by Jenkins and colleagues (2008) has demonstrated repetition suppression effects in the MPFC.

When comparing perceptually familiar faces with familiar faces previously paired with person-knowledge, more activity was found in the fusiform cortex. Speculatively, this increased activity in the fusiform might indicate greater perceptual elaborations created when perceivers formed impressions of faces for which no other sources of information was available.

The influence of person knowledge on MPFC activity

Although first impressions can efficiently be formed solely based on perceptual information, the availability of person-knowledge is particularly useful when construing others on a more individuated basis (Fiske & Neuberg, 1990). It is notable that the MPFC, a brain region recruited by various social cognitive and “theory of mind” tasks, is also part of an extended network of brain regions supporting the perception of familiar faces (Gobbini & Haxby, 2007; Gobbini et al., 2004; Leibenluft et al., 2004). The current results provide evidence for the hypothesized role of this brain region in accessing person-knowledge about social targets

(Mitchell, Cloutier, Banaji, & Macrae, 2006; Mitchell et al., 2002; Todorov et al., 2007), irrespective of their perceptual familiarity.

Indeed, both novel and familiar faces described by person-knowledge elicited preferential MPFC activation when compared, respectively, to novel faces or perceptually familiar faces without person-knowledge. Since perceptual familiarity with the faces cannot account for these effects, activation of MPFC when viewing faces paired with person-knowledge most likely indicates operations supporting the access of specific personality characteristics and mental states describing the social targets. These results confirm that person-knowledge itself is sufficient to elicit activity in MPFC in response to a face (see also Todorov et al., 2007). Furthermore, they suggest a role for the MPFC in representing or retrieving person-knowledge rather than the strong emotional connotations associated with personally familiar others. Indeed, contrary to previous studies where personally familiar social targets were presented (Gobbini et al., 2004; Leibenluft et al., 2004), perceivers in the current study never interacted with the social targets for which they learned descriptive information.

Much remains to be accomplished to clarify the roles played by the MPFC in person perception and social cognition more broadly (Amodio & Frith, 2006). Nevertheless, the current study suggests a role for this region in the representation of person-knowledge. It is noteworthy that self-referential information (e.g., person-knowledge about oneself) is also systematically shown to activate a similar, albeit more ventral, region of the MPFC (Kelley et al., 2002; Moran et al., 2006). It is conceivable that the MPFC might support elaborate social construal by representing the various unique attributes of social targets, being either a conspecific or oneself. These conceptual representations about human entities might also support theory of mind tasks and social cognition more broadly. The current results do not completely exclude the possibility that specific processes, rather than specific type of representations, might underlie involvement of the MPFC in these social cognitive abilities. Nevertheless, the fact that perceivers performed the same judgments on all social targets (i.e., impression formation) and that person-knowledge elicited preferential MPFC activity (not perceptual familiarity) warrants further considerations of a representational role for the MPFC (Mason, Banfield, & Macrae, 2004; Mitchell et al., 2002).

Other regions in addition to the MPFC were preferentially recruited by person-knowledge. Among these regions, greater activity in VLPFC was obtained when perceivers formed impressions of both novel and familiar faces paired with person-knowledge compared to novel and familiar faces without person-knowledge, respectively. The VLPFC is believed to play a role in the integration of visual and somatosensory information (Price, 2008) as well as in emotional and cognitive regulation operations (Ochsner, & Gross, 2005; Thompson-Schill et al., 2005). It is therefore possible that in the current context it supported the integration of the conceptual and perceptual information available when forming impressions of social targets paired with person-knowledge. Speculatively, the VLPFC might also play a role in retrieving these integrated impressions of familiar social targets for which person-knowledge is available (Thompson-Schill et al., 2005).

CONCLUSIONS

Research on the topic of face perception has led to the elaboration of extensive models of the neural systems supporting various aspects of face processing (Adolph, 2009; Haxby et al. 2001; Gobinni, & Haxby, 1997; 1996). Nevertheless, the exact role of each component of this network is still not fully understood. The current findings consolidate and extend our knowledge of face perception by demonstrating that faces for which person-knowledge is available, experimentally controlling for perceptual familiarity, recruit a network of brain

regions involved in social cognition. Among these regions, the MPFC possibly plays a role in representing person-knowledge about social targets.

Further investigations of how contextual variables influence the neural substrates of face perception will offer important insights towards understanding person perception and social cognition as a whole. Indeed, social cognitive investigations reveal the importance of variables related to social targets (e.g., person-knowledge available) and perceivers (e.g., motivations and processing goals) during person perception processes. Future studies should explore how these variables impact the neural substrates underlying face perception and interact with the processing of specific facial features (i.e., emotional expressions or facial attractiveness). This would not only help us better understand person perception operations but also help us elucidate the functions supported by components of the face perception network.

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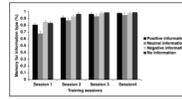


Figure 1. Behavioral results from the training sessions. The results demonstrate that, by the end of training, participants were able to correctly attribute the information type (i.e., positive, neutral, negative or no information) associated with the faces an average of 90% of the time.

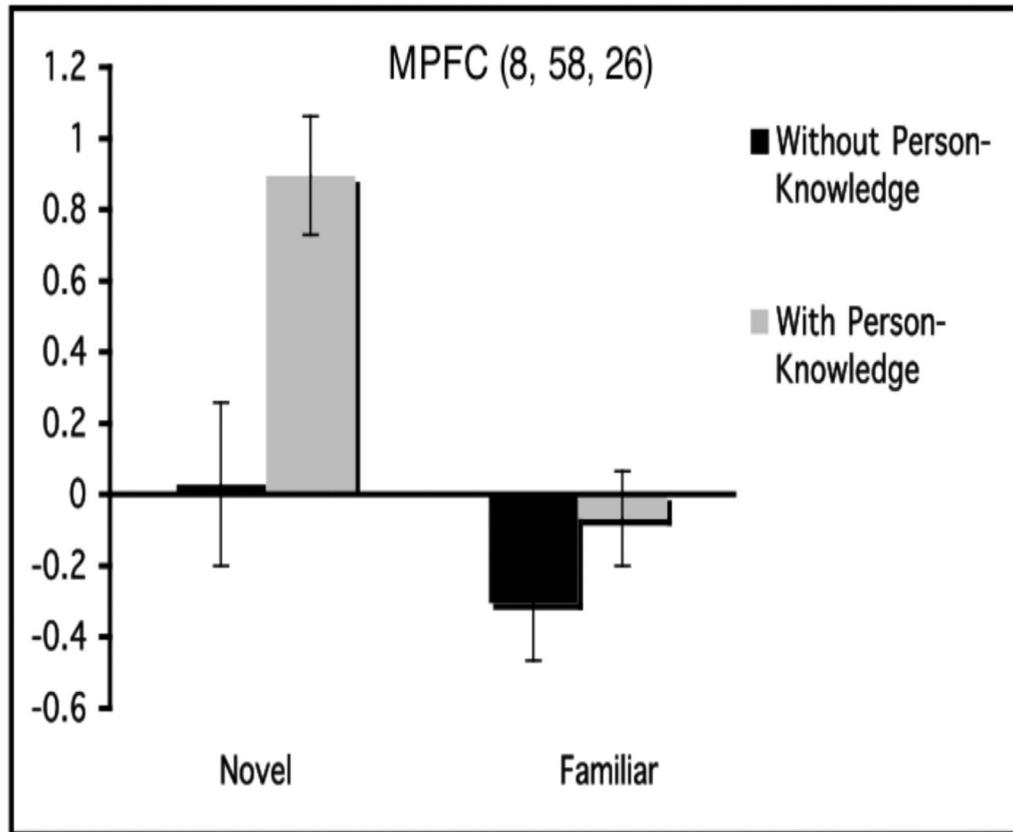


Figure 2. Graph displays a signal change (parameter estimates) for all conditions (novel faces without person-knowledge, novel faces with person-knowledge, familiar faces without person-knowledge and familiar faces with person-knowledge) relative to the baseline fixation. Error bars indicate standard error of the mean. Activation was greater to novel than familiar faces and to faces for which person-knowledge was available compared to those for which person-knowledge was not available.

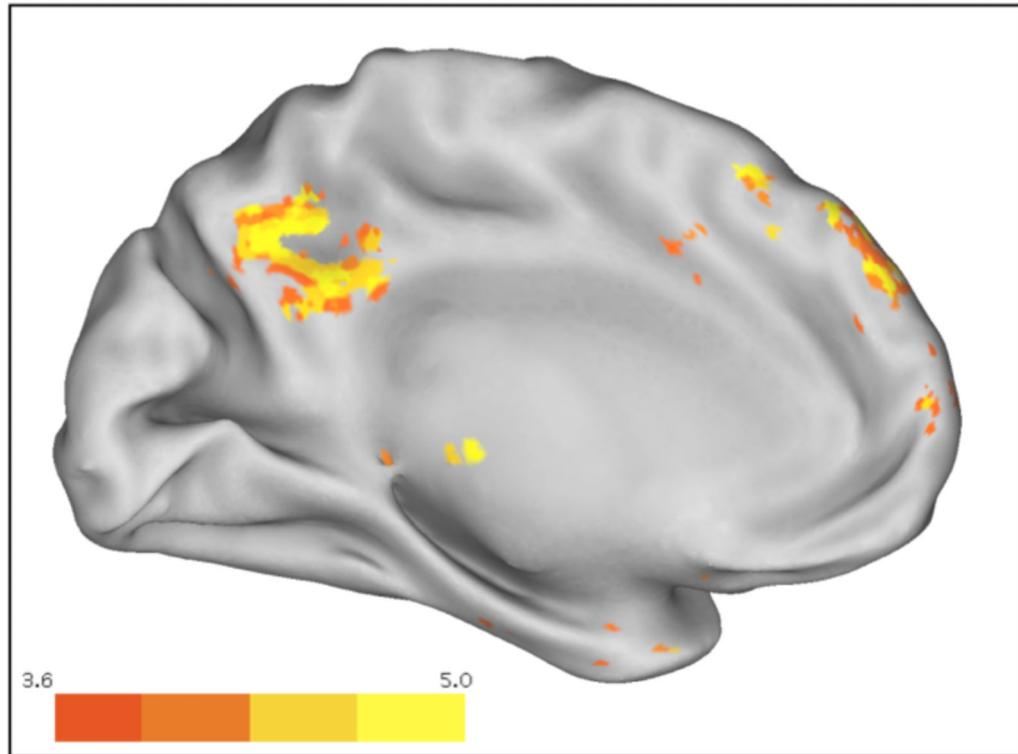


Figure 3. Sagittal views displayed on an inflated Colin Brain template. Figures display greater activity in MPFC and Precuneus when forming impressions of novel faces paired with person-knowledge compared to novel faces without person-knowledge.

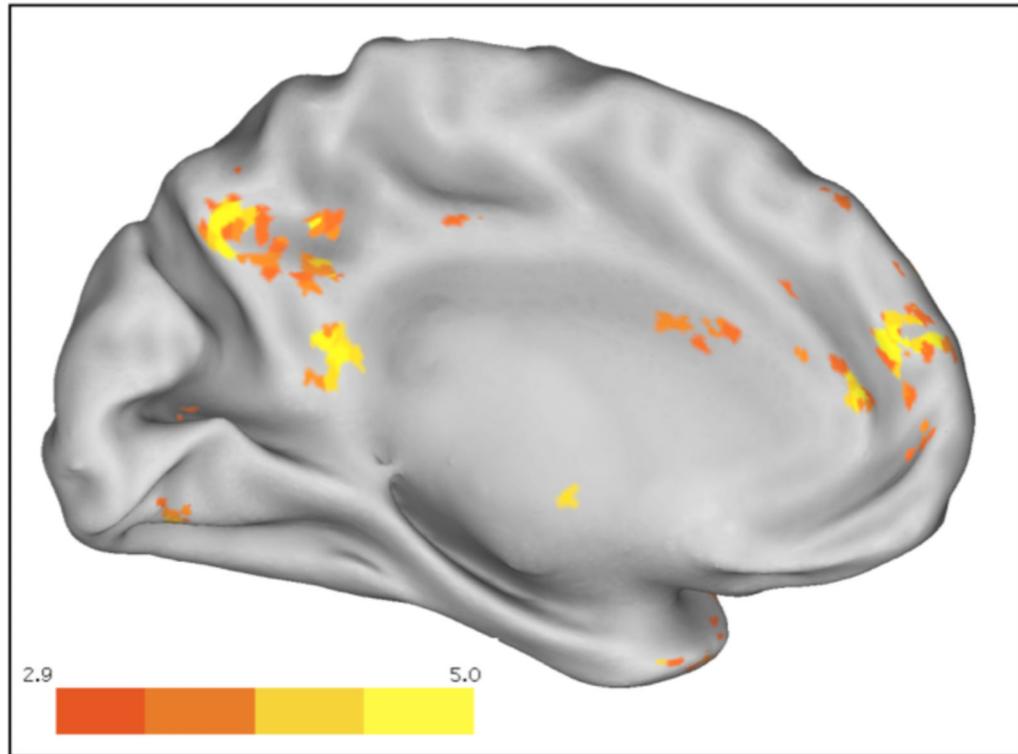


Figure 4. Sagittal views displayed on an inflated Collin Brain template. Figures display greater activity when forming impressions of familiar faces previously paired with person-knowledge compared to perceptually familiar faces.

Table 1

Identification of BOLD signal differences between novel faces without information and novel faces with information.

Brain Region	T	k	x	y	z
<u>Novel with info > Novel without info</u>					
BA9 Medial Frontal Gyrus	6.76	139	0	48	31
BA47 R Ventral Lateral Prefrontal Cortex*	6.47	18	45	26	-14
BA20 L Inferior Temporal Gyrus	6.44	41	-53	-7	-30
R Insula	6.34	27	45	-17	12
R Cerebellum	6.29	133	36	-77	-29
BA7/BA23 Precuneus/Posterior Cingulate	6.23	259	-6	-53	39
BA47 L Ventral Lateral Prefrontal Cortex	6.04	37	-39	37	-12
BA39 L Inferior Parietal Lobule	5.79	282	-42	-66	28
BA20 R Inferior Temporal Gyrus	5.38	36	50	-10	-25
L Thalamus	5.21	22	-12	-20	4
<u>Novel without info > Novel with info</u>					
BA5 R Superior Parietal Lobule	6.98	57	33	-47	47
BA18 L Inferior Occipital Gyrus	6.38	181	-30	-90	7
BA7 L Superior Parietal Lobule	5.97	21	-18	-58	55
BA40 L Inferior Parietal Lobule	5.81	23	-62	-19	29
BA7 L Precuneus	5.45	29	6	-53	55
BA9 R Middle Frontal Gyrus	5.30	27	42	40	34

Activations determined to be significant ($p < 0.001$, uncorrected at voxel-level and $p < 0.05$, corrected at cluster-level) are listed along with the best estimate of their location (* with the exception of the R Ventral Lateral Prefrontal Cortex which had a $p < .007$ corrected at cluster-level). BA = approximate Brodmann's area location. Coordinates are from the Talairach & Tournoux atlas. Locations of the activations are determined based on the functional responses superimposed on averaged anatomical MRI images and are referenced to the Talairach atlas.

Table 2

Identification of BOLD signal differences between perceptually familiar faces and novel faces without information.

Brain Region	T	k	x	y	z
<u>Familiar Perceptually > Novel without info</u>					
BA31	5.15	26	-15	-57	25
<u>Novel without info > Familiar Perceptually</u>					
BA19/37	6.23	93	50	-67	-9
BA38	6.11	39	50	14	-13
BA6	5.90	35	-30	-6	61
BA37	5.72	24	-48	-67	1
BA1	5.69	25	-53	-21	40
BA40	5.57	58	53	-42	27
	5.48	25	36	-62	-20
	5.35	28	-30	-71	-17
BA19	4.74	22	-27	-84	18

Activations determined to be significant ($p < 0.001$, uncorrected at voxel-level and $p < 0.05$, corrected at cluster-level) are listed along with the best estimate of their location. BA = approximate Brodmann's area location. Coordinates are from the Talairach & Tournoux atlas. Locations of the activations are determined based on the functional responses superimposed on averaged anatomical MRI images and are referenced to the Talairach atlas.

Table 3

Identification of BOLD signal differences between knowledge-based and perceptual-based face familiarity.

Brain Region	T	k	x	y	z
<i>Familiar Knowledge > Familiar Percept.</i>					
BA9 L Medial Frontal Gyrus	5.59	142	-6	42	12
BA31 R Precuneus	5.02	107	3	-65	36
BA47 L Ventral Lateral Prefrontal Cortex	4.17	84	-48	24	-6
BA22 L Posterior Superior Temporal Sulcus	4.15	-50	-50	-60	22
<i>Familiar Percept. > Familiar Knowledge</i>					
BA37 R Fusiform Gyrus	5.55	82	42	-56	-10
BA19 R Middle Occipital Gyrus	5.44	66	30	-77	31

Activations determined to be significant ($p < 0.001$, uncorrected at voxel-level and $p < 0.05$, corrected at cluster-level) are listed along with the best estimate of their location. BA = approximate Brodmann's area location. Coordinates are from the Talairach & Tournoux atlas. Locations of the activations are determined based on the functional responses superimposed on averaged anatomical MRI images and are referenced to the Talairach atlas.