

Spontaneous retrieval of affective person knowledge in face perception

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Abstract

In a functional magnetic resonance imaging experiment, we explored whether affective person knowledge based on memories formed from minimal information is spontaneously retrieved in face perception. In the first stage of the experiment, participants were presented with 120 unfamiliar faces. Each face was presented with a description of one of four types of behaviors: aggressive, disgusting, neutral, and nice. In the second stage, participants were scanned while engaged in a one-back recognition task in which they saw the faces that were associated with behaviors and 30 novel faces. Although this task is a simple perceptual task that neither demands person evaluation nor retrieval of person knowledge, neural responses to faces differed as a function of the behaviors. Faces associated with behaviors evoked stronger activity than did novel faces in regions implicated in social cognition—anterior paracingulate cortex and superior temporal sulcus. Explicit memory for the behaviors enhanced the neural response in these regions. Faces associated with disgusting behaviors evoked stronger activity in left anterior insula than did faces associated with aggressive behaviors. This effect was equally strong for faces associated with explicitly recalled behaviors and faces associated with non-recalled behaviors. The findings suggest that affective person knowledge acquired from minimal information is spontaneously retrieved in face perception, engaging neural systems for analysis of social cognition and emotions.

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1. Introduction

People are able to maintain distinct mental representations of a practically unlimited number of individuals, and as the great social psychologist Solomon Asch remarked “impressions form with remarkable rapidity and great ease” (Asch, 1946, p. 258). Impression formation has been a central topic of research for social cognition (Fiske, Lin, & Neuberg, 1999; Macrae & Bodenhausen, 2000). This research has shown that when people intend to form impressions of other people, these impressions are formed on-line with a disproportionate influence of initial information. Mental representations of other people are structured around a set of inferred traits and an overall evaluation of the person (Wyer & Srull, 1989). One source of trait inferences is the behavior of others. Numerous studies have shown that people make quick unreflective trait inferences from minimal behavioral information, often ignoring the context of the behavior (Gilbert & Malone, 1995; Trope & Alfieri, 1997).

People make trait inferences about other people even when they do not intend to do so (Uleman, Blader, & Todorov,

2005; Uleman, Newman, & Moskowitz, 1996) and such spontaneous trait inferences can be dissociated from the memory for the behaviors, which triggered the inferences (Carlston & Skowronski, 1994; Carlston, Skowronski, & Sparks, 1995; Todorov & Uleman, 2002). Todorov and Uleman (2003) also showed that spontaneous trait inferences occur when the cognitive resources of participants are severely constrained, suggesting that the inference process is fairly automatic (Bargh, 1994). In this paper, we explore the neural correlates of spontaneous retrieval of trait inferences during face perception. Understanding how such inferences affect face perception is critical for building neural models of the processes that associate the visual appearance of a face with a rich contextual representation of a person.

In one of the first attempts to outline a neural model of social cognition, Brothers wrote that “the visual appearance of a face in social cognition is analogous to a stream of speech in linguistic processing: the face stimulus is immediately and obligatorily transformed into the representation of a person (with dispositions and intentions) before having access to consciousness” (Brothers, 1990, p. 35). We decided to use functional brain imaging to study the neural correlates of the spontaneous retrieval of affective person knowledge during face perception. More specifically, we tested whether faces that are associated with specific

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traits (e.g., aggressive) – based on hearing about a single behavior – evoke distinctive neural responses while performing a task that does not explicitly require person evaluation or retrieval of information associated with the person.

The present research builds on and extends previous work on perception of personally familiar individuals. Using fMRI, Gobbini, Leibenluft, Santiago, and Haxby (2004) demonstrated that perception of personally familiar individuals causes changes in a distributed network of areas that extend beyond a visual memory for a face. Faces of personally familiar individuals evoked a stronger response than faces of famous familiar faces and unfamiliar faces in areas associated with social cognition. The response modulation in these areas might reflect the spontaneous retrieval of social knowledge about the personality and attitudes of close friends and relatives. This type of information is critical for appropriate social behavior and can be tightly linked to the visual representation of the face. While the work of Gobbini et al. focuses on retrieval of information that is acquired over long periods of time and repeated interactions, in this paper,

we explore the retrieval of person knowledge acquired from minimal information.

The experiment was modeled upon behavioral studies showing that a single behavior is sufficient to trigger a trait inference (Todorov & Uleman, 2002, 2004). In the first stage of the experiment, participants were presented with a large number of unfamiliar faces (120) paired with verbal descriptions of behaviors. Participants were instructed to memorize the behaviors. We used four classes of behaviors: aggressive, disgusting, nice, and neutral (Fig. 1A). For each participant, behaviors were randomly assigned to faces. Thus, the same faces appeared with different behaviors for different participants. The neural responses to faces were measured with fMRI in the second stage of the experiment in a rapid event-related design (Fig. 1B). Participants were presented with all faces from the learning task intermixed with novel faces and were scanned while performing a one-back recognition task. This task is a simple perceptual matching task that requires neither evaluation of the faces nor retrieval of the behavioral information. Thus, it measures implicit evaluation of

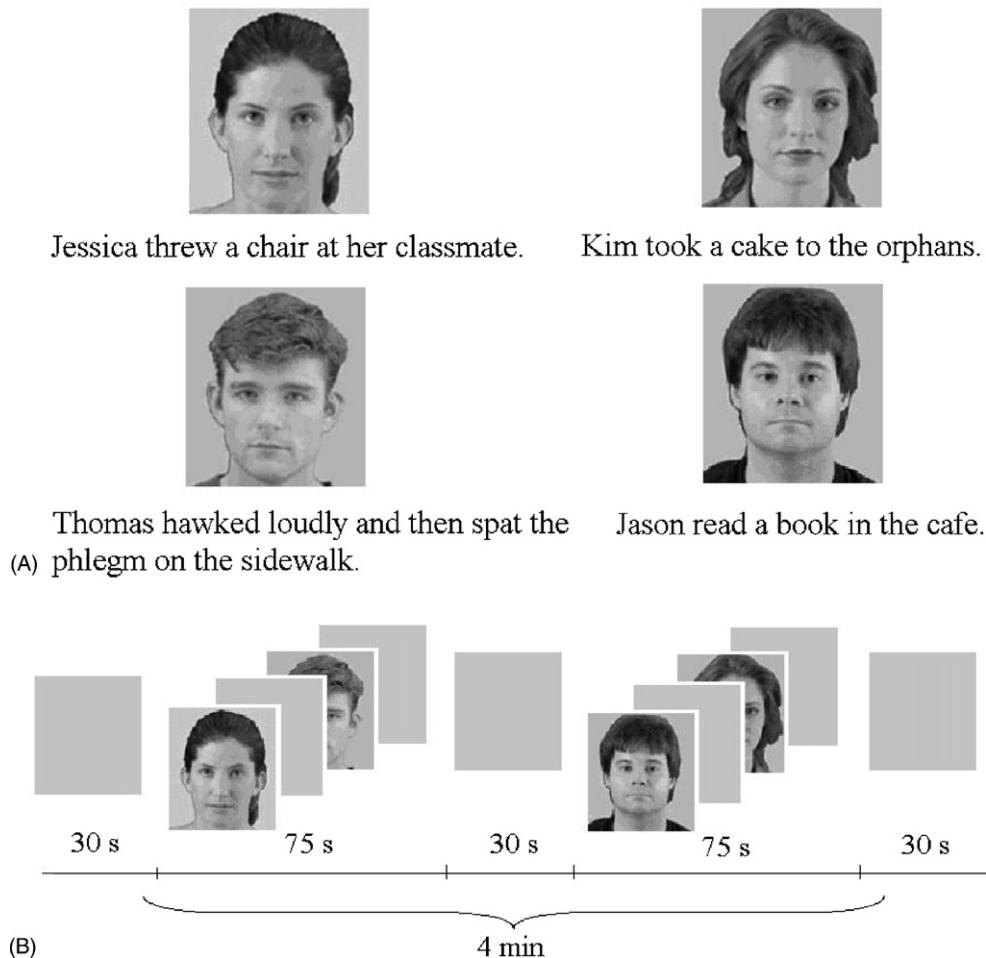


Fig. 1. (A) Examples of categories of stimuli used in the experiment. Each face was paired with a single behavior from one of four categories: aggressive, disgusting, nice, or neutral. For each participant, behaviors were randomly assigned to faces. Thus, the same face appeared with different behaviors for different participants. Each face-behavior pair was presented for 5 s. The order of face-behavior pairs was randomized. Participants were told that this was a memory experiment and instructed to memorize the behaviors. (B) Temporal sequence of stimuli in a time series. Faces were presented on gray-white background in a pseudo-random order in which there was an equal probability that a face from any of the five categories (novel, aggressive, disgusting, nice, and neutral) would follow the preceding face. A time series consisted of three 30 s fixation epochs, separating two blocks of presentations of 25 faces for 1 s each, with an inter-trial interval of 2 s. There were six time series, each lasting 4 min.

faces. After the second stage, we measured explicit memory for the behaviors.

We selected the four classes of behaviors – aggressive, disgusting, nice, and neutral – because they allowed us to test theoretically meaningful and statistically independent contrasts. First, we tested whether the neural response to faces associated with behaviors was different from the response to novel faces. Perception of familiar individuals, especially when they have personal significance, evokes neural activity in regions implicated in social cognition (Gobbini et al., 2004; Gobbini & Haxby, 2007). However, it is unclear whether trait knowledge acquired from minimal information would evoke neural activity in these regions. Second, we tested whether the neural response to faces associated with negative behaviors is different from the response to faces associated with positive behaviors.¹ For example, it is possible that spontaneous retrieval of trait knowledge acquired from minimal information involves only general good/bad discrimination rather than specific trait knowledge. Finally, we tested whether the responses to faces that are associated with negative behaviors differ based on the type of negative behavior. Specifically, we tested whether the response to faces associated with disgusting behaviors was different from the response to faces associated with aggressive behaviors. Although both of these behaviors are negative, their implications are clearly different. If specific trait knowledge is spontaneously retrieved in face perception, then we should observe differences between responses to these faces. We selected disgusting behaviors because of prior research implicating anterior insula in processing of disgust-related stimuli (Calder, Keane, Manes, Antoun, & Young, 2000; Murphy, Nimmo-Smith, & Lawrence, 2003; Phan, Wager, Taylor, & Liberzon, 2002; Phillips et al., 1997). Thus, faces associated with disgusting behaviors should evoke stronger activity in anterior insula than faces associated with aggressive behaviors.

The large number of faces and behaviors also allowed us to test whether spontaneous retrieval of affective person knowledge is independent of explicit memory for the behaviors, which triggered these inferences. Consistent with prior behavioral work (Carlston & Skowronski, 1994; Todorov & Uleman, 2002), it is possible that explicit memory for the behaviors may not be necessary for evoking the inference-associated pattern of neural responses to faces. However, it is also possible that differences in neural responses to faces as a function of the associated behaviors could be observed only if participants explicitly recall the behaviors.

We expected to see changes in neural response in two sets of brain regions: regions associated with social cognition, especially the representation of the personal traits and mental states of others, and regions associated with emotion, especially the anterior insula because of its specific role in the representation of disgust. A number of functional imaging studies have investigated brain activity during tasks that require attribution of mental states (Gallagher & Frith, 2003). Across different tasks

and modalities, three areas have been consistently activated in ‘theory of mind’ tasks: anterior paracingulate cortex (APC), posterior STS, and temporal poles (Frith & Frith, 1999; Gallagher & Frith, 2003). Perception of personally familiar faces (e.g., friends and relatives) also activates the same network of brain areas involved in ‘theory of mind’ tasks (Gobbini et al., 2004). Thus, it is likely that these areas will be important for perception of faces associated with affective traits (Mitchell, Banaji, & Macrae; Mitchell, Heatherton, & Macrae, 2002; Mitchell, Macrae, & Banaji 2004, 2005). Moreover, Harris, Todorov, and Fiske (2005) have recently shown that APC and posterior STS were specifically activated when participants were making dispositional inferences about other people. In light of these findings, we expected that faces associated with behaviors would evoke stronger responses in both APC and STS than novel faces.

2. Methods

2.1. Participants

Eleven healthy adults (8 males and 3 females) participated in the experiment. All participants were right-handed except for one. Their ages ranged from 18 to 32 years and the mean age was 21 years. One participant was removed from the analysis because of a large motion artifact and another was removed because of a large susceptibility artifact. Participants were recruited using a flyer that was posted in the Psychology Department and were paid for their participation. We acquired informed consent for their participation using a standard consent form approved by the Institutional Review Board for Human Subjects at Princeton University.

2.2. Stimuli

2.2.1. Faces

The photo stimuli were grayscale frontal images of 150 faces (75 males and 75 females) that were selected from a college yearbook. In order to ensure that none of the photos would be recognizable to our participants, we used photos of students who have long since left school and from an institution that is geographically distant from our experimental location. The gaze of all stimuli was directed forward. Stimuli were adjusted to be of equal size and luminance. In the behavioral stage of the experiment, the faces were presented on a Dell PC (13 in. screen). In the fMRI stage, the faces in the scanner were projected onto a screen and viewed in a mirror over the participant’s forehead.

2.2.2. Behaviors

We used 120 verbal descriptions of behaviors—four sets of 30 different behaviors. Each set represented a specific trait dimension: aggressive, disgusting, nice, and neutral (see Fig. 1A for examples). To create the final sets of behaviors, we used previously validated behaviors for their trait diagnosticity (Uleman, 1988), as well as behaviors from studies on aggression and disgust. Some aggressive behaviors were taken from previous studies and particularly from work on adolescent aggression (Xie, Cairns, & Cairns, 2002). The disgusting behaviors were based upon previous work on disgust elicitors (Haidt, McCauley, & Rozin, 1994). The neutral and nice behaviors were based on everyday situations and were chosen for their generality across age and gender (the list of all behaviors is available from the authors on request).

2.3. Procedures

2.3.1. Behavioral session

In the first stage of the experiment, participants were told that they would engage in a passive memorization task, during which they would be asked to look at a series of photos and sentences and remember them as best as they can for a task later in the experiment. They were also told that it was easiest to remember the stimuli by imagining the person depicted actually performing the behavior

¹ As explained below, faces associated with neutral behaviors were classified as positive and this contrast collapsed across nice and neutral behaviors.

that appeared with the face. Each participant saw two presentation blocks of 120 face–behavior pairs, with a self-regulated break between the two blocks. Each face–behavior pair was presented twice (once in each block). Each face–behavior pair was presented for 5 s, with an inter-trial interval of 1 s, and the order of the pairs was randomized for each participant. For each participant, behaviors were randomly assigned to faces. The memorization task took approximately 30 min to complete. The fMRI session immediately followed the completion of this task.

2.3.2. FMRI session

In the scanner, participants were asked to perform one-back recognition task. The task was to indicate, by press of a button, whether the current face on the screen was the same as or different from the one immediately preceding it. Thirty novel faces were intermixed with the 120 faces presented in the first stage of the experiment. There were six time series, each lasting 4 min. A time series consisted of a 30 s fixation epoch followed by a block of 25 faces, a 30 s fixation epoch, a second block of 25 faces, and a final 30 s epoch (see Fig. 1B). Faces were presented for 1 s each, with an inter-trial interval of 2 s. Faces were presented on gray–white background in a pseudo-random order in which there was an equal probability that a face from any of the five categories (novel, aggressive, disgusting, nice, and neutral) would follow the preceding face. Each time series contained a unique presentation order and the order of these sequences was randomized across participants, so that each participant had a different sequence presentation across scans. Over the six time series, the entire set of 150 faces (30 associated with aggressive behaviors, 30 with disgusting behaviors, 30 with nice behaviors, 30 with neutral behaviors, and 30 novel) was presented twice.

2.3.3. Post-fMRI behavioral session

After the completion of the fMRI session, participants were asked to make person judgments of all 150 faces and after this task to recall the behaviors that had been presented with the faces in the first stage of the experiment. In the judgment task, participants were given a forced choice categorization task in which they were asked to indicate whether each face was associated with one of four categories: aggressive, disgusting, nice, or none of these. After all 150 faces had been categorized, participants were asked to recall as much of the behavioral information as they could possibly remember. Each face was presented with a text box and participants were asked to type everything they could remember. If they could not remember the whole sentence, they were asked to write down anything that they remembered as being associated with the face. The time taken to complete this section ranged from 30 to 50 min.

Due to a computer failure, the recall data for one participant were lost, leaving us with recall data for eight participants. Two independent judges coded the accuracy of the behavior recall according to a liberal gist criterion. For example, “hit a child” was coded as correct recall of “Andrew took a swing at the helpless boy”. The agreement between the judges ranged from 81 to 100% for the eight participants. Across participants, the overall agreement was 95%. Cases for which the judges disagreed were resolved by a third judge.

2.4. Image acquisition

fMRI scans were obtained using a 3T Siemens Allegra head-only scanner. Blood oxygen level dependent (BOLD) images were obtained using gradient echoplanar imaging. The data were obtained with a 3 mm × 3 mm × 3 mm resolution using a head coil (64 × 64 matrix, FOV = 192 mm, TR = 2 s, TE = 30 ms, and flip angle = 90°). One hundred and twenty brain volumes were acquired in each time series. Each volume covered the whole cerebrum and consisted of 32 transverse slices (3 mm thick with 1 mm gap). Six time series were obtained for each participant in a single fMRI session. High resolution T1-weighted structural images were also acquired for anatomical coregistration for each participant in the beginning of the fMRI session.

2.5. Image analysis

Data were analyzed using the Analysis of Functional Neuro-images software package (AFNI; <http://afni.nimh.nih.gov/afni/>). All functional volumes were motion corrected, and the data were smoothed with a 4 mm Gaussian kernel.

Functional image data were analyzed on a voxel-wise basis with multiple regression. Faces associated with different categories of behaviors were presented in a random, intermixed sequence in an event-related design. We performed two regression analyses. In the first analysis, five regressors of interest were used to measure the strength of response to the five categories of faces (novel, aggressive, disgusting, neutral, and nice). In the second analysis, faces were classified according to the behavioral responses of participants as explained below, and nine regressors of interest were used (novel, aggressive-recalled, aggressive-non-recalled, disgusting-recalled, disgusting-non-recalled, neutral-recalled, neutral-non-recalled, nice-recalled, and nice-non-recalled). The objective of the first analysis was to identify regions that were more active for conditions of prior theoretical interest. The objective of the second analysis was to extract the percent signal change in these regions as a function of both face category and memory for the behaviors. In both regression models, regressors of no interest were included to factor out variance that could be attributed to between-time-series changes in intensity, linear and quadratic changes in intensity within a time series, and changes attributable to head movement. The beta weights for selected regressors were converted to indices of response strength, expressed in units of percent signal change relative to a baseline—the 30 s blank screens separating the blocks of faces. The maps of response magnitudes for each participant were converted to Talairach space (Talairach & Tournoux, 1988) to allow for a group analysis of the data.

The significance of effects in the group analysis was tested using a random effects model. A group analysis, based on the first regression analysis, was performed to test the following statistically orthogonal contrasts using *t*-tests: (1) faces associated with behaviors versus novel faces; (2) faces associated with negative behaviors versus faces associated with nice and neutral behaviors; (3) faces associated with disgusting behaviors versus faces associated with aggressive behaviors. Significant clusters were defined as contiguous voxels with $p < 0.005$ (uncorrected for multiple comparisons), $t(8) > 3.83$, and a minimum volume of 100 mm³.

For each participant, based on their behavioral responses in the final stage of the experiment, we divided the faces into faces associated with explicitly recalled behaviors and faces associated with non-recalled behaviors. This classification created two (recall) × four (behavior) face categories. Correspondingly, we used eight regressors, as well as a regressor for novel faces, to compute the response strength, expressed in units of percent signal change relative to the baseline. Specifically, after identifying significant clusters of theoretical interest in the group analysis ($p < 0.005$, a minimum volume of 100 mm³), based on the first regression analysis, we used the results of the second regression analysis to extract the percent signal change in these regions as a function of the associated behavior and the memory for the behavior (e.g., response to faces associated with recalled aggressive behaviors, response to faces associated with non-recalled aggressive behaviors, etc.). Finally, we tested whether the pattern of responses varied as a function of explicit memory for the behaviors using analysis of variance (ANOVA) and *t*-tests.² We conducted two different analyses: on the mean response averaged across all voxels in the cluster and on the voxel with maximum activation in the cluster. Because both analyses provided practically the same results, we report only the latter analysis.

3. Results

3.1. Behavioral data

Although participants were presented with a large number of unfamiliar faces and behaviors, they were better than chance

² For the contrast of faces associated with disgusting behaviors and faces associated with aggressive behaviors, the same procedures were followed to extract the signal change as a function of the explicit categorization of the faces (Table 1), creating regressors based on the categorization performance (e.g., faces associated with disgusting behaviors classified correctly, faces associated with disgusting behaviors classified incorrectly, etc.), and test whether the pattern of responses varied as a function of this categorization. The rationale for this analysis is explained in the section discussing this contrast.

Table 1

Means (S.D.) of proportions of face categorizations as a function of the behaviors associated with the faces

Behavior	Person judgment			
	Aggressive	Disgusting	Nice	Neutral
Aggressive	0.47 (0.24)	0.14 (0.08)	0.21 (0.21)	0.18 (0.13)
Disgusting	0.13 (0.05)	0.49 (0.18)	0.25 (0.26)	0.13 (0.13)
Nice	0.11 (0.05)	0.11 (0.07)	0.60 (0.11)	0.18 (0.14)
Neutral	0.10 (0.08)	0.12 (0.10)	0.42 (0.21)	0.36 (0.28)
Novel faces	0.08 (0.07)	0.10 (0.09)	0.21 (0.23)	0.61 (0.34)

(0.25 correct) at categorizing the faces as a function of the associated behavior. As shown on the diagonal in Table 1, 47% of the faces associated with aggressive behaviors were categorized as aggressive, $t(8) = 2.85$, $p < 0.021$, 49% of the faces associated with disgusting behaviors were categorized as disgusting, $t(8) = 3.89$, $p < 0.005$, and 60% of the faces associated with nice behaviors were categorized as nice, $t(8) = 9.66$, $p < 0.001$. Faces associated with neutral behaviors were more likely to be categorized as nice than as neutral, and only the former categorization was significantly higher than chance, $t(8) = 2.34$, $p < 0.045$. This person positivity bias (Sears, 1983) was also apparent in the participants' categorization errors. Participants were almost twice more likely to classify faces associated with negative behaviors as positive ($M = 0.19$, S.D. = 0.09) than to classify faces associated with positive or neutral behaviors as negative ($M = 0.11$, S.D. = 0.05), $t(8) = 3.06$, $p < 0.016$. In contrast to the categorization of faces associated with neutral behaviors, the dominant categorization of novel faces was neutral, $t(8) = 3.19$, $p < 0.013$. Novel faces were significantly more likely to be classified as neutral than faces associated with neutral behaviors, $t(8) = 3.80$, $p < 0.005$, and significantly less likely to be classified as nice, $t(8) = 3.92$, $p < 0.004$.

Participants recalled 37% (S.D. = 25) of aggressive behaviors, 37% (S.D. = 20) of disgusting behaviors, 30% (S.D. = 20) of nice behaviors, and 33% (S.D. = 20) of neutral behaviors.

3.2. fMRI data

3.2.1. Faces associated with behaviors versus novel faces

As we expected, faces associated with behaviors evoked a stronger response than novel faces in the APC and two regions of the STS (Table 2). We further analyzed whether the response

Table 2

Areas showing significantly greater activity for faces associated with behaviors than for novel faces

Region	Cluster size (mm ³)	x	y	z	t-Value
Left anterior paracingulate cortex	417	-5	50	37	3.86, $p < 0.005$
Left anterior cingulate gyrus	180	-14	31	31	4.28, $p < 0.003$
Left orbitofrontal cortex	769	-26	26	-9	4.25, $p < 0.003$
Left anterior superior temporal sulcus	724	-51	-18	-10	3.95, $p < 0.004$
Left posterior superior temporal sulcus	149	-38	-52	18	4.11, $p < 0.003$
Left middle temporal gyrus	150	-48	-41	-11	3.99, $p < 0.004$
Left middle temporal gyrus	137	-54	-7	-17	3.95, $p < 0.004$
Left hippocampus	176	-31	-30	-9	4.02, $p < 0.004$
Left occipital temporal sulcus	298	-36	-46	-3	3.94, $p < 0.004$

Note: The t -value for the voxel with maximum activation in the cluster is reported. Coordinates of this voxels are reported in Talairach space.

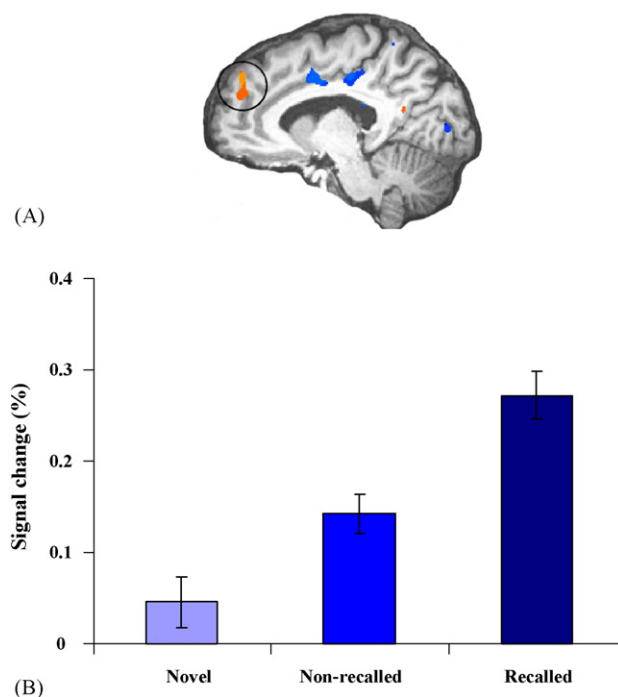


Fig. 2. (A) Area in left anterior paracingulate cortex showing a significantly stronger activation to faces associated with behaviors than to novel faces and (B) average percent signal change in the voxel of maximum activation as a function of category of face and explicit memory for the behavior information (error bars show within-subjects standard errors).

in these regions varied as a function of explicit memory for the behaviors. As Fig. 2 shows, the strongest response in the APC was to faces for which participants recalled the associated behavior. The weakest response was to novel faces. The linear trend was significant, $F(1, 7) = 20.61$, $p < 0.003$. Both simple effects were also significant. The response to faces associated with recalled behaviors was stronger than the response to faces associated with non-recalled behaviors, $t(7) = 2.77$, $p < 0.028$, and the response to the latter faces was stronger than the response to novel faces, $t(7) = 4.30$, $p < 0.004$. A similar pattern of response was found in an adjacent region on the border between APC and anterior cingulate cortex ($F(1, 7) = 24.59$, $p < 0.002$, for the linear trend).

As shown in Fig. 3, the pattern of response was the same in both regions of the STS. The response to faces associated

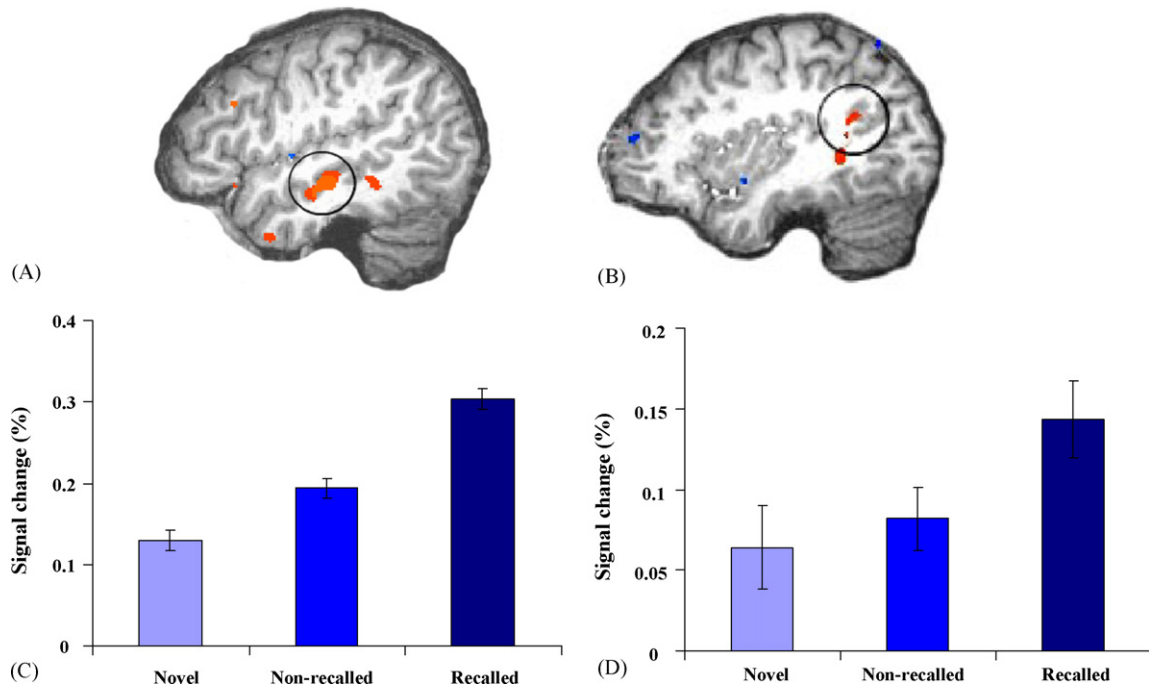


Fig. 3. (A) Area in left anterior superior temporal sulcus showing a significantly stronger activation to faces associated with behaviors than to novel faces, (B) area in left posterior superior temporal sulcus showing a significantly stronger activation to faces associated with behaviors than to novel faces, (C) average percent signal change in the voxel of maximum activation as a function of category of face and explicit memory for the behavior information in the anterior region of STS (error bars show within-subjects standard errors) and (D) average percent signal change in the voxel of maximum activation as a function of category of face and explicit memory for the behavior information in the posterior region of STS (error bars show within-subjects standard errors).

with recalled behaviors was stronger than the response to faces associated with non-recalled behaviors, $t(7) = 2.55$, $p < 0.038$ for the anterior region and $t(7) = 2.47$, $p < 0.043$ for the posterior region, and the response to the latter was stronger than the response to novel faces, $t(7) = 2.99$, $p < 0.020$ for the anterior region, although this difference was not significant in the posterior region, $t(7) = 1.37$, $p > 0.21$. In both regions, the linear trend was significant, $F(1, 7) = 14.01$, $p < 0.007$ for the anterior region, and $F(1, 7) = 11.75$, $p < 0.011$ for the posterior region.

In addition to the APC and STS, faces associated with behaviors evoked a stronger response than novel faces in left orbitofrontal cortex and in brain regions implicated in retrieval of memories: left hippocampus and two regions in left middle temporal gyrus (Table 2). In all these regions, the pattern of response was the same as in the APC and STS: faces associated with recalled behaviors evoked a stronger response than faces associated with non-recalled behaviors, which in turn evoked a stronger response than novel faces. The linear trends were significant in all regions: $F(1, 7) = 15.12$, $p < 0.006$, for left orbitofrontal cortex; $F(1, 7) = 26.28$, $p < 0.001$, for left hippocampus; $F(1, 7) = 11.15$, $p < 0.012$, for the more anterior region in left middle temporal gyrus; $F(1, 7) = 13.13$, $p < 0.008$, for the other region in left middle temporal gyrus.

3.2.2. Faces associated with negative behaviors versus faces associated with nice and neutral behaviors

Because participants classified faces associated with neutral behaviors as nice, we collapsed across faces associated with nice

behaviors and faces associated with neutral behaviors for this contrast. The only region, which met our criteria for significance, was a region in left STS (cluster volume 355 mm^3 , Talairach coordinates: $-44, -37, 6$, $t(8) = 4.28$, $p < 0.003$).

A two (behavior) \times two (recall) ANOVA showed that both the effect of behavior, $F(1, 7) = 14.99$, $p < 0.006$, and the effect of recall, $F(1, 7) = 9.57$, $p < 0.017$, were significant. Faces associated with negative behaviors evoked stronger activity than faces associated with positive behaviors, and faces associated with recalled behaviors evoked stronger activity than faces associated with non-recalled behaviors. However, these main effects were qualified by a significant interaction, $F(1, 7) = 6.64$, $p < 0.037$, indicating that the difference between faces associated with negative behaviors and faces associated with positive behaviors was significant only when these behaviors were recalled ($M = 0.28$, S.E. = 0.03 versus $M = 0.15$, S.E. = 0.02, respectively), $t(7) = 3.23$, $p < 0.014$. When the behaviors were not recalled ($M = 0.15$, S.E. = 0.01 versus $M = 0.14$, S.E. = 0.01), the difference was not significant, $t(7) = 1.28$, $p > 0.24$.

3.2.3. Faces associated with disgusting behaviors versus faces associated with aggressive behaviors

As shown in Fig. 4, faces associated with disgusting behaviors evoked a stronger response in left anterior insula than faces associated with aggressive behaviors. The only significant effect was the effect of behavior ($F(1, 7) = 18.85$, $p < 0.003$; effect of recall: $F(1, 7) = 1.23$, $p > 0.30$; $F < 1$ for the interaction). That is, the neural response was not dependent on the participants' explicit

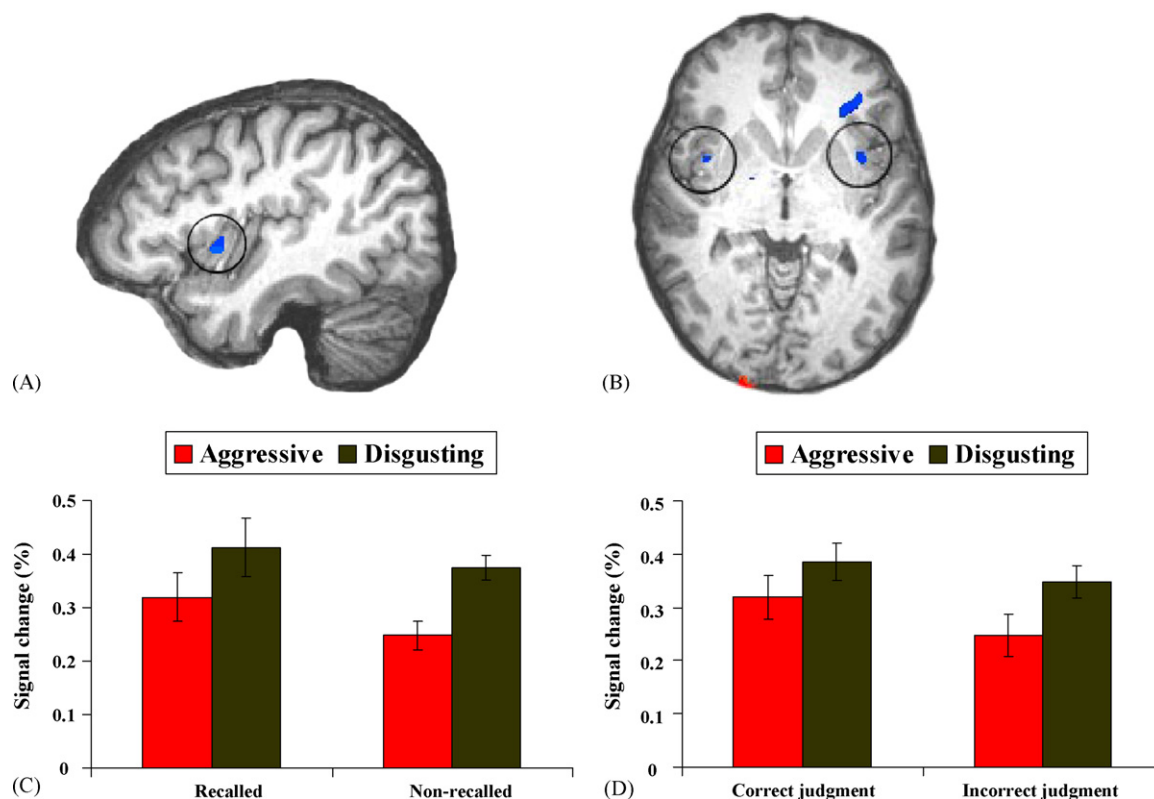


Fig. 4. (A) Area in left anterior insula showing a significantly stronger activation to faces associated with disgusting behaviors than to faces associated with aggressive behaviors, (B) areas in left and right anterior insula showing a significantly stronger activation to faces associated with disgusting behaviors than to faces associated with aggressive behaviors, (C) average percent signal change in the voxel of maximum activation in left anterior insula as a function of category of face and explicit memory for the behavior information (error bars show within-subjects standard errors) and (D) average percent signal change in the voxel of maximum activation in left anterior insula as a function of category of face and correct classification of faces (error bars show within-subjects standard errors).

Table 3

Areas of significant activity for the contrasts of faces associated with disgusting behaviors vs. faces associated with aggressive behaviors

Region	Cluster size (mm ³)	x	y	z	t-Value
Faces associated with disgusting behaviors greater than faces associated with aggressive behaviors					
Left orbitofrontal cortex	570	-33	35	-8	3.96, $p < 0.004$
Left inferior frontal gyrus	127	-57	8	14	3.92, $p < 0.004$
Right anterior cingulate gyrus	206	1	6	35	3.84, $p < 0.005$
Left anterior insula	361	-44	4	1	3.99, $p < 0.004$
Right superior temporal gyrus	561	61	-26	20	3.89, $p < 0.005$
Right superior temporal sulcus	284	45	-19	5	3.87, $p < 0.005$
Left cingulate gyrus	721	-1	-25	42	3.94, $p < 0.004$
Left cingulate gyrus	195	-3	-8	45	3.84, $p < 0.005$
Right thalamus	268	23	-18	13	4.20, $p < 0.003$
Left precentral gyrus	147	-22	-26	54	4.06, $p < 0.004$
Right post-central gyrus	488	30	-31	40	3.87, $p < 0.005$
Left paracentral lobule	211	-1	-36	58	4.79, $p < 0.001$
Right precuneus	100	12	-39	45	3.98, $p < 0.004$
Left intraparietal sulcus	551	-13	-77	43	6.09, $p < 0.001$
Right cuneus	622	1	-77	29	4.65, $p < 0.002$
Right lingual gyrus	113	21	-51	3	3.97, $p < 0.004$
Right middle occipital gyrus	160	42	-70	22	4.50, $p < 0.002$
Faces associated with aggressive behaviors greater than faces associated with disgusting behaviors					
Right cuneus	117	18	-98	0	3.91, $p < 0.004$
Right cerebellum	156	37	-50	-28	4.22, $p < 0.003$

Note: The *t*-value for the voxel with maximum activation in the cluster is reported. Coordinates of this voxels are reported in Talairach space.

memory for the behaviors. As shown in Fig. 4B, faces associated with disgusting behaviors also evoked a stronger activity in right anterior insula, although the cluster was smaller than our criterion for significance (the volume for this cluster was 35 mm^3 ; the coordinates for the voxel with maximum activation were: 40, 5, 0, $t(8) = 3.84$, $p < 0.005$).

Although the neural response in left anterior insula did not depend on explicit memory for the behaviors, it is still possible that the difference between faces associated with disgusting and aggressive behaviors was driven by explicit trait knowledge. For example, rates of recall (37%) were generally lower than the rates of correct categorization of the faces (47% for aggressive and 49% for disgusting; see Table 1 and text above). That is, although for some faces participants did not recall the associated behaviors, they could recall the trait implications of these behaviors. We used the performance on the face categorization task to control for explicit associations of faces and trait knowledge (see footnote 2). If the retrieval of affective person knowledge is an implicit effect, then the response to faces associated with disgusting behaviors should be stronger than the response to faces associated with aggressive behaviors independent of the categorization judgment of the participants. To test this hypothesis, we followed the same procedures for the participants' judgments as in the case of their recall. A two (judgment: correct versus incorrect) \times two (behavior) ANOVA revealed a significant effect of behavior, $F(1, 8) = 14.78$, $p < 0.005$ (Fig. 4D). This was the only significant effect; $F(1, 8) = 1.05$, $p > 0.34$, for the effect of recall, and $F < 1$ for the interaction.

In addition to left anterior insula, faces associated with disgusting behaviors activated more strongly a number of different regions, including right STS, left cingulate gyrus, right anterior cingulate gyrus, left intraparietal sulcus, left inferior frontal gyrus, and right precuneus (Table 3). Faces associated with aggressive behaviors evoked a stronger response only in two regions—right cerebellum and right cuneus.

4. Discussion

Previous behavioral studies have shown that people spontaneously and effortlessly make trait inferences about other people based on minimal behavior information (e.g., Carlston & Skowronski, 1994; Todorov & Uleman, 2003; Uleman et al., 2005). Building on this behavior work, we tested the consequences of such inferences for face perception. Does prior person knowledge, acquired from minimal information within a short period of time, modify neural representation of faces? Specifically, we tested whether such person knowledge is spontaneously retrieved in face perception. Despite the large number of unfamiliar faces, the impoverished nature of the behavior information, and the poor explicit memory for the information, we obtained evidence for spontaneous retrieval of person knowledge in a perceptual task that neither demanded person evaluation nor information retrieval.

Relative to novel faces, faces associated with behaviors evoked a stronger activity in APC and STS—core regions underlying thinking about other people (Gallagher & Frith, 2003). Both APC (Mitchell et al., 2002, 2004; Mitchell, Banaji et al.,

2005; Mitchell, Macrae et al., 2005) and STS are involved in inferring intentions and person attributes of other people (Winston, Strange, O'Doherty, & Dolan, 2002). The activity observed in these regions in the current study suggests that participants spontaneously retrieved person attributes during face perception. The findings are consistent with previous work on perception of personally familiar individuals (Gobbini et al., 2004; Gobbini & Haxby, 2007). As noted in Section 1, Gobbini et al. have shown that faces of personally familiar individuals activate a number of brain regions implicated in social cognition, including APC and STS. However, in the case of such individuals, the knowledge is acquired over years with numerous and varied interactions. In contrast, in the present study, the person knowledge was acquired from minimal information: two 5 s pairings of a picture of a face with one statement of behavior. Nevertheless, this newly acquired knowledge engaged neural systems for analysis of social cognition.

APC is involved not only in thinking about other people but also in thinking about oneself or self-referential processing (Mitchell, Banaji et al., 2005; Mitchell, Macrae et al., 2005; Ochsner et al., 2004). Mitchell et al. argued that whereas the ventral part of the APC is involved in self-referential processing, the dorsal part of APC is involved in judgments about others. Consistent with this hypothesis, we observed activity in the dorsal part of the APC. Ochsner et al. (2004) argued that the ventral part is involved in basic assessment of the affective value of stimuli whereas the dorsal part is involved in meta-cognitive tasks involving some self-reflection (e.g., "I remember the aggressive behavior of this person"). This latter possibility is also consistent with our data. In the debriefing, participants reported that they had spontaneous recollections of behaviors for some of the faces. In fact, the response in the dorsal part of the APC increased linearly as a function of the familiarity of faces. Further, APC did not seem to be involved in discriminating between familiar faces as a function of their associated behaviors. This pattern of findings suggests that activity in APC can simply mark the significance of perceived faces (and possibly meta-cognitive activity) and that the discrimination between different types of associated knowledge is computed in different brain regions (e.g., disgust in anterior insula).

In addition to APC and STS, faces associated with behaviors activated several regions in the left temporal lobe found to be active in retrieval of information about other people (Graham, Lee, Brett, & Patterson, 2003; Leveroni et al., 2000; Paller et al., 2003). Consistent with these studies, we found that explicit memory for the behaviors enhanced the neural responses to faces in these regions. Most of these studies have compared perception of famous with perception of unfamiliar individuals. However, in Paller et al. (2003) study, participants learned biographical facts about unfamiliar faces. Relative to novel faces, faces associated with biographical facts evoked stronger activity in left hippocampus and left middle temporal gyrus—regions that were also more active for faces associated with behaviors than novel faces in our study. On the other hand, Paller et al. did not observe stronger activity in APC and STS for newly learned faces. An interesting possibility is that regions in the temporal lobe underlie retrieval of person specific facts but not retrieval of abstracted

person attributes and affective knowledge. Work with patients is consistent with this possibility. Johnson, Kim, & Risse (1985) have shown that patients with amnesia not only can acquire affective reactions to people based on biographical information but also that these reactions can persist despite the complete loss of memory for the biographical information. Tranel and Damasio (1993) described a patient with a bilateral damage to the entire medial temporal lobe. Although this patient neither explicitly nor implicitly (e.g., increased galvanic skin response) recognized familiar faces, he showed a reliable preference for caregivers who were consistently nice to him. These findings suggest that different neural systems can underlie storage and retrieval of affective person information and biographical person information.

Within the class of faces associated with behaviors, there were important differences as a function of the associated knowledge. Faces associated with negative behaviors evoked a stronger response in left STS than faces associated with positive behaviors. Negative behaviors have higher informational and affective value than positive behaviors (Skowronski & Carlston, 1989). Thus, it is possible that faces associated with negative traits would engage more strongly regions underlying analysis of social intentions. Interestingly, faces associated with negative behaviors and faces associated with positive behaviors were differentiated only when participants recalled the behaviors. This finding suggests that activity in areas of STS could be modulated only by explicit person knowledge. However, given that we did not predict this pattern of response, the finding should be interpreted with caution.

Do people spontaneously activate specific affective knowledge in face perception? Our findings suggest that they do. Consistent with studies implicating anterior insula in processing of disgust-related stimuli (Calder et al., 2000; Murphy et al., 2003; Phan et al., 2002; Phillips et al., 1997), faces associated with disgusting behaviors activated anterior insula more strongly than faces associated with aggressive behaviors. Although both aggressive and disgusting behaviors are negative, faces associated with these behaviors were differentiated according to the specific trait implications of the behavior. Further, the response in anterior insula was completely independent of both explicit memory for the behaviors and even explicit classification of the faces. This finding suggests that emotional responses can be dissociated from explicit person judgments, a possibility consistent with research on implicit and explicit social cognition (Greenwald & Banaji, 1995; Wilson, Lindsey, & Schooler, 2000), as well as evidence for implicit associative memory (Carlesimo, Perri, Costa, Serra, & Caltagirone, 2005; Goshen-Gottstein, Moscovitch, & Melo, 2000; Graf & Schacter, 1985; Schacter & Graf, 1986).

Our experiment investigated spontaneous evocation of affective person knowledge about traits that are associated with a person *in memory*, not traits that are inferred based on the physical appearance of a face. People often make trait inferences based solely on the person's facial appearance (Todorov, Mandisodza, Goren, & Hall, 2005; Zebrowitz, 1999). Recent evidence also suggests that such inferences can be unintentional and automatic (Willis & Todorov, *in press*). Winston et al. (2002) have

shown that faces perceived as untrustworthy evoke a stronger amygdala response than trustworthy faces even when participants did not judge the faces' trustworthiness. In this case, as well as in cases of differential neural responses to attractive and unattractive faces (Aharon et al., 2001; O'Doherty et al., 2003), neural responses are dependent on the visual appearance of the face. A computational mechanism that links particular perceptual features (or a configuration of features) to conceptual (trait) representations could account for differential neural responses. In this paper, we showed that the same facial appearance could trigger different neural responses as a function of prior behavior information associated with the face.

Recently, Singer, Kiebel, Winston, Dolan, and Frith (2004) obtained conceptually similar findings. Participants repeatedly interacted with other people in a prisoner's dilemma game, in which people can either cooperate with their partner or defect. In a subsequent face perception task, Singer et al. obtained meaningful differences in neural responses to cooperators' faces and defectors' faces, although these faces were randomly assigned to these roles. Singer et al.'s and our findings show that affective significance acquired in an interaction context can modulate neural representation of faces. We further show that the required interaction is minimal and that neural responses can be independent from explicit memory for the information obtained in the interaction.

In sum, affective person knowledge extracted from minimal information is spontaneously retrieved in face perception. The same face could trigger different neural responses as a function of the information associated with the face. The simple act of making a person inference from minimal information changes the processes that are recruited when that person's face is perceived, involving the spontaneous activation of neural systems for analysis of social intentions and analysis of emotions. Understanding how the retrieval of stored affective person knowledge is neurally represented is essential for building models of the social brain.

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