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Stereotype-based modulation of person perception

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ABSTRACT

A core social–psychological question is how cultural stereotypes shape our encounters with other people. While there is considerable evidence to suggest that unexpected targets—such as female airline pilots and male nurses—impact the inferential and memorial aspects of person construal, it has yet to be established if early perceptual operations are similarly sensitive to the stereotype-related status of individuals. To explore this issue, the current investigation measured neural activity while participants made social (i.e., sex categorization) and non-social (i.e., dot detection) judgments about men and women portrayed in expected and unexpected occupations. When participants categorized the stimuli according to sex, stereotype-inconsistent targets elicited increased activity in cortical areas associated with person perception and conflict resolution. Comparable effects did not emerge during a non-social judgment task. These findings begin to elucidate how and when stereotypic beliefs modulate the formation of person percepts in the brain.

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Introduction

The ability of the human brain to transform complex three dimensional visual stimuli that are encountered under varying processing conditions (e.g., lighting, distance, and viewpoint variations) into meaningful representations of persons is nothing short of astonishing. According to a large corpus of neuroscientific work, this feat requires the recruitment of an extensive and partially unique set of brain regions. Their interplay is often portrayed in a hierarchical fashion. More specifically, visual person-related information is assumed to travel from photoreceptor cells located in the back of the eye through the optic nerve to the thalamus and via primary visual cortices to what has been termed the core system of person perception (Gobbini and Haxby, 2007; Haxby et al., 2000; Rossion, 2008; Sergent et al., 1992; Weiner and Grill-Spector, 2010). In this core system the structural analysis of human faces and bodies is accomplished (i.e., person perception), before the information gets used by an extended system of brain sites to infer person knowledge such as an individual's emotional state, intentions and/or personality (Gobbini and Haxby, 2007; Haxby et al., 2000; Ishai, 2008).

It has also been observed, however, that brain connectivity is mostly bidirectional and that initial information reaching a cortical

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region is often processed under the influence of intra- and crossregional cortical interactions (Felleman and van Essen, 1991; Friston, 2005; Tononi et al., 1992). In addition, from a computational point of view it has been deemed unlikely that feedforward mechanisms alone can achieve flexible and invariant visual recognition in a complex and rapidly changing environment (Ahissar and Hochstein, 2002; Deco and Rolls, 2004; Lamme and Roelfsema, 2000; Mumford, 1992). Therefore, an alternative perspective has emerged that characterizes person perception as dynamic, flexible and specialized to a perceiver's learning history, expectations and current processing goals (Amodio, 2010; Egner et al., 2010; Ofan et al., 2011; Peelen et al., 2009; Puri et al., 2009; van Bavel et al., 2008; in press). At the heart of this topdown perspective lies the idea that perceivers do not merely interpret their surroundings by analyzing incoming information, but rather that they try to understand sensory input by linking it to previous experience (Bar, 2009; Bruner, 1973; Friston, 2005; Gilbert and Sigman, 2007). According to this approach, person perception may not only inform person inferences, but person inferences may also influence person perception.

In everyday life, a well-traveled route to infer knowledge about others lies in the process of social stereotyping. As culturally embedded beliefs based on people's social group memberships, stereotypes provide predictions about the apparent personalities and deeds of others without the cumbersome necessity of getting to know them. Although stereotypic beliefs frequently shape the unfolding of human interactions (Brewer, 1988; Fiske and Neuberg, 1990), the extent of their activation and application during an

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encounter typically depends on a target's specific appearance as well as a perceiver's temporary processing goal (for a review see Macrae and Quadflieg, 2010). Once activated, however, stereotypic beliefs profoundly bias the way in which information about others is sought out, attended to, interpreted and remembered (Cameron and Trope, 2004; Jussim and Fleming, 1996; Trope and Thompson, 1997).

The propensity to stereotype others also draws attention to individuals who may warrant further scrutiny. In particular, people tend to direct their interest toward others who violate prevailing cultural stereotypes, such as female motor mechanics (Hutter et al., 2009) and accomplished African Americans (Kernahan et al., 2000). That atypical individuals merit additional analysis (i.e., stereotypic beliefs cannot explain their behavior) is evidenced in the post-perceptual operations that follow target registration. Stereotype-discrepant persons, for instance, trigger elaborative processes that strive to resolve apparent categorical inconsistencies and enhance person memory (Crocker et al., 1983; Jackson et al., 1993; Macrae et al., 1999). While there is accumulating evidence that an encounter with an atypical group member can impact inferential and memorial aspects of person construal, it is unclear whether equivalent effects emerge during the formation of person percepts. Based on the assumption that perception ultimately comprises an interaction between available stimulus input and the brain's predictions regarding likely stimulus identities (Cavanagh, 1991; Gilbert and Sigman, 2007; Gregory, 1997; Sterzer et al., 2009), however, stereotypes may also guide fundamental aspects of person perception.

Serving as critical groundwork to address this claim is work that explores how the brain undertakes the perceptual analysis of static human faces and bodies. Based on a large corpus of neuroimaging and brain-damaged patient studies, the core neural system of person perception is currently thought to comprise several areas in the ventral visual stream which have been termed the occipital face area (OFA, e.g., Gauthier et al., 2000), fusiform face area (FFA, Kanwisher et al., 1997), extrastriate body area (EBA, Downing et al., 2001) and the fusiform body area (FBA, Peelen and Downing, 2005). While both the OFA and FFA show increased activity when people view human faces compared to other objects (Haxby et al., 1999; Rossion, 2008; Sergent et al., 1992; Yovel and Kanwisher, 2005), the EBA and FBA display enhanced activity to human bodies (Peelen and Downing,

2007). It is through the combined effort of these four cortical regions that the structural representation of an individual's facial and bodily appearance can be achieved (Gobbini and Haxby, 2007; Haxby et al., 1999, 2000; Peelen and Downing, 2007; Weiner and Grill-Spector, 2010; Yovel and Kanwisher, 2005). What remains to be determined is whether social expectations such as those arising from stereotypic beliefs can influence the processing of visual face and body information in this set of areas.

To address this issue, we invited participants to complete a localizer task while undergoing functional magnetic resonance imaging (fMRI) to identify critical components of their core person-perception network (i.e., FFA, OFA, EBA, FBA). In addition, participants were asked to make judgments about men and women depicted in various stereotype-consistent and stereotype-inconsistent occupations (see Fig. 1). Specifically, participants reported either the sex of each target (i.e., person categorization) or the color of a dot (i.e., color classification) that was located on the image. Goal orientation was manipulated in this way as prior research has suggested that stereotype activation is impeded when non-social processing goals guide target appraisal (Macrae et al., 1997; Wheeler and Fiske, 2005). In line with previous work, we anticipated that target typicality (i.e., stereotype-inconsistent > stereotype-consistent) would modulate activity in brain regions dedicated toward person perception, but only under social-processing conditions.

Material and methods

Participants

Eighteen Caucasian undergraduate students from the University of Aberdeen (9 men), aged between 19 and 26 years (mean: 22.4 years) participated in the imaging study. All volunteers were native English speakers, right-handed as determined by the Edinburgh handedness inventory (Oldfield, 1971), and reported normal or corrected-to-normal vision. Two additional participants were recruited but excluded from analysis due to study interruption caused by a feeling of claustrophobia (1 male) and excessive head motion in the scanner (1 male). None of the participants had a history of neurological or neuropsychiatric disorders or were currently taking psychoactive medications. Informed consent



Fig. 1. Examples of stimuli used during the categorization task: (A) cleaner, (B) judge, (C) florist, and (D) footballer.

was obtained from all individuals and the study protocol was approved by the School of Psychology Ethics Committee of the University of Aberdeen.

fMRI paradigm and stimuli

During the person perception localizer task participants viewed blocks of subsequently presented pictures and performed a 1-back repetition detection task, requiring them to press a button for any immediate repetition of the same picture. Pictures comprised 6 different types of visual stimuli seen from a front view perspective including faces (42 different identities, 21 female), bodies (42 different identities, 21 female), and cars (42 different models), as well as their phasescrambled controls. Stimuli used in the localizer task were not used at any other point during the study. Faces displayed a neutral facial expression, had no visible accessories or facial hair, depicted direct eye gaze, and were cropped so that no hair was present. Bodies were cropped so that they did not contain any head or neck information. All stimuli were presented in color, embedded in the same uniform gray background, standardized to a common size of 184 (width)×210 (height) pixels, and matched on mean luminosity as well as mean contrast. Image scrambling was realized by using Fourier phase randomization (Sadr and Sinha, 2004).

The localizer task comprised two separate runs, each lasting about 14 min. In each run, participants encountered 5 blocks of each of the 6 types of visual stimuli resulting in a total of 30 alternating blocks per run. Each block consisted of 18 stimuli from the same visual category and lasted 18 s. Within each block each stimulus was presented for 750 ms followed by a blank screen for 250 ms. One or two out of the 18 stimuli per block were repeated resulting in 6 repetitions for each visual category per run. On each trial, image presentation on the screen's uniform black background was varied slightly in location (X = ~5%; Y = ~5%) to prevent participants from adapting to low level cues and to avoid repetition decisions based on the inspection of only small sectors of the images. Between blocks a white fixation cross was shown for 9 s epochs. For each localizer run a fixed, pseudo-randomized block order was created so that the same visual category was never run back-to-back and every visual category followed any other category exactly once. By necessity the visual category that was shown first in a run followed only 4 out of the possible 5 other categories. Responses were given by pressing a button on a button box with the index finger of the right hand.

The categorization task was set up as an event-related fMRI experiment during which colored photographs depicting people in specific occupational roles were shown. For each photograph participants were asked to report the sex of the person displayed (male vs. female) or to indicate the color of a dot included in the image (orange vs. purple) via a button press. In the dot judgment task, the dot was located randomly somewhere on the displayed person so that participants not only had to determine its color but also its position encouraging them to process each image as a whole (see Dubois et al., 1999; Macrae et al., 1997; Wheeler and Fiske, 2005). For the dot as well as the sex judgments, the same 60 photographs were presented in different, pseudorandom orders resulting in a total of 120 experimental trials presented in one run (lasting about 12 min). On each trial, participants first saw an instruction screen for 1000 ms with one of two words ("Gender?", "Color?") informing them which judgment was to be performed. After the instruction screen, a white fixation cross appeared for 300 ms, which was then replaced by a target photograph presented centrally on a uniform black background and remaining on the screen for 1700 ms followed by a second white fixation cross for 1000 ms. Thus, a participant had up to 2700 ms to respond to each target.

The 60 target photographs depicted Caucasian individuals in 30 different occupational roles. Fifteen of the chosen occupations were stereotypically associated with females (e.g., babysitter, cleaner, elementary school teacher, flight attendant, florist, hair dresser, hotel

receptionist, homemaker, maid, midwife, nurse, seamstress, secretary, sales person, waitress), whereas the remaining fifteen were stereotypically associated with males (e.g., bricklayer, cinematographer, chef, construction worker, judge, mechanic, firefighter, footballer, pilot, police officer, racing driver, referee, sailor, soldier, vicar). For each occupation, the internet was searched until a picture displaying a very obvious individual of the profession was found. Particular attention was paid to the fact that the bodies and the clothing of the selected individuals were ambiguous with regard to sex. Thus, naturally occurring differences in male and female body shapes were either invisible due to profession-specific uniforms (e.g., the wide robes of a vicar or a judge) or because the chosen individuals held profession-defining objects so that primary sex markers such as breasts were covered (e.g., a maid holding towels covering the chest area). Using Adobe Photoshop (Version 8.0) the chosen individuals' were then altered such that their head was removed. The remaining bodies were optimized so that a slightly masculinized and feminized version of each body was created. This was done by minimally stretching or squashing the image, and by adding or removing clothing folds in the appropriate places to take away or add indications of breasts or muscles. Each of the resulting 30 feminized bodies was then paired with one of 30 female faces, and each of the 30 masculinized bodies with one of 30 male faces. All faces depicted neutral facial expressions, had no visible accessories (i.e., glasses, jewelry) or facial hair and displayed direct eye gaze. The final pictures were standardized to a common size of 400×400 pixels. Half of the stereotype-consistent (e.g., male sailor) and half of the corresponding stereotype-inconsistent pictures (e.g., female sailor) were marked with an orange dot, whereas the remaining pictures were marked with a purple dot. The applied dots (24 pixels in diameter) were placed randomly on the individuals (anywhere on the face and body area) with the limitations that the dot was in the same position and of the same color for the masculinized and feminized version of each image (for examples see Fig. 1).

Intermixed with the trials of interest in the categorization task were 69 rest trials. These trials were included to introduce "jitter" into the time series so that unique estimates of the hemodynamic responses for the trial types of interest could be computed (Ollinger et al., 2001). Rest trials consisted of the presentation of a white fixation cross which remained on the screen for 1000 up to 11000 ms. The order of trials of interest and rest trials was pseudo-randomized using optseg2 software. Three different versions of pseudo-randomized trial orders were created and each version was used with one third of the participants. Responses during the categorization task were given by pressing one of two buttons on a button box with the index or middle finger of the right hand. All participants classified male individuals and orange dots with their index finger and female individuals and purple dots with their middle finger so that in both tasks on half of the trials of the gender-consistent and gender-inconsistent condition the reply was given with the index finger, and on the other half of the trials with the middle finger.

The order of the three experimental runs (2 localizer runs, 1 categorization run) was counterbalanced across participants. All stimuli were back projected onto a screen visible via a mirror mounted on the MRI head coil (visual angle $\sim 13.5 \times 13.5^\circ$). Stimulus presentation and recording of participants' responses and associated latencies was accomplished using Presentation® software (version 9.13, Neurobehavioral Systems, inc., Albany, California). To familiarize participants with both tasks, they completed 2 practice blocks of the localizer task (1 face block, 1 scrambled cars block) and 8 practice trials of the categorization task (4 sex judgments, 4 color judgments) on a Toshiba Laptop computer outside the scanner. None of the practice stimuli were included in the experiment proper.

Image acquisition

Image acquisition was undertaken on a 3 T whole body scanner (Philips Medical Systems, Best, The Netherlands) with an 8-channel

phased array head coil. For registration purposes anatomical images were acquired using a high-resolution 3-D fast field echo sequence (FFE; 170 sagittal slices, TE=3.8 ms, TR=8.2 ms, flip angle=8°, voxel size=.94×.94×1 mm). Functional images were collected using a gradient echo, echo-planar sequence sensitive to BOLD contrast (TR=2000 ms, T2* evolution time 40 ms, flip angle=90°, 1.88×1.88 in-plane resolution; matrix 128×128, field of view 24 cm²). For each volume 24 axial slices; 4 mm slice thickness, 1 mm skip between slices were acquired. In total, 417 volumes were collected for each of the two runs of the localizer task and 332 volumes during the categorization task. For each run the first six volumes were discarded to account for T1 saturation effects.

Data analysis

Behavioral data were analyzed using SPSS for Windows. For image analyses we used SPM8 (Wellcome Department of Imaging Neuroscience, London, UK). For the localizer task, pre-processing began by realigning and unwarping the functional data using a least square approach and a 6 parameter (rigid body) spatial transformation to minimize the effects of head movements on data analysis. The direction and magnitude of motion for each participant over the course of each run were examined, and participants who moved over 2.5 mm in any direction were excluded from the analysis (1 participant). Following realignment, the mean EPI image was registered to the high-resolution gray matter segment for each participant, using SPM8's rigid body transformation. Individual gray matter segments were extracted using SPM8's "segment" function. To ensure that the procedure was successful all extracted segments were inspected visually and if necessary cleaned from remaining bits of dura mater using MRIcroN (http://www.cabiatl.com/mricro/mricro/index. html). Subsequent to coregistration, functional data were transformed into standard anatomical space by determining the normalization parameters required to warp each individual's coregistered gray matter segment onto the gray matter MNI template. These parameters were then applied to a person's functional and structural volumes using an isotropic voxel size of $2 \times 2 \times 2$ mm for the former and $1 \times 1 \times 1$ mm for the latter. Finally, the normalized functional images were spatially smoothed applying a 6 mm full-width-half-maximum Gaussian kernel to reduce noise. Thereafter, a two-run block design was modeled using a canonical hemodynamic response function and its temporal derivative to create regressors of interest for each experimental condition. Furthermore, a high-pass temporal filter (cut-off 300 s) was applied to the data to remove low frequency noise and slow-drifts in the MR signal, Statistical parametric maps were computed individually for each participant and for each condition of interest (i.e., each predictor of interest against baseline). Based on the resulting contrast effect maps face-specific and body-specific ROIs were determined for each participant.

To identify face ROIs (OFA, FFA) a conjunction of the contrasts faces versus cars and faces versus scrambled faces [(faces-car) and (facesscrambled faces)] was computed to isolate areas responding preferentially to faces as compared to objects and for which this preference cannot be accounted for by low-level visual cues (see Rossion et al., 2011). Similarly, to identify body ROIs (EBA, FBA) a conjunction of the contrasts bodies versus cars and bodies versus scrambled bodies [(bodies-car) and (bodies-scrambled bodies)] was computed. ROIs were defined based on the specified conjunctions as the set of contiguous voxels that were significantly activated (all p < .001, uncorrected) within a 9 mm cube surrounding a region-specific peak voxel. This procedure was chosen to ensure that ROIs could be segregated from nearby activations and to roughly equate the number of voxels included across different ROIs (Peelen et al., 2006). Thus, based on the first conjunction, the FFA for each person was defined as the set of contiguous voxels that were significantly activated within a 9 mm cube surrounding a peak voxel located in the middle fusiform gyrus (in each hemisphere). Based on the same conjunction, the peak voxel of the OFA was located for each person in the inferior occipital gyrus. In addition, based on the second conjunction, a peak voxel located in the middle fusiform gyrus was defined for each person as basis for the FBA. Finally, the same conjunction was also used to determine for each person a peak voxel located in the lateral occipitotemporal cortex indicative of the EBA.

For the categorization task, pre-processing was equivalent but began by slice-time correcting the functional data to the twelfth slice of each whole-brain volume using SPM8's Fourier phase shift interpolation. A standard two-level statistical analysis approach was chosen to analyze the obtained data. Thus, a single-run event-related design was modeled using a canonical hemodynamic response function and its temporal derivative to create regressors of interest for each experimental condition. Furthermore, a high-pass temporal filter of 1/118 s was applied. Statistical parametric maps were computed individually for each participant and for each condition of interest (i.e., each predictor of interest against baseline). The resulting contrast effect maps were entered into a full-factorial second-level repeated measures analysis of variance with the factors task (sex vs. color categorization) and target typicality (stereotype-consistent vs. stereotype-inconsistent), treating participants as a random effect. To minimize false-positive results, effects were considered statistically significant using a voxelwise threshold of p<.001 and a cluster-based threshold of p < .05 (FWE corrected). In addition, the mean parameter estimates during the categorization task were extracted for each participant and ROI as identified in the localizer task. These estimates were then submitted to a 2 (target typicality: stereotype-consistent vs. stereotype-inconsistent) × 2 (task: sex vs. color judgments) repeated measures ANOVA. Follow-up simple effects analyses were used to elucidate the nature of the identified interaction effects.

The effective connectivity analysis was conducted according to the psychophysiological interaction (PPI) approach as suggested by Friston et al. (1997). As the seed region of interest for the PPI we chose an area in the dorsolateral prefrontal cortex (DLPFC) that showed enhanced activity during stereotype-inconsistent compared to stereotypeconsistent sex judgments. Thus, the first eigenvariate of a 6 mm sphere around a local maximum closest to the previously identified peak voxel of the right DLPFC was extracted for each person based on the full omnibus F-test of all four experimental conditions (stereotype-consistent sex judgment, stereotype-inconsistent sex judgment, stereotype-consistent color judgment, stereotype-inconsistent color judgment) against baseline (p<.001, k>5). Significant voxels could be identified in this region in sixteen out of the eighteen participants. The PPI analysis function in SPM8 was applied to build a design matrix suitable to estimate the PPI, including three columns reflecting the time course of the right DLPFC, the psychological variable (1 while participants viewed stereotypeinconsistent pictures under a sex categorization goal, -1 while participants viewed stereotype-consistent pictures under a sex categorization goal), and the product of physiological and psychological variable (PPI regressor). The resulting general linear model was used to determine the parameter estimates of these three components and the parameter estimates obtained for the interaction were eventually entered into a ttest. In this second-level random effects analysis an explicit brain mask was applied that comprised the fusiform gyrus and the occipital lobe bilaterally as specified in the WFU pickatlas (version 2.4; Maldjian et al., 2003) to limit the results of the analysis to brain regions of theoretical interest (i.e., person perception areas). Brain sites showing stronger effective connectivity during the stereotype-inconsistent sex trials compared to the stereotype-consistent sex-trials were determined based on a voxelwise threshold of p<.005, a cluster-based threshold of p<.05, and a minimal cluster size of 10 voxels.

Results

Behavioral analysis

Accuracy scores on the categorization task were submitted to a 2 (target typicality: stereotype-consistent vs. stereotype-inconsistent) \times 2

(task: sex vs. color judgment) repeated measures analysis of variance (ANOVA). None of the main or interaction effects reached statistical significance, indicating that accuracy was equivalent across conditions [M=97%, SD=5%]. Error trials were excluded from further statistical analyses and median response times were calculated for each experimental condition. When these data were submitted to the same 2×2 repeated measures ANOVA, the only significant effect to emerge was a target typicality \times task interaction [F(1,17)=6.81, p<.05]. Follow-up simple effect analyses revealed that, in the sex-categorization task, response times were faster when targets were displayed in stereotype-consistent (M=675 ms, SD=137 ms) than stereotype-inconsistent occupations [M=704 ms, SD=145 ms; F(1,17)=5.74, p<.05]. During the color-judgment task response times were comparable for both types of targets [stereotype-consistent: M=681 ms, SD=130 ms; stereotype-inconsistent: M=672 ms, SD=137 ms; F(1,17)=.63, ns].

Localizer-based fMRI analysis

Table 1 lists the mean coordinates of all four regions of interest (ROIs: OFA, FFA, FBA, EBA) based on the localizer task. The findings replicate previous work, such that face-selective activity was more consistently found in the FFA than the OFA (e.g., Andrews et al., 2010; Rossion et al., 2003a). Mean parameter estimates in all four ROIs were extracted from the categorization task for each participant (see Fig. 2) and submitted to a 2×2 repeated measures ANOVA. For the OFA, this analysis returned no significant main or interaction effects in either hemisphere [all F(1,15)'s<1.15, ns]. For the right and left FFA, however, a main effect of task emerged [right: F(1,17) = 7.99, p < .05; left F(1,16) = 15.23, p < .05] that was qualified by a target typicality × task interaction in both hemispheres [right: F(1,17) = 5.09, p < .05; left: F(1,16) = 3.17, p = .09]. Follow-up simple effect analyses indicated that activity in the bilateral FFA was significantly increased for stereotype-inconsistent compared to stereotype-consistent targets during sex judgments [right: F(1,17) = 6.07, p < .05, left: F(1,16) = 4.70, p<.05], but not during color judgments [right: F(1,17) = 1.13, ns; left: F(1,16) = .05, ns].

For both the right and left EBA, a target typicality × task interaction [right: F(1,17) = 4.90, p < .05; left: F(1,17) = 4.23, p = .06] emerged. Again, activity was increased for stereotype-inconsistent compared to stereotype-consistent targets during sex judgments [right: F(1,17) =6.35, p < .05; left: F(1,17) = 4.48, p < .05, but not during color judgments [right: F(1,17) = 0.78, ns; left: F(1,17) = .06, ns]. For the right and left FBA a main effect of task [right: F(1,17) = 6.05, p < .05; left: F(1,17) =21.60, p < .05] was qualified by a target typicality × task interaction [right: F(1,17) = 4.11, p = .06; left: F(1,17) = 4.98, p < .05]. Activation in the FBA was increased for stereotype-inconsistent compared to stereotypeconsistent targets during sex judgments [right: F(1,17) = 4.00, p = .06; left: F(1,17) = 7.07, p < .05], but not during color judgments [right: F(1,17) = 7.07, p < .05] (1,17) = .17, ns; left: F(1,17) = .03, ns]. Importantly, none of the above effects was notably impacted by including an additional parametric response time (RT) regressor (according to the variable impulse model, see Grinband et al., 2008; Yarkoni et al., 2009) in

Table 1Mean MNI coordinates of face- and body-selective regions of interest as determined based on the localizer task.

Region	Hemisphere	n	Х	у	Z
Extrastriate body area (EBA)	L	18	-49	-78	3
	R	18	50	-74	-1
Fusiform body area (FBA)	L	18	-43	-49	-21
	R	18	43	-48	-20
Fusiform face area (FFA)	L	17	-41	-53	-21
	R	18	41	-52	-21
Occipital face area (OFA)	L	16	-37	-83	-15
	R	16	39	-82	-12

the general linear model to account for potential response time differences between trials for each participant.

Whole-brain fMRI analyses

Exploratory whole-brain analyses were undertaken to examine the effects of the experimental manipulations beyond that observed in regions of the person perception network. In the first set of analyses, stereotype-consistent and stereotype-inconsistent sex trials were compared. This contrast (i.e., stereotype-consistent>stereotype-inconsistent) yielded no significant effects. The reverse contrast, however, revealed an enhanced response in the right DLPFC [number of voxels: 177; peak voxels: x = 34, y = 22, z = 16, t = 4.15 and x = 44, y = 18, z = 22, t = 4.06 (coordinates in MNI stereotaxic space)]. To establish if this effect was task-specific, the mean parameter estimates for both sex and color judgments were extracted for this cluster and submitted to a 2×2 repeated measures ANOVA. This analysis revealed main effects of target typicality [F(1,17) = 11.98, p < .05] and task [F(1,17) = 11.98, p < .05](1,17) = 11.17, p<.05] that were qualified by a significant target typicality \times task interaction [F(1,17) = 14.13, p < .05; see Fig. 3, panel A]. Follow-up simple effects analyses indicated that activation was significantly enhanced for stereotype-inconsistent compared to stereotypeconsistent targets during sex judgments [F(1,17) = 20.38, p < .05], but not during color judgments [F(1,17) = .03, ns]. Repetition of the analysis with the RT controlled data led to a reduction in extent and magnitude of DLPFC activity [number of voxels: 32; peak voxels: x = 36, y = 10, z = 20, t=3.83 and x=44, y=18, z=22, t=3.59, p<.05, uncorrected]. Nevertheless, mean parameter estimates extracted from the modified cluster remained to show the previously reported pattern of activity.

A second set of analyses investigated the main effects of target typicality and task (see Table 2). When neural activity between stereotype-consistent and stereotype-inconsistent trials was compared regardless of judgment type, neither the comparison of stereotype-consistent > stereotype-inconsistent nor the reverse contrast revealed any significant effects. When neural activity between color and sex judgments was contrasted, color > sex judgments yielded enhanced activity in the lingual gyrus with local maxima located in both hemispheres. Additionally, the reverse contrast (sex > color judgments) yielded enhanced activity in the dorsomedial prefrontal cortex (DMPFC), the dorsolateral prefrontal cortex (DLPFC), the ventrolateral prefrontal cortex (VLPFC), the middle temporal gyrus (MTG) and the posterior cingulate cortex (PCC).

Psychophysiological interaction analysis

Exploration of the connectivity pattern via PPI revealed that during stereotype-inconsistent compared to stereotype-consistent trials, effective connectivity with the right DLPFC was enhanced in brain areas located in the left and right mid fusiform gyrus as well as the right middle occipital gyrus (see Table 3 and Fig. 3, panel B). The peak coordinates of these regions fell close to those of the left and right FBA/FFA region and the right EBA identified using the localizer task.

Discussion

From furniture and automobiles to animals and tools, people routinely perceive their surroundings in a category-based manner (Rosch, 1978). They do so for good reason. By classifying stimuli as instances of generic categories, people can avoid the difficulty of individuating every object they encounter. In this way, categorization streamlines information processing and response generation (Harnad, 2005). Unsurprisingly, person perception frequently takes a similar course. Following the detection of category-specifying cues, individuals can be assigned to a small number of core social groupings (i.e., sex, race, age) that serve as the building blocks of person inferences (Brewer, 1988; Fiske and Neuberg, 1990; Macrae and Bodenhausen, 2000).

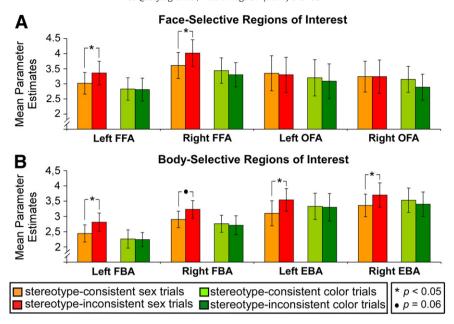


Fig. 2. Panel A: Mean parameter estimates across experimental conditions for face-selective regions of interest. Panel B: Mean parameter estimates across experimental conditions for body-selective regions of interest. Error bars reflect between-subject standard error.

Just as people are sensitive to the representativeness of exemplars from object categories (Medin, 1989; Rosch and Mervis, 1975), however, so too are they attuned to the typicality of members of social groups (Blair et al., 2004; Maddox, 2004). While perceivers are known to engage in elaborative attributional searches upon encountering atypical group members (Crocker et al., 1983; Jackson et al., 1993; Macrae et al., 1999), it is not yet known whether the violation of social expectancies can also impact fundamental processes of person perception. To explore this issue, we asked participants to view a series of stereotyped individuals with either a sex (i.e., social) or color (i.e., non-social) categorization goal in place.

Analyses of the resulting neuroimaging data revealed that completion of these two tasks recruited fundamentally divergent neural substrates. While a non-social judgment engaged low-level visual areas within the lingual gyri (likely to involve color-sensitive populations of neurons, see Chao and Martin, 1999; Sakai et al., 1995; Zeki, 1990), social judgments elicited enhanced activation in DMPFC, middle temporal gyrus and PCC. The DMPFC has previously been implicated in aspects of social cognition, notably mental state and personality attribution (Saxe, 2006; van Overwalle, 2009). In combination with

activity in the temporal lobes and PCC, this region has been argued to play a prominent role during impression formation (Schiller et al., 2009). What the current findings suggest is that, depending on their temporary processing objectives, participants construed targets as either simple perceptual entities or meaningful social agents.

Importantly, only during trials that required the sex-categorization of stereotype-inconsistent targets was increased activity observed in core person perception areas, such as the FFA, FBA and EBA. Initial evidence suggests that activity in these regions can index the effort required to form coherent person percepts. Sex judgments on visually unfamiliar compared to familiar faces, for example, have previously been found to elicit enhanced FFA activity (Rossion et al., 2003b). Greater FFA activity has also been observed during facial individuation when perceptual information was impoverished and harder to extract [e.g., following facial blurring (Bokde et al., 2005)]. Finally, increased FFA activity has been associated with the enhanced in-depth processing of faces due to social-motivational forces such as a target's in-group membership (van Bavel et al., 2008; in press). In the context of the current paradigm, amplified activation in the FFA, FBA, and EBA may therefore signal that forming a coherent person representation

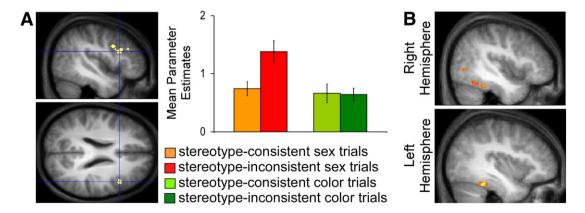


Fig. 3. Panel A: The right dorsolateral prefrontal cortex (DLPFC) displaying greater activity during stereotype-inconsistent than stereotype-consistent sex trials. Error bars of the displayed mean parameter estimates reflect between-subject standard error. Panel B: Brain regions in the fusiform gyrus and the occipital lobe showing significantly enhanced effective connectivity with the right DLPFC during stereotype-inconsistent compared to stereotype-consistent sex trials. All activations were overlaid on the structural anatomy averaged across all 18 participants.

Table 2 Exploratory whole brain fMRI analyses: peak voxel and number of voxels for brain regions obtained for the main effects of target typicality and task (voxelwise threshold of p<.05, FWE corrected; coordinates in MNI stereotaxic space).

Region	Voxels	х	у	Z	t-value		
Stereotype-consistent>stereotype-inconsistent trials No suprathreshold activation							
Stereotype-inconsistent>stereotype-consistent trials No suprathreshold activation							
Color categorization>sex categorization							
Lingual gyrus (right)	977	20	-74	-14	5.23		
Lingual gyrus (left)		-20	-74	-14	4.85		
Sex categorization > color categorization							
Dorsomedial prefrontal cortex	1391	0	32	54	5.65		
Dorsolateral prefrontal cortex (right)	613	50	24	24	4.82		
Dorsolateral prefrontal cortex (left)	643	-50	20	20	5.92		
Ventrolateral prefrontal cortex (right)	328	42	28	-16	5.00		
Posterior middle temporal gyrus (left)	296	-58	-48	-4	5.07		
Middle temporal gyrus (left)	147	-58	-16	-14	4.65		
Posterior cingulate gyrus	98	2	-52	22	4.12		

during sex categorization occurred at greater depth and was more demanding when targets failed to confirm prevailing gender stereotypes, a conclusion that is supported by the response time data. This observation is particularly noteworthy given that sex categorization is considered to be a highly routinized perceptual inference that can occur as quickly as 150–200 ms after the presentation of a face (Mouchetant-Rostaing et al., 2000; Smith et al., 2009). In line with so-called hierarchical predictive coding models of visual representation, the recruitment of additional processing resources as found in the current study is likely to reflect the brain's attempt to resolve stereotype-driven prediction errors (Egner et al., 2010; Friston, 2005; Furl et al., 2007; Puri et al., 2009).

A further important feature of hierarchical predictive coding models is the idea that predictions are mediated by backward connections from more advanced brain regions (Bullier et al., 2001; Hupé et al., 1998; Hochstein and Ahissar, 2002; Mumford, 1992). Supporting this assumption, during sex categorization, stereotype-inconsistent targets also elicited enhanced activity in the right DLPFC. An extensive literature indicates that the DLPFC is routinely engaged during complex cognitive tasks. In particular, it plays a pivotal role in representing and maintaining task objectives (Mansouri et al., 2009), especially when they require overcoming a habitual or prepotent response (Bunge et al., 2002; Liddle et al., 2001). In line with these observations, DLPFC involvement has been reported when participants are required to refrain from stereotypical thinking in reasoning or associative tasks (Beer et al., 2008; De Neys et al., 2008; Knutson et al., 2007). Corroborating these observations, DLPFC engagement occurred in the current study when participants had to ignore stereotypic associations triggered by occupational roles that conflicted with a target's actual sex. Additionally, a PPI analysis revealed that the interplay between the right DLPFC and person perception areas was tighter when targets violated rather than confirmed participants'

Table 3 Peak voxel and number of voxels for brain regions in the fusiform gyrus and the occipital lobe showing stronger effective connectivity with the right DLPFC during stereotype-inconsistent than stereotype-consistent sex judgments (voxelwise threshold of p<.005; cluster-based threshold of p<.05; k>5; coordinates in MNI stereotaxic space).

Region	Voxels	Х	у	Z	t-value
Fusiform gyrus (right)	68	44	-42	-22	5.28
		40	-54	-18	4.56
Fusiform gyrus (left)	95	-44	-42	-22	8.87
Middle occipital gyrus (right)	57	42	-70	0	4.84
		54	-70	2	4.27

stereotypic beliefs during sex judgments. In so doing, the current study complements previous research suggesting that the DLPFC is a likely candidate to act as a modulator for visual processing (Gazzaley and D'Esposito, 2007; Gilbert and Sigman, 2007; Kastner and Ungerleider, 2000).

Admittedly, it is worth keeping in mind that a PPI analysis reflects a mere correlational statistical approach. Therefore, it is also possible that activity in the core person perception network modulated activity in the right DLPFC rather than vice versa. In context of the current study, however, we consider this alternative largely implausible. There is no reason to assume that perceptual abnormalities (which could potentially modulate activity in the core person perception network and then be fed forward) were more strongly embedded in unexpected rather than expected targets. During stimulus creation, all pictures were artificially altered in the same manner. If the picture of a male police officer acted as an original, for instance, we removed the person's head and then paired the body with a new male and female head to ensure that head-body pairings did not seem more natural in one of the conditions because they reflected "real" pairings. Additionally, modifications of bodies to create male and female versions did not always occur in such a way that occupation-consistent bodies were altered into inconsistent bodies. During body search, care was taken to include stereotypeconsistent (a male sailor, a female nurse) and inconsistent bodies (e.g., a female soldier, a male cleaner) which were then slightly altered to fit the opposite sex. Thus, stimulus creation was optimized to ensure that the conflict between body and face information resulted from a stereotype-based expectation rather than from a mere perceptual abnormality.

Furthermore, if stereotype-inconsistent targets had been systematically different from stereotype-consistent targets on a perceptual level, differential activity depending on target type in person perception areas should also have occurred during dot categorization. It was found, however, that only during social processing did stereotypic expectations impact activity in the core person perception network. This observation is also noteworthy given that several influential theoretical models of person perception suggest that perceivers automatically stereotype others according to sex following the detection of available facial and bodily cues (Brewer, 1988; Fiske and Neuberg, 1990). In line with the current findings previous empirical work has begun to challenge this assumption (Gilbert and Hixon, 1991; Macrae et al., 1997; Wheeler and Fiske, 2005). What has not yet been addressed, however, is whether individuals who explicitly violate stereotypic expectations attract particular attention irrespective of a perceiver's processing goal. In social interactions, the violation of category-based expectations has been found to trigger a cardiovascular threat reaction (Mendes et al., 2007) as well as attributional searches through which the apparent inconsistency may be resolved (Hutter et al., 2009; Jackson et al., 1993; Kernahan et al., 2000). The current data failed, however, to find evidence that merely perceiving stereotype-violating targets resulted in the automatic capture of enhanced processing resources.

It is also unlikely that this absence of stereotype-based modulation of neural activity in cortical areas associated with person perception during dot categorization can be traced back to participants' mere inability to detect conspecifics in the presented stimuli. Comparison of activity between sex-consistent trials and color categorization trials shows that both trial types elicited similar levels of activity across the person perception network (see Fig. 2). Previous studies using the Rubin face–vase figure as stimulus input have demonstrated a reduction in FFA activity when the same visual information is perceived as a vase instead of a face (Andrews et al., 2002; Hasson et al., 2001). The lack of a general diminished response in the OFA, FFA, FBA and EBA during color judgments in the current study indicates that, under both processing goals, grouping processes turned local visual features into representations of human faces and bodies. Nevertheless, the extraction of social meaning (and potential categorical conflict) from such perceptual input

depended on the specific processing goal that was in place (Harnad, 2005).

Finally, during the revision of this paper a more widely debated topic was raised—the issue of how to deal with systematic response time differences between experimental conditions. Though these differences are often neglected during the analyses of brain imaging data, recent evidence indicates that many brain regions tend to show a "time-ontask" effect. Therefore, it has been recommended to report findings with and without the inclusion of a RT regressor to be able to assess the effect of RT differences across experimental conditions (Yarkoni et al., 2009). It is worthwhile to consider, however, that differences in response times across experimental conditions are not necessarily "noise" that needs to be controlled for. Importantly, in context of the current study, participants were expected to solve the conflict between perceptual and stereotypic sex cues during stereotype-inconsistent trials. In this regard, both enhanced activity in the DLPFC as well as increased response times during these trials can be thought of as an indicator of the same phenomenon of interest. As would be expected based on this reasoning, controlling for variation in one of the two variables (such as RT differences) also partially reduced the effect in the other (i.e., differential DLPFC activation across conditions). The same effect was not found in person-perception related ROIs, however, further supporting the idea that visual information was not merely sampled for longer but at a finergrained level.

In sum, the current study demonstrated that the presentation of targets that violated stereotypic beliefs (e.g., male hairdressers and female airline pilots) increased neural activity in areas dedicated toward person perception (i.e., FFA, FBA, EBA) and executive control (i.e., DLPFC) under a social, but not a non-social processing orientation. In so doing, the current work begins to elucidate how and when stereotypes modulate the formation of person percepts in the brain and extend recent efforts to elucidate top-down influences on person perception (Amodio, 2010; Ofan et al., 2011; van Bavel et al., 2008; in press). As such, the data provide further empirical support for the idea of the constructive nature of visual perception, regardless whether objects, scenes or other human beings are concerned (Eger et al., 2007; Egner et al., 2010; Gilbert and Sigman, 2007; Lupyan et al., 2010; Sterzer et al., 2009).

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