1 A behavioral face preference deficit in a monkey with an incomplete face
2 patch system

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Abstract

Primates are experts in face perception and naturally show a preference for faces under free-viewing conditions. The primate ventral stream is characterized by a network of face patches that selectively responds to faces, but it remains uncertain how important such parcellation is for face perception. Here we investigated free-viewing behavior in a female monkey who naturally lacks fMRI-defined posterior and middle lateral face patches. We presented a series of content-rich images of scenes that included faces or other objects to that monkey during a free-viewing task and tested a group of 10 control monkeys on the same task for comparison. We found that, compared to controls, the monkey with missing face patches showed a marked reduction of face viewing preference that was most pronounced for the first few fixations. In addition, her gaze fixation patterns were substantially distinct from those of controls, especially for pictures with a face. These data demonstrate an association between the clustering of neurons in face selective patches and a behavioral bias for faces in natural images.

Keywords

fMRI; face patch; free-viewing; rhesus macaque; face perception

1. Introduction

Primates are social animals relying primarily on a highly developed visual system. Faces are amongst the most important visual stimuli for social interactions, and as a result primates are expert in fast and accurate detection and recognition of faces (Crouzet et al., 2010; Freiwald et al., 2016; Leopold and Rhodes, 2010). The specialization in face perception is thought to be enabled by a dedicated network of face patches, which are characterized by face-selective activations in fMRI localizers (Kanwisher and Yovel, 2006; Tsao et al., 2008). In macaques, these face patches contain a high proportion of face-selective neurons (Tsao et al., 2006) and are strongly interconnected (Grimaldi et al., 2016; Moeller et al., 2008; Premereur et al., 2016). Several studies have established a causal link between the macaque face patch

system and face perception, by showing that pharmacological, electrical, or optogenetic perturbation has a negative impact on face gender discrimination (Afraz et al., 2015), a same-different face individuation task (Moeller et al., 2017), and face detection (Sadagopan et al., 2017). Face-selectivity of fMRI responses in these face patches only emerge after birth over the first year of development (Livingstone et al., 2017) and fail to develop if macaques are reared without exposure to faces (Arcaro et al., 2017).

Here we report a case study of a rhesus monkey with a naturally occurring incomplete face patch system. Monkey D has no face-selective patches in posterior inferotemporal cortex and the middle lateral superior temporal sulcus (STS) and misses one anterior face patch (Vinken et al., 2018), despite, as far as we know, having grown up with a normal exposure to a social environment and its visual stimuli and with no unusual medical history. Thus, in contrast with the face deprivation study by Arcaro et al. (2017), this monkey represents natural variability of the face patch system. It is unclear whether this lack of most face patches has any perceptual consequences. Perhaps face processing functions normally and the inferotemporal neurons merely lack the large-scale clustering that defines face-selective patches (Aparicio et al., 2016). In a previous study we trained monkey D successfully on a same-different face identity task (Vinken et al., 2018), but we cannot rule out that the monkey relied on low-level visual features. Free-viewing behavior is not subject to this confound and the natural tendency to fixate on faces can be exploited to investigate face processing. In humans, the behavioral saliency of faces is so strong that observers spontaneously look at a face in natural scenes within the first few fixations regardless of low-level visual saliency (Cerf et al., 2007). This tendency to look at faces or face-like stimuli is already present in newborn infants (Farroni et al., 2005) and in macaques when they are not bound by any particular task constraints (Arcaro et al., 2017; Sugita, 2008; Taubert et al., 2017). A recent study showed that the amygdala has an important role in this behavior (Taubert et al., 2018), but it most likely also relies on face processing within the visual system. Interestingly, the face-deprived monkeys of the study by Arcaro et al. (2017), whom had not developed any face patches, also did not show a face preference in a free-viewing task. Thus, face

looking in a free-viewing task can be used to implicitly assess face processing while avoiding the confound of unrelated strategies that can be learned.

In humans, natural variability in face processing and face perception has been related to several pathologies. First, developmental prosopagnosia (DP) refers to a severe impairment in the ability to recognize faces without any cognitive or early visual processing deficit. Overall, functional imaging studies suggest a reduced but not absent face selectivity in individuals with DP throughout posterior and anterior face areas (Jiahui et al., 2018). However, behavioral investigations into the nature of DP suggest that it is a heterogeneous condition that cannot be related to any single aspect of face processing (Garrido et al., 2008). Indeed, cases of DP with no face-selective activations have been reported (e.g. Bentin et al., 2007; Hadjikhani and De Gelder, 2002). Interestingly, a recent free-viewing study also suggested that individuals with DP generally spend less time looking at faces in social scenes (Bobak et al., 2017). Second, autism spectrum disorders (ASD) are characterized by an impairment in several aspects of face processing (Golarai et al., 2006). Earlier functional imaging studies reported reduced activations by faces in the fusiform face area (FFA) for subjects with ASD (for an overview, see Schultz, 2005). However, this supposed lack of FFA activations in ASD may be explained by differences in fixation behavior (see Discussion). Free-viewing of natural stimuli is atypical in ASD, with again a decreased tendency to fixate faces (Constantino et al., 2017; Wang et al., 2015).

To investigate whether the incomplete face patch system found in monkey D is related to atypical face viewing behavior, we presented a series of content-rich pictures that included faces or other objects during a free-viewing task. We tested a group of 10 control monkeys for comparison on the same task, and predicted that monkey D should have a reduced face preference similar to face-deprived monkeys. Additionally, we assessed the inter-individual fixation pattern dissimilarities in order to compare spatial distributions of fixations across image categories.

2. Materials and Methods

2.1. Subjects

Monkey D is a female adult rhesus monkey (*Macaca mulatta*) of 11 years old at the time of testing. Ten rhesus monkeys (two female; 4-12 years old) from our animal facility served as control subjects (monkeys C1-C10). All subjects had, for other experiments, a magnetic resonance imaging (MRI) compatible head post implanted during aseptic surgery under deep isoflurane gas anesthesia. Animal care and experimental procedures were in accordance with the national and European guidelines and approved by the KU Leuven Animal Ethics Committee.

2.2. Face patch localization

Face patch localization for monkey D was part of a previous study (Vinken et al., 2018). Briefly, the stimulus set of Tsao et al. (2003) was used, consisting of 5 categories of 16 stimuli each: human faces, human (headless) bodies, fruits, manmade objects, and hands. Images were presented at a size of 8° on a grey background with a red fixation dot in the middle, and the monkey was rewarded with juice for continuous fixation (2 x 2° window). The order of presentation was a pseudo-random block design, with one block of 16 s per stimulus category. Within each block, the corresponding 16 images were presented in shuffled order, without inter-stimulus interval, and at 1 s per image. All five categorical blocks were presented 5 times per run (490 s) with the restriction that all five needed to be presented once before they were repeated and every fifth categorical block presentation was followed by a 16 s fixation block.

A total of 31 functional scans of ~8 min (i.e. runs) were acquired using a gradient-echo T2*-weighted echo-planar imaging sequence of 40 horizontal slices (TR = 2 s, TE = 18 ms, flip angle = 90°, 1.25 mm isotropic voxels), with a 3 T full-body scanner (MAGNETOM Prisma, Siemens). The percentage fixation in the 2 x 2° window was >90% for the entire duration of each run. Before each scanning session, a MION contrast agent (monocrystalline iron oxide nanoparticle, Rienso: Takeda, 8-11 mg/kg) was injected intravenously

to enhance the signal-to-noise ratio (Vanduffel et al., 2001). The functional images were preprocessed using SPM12 for slice-time correction and spatial alignment, and JIP (V3.1) for co-registration with a skull-stripped anatomical MRI. Next, the images were resliced into 1 mm isotropic voxels and spatially smoothed with a 2 mm isotropic FWHM Gaussian kernel using SPM12. Finally, *t*-maps (testing across runs) were estimated using a general linear model (SPM12) that included regressors for each block type as well as motion and eye movement regressors of no interest. All regressors were convolved with a MION response function (Vanduffel et al., 2001).

2.3. Free-viewing experiment

The behavioral assessment was based on the free-viewing experiment reported by Arcaro et al. (2017), but we used mostly other natural stimuli. The full set consisted of 264 pictures of scenes, which can be divided in 5 broad categories: scenes that included faces (primates only), animals (non-primate), visually well-defined foreground objects at a close range, indoor scenes taken at a relatively greater distance, and outdoor scenes. The largest category was faces with a total of 54 pictures, consisting of the subset of 19 pictures with clearly visible hands and faces used by Arcaro et al. (2017) and 35 pictures of rhesus monkeys and humans taken at our lab (all with clearly visible hands and faces). The other 4 categories each contained 30 pictures, of which 19 indoor scene or object pictures were taken from the SUN database (Xiao et al., 2010), and the rest is owned by the first author or the lab.

For each monkey, each picture was presented nine times, spread across three sessions (days) and in three runs per session. In each run, all 264 pictures were presented in random order in the middle of a black screen. Each was shown for 3 s at a size of 22.6 x 22.6°, with an inter-stimulus interval of 200 ms. There was no fixation dot, and the monkeys received a juice reward every 500-1500 ms for as long as their gaze stayed inside a fixation window of 29 x 29° centered around the images. In other words, the monkeys were rewarded for as long as their gaze was on or just next to the picture, regardless of what they were

looking at. Throughout each run, the monkey's gaze was continuously tracked using a video-based eye tracker for the right eye (EyeLink 1000, SR Research; sampling rate 1 kHz).

In order to map the monkey's gaze to the image's pixel space, we performed an eye tracking calibration experiment at the start of each session. During this experiment, a fixation point was presented on a grey background at 13 locations in random order, covering the full square area where pictures would be presented (**Figure 3 A**). On each trial, the fixation point was presented at a new location and the monkey received a juice reward for making a saccade toward the fixation point and fixating it for 1 s. The experiment was run for a minimum of 16 successful trials per location. The medians of those 16+ fixations for each location were then used to transform gaze coordinates to pixel coordinates, using second order polynomial regression.

After transformation to pixel space closed-eye epochs (e.g. eye blinks) were removed and the data were smoothed with a Gaussian filter (SD = 10 ms). As in Arcaro et al. (2017), fixations were defined as epochs where eye velocity was $<20^\circ/\text{s}$ and fixation duration was >99 ms but <2 SD above the run mean. For the fixation density heat maps, fixations were summed over multiple presentations of the same picture, smoothed by a Gaussian filter (SD = 0.5° for individual monkeys, SD = 0.25° when pooling over multiple monkeys), and normalized by the maximum.

2.3.1. Eye coordinate shift

After running the free-viewing experiment for monkey D and several controls (C1-4), we noticed a systematic shift between fixation patterns and image content (see **Figure 3 B**). We determined that the cause of this shift was the difference between the luminance during the eye calibration task (background at 57% of maximum screen brightness) versus the free-viewing experiment (images on average at 23% brightness, SD = 9%). Thus, for the remaining controls (C5-10) we ran several calibration experiments with difference background luminance to estimate this effect (note that for the analysis of the data of the main

experiment we always used the calibration at 57% luminance to be consistent with monkeys D and C1-4). Such a difference in luminance typically causes deviations from the calibrated position through changes in pupil size (Choe et al., 2016; Drewes et al., 2014). Importantly, this shift seemed to vary between subjects and days, causing the inter-individual variability to be inflated in further analyses. To correct for this deviation, we estimated (per monkey and per day) for each image independently a shift that optimized the percentage of time the monkey looked at target areas in the remaining images (thus excluding the image for which the shift was actually computed). These target areas covered salient parts of the image that were relevant for further analyses: faces, animal heads, or other points of interest (see **Figure 3**). Note that the shift correction was based on independent data, that is, no image was ever used to estimate a shift for its own corresponding eye tracking data. This ensures that the procedure could not artificially inflate the time the monkey looked at target areas. The optimization was done by performing a grid search covering an area of $6 \times 6^\circ$ centered on the calibrated position in steps of 0.5° . We validated this procedure for control monkeys C5-10, using the calibration data with several levels of background luminance (Figure S1).

2.3.2. Fixation pattern dissimilarity

In order to quantify the dissimilarities of fixation patterns, we divided the square image area into 22×22 square tiles of $\sim 1 \times 1^\circ$ and calculated the number of fixations in each tile per image and monkey, summed across presentations. These fixation distributions were first normalized to the maximum for each image and then correlated for all possible monkey pairs (Pearson correlation), resulting for each monkey pair in a pair-wise correlation matrix M_i per image i . Each off-diagonal element in these matrices was then normalized to the expected maximum correlation (Op de Beeck et al., 2008). Briefly, for each fixation distribution (thus per image and monkey) we estimated its reliability by calculating the Spearman-Brown corrected split-half correlation coefficient (1000 random splits of the number of fixations). Then, per image, we used these reliabilities to estimate the maximal possible correlation between fixation

distributions of two monkeys: $\sqrt{r_j \times r_k}$ (with fixation distribution reliabilities r_j and r_k for monkey j and k , respectively). After dividing the correlation matrices by the expected maximum correlation, we subtracted the values from 1 to get dissimilarity matrices D_i where a value of 0 and 2 indicates minimal and maximal dissimilarity, respectively, between the fixation patterns of the two monkeys .

2.4. Statistical analysis

For statistical inference we calculated p-values using a one-sample permutation test for the mean (10^6 randomizations of the sign of each data point). The reported p-values are not corrected for multiple comparisons.

3. Results

We investigated the free-viewing behavior in monkey D and 10 control monkeys, using a rich set of pictures containing faces, non-primate animals, objects, or indoor and outdoor scenes. The monkeys were only rewarded for directing their gaze towards the general location of the stimuli and could freely choose where to look within each picture. For each monkey, each picture was presented 9 times (3 days with 3 runs per day) while we recorded their gaze using video-based eye tracking. If an intact face-patch system is strongly linked to a preference to fixate on faces (Arcaro et al., 2017), we predict that monkey D, who lacked face patches, will spend substantially less time spontaneously looking at faces.

3.1. Missing posterior and middle face patches in monkey D

First, we describe the results of the fMRI face patch localizer for monkey D. Typically, six or more patches of face-selective cortex (Tsao et al., 2008) can be defined contrasting faces with bodies, fruits, manmade objects, and hands. These six prototypical patches in IT cortex are: posterior lateral (PL), middle lateral (ML), middle fundus (MF), anterior lateral (AL), anterior fundus (AF), and anterior medial (AM) face patch. Using the face patch localizer in monkey D (Vinken et al., 2018), we found visual activations for faces (face versus fixation) throughout the ventral stream (see **Figure 1**; see also EPI images in Figure S2 A). However,

we only found evidence for face-selective activations (face versus other categories) in two anterior face patches, namely AL bilaterally and AM in the right hemisphere (and perhaps a hint of MF at lower thresholds; see Figure S2 B, C). Thus, despite the fact that these voxels were responsive to faces, there was neither evidence for posterior and middle (lateral) face patches nor for anterior patch AF. On the other hand, by contrasting bodies with the remaining categories in the fMRI localizer, we did find evidence for a body selective patch in the middle superior temporal sulcus (MSB), in addition to the anterior temporal sulcus (ASB) and anterior middle (AMB) body patches (Popivanov et al., 2014, 2012). Taken together, these pieces of evidence show that the missing face patches in the localizer were not the result of a lack of signal or an fMRI-related technical issue.

In the left hemisphere, we confirmed the absence of a face-selective patch ML by measuring spiking activity at the location where ML was expected to be (see **Figure 1** A, C). Specifically, in our previous study (Vinken et al., 2018), we assessed face selectivity on-line at 18 different grid positions in order to localize ML (by presenting 16 faces and 16 non-faces from the fMRI localizer). For the purpose of that study we required at least face-responsive, but preferably face-selective sites. Thus, after not finding ML, we decided to record data from face-responsive multiunit sites and preferably face-selective single neurons, at the two grid positions that were most activated by faces. We reported a mean face selectivity index $[(\text{net response to faces} - \text{net response to non faces}) / (|\text{net response to faces}| + |\text{net responses to non faces}|)$ (Tsao et al., 2006)] of 0.06 (SD = 0.62, n = 67) for multiunit sites and of 0.35 (SD = 0.44, n = 33) for single neurons. The index is >0 for neurons or multiunit sites that respond more to faces than non-faces and <0 vice versa. Thus, face-responsive multiunit sites in monkey D showed on average no face selectivity, but we could find face selective single neurons as expected from recordings outside fMRI-defined face patches (Taubert et al., 2015a). In contrast, for the second monkey of Vinken et al. (2018; C8 in the present study), the mean face selectivity indices for in this case unbiased samples from ML were 0.71 (SD = 0.35, n = 219) for multiunit sites and 0.69 (SD = 0.38, n = 168) for single neurons, indicating

strong and consistent face selectivity. In **Figure 1 D** we provide spiking activity time courses from the recordings of these experiments, with corresponding time courses for the face selectivity index. Note that the neural responses for monkey D were in general more transient compared to monkey C8, but there was no transient temporal pattern in face selectivity.

Figure 1. fMRI localized face and body patches in monkey D, based on 31 runs. For face patch localization, we used t -maps based on the contrast faces versus bodies, fruits, manmade objects, and hands. For body patch localization, we used bodies versus the remaining four categories. **A** Left and right hemispheres with face selective (dark yellow) and body selective (blue) areas defined by a contrast with $t > 4.76$ ($p < 0.05$, FEW corrected). Light yellow indicates areas that showed an unselective visual response to faces (contrast faces versus fixation, $t > 4.76$). Text labels indicate face and body patches. Note that there are no middle (or posterior) face patches, despite the presence of the body patch MSB. Even at lower contrast thresholds these face patches were absent (except perhaps right MF, see Figure S2). Red markers indicate locations where we measured spiking activity to directly assess neural selectivity (79 penetrations spread across 18 different grid positions). Grey contour lines indicate coronal sections displayed in panel B. Axis units are in mm, with the origin centered at the auditory meatus. Thick arrows indicate anterior (A), posterior (P), left (L), right (R), dorsal (D) and ventral (V) directions. **B** coronal sections of an anatomical MRI scan of monkey D, with heat maps superimposed for the face patch (T faces) and body patch (T bodies) localization contrasts. **C** bottom view of the brain, same conventions as in A. **D** Neural face selectivity measured as part of a different study (Vinken et al., 2018) at the grid positions activated most by faces in the expected ML area of monkey D (black cross in A and C) and from the fMRI defined ML of control

monkey C8. **i)** Time courses of average single neuron firing rates (top) and of the corresponding face selectivity index (bottom), with 95% bootstrap confidence bounds. Note that for monkey D (left) we searched for and recorded from preferably face selective neurons, in contrast with monkey C8 where no such selective search was required. As such, the weak face selectivity in D is consistent with recordings outside fMRI-defined face patches (Taubert et al., 2015a). **ii)** Time courses for multiunit sites, which we required to be face responsive (same plotting conventions as above). Average responses are no longer face selective for monkey D, demonstrating a striking difference with monkey C8.

We have fMRI mapping data of face patches in 4 out of 10 control monkeys (**Figure 2**): monkeys C4 and C8 (monkeys D and G, respectively in Premereur et al., 2016; Taubert et al., 2015a), monkey C5 (monkey M1 in Li et al., 2017), and monkey C7 (Figure S3). Monkey C5 had implanted coils that produced a low signal in anterior temporal cortex, precluding the detection of the anterior face patches. However, this monkey showed the typical posterior face patches (PL, ML and MF) bilaterally. We could not detect AM in the right hemisphere of control monkey C8, but AM was present in its left hemisphere. Thus, in each of the 4 animals, face patches were present at least unilaterally when signal strength was sufficiently strong and each of the control animals had the typical posterior face patch system (PL, ML and MF). However, ML, which is typically activated strongly, was lacking in both hemispheres of monkey D. We did not perform fMRI mapping of face patches in the remaining 6 control monkeys, assuming that these showed the typical pattern.

Figure 2. Overview of fMRI localized temporal face patches in monkey D and controls. Red indicates that the face patch was absent for a contrast with threshold at $p < 0.05$ (FWE corrected). MF in the right hemisphere of monkey D was colored light red because there was some weak evidence at lower thresholds (Figure S2 B, C). Unlike the others, monkey C5 was scanned at sub-millimeter resolution using implanted coils. The resulting signal was too weak at the anterior temporal cortex to detect any anterior face patches, so we cannot make any claims about their presence or absence (indicated with red and white hatching). LH: left hemisphere, RH: right hemisphere. ¹(Premereur et al., 2016; Taubert et al., 2015a), ²(Li et al., 2017), ³see Figures S3 and S4.

3.2. Reduced face-viewing preferences

We recorded the eye movements of monkey D and 10 control monkeys during the presentation of pictures in a free-viewing behavioral experiment. The eye tracking data were corrected for deviations from the calibrated gaze position (**Figure 3 A,B**), which resulted from a luminance difference between the calibration task and the free-viewing experiment (see Materials and methods, Free-viewing experiments, Eye coordinate shift). Because the shift correction for each image was based on all other images, the exact estimated shift value varied across images, but this variability was negligible: the standard deviation across 264 images was between 0 and 0.21° ($M = 0.03$). The average estimated shift was 0.7° ($SD = 0.4^\circ$ across monkeys), with an average shift of 0.8° for monkey D. Monkey C4 had the largest average shift of 1.5° . Overall, the correction for gaze deviation led to qualitatively the same results as without correction, but reduced inter-individual variability. Therefore, we used gaze-shift corrected eye tracking coordinates for all further analyses.

Figure 3 C shows example images illustrating that control monkeys consistently looked disproportionately toward faces (I-X) and a variety of points of interest in other picture categories, such as the head of a cockroach (XI), fruits spread on cage bedding (XII), a circular mark on a round pillow (XIII), or the center of a Ferris wheel (XIV). On the other hand, face preference of monkey D could be absent (I-III), reduced (IV-VII), or similar compared to controls (VIII-X). Similarly, monkey D showed variability in the preference for other points of interest (XIV). In order to quantitatively assess viewing preferences, we used several target areas that were selected independently of fixation data: faces and hands (as in Arcaro et al., 2017) and non-primate animal heads (**Figure 3 C I-X and XI**). In addition, in several images of the object and scene images categories we noticed a preference for certain image locations as well (**Figure 3 C XII-XIV**). Such points of interest were selected based on inspection of the average fixation densities of control monkeys (thus excluding monkey D). In total, there were faces and hands in 54 pictures, animal heads in 29, and other points of interest in 9 object, 11 indoor scene, and 15 outdoor scene pictures.

Figure 3. Gaze calibration and example images with fixation densities for monkey D and controls. **A** Gaze calibration fixation points. Red markers indicate the locations of the dots on the screen (gray rectangle). The dots cover the entire square area where pictures were presented on the screen during the free-viewing experiment. **B** Correction for gaze deviation based on the optimization for all other images (see Materials and methods, Free-viewing experiments, Eye coordinate shift). Left: an example of monkey D, who had an average shift of 0.8° . In the uncorrected image the peak fixation spot is slightly above the eye of the rabbit, while after correction (using different pictures) it overlaps with the eye. Right: an example of monkey C4, which had an average shift of 1.5° (largest of all monkeys). After correction (using different pictures), the peak fixation spot is shifted towards the salient object. **C** First rows show example images of all five stimulus categories. The second and third rows show shift-corrected normalized fixation density heat maps for monkey D (pooled across all 9 stimulus presentations) and controls (pooled across

presentations and monkeys), respectively. Boxes indicate target areas: faces (full lines) and hands (dashed lines) in all face images (I-X), heads in non-primate animal images (XI), and points of interest in selected object images, indoor scenes, outdoor scenes (XII-XIV). All target areas were used for the correction for gaze deviation (except hands, which were not particularly fixated by the monkeys).

When considering the entire 3 s interval during which the pictures were presented, the percentage fixation time was above chance (assuming a uniform distribution of the gaze) for all four types of target areas (**Figure 4 A**). Interestingly, for monkey D the percentage face fixation was >2.5 SD below the mean of controls (SD calculated across controls), meaning that the probability of observing a percentage face fixation as low as or lower than monkey D is smaller than 1 in 150 (given controls and assuming a normal distribution). The viewing preference of monkey D was reduced to a lesser extent for animal heads (-2.2 SD), and other points of interest (-1.5 SD), but not for hands ($+1.1$ SD). For one control monkey C7, face-viewing preference was almost as low as monkey D, even though the fMRI localizer (Tsao et al., 2003) showed that the face patch system was intact (Figure S3). On the other hand, the time courses of the percentage of face fixations reveal that monkey C7 showed an initial preference for faces that decreased throughout the 3 s presentation of the stimulus (**Figure 4 B**). Such an initial peak followed by a decrease is shared by most other monkeys and likely reflects a monkey's first fixations on what is relevant for the monkey before starting to explore the remaining, less interesting content of the picture.

In order to investigate the initial face preference, we focused on an early time window starting with the presentation of the stimulus and ending at 377 ms post stimulus onset, which was the point at which the time course of face fixation averaged across all monkeys peaked (**Figure 4 B**). In this time window (0-377 ms), the percentage fixation time was above chance for faces, animal heads, and other points of interest, but not for hands (**Figure 4 C**). Importantly, when considering preferences in this initial time window, percentage face fixation was substantially reduced for monkey D only, with a value that was >2.8 SD below the mean of controls (SD calculated across controls). This means that the probability of observing a value as low as or lower than monkey D is < 1 in 400 (given controls and assuming a normal distribution).

329 Comparing all 10 controls with monkey D at 377 ms (**Figure 4 D**), the gross percentage fixation of faces
330 was between 2.3 and 4.6 times higher, with an average of 3.4 (SD = 0.8, $p = 0.002$ compared to a mean of
331 1). On average, controls also fixated more than monkey D animal heads and other points of interest, with
332 a relative percentage fixation of 1.3 (SD = 0.4, $p = 0.055$), and 1.6 (SD = 0.4, $p = 0.002$) respectively, but
333 less hands, with a relative percentage fixation of 0.48 (SD = 0.15, $p = 0.002$). Finally, for the controls, the
334 relative percentage fixation time was higher for faces than for animal heads (mean difference $M = 2.1$, SD
335 = 0.7, $p = 0.002$), other points of interest ($M = 1.8$, SD = 0.7, $p = 0.002$), and hands ($M = 2.9$, SD = 0.9, $p =$
336 0.002).

337 In sum, face-viewing preference across the full 3 s of stimulus presentation was significantly reduced for
338 monkey D compared to controls. In addition, albeit to a lesser degree, viewing preference for animal heads
339 and other points of interest was also reduced, while that for hands was higher. In particular, when focusing
340 on the early time window ending at 377 ms after picture onset, monkey D was a distinct outlier for face-
341 viewing preference, but not for the other stimulus categories, compared to every single control monkey
342 (**Figure 4 C**).

Figure 4. Viewing preferences for faces (F), animal heads (A), points of interest (PI), and hands (H). **A** Average percentage time looking in target areas (i.e. boxes in **Figure 3 C**) minus the percentage of the image area covered by the boxes. Each marker indicates a different monkey. Red: monkey D. Light blue: control monkey C7, which is highlighted because of its reduced face preference over the entire 3 s presentation interval. Dark blue: control monkey C2 (see Results, Irregular fixation patterns). The horizontal black lines indicate means across controls, whereas the gray boxes indicates SD across controls. **B** Face-viewing preference across the picture presentation interval per monkey. Black: average across all monkeys (including D), which peaks at 377 ms. **C** Same as in A for the first 377 ms of picture presentation. **D** Average percent time looking at target areas (0-377ms window) for each control monkey, divided by the average for monkey D (same conventions as in A). For data and the same analysis without gaze-shift correction, see Figure S5.

3.3. Irregular fixation patterns

The previous analysis focused on viewing time for specific targets such as faces, based on predefined regions of interest in the pictures. In contrast, our stimuli are rich in content and the monkeys are likely to fixate reliably on salient features both inside as well as outside the target boxes. Here, we further investigate monkey D's viewing preferences by comparing her fixation patterns for each picture category with those of controls. In order to do this, we calculated for each monkey pair and image a dissimilarity matrix D_i , where the value for each cell indicates the pair-wise dissimilarity in fixation patterns of two monkeys (a value of 0 indicates maximal similarity). Next, we averaged these dissimilarity matrices D_i across images of the same category (i.e. those with faces and hands, animal heads, other points of

interest, or the remaining images). Finally, the category-average dissimilarity matrices were normalized by the average pairwise dissimilarity for control monkey pairs only. Thus, a value of 1 indicates a viewing pattern dissimilarity equal to the average dissimilarity between control monkeys, whereas a value of 2 indicates a dissimilarity of twice the control average.

In **Figure 5 A** we show the normalized dissimilarity matrices for images with faces and hands (i), with animal heads (ii), with other points of interest (iii), or the remaining images which had no target boxes (iv). The figure suggests that fixation patterns for monkeys D and C2 were more distinct from those of other monkeys, and in particular for monkey D in case of face images (**Figure 5 Ai**). To show this more clearly, in **Figure 5 B** we averaged for each monkey the dissimilarities from all other monkeys (i.e. row averages excluding the diagonal cells). The results show in general that fixation pattern dissimilarities of controls were tightly distributed around 1 and thus more or less equally similar to each other. Note that this figure does not show monkey C7 as an outlier, despite the reduced face-viewing preference computed for the whole 3 s presentation (**Figure 4 A**). However, fixation patterns were consistently more distinct for monkey C2 (~1.5 times the average for controls), regardless of stimulus category. This likely reflects the tendency of that monkey to fixate the upper part and even just above the pictures. Importantly, there was no relation with image category and this monkey showed normal face-viewing preference (**Figure 4**). On the other hand, monkey D showed unusually distinct fixation patterns with a clear effect of stimulus category. Indeed, in **Figure 5 C** we show each fixation pattern dissimilarity from monkey D for each of the 10 control monkey's (i.e. the first row of each matrix, excluding the diagonal cell), which is higher for faces than for animal heads (mean difference $M = 0.34$, $SD = 0.17$, $p = 0.004$), other points of interest ($M = 0.49$, $SD = 0.16$, $p = 0.002$), and the remaining images ($M = 0.58$, $SD = 0.14$, $p = 0.002$). Note that monkey C2 is also the most different from monkey D.

In sum, fixation patterns were significantly more distinct for monkey D and more so for images containing faces (and hands) than for other images. Control monkey C2 was also an outlier in terms of fixation patterns, but this was independent of stimulus category.

Figure 5. Fixation pattern dissimilarities for pictures with faces (F), animal heads (A), points of interest (PI), and remaining pictures (R). **A** Dissimilarity matrices normalized by the average pair-wise dissimilarity for controls (C1-C10). Values of 1 indicate average dissimilarity, values >1 indicate higher than average dissimilarity. **B** Average fixation pattern dissimilarities from all other monkeys. Each marker indicates a different monkey. Red: monkey D. Dark blue: control monkey C2, which is highlighted for its distinct fixation patterns. Light blue: control monkey C7, which had reduced face preference at 3 s (see Results, Reduced face-viewing preferences). The horizontal black lines indicate means across controls, whereas the gray boxes indicate SD across controls. **C** Fixation pattern dissimilarity from monkey D for each control monkey (same conventions as in B). For the same data and analysis without gaze-shift correction, see Figure S6.

4. Discussion

Here we report atypical face-viewing in a rhesus monkey D with an incomplete face patch system. The monkey, which is missing PL, ML, AF, and perhaps MF, showed a strongly reduced face-viewing preference that is most pronounced for the first few fixations. In addition, but to a smaller degree, the preference for animal heads and other points of interest was also reduced, while that for hands was slightly increased, but unlike for faces, there was overlap in viewing preference for these categories with controls. Finally,

the fixation patterns of monkey D were generally more distinct compared with controls, and this difference is by far most pronounced for pictures with a face. Together, these results demonstrate an atypical viewing of natural images, in particular when faces are present, in a monkey with missing face-selective areas in the inferior temporal cortex.

Our behavioral results are similar to those of the face-deprived monkeys described by Arcaro et al. (2017). One difference is that the deprived monkeys had a stronger tendency to look disproportionately at hands (almost as much as the controls had for faces) than monkey D. For face-deprived monkeys, this suggests that they had acquired a preference for what is arguably the most behaviorally relevant visual stimulus of their daily environment. For monkey D, we think she might just look slightly more at hands compared to controls because she is looking less at faces. Overall, this demonstrates that missing face patches that occur naturally without any obvious visual deprivation are associated with a decreased face preference bias. However, it is impossible to say which came first. That is, whether an anatomo-functional defect in the visual system led to a lower face preference, or whether the latter led to some underdeveloped face patches. It is plausible that a primate might just not develop a preference for looking at faces, if abilities such as face discrimination (Afraz et al., 2015; Moeller et al., 2017), face detection (Sadagopan et al., 2017), or social gaze following (Roy et al., 2014) are impaired because of a defect face processing system. On the other hand, the formation of category selective domains such as the face patch system require exposure to these categories (Arcaro et al., 2017; Srihasam et al., 2014). Therefore, it is also plausible that normal development of the face patch network is disrupted if a primate avoids looking at faces. Although this raises the question of why monkey D would have developed particularly anterior face patches AL and AM. The presence of fMRI defined anterior face patches, despite the absence of the more posterior ones, might be counterintuitive given the dominant view of the face patch system as a posterior to anterior face processing hierarchy. Still, without a detailed investigation of the response characteristics of the neurons it is impossible to tell whether or not normal functioning of AL and AM is also impaired. Furthermore, it is

still possible that earlier stages just lack the typical clustering of face selective neurons in face patches, while the same information is still available in a spatially distributed way. Note that the behavioral impairment in monkey D would then suggest that the presence of face selective neurons but without clustering would impact a preference for faces during free viewing.

Our results are also in agreement with Sadagopan et al. (2017), who found that during unilateral inactivation of face patch ML, monkeys showed a visual search deficit for faces embedded in noise during free-viewing. Thus, it is tempting to speculate that the face preference deficit in monkey D results from the absence of ML. A reduction in the percentage of face fixations can result from a perceptual deficit in face detection and/or a deficit in preference for faces without a concomitant detection deficit. For instance, in theory it is possible to have a deficit in preference for faces but a normal perceptual threshold in a face detection task in which foveally presented faces are embedded in noise. Although our data cannot dissociate these two possible causes of the behavioral deficit we (and Sadagopan et al., 2017) observed, it is assumed that ML and other face patches that are missing in monkey D contribute to the processing of face features, which suggests that her behavioral deficit results from a perceptual face detection deficit.

Taubert et al. (2018) reported that monkeys with bilateral amygdala lesions show no preference for faces during free-viewing. Whether the absence of face preference with amygdala lesions result from the amygdala itself or reflects absent modulation of face patches by the amygdala was unclear. The latter possibility would be in line with our finding of a face preference deficit in a monkey with a reduced face patch system. Note that only anterior face patches that were preserved in monkey D project to the amygdala (Moeller et al., 2008) while there is no evidence for direct connections between the amygdala and the face patches that were absent in monkey D. This and assuming normal amygdala function in monkey D, suggests that an intact anterior face patch – amygdala network is not sufficient for typical face preference behavior and that the latter critically depends on more posterior face patches.

In humans, the preferential bias for faces is partly genetically controlled (Constantino et al., 2017). In particular, there seems to be a specific reduction in that bias in individuals with ASD (Constantino et al., 2017; Wang et al., 2015). However, the neural basis for this reduced face preference is unclear. Neuroimaging studies have described a hypoactivation of face-selective areas in ASD (Schultz, 2005), but a major concern with these experiments is that they did not control for face scanning strategies (Kanwisher and Yovel, 2006). For example, even when looking at faces, subjects with ASD might avoid looking at the eye region (Klin et al., 2002). Therefore, in studies where subjects are not required to fixate, a hypoactivation of face-selective areas could depend on a tendency to avoid the eyes or even the face. Indeed, there is evidence that fusiform gyrus activations to faces in subjects with ASD are positively correlated with eye fixation duration (Dalton et al., 2005) and that they are typical when the subjects are required to fixate (Hadjikhani et al., 2004; Perlman et al., 2011). In addition, even the systematic shift and higher inter-individual variability in location of the face-selective fusiform gyrus for subjects with ASD (Scherf et al., 2010) could be explained by a systematic difference in face scanning strategy, with higher inter-individual variability. In contrast, monkey D was required to fixate on a central fixation dot during fMRI mapping, so an abnormal face scanning strategy cannot explain the lack of face patches in her case. Similarly, whereas individuals diagnosed with DP might show a reduced preference for looking at faces (Bobak et al., 2017), there is no general absence of face selectivity in their visual cortex (Jiahui et al., 2018). Rather, DP seems to be overall associated with a reduced face, body, and scene selectivity in face, body, and scene-selective areas throughout visual cortex, respectively (Jiahui et al., 2018). Monkey D on the other hand showed body selective fMRI responses in the expected location of the body patches (Popivanov et al., 2014, 2012). Then again, because DP is such a heterogeneous condition, making general claims might be unwarranted.

The homology of face category areas in humans and macaques is not firmly established (see Yovel and Freiwald, 2013). However, when considering the functional maps for color, places, bodies, and faces in

humans and monkeys (Caspari et al., 2014; Lafer-Sousa et al., 2016), PL and ML, which are missing in monkey D, appear to be at similar relative locations as the human occipital face area (OFA) and FFA, respectively. The anterior face patches AL or AM, which were present in monkey D, might in that scheme correspond to the human anterior temporal face patch (ATFP), whereas the missing dorsal face patches MF and AF might correspond to the human STS face areas. The homologies between PL/ML/AL and OFA/FFA/ATFP are also supported by warping of the functional activations from monkey to human cortex (Rajimehr et al., 2009). On the other hand, Ku et al. (2011) raised doubt about the homology of ML, which is located in the STS, and the more ventrally located FFA, by reporting ventrally located face patches in inferior temporal cortex of the monkey. However, the STS face patches do not appear to project to these putative ventrally located face patches, raising doubts about their consistent existence (Grimaldi et al., 2016). More disturbing is the finding that fMRI activation patterns are similar for mirror-symmetric views of faces in FFA (Axelrod and Yovel, 2012), but not in OFA, while single unit responses (Freiwald and Tsao, 2010) and fMRI activation patterns in macaque ML are selective for mirror-symmetric views (Dubois et al., 2015). However, retinotopic mapping suggests a homology between human OFA and macaque PL (Janssens et al., 2014) and by extrapolation between FFA and ML.

Finally, before this study, monkey D had participated in experiments involving faces as part of an upright-inverted or a same-different task (Vinken et al., 2018). Therefore, she had been exposed extensively to face images and one might argue that this caused her to lose interest in faces. However, control monkey C8 had undergone the same training and experiments, in addition to being part of previous studies with faces (Taubert et al., 2016, 2015a, 2015b), of which monkey C4 was also part. Both monkeys show a typical face-viewing preference as well as regular fixation patterns, so it is highly unlikely that the behavioral face preference deficit of monkey D can be explained by her training history.

In sum, we found that a monkey whom lacks most face patches has a marked reduction of the tendency to foveate faces in natural images and displays atypical eye movement scanning patterns for natural

images that contain faces. These deficits were face specific and show that a behavioral bias for faces in natural images is associated with the clustering of neurons in face selective patches.

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