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Face perception is mediated by a distributed cortical network

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Abstract

The neural system associated with face perception in the human brain was investigated using functional magnetic resonance imaging (fMRI). In contrast to many studies that focused on discreet face-responsive regions, the objective of the current study was to demonstrate that regardless of stimulus format, emotional valence, or task demands, face perception evokes activation in a distributed cortical network. Subjects viewed various stimuli (line drawings of unfamiliar faces and photographs of unfamiliar, famous, and emotional faces) and their phase scrambled versions. A network of face-responsive regions was identified that included the inferior occipital gyrus, fusiform gyrus, superior temporal sulcus, hippocampus, amygdala, inferior frontal gyrus, and orbitofrontal cortex. Although bilateral activation was found in all regions, the response in the right hemisphere was stronger. This hemispheric asymmetry was manifested by larger and more significant clusters of activation and larger number of subjects who showed the effect. A region of interest analysis revealed that while all face stimuli evoked activation within all regions, viewing famous and emotional faces resulted in larger spatial extents of activation and higher amplitudes of the fMRI signal. These results indicate that a mere percept of a face is sufficient to localize activation within the distributed cortical network that mediates the visual analysis of facial identity and expression.

Keywords: Functional MRI; Passive viewing; Orbitofrontal cortex

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1. Introduction

Face perception is a highly developed visual skill in primates. Converging evidence from neuropsychology, neurophysiology, and cognitive development indicates that face perception may be mediated by a specialized neural system in the brain [9]. In the past decade, with the advent of functional brain imaging techniques, it has been shown that face perception consistently activates a region in the lateral fusiform gyrus [17,30,33,46]. It has been proposed that the ‘fusiform face area’ is a module specialized for face perception [30]. This region, however, also responds significantly to other categories of objects (e.g., houses, chairs, and tools), thus ruling out its status as a face “module” [4,21,27,28]. Furthermore, it has been shown that neural activation within the fusiform face-selective region is modulated by expertise [12,13], attention [37], visual imagery [24,26,36], and emotion [51]. These findings suggest that the response to faces in extrastriate cortex is not the result of a mere hierarchical, bottom-up, ‘feature’ analysis, but is modulated by top-down effects, likely originating in parietal and frontal regions.

The recognition of identity is based on invariant facial features, while changeable aspects of the face, such as speech-related movement and expression, contribute to social communication. When looking at faces, we automatically perceive the gender, expression, and mood. Processing the information gleaned from the faces of others therefore requires the integration of activation within a network of cortical regions. Numerous face perception studies have reported activation not only in the fusiform gyrus, but also in other regions in the

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visual cortex, limbic system, and prefrontal cortex [24,25]. Haxby et al. have suggested that face perception is mediated by a distributed neural network in the human brain and have proposed a new model that includes a ‘core’ system and an ‘extended’ system [20]. The core system is comprised of the inferior occipital gyrus (IOG), fusiform gyrus (FG), and the superior temporal sulcus (STS). The ventral regions (IOG and FG) mediate the recognition of individuals. The more dorsal regions (STS) participate in the perception of social signals such as the direction of gaze, speech-related lip movements, and facial expressions [22,41]. The extended system includes the amygdala and the insula, which mediate the perception of emotional facial expressions, in particular fear, anger, and disgust [2,25,34,39]. Additionally, it has been shown that assessment of facial attractiveness evoked activation in prefrontal cortex [35] and the reward circuitry, in particular the amygdala and nucleus accumbens [1]. It is important to note, however, that not a single study has shown activation within all regions of both the core and the extended systems.

The aim of this study was to test whether activation in regions of the distributed neural system associated with face perception could be localized with a simple task, namely passive viewing of various face stimuli. Previous studies focused on activation within the fusiform gyrus [16], or compared activation evoked by specific face stimuli, such as familiar versus unfamiliar faces [44]. We adopted a more general approach, instructing subjects to view different face stimuli (line drawings of unfamiliar faces and photographs of unfamiliar, famous, and emotional faces) and analyzing all face-responsive regions in the brain. Our results indicate that viewing faces evokes activation in a distributed network that includes multiple, bilateral regions in the visual cortex, limbic system, and prefrontal cortex. Within this network, the response to famous and emotional faces is stronger than the response to unfamiliar faces.

2. Experimental procedures

2.1. Subjects

Thirteen healthy, drug-free volunteers (eight males, five females, mean age 26 ± 4 years) with normal vision participated in the study. All subjects gave written informed consent prior to the examination.

2.2. Stimuli and task

Subjects were presented with four different types of face stimuli: black and white line drawings of unfamiliar faces, and gray scale photographs of unfamiliar, famous, and emotional faces. Phase scrambled versions of these faces were used as visual baseline. The scrambled pictures were generated by randomizing the phase information after Fourier transformation using an in-house Matlab script. Each stimulus was presented for 3 s. Each time series included three alternating epochs of faces (36 s) and scrambled faces (24 s). Five runs (line drawings, famous, emotional, and two runs with unfamiliar faces) were collected for each subject and the order of stimulus formats was randomized. Stimuli were generated using SCOPE V2.5.4 (Max R. Duersteler, University Hospital Zurich, Switzerland) and were projected with a magnetically shielded LCD video projector onto a translucent screen. The subject viewed the screen through a mirror system.

2.3. Data acquisition

Data were collected using a 3T Philips Intera whole body MR scanner (Philips Medical Systems, Best, The Netherlands) equipped with a transmit–receive body coil and a commercial eight-element head receiver array (MRI Devices Corporation, Waukesha, WI, USA). Functional data were obtained from 39 transverse slices covering the whole brain with a spatial resolution of 2.3 mm × 2.3 mm × 3 mm (acquisition matrix 96 × 96), using a sensitivity encoded single-shot gradient-echo planar sequence [40] with an acceleration factor of 2.0. Other functional imaging parameters were FOV = 220 mm, TR = 3000 ms, TE = 35 ms, and $\theta = 82^\circ$. High-resolution spoiled gradient recalled echo structural images were obtained with 1 mm × 1 mm × 0.8 mm spatial resolution (acquisition matrix 224 × 224), TE = 2.30 ms, TR = 20 ms, $\theta = 20^\circ$. These T1-weighted images provided detailed anatomical information for the region of interest (ROI) analysis.

2.4. Data analysis

Data were analyzed using the SPM2 software (Wellcome Department of Cognitive Neurology, London, UK, www.fil.ion.ucl.ac.uk/spm/). All volumes were realigned to the first volume, corrected for motion artefacts, mean-adjusted by proportional scaling, normalized into standard stereotactic space (template provided by the Montreal Neurological Institute) and smoothed using a 5 mm full-width-at-half-maximum Gaussian kernel. The time series were high-pass filtered to eliminate low-frequency components (filter width 128 s) and adjusted for systematic differences across trials. The main effect of faces (i.e., the response to faces as compared with the response to scrambled faces) was analyzed using a linear convolution model with an assumed hemodynamic response function [10,11]. Clusters were selected that showed a significant effect ($P < 0.001$, uncorrected) with four or more contiguous voxels. Statistical parametric maps indicating the main effect of faces were used to identify a set of ROIs for each subject, including bilaterally the inferior occipital gyrus (IOG), fusiform gyrus (FG), superior temporal sulcus (STS), amygdala, hippocampus, and the inferior frontal gyrus (IFG). As activation in the orbitofrontal cortex (OFC) was found medially and the clusters were small, the ROI analysis for this region included both hemispheres.

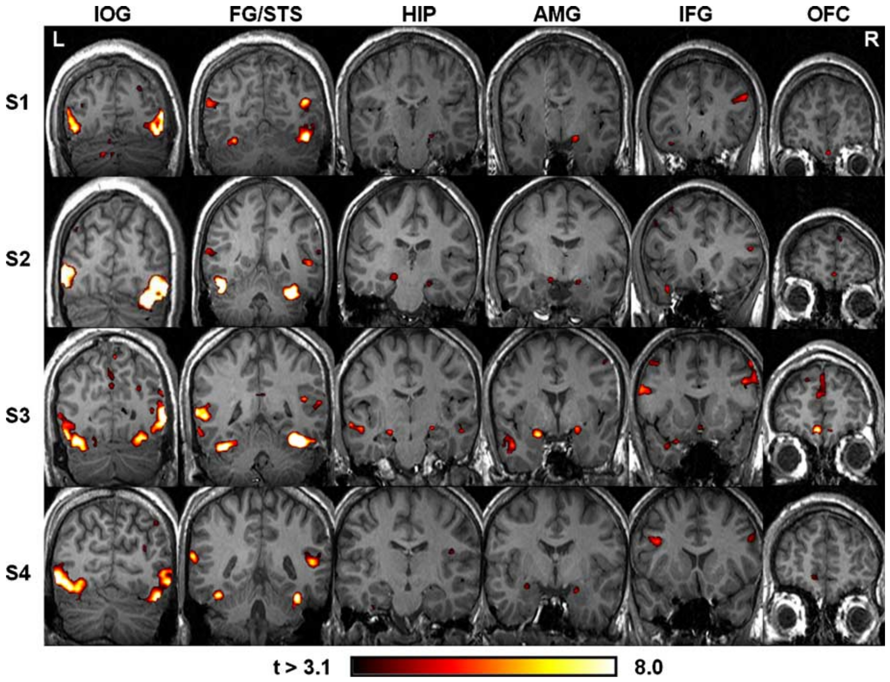

Fig. 1. A network of face-responsive regions. Shown from left to right are coronal sections illustrating activation in the inferior occipital gyrus (IOG), fusiform gyrus (FG), superior temporal sulcus (STS), hippocampus (HIP), amygdala (AMG), inferior frontal gyrus (IFG), and orbitofrontal cortex (OFC). Statistical maps, indicating the main effect of faces ($P < 0.001$, with cluster size of four or more contiguous voxels), are shown for four individual subjects.

The anatomical locations of these clusters were determined by superimposing the statistical maps on the coplanar high-resolution structural images. ROI masks were created using MRIcro (www.psychology.nottingham.ac.uk/). For each subject and each ROI, a mean time series averaged across all activated voxels in a region and across all repetitions for each stimulus format was calculated. These means were used for between-subjects random-effects analyses. Separate repeated measures ANOVAs analyzed the effect of the various face formats in each region and each hemisphere.

3. Results

3.1. Activation evoked by visual perception of faces

Visual perception of faces, as compared with scrambled faces, significantly activated the IOG, FG, STS, amygdala, hippocampus, IFG, and the OFC (Fig. 1). Within these face-responsive regions, bilateral activation was found in all subjects (see Table 1 for cluster size and brain atlas coordinates), however stronger responses were observed in the right hemi-

Table 1
Main effect of faces

Region	*N*	Mean cluster size (cm^3)	Mean coordinates			Mean *t*-value
			x	*y*	*z*	
L. IOG	13	3.05 (0.62)	−41 (1)	−81 (1)	−7 (1)	5.60 (0.28)
R. IOG	13	3.98 (0.67)	41 (2)	−82 (2)	−4 (1)	5.91 (0.36)
L. FG	13	2.92 (0.41)	−42 (1)	−58 (2)	−18 (1)	5.61 (0.28)
R. FG	13	4.42 (0.55)	40 (1)	−57 (2)	−17 (1)	6.08 (0.29)
L. STS	10	0.59 (0.19)	−54 (3)	−48 (4)	4 (3)	4.06 (0.20)
R. STS	13	0.80 (0.22)	53 (1)	−45 (3)	7 (2)	4.14 (0.15)
L. HIP	6	0.23 (0.09)	−24 (4)	−23 (1)	−16 (2)	3.63 (0.13)
R. HIP	7	0.21 (0.05)	26 (2)	−22 (1)	−16 (2)	3.60 (0.04)
L. AMG	8	0.64 (0.17)	−18 (2)	−7 (1)	−16 (1)	3.92 (0.20)
R. AMG	11	0.65 (0.16)	19 (1)	−7 (1)	−16 (1)	3.85 (0.10)
L. IFG	7	0.87 (0.29)	−47 (2)	19 (2)	22 (3)	3.83 (0.19)
R. IFG	11	1.41 (0.46)	52 (1)	23 (3)	22 (2)	4.04 (0.11)
M. OFC	8	0.79 (0.34)	−2 (2)	50 (1)	−21 (2)	4.03 (0.17)

N indicates the number of subjects who showed significant response to faces as compared with scrambled faces ($P < 0.001$, with cluster size of four or more contiguous voxels). Volumes were calculated before spatial normalization. Coordinates are in the normalized space of the brain atlas [48]. For each region, mean volume and mean coordinates were averaged across all subjects who showed the effect. Standard errors of the mean (S.E.M.) are indicated in parentheses. L, left; R, right; M, medial.

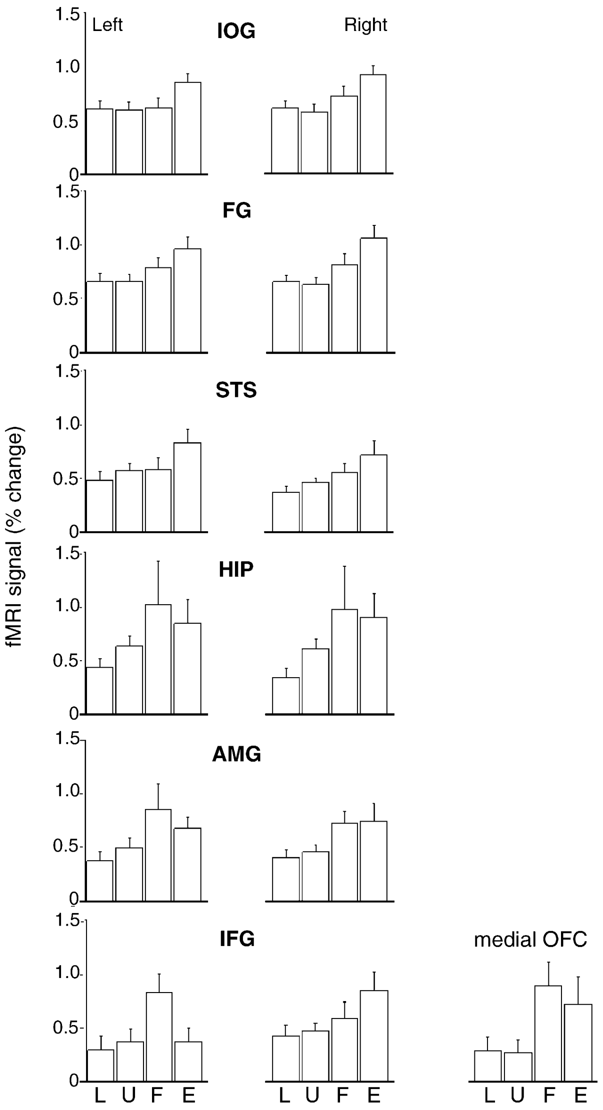

Fig. 2. Activation evoked by various stimulus formats: black and white line drawings of unfamiliar faces (L), and gray scale photographs of unfamiliar (U), famous (F), and emotional (E) faces. Within each region of interest, the mean amplitude of the fMRI signal was averaged across all subjects who showed a significant response to faces ($P < 0.001$, with cluster size of four or more contiguous voxels). Error bars indicate S.E.M.

sphere. In the IOG, FG, STS, and IFG this hemispheric asymmetry was manifested by larger clusters of activation ($P < 0.0001$) and higher t-values ($P < 0.001$) in the right hemisphere. Finally, in all face-responsive regions, more subjects showed activation in the right than in the left hemisphere ($P < 0.01$).

3.2. *Differential responses to various face formats*

Having localized the visual activation evoked by faces, an ROI analysis was performed in order to estimate the amplitude of the response associated with specific stimulus formats (Fig. 2). Line drawings of unfamiliar faces and photographs of unfamiliar, famous, and emotional faces evoked significant, bilateral activation within all regions. In terms of the spatial extent of the activation, all face formats evoked stronger activation in the right hemisphere ($P < 0.001$). A similar trend of hemispheric asymmetry was also observed for the t-values ($P < 0.01$) and the number of subjects who showed the effects ($P < 0.01$) (see Table 2). It is of interest that famous and emotional faces evoked activation in larger clusters than both line drawings and photographs of unfamiliar faces ($P < 0.01$). Within the “core” system, namely the IOG, FG, STS, and the right IFG, emotional faces evoked larger amplitudes of the fMRI signal in both hemispheres ($P < 0.01$). Famous faces were associated with stronger fMRI signals in regions of the “extended” system, namely the left amygdala, left IFG, and bilaterally in the hippocampus ($P < 0.001$). Finally, we did not observe any significant differences between the fMRI signal evoked by black and white line drawings of unfamiliar faces and gray scale photographs of unfamiliar faces [except for the hippocampus, where the response to photographs was stronger in one subject ($P < 0.05$)].

4. Discussion

The neural response evoked by passive viewing of faces was investigated using fMRI. Activation was found in a network of face-responsive regions, including the IOG, FG, STS, amygdala, hippocampus, IFG, and OFC. Within these regions, all stimuli (line drawings of unfamiliar faces and photographs of unfamiliar, famous, and emotional faces) evoked significant activation, with stronger responses in the right hemisphere. Furthermore, the response to famous and emotional faces was stronger than the response to unfamiliar faces.

Consistent with previous studies, viewing faces evoked activation in multiple, bilateral regions of the distributed cortical network for face perception [20]. We found activation in the “core” system, namely in the IOG and lateral FG, the extrastriate regions that mediate face detection and identification [13,16,19,24,30] and the STS, where information about social communication, such as the direction of gaze, is processed [22,41]. Interestingly, a recent monkey fMRI study has reported the existence of similar face-selective patches in TE and STS, suggesting that the core system, presumably due to the biological significance of faces, is evolutionary preserved in primates [50]. We also found activation in the “extended” system, namely in the amygdala, hippocampus, IFG, and OFC, where information about facial expression is processed [2,25,34,39].

Although viewing faces evoked bilateral activation within all face-responsive regions, stronger responses were found in the right hemisphere. This hemispheric asymmetry was manifested by larger and more significant clusters of activation, and larger number of subjects who showed the effect. Previous studies, in which the response to faces was compared with the response to scrambled faces, have reported

Table 2
The differential effects of various face stimuli

Region	Line drawings			Unfamiliar faces			Famous faces			Emotional faces		
	N	Mean cluster size (cm^3)	Mean *t*-value	*N*	Mean cluster size (cm^3)	Mean *t*-value	*N*	Mean cluster size (cm^3)	Mean *t*-value	*N*	Mean cluster size (cm^3)	Mean *t*-value
L. IOG	11	1.75 (0.42)	4.13 (0.17)	12	1.81 (0.56)	4.51 (0.21)	12	1.27 (0.31)	4.06 (0.12)	13	1.94 (0.44)	4.23 (0.16)
R. IOG	12	1.82 (0.33)	4.30 (0.22)	11	2.63 (0.64)	4.79 (0.26)	13	1.99 (0.42)	4.30 (0.11)	13	2.37 (0.43)	4.48 (0.20)
L. FG	13	1.15 (0.33)	4.02 (0.15)	13	1.32 (0.38)	4.56 (0.22)	12	1.59 (0.33)	4.20 (0.17)	13	1.53 (0.24)	4.36 (0.14)
R. FG	13	2.11 (0.45)	4.18 (0.18)	13	2.15 (0.52)	4.67 (0.21)	13	2.26 (0.46)	4.43 (0.16)	13	2.62 (0.45)	4.59 (0.18)
L. STS	4	0.10 (0.03)	3.45 (0.12)	6	0.28 (0.08)	3.84 (0.10)	7	0.26 (0.09)	3.86 (0.08)	8	0.53 (0.17)	3.74 (0.13)
R. STS	5	0.14 (0.09)	3.52 (0.07)	7	0.38 (0.14)	4.02 (0.20)	9	0.33 (0.18)	3.61 (0.06)	8	1.13 (0.26)	4.11 (0.14)
L. HIP	1	0.04 (0.00)	3.25 (0.00)	2	0.09 (0.02)	3.45 (0.17)	4	0.31 (0.15)	3.60 (0.11)	3	0.33 (0.13)	3.77 (0.17)
R. HIP	1	0.04 (0.00)	3.34 (0.00)	1	0.13 (0.00)	3.46 (0.00)	4	0.13 (0.03)	3.39 (0.05)	5	0.15 (0.05)	3.45 (0.09)
L. AMG	2	0.19 (0.10)	3.53 (0.04)	4	0.39 (0.07)	3.57 (0.04)	8	0.51 (0.20)	3.78 (0.15)	7	0.38 (0.20)	3.56 (0.14)
R. AMG	3	0.12 (0.06)	3.46 (0.11)	5	0.42 (0.22)	3.68 (0.13)	7	0.28 (0.09)	3.75 (0.12)	7	0.47 (0.19)	3.60 (0.11)
L. IFG	6	0.82 (0.64)	3.52 (0.12)	4	0.73 (0.43)	3.62 (0.11)	8	1.11 (0.48)	3.87 (0.12)	3	0.30 (0.26)	3.47 (0.12)
R. IFG	8	1.11 (0.59)	3.68 (0.15)	6	0.53 (0.16)	3.77 (0.08)	10	0.47 (0.11)	3.62 (0.06)	9	1.37 (0.57)	3.86 (0.17)

N indicates the number of subjects who showed significant response to faces as compared with scrambled faces ($P < 0.001$, with cluster size of four or more contiguous voxels). Volumes were calculated before spatial normalization. Coordinates are in the normalized space of the Talairach and Tournoux brain atlas. For each region, mean volume and mean coordinates were averaged across all subjects who showed the effect. S.E.M. are indicated in parentheses. L, left; R, right.

bilateral activation in multiple regions [19,24,25,28]. In contrast, when a face “localizer” was employed, namely when the response to faces was contrasted with the response to assorted common objects, stronger activation was reported in the right hemisphere, thus identifying the highly-selective face-responsive patches [30]. It is of interest that right unilateral lesions in ventral occipitotemporal cortex are sufficient to produce prosopagnosia, the inability to recognize familiar faces [6,31], although most patients have bilateral lesions [5]. Future studies will determine the specific role of each hemisphere in face perception.

Similar patterns of activation were evoked by line drawings and gray scale photographs of unfamiliar faces, consistent with previous findings [27,28]. Interestingly, the face-selective patches in the macaque brain also respond similarly to both line drawings and photographs of faces [50]. It therefore seems that in the primate brain, the extrastriate face-responsive regions detect a high-level gestalt of facial forms, and not merely low-level features. We also found that emotional faces evoked greater activation in all face-responsive regions, consistent with previous reports of valence enhancement [25,38,51].

Previous functional brain imaging studies of familiar faces have used a variety of stimuli (e.g., celebrities, personally familiar faces, newly learned faces) and tasks, yet activation was found in similar visual areas that were activated by unfamiliar faces, most consistently in the fusiform gyrus [14,15,32,46]. In some studies, additional activation was found in an anterior middle temporal region, the locus proposed for the analysis of unique semantic attributes [8,14,15,32,44,46]. It should be noted that activation in this anterior middle temporal region was found only when familiar and unfamiliar faces were directly compared. We found that in the left IFG famous faces evoked the strongest response. This region was previously implicated in the retrieval of face–name association [3,29] and controlled semantic retrieval [52]. Our database of famous faces consisted of contemporary celebrities [24] and post-scanning debriefing revealed that all subjects recognized and were able to name most of these faces.

In some subjects, viewing faces evoked bilateral activation in the hippocampus, where the maximal response was evoked by famous faces. Previous studies indicated the involvement of the hippocampus during encoding of novel faces [18], and during the encoding of novel face–name associations [47], concurrent with its role in associative memory processing [7]. Recent fMRI studies reported activation in the hippocampus during active maintenance of novel faces in working memory [42] and during visual imagery of famous faces [24].

It is of interest that passive viewing of faces evoked activation in orbitofrontal cortex, a region prone to susceptibility-related signal dephasing [45]. Electrophysiological studies in monkeys and functional brain imaging studies in humans have shown that the OFC represents the reward value of taste and olfactory inputs and has a major role in rapid stimulus-reinforcement association learning and its reversal in a changing environment [43]. The existence of face-selective neurons in the OFC [49], and the inability of patients with OFC lesions to identify emotional facial expressions [23], suggest that this region has an important role in the processing of facial cues required for social reinforcement.

Taken collectively, our findings indicate that the mere percept of a face, without the performance of any explicit task, is sufficient to activate a network of regions in the visual cortex, limbic system, and prefrontal cortex, where information about facial identity and expression is processed.

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