Visual areas PPA and pSTS diverge from other processing modules during perceptual closure: Functional dichotomies within category selective networks

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A B S T R A C T

The nature of neural processing within category-preferring visual networks remains an open topic in human neuroscience. Although the topography of face, scene, and object-preferring modules in the human brain is well established, the functional characterization, in terms of dynamic selectivity across their nodes is still elusive.

Here, we use long trials of perceptually impoverished images of faces and objects to assess the dynamics of BOLD activity and selectivity induced by perceptual closure within these regions of interest. Departing from paradigms involving immediate percepts, we used ambiguous images favoring holistic search and independence from low level stimulus properties.

By assessing the neural responses to images that go beyond the preferred category of the studied ROIs we could dissect the specificity of these processes as a function of the timing of perceptual closure and contribute to the debate regarding specialization of these modules.

We found that pSTS is a notable exception to the observation that category selective high-level visual areas also participate on the perceptual closure of their non-preferred category. A similar observation was found for PPA responses to faces. Most importantly, these observations directly link the pSTS region with the social processing network, which cannot be engaged by object stimuli.

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1. Introduction

Since the first fMRI studies involving the fMRI response to objects (Malach et al., 1995) many neuroimaging studies have attempted to identify regions that preferentially process a few given image categories. Among these, particular focus has been given to the study of neural responses to images of objects, scenes and faces (Malach et al., 1995; Epstein & Kanwisher, 1998; Kanwisher, McDermott, & Chun, 1997). Recent work has emphasized methodological issues, standardization of paradigms and analyses, which has helped to establish the cortical topography and general organization of these high-level selective visual regions in the ventral stream (Fox, Iaria, & Barton, 2009; Rossion, Hanseeuw, & Dricot, 2012).

The core face-preferring network (Haxby, Hoffman, & Gobbini, 2000), comprises the Fusiform Face Area (FFA) (Kanwisher et al.,

1997), the Occipital Face Area (OFA) (Gauthier et al., 2000), and a region on the posterior bank of the Superior Temporal Sulcus (pSTS) (Puce, Allison, Bentin, Gore, & McCarthy, 1998). According to Haxby's model, the OFA is thought to drive other face-selective regions by analyzing lower-level features of a face, while the FFA underlies holistic processing and the STS extracts higher level social and emotional aspects.

Regarding object processing in the visual cortex, an extensive area comprising parts of the inferior temporal and the lateral occipital cortex, called the lateral occipital complex (LOC) (Malach et al., 1995) shows larger responses to objects than textures or scrambled images. (Grill-Spector et al., 1999a). This area can be subdivided into a fusiform region and a lateral occipital region. Mimicking the OFA and FFA hierarchy, while the lateral occipital region performs lower-level analysis and extraction of features, the posterior fusiform region shows more invariance to basic properties such as viewpoint.

Scene selective regions include the parahippocampal place area (PPA) (Epstein & Kanwisher, 1998), the retrosplenial cortex (RSC) (Maguire, 2001) and the Transverse Occipital Sulcus (TOS) (Nakamura et al., 2000), which is also known as the Occipital Place Area (OPA) (Dilks, Julian, Paunov, & Kanwisher, 2013). While the

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PPA is more concerned with scene processing and individuation, the RSC is more directly involved in visual navigation and integration (Park & Chun, 2009).

However, these functional specializations and processing at each node of the networks do not go without controversy, (for a review on the face-network arquitecture see Atkinson & Adolphs, 2011) and the degree to which they can be engaged by non-preferred categories is still controversial. In fact, the assessment of how truly specialized is the processing in these high-level regions is fundamental to the understanding of the concept of selectivity in visual areas.

Here, we addressed this question by studying temporal dynamics of activity using images that imply delayed perceptual closure and categorization. We compared closure across categories for all networks irrespective of their preference.

Perceptual closure refers to the well known Gestalt principle of perceptual organization that reflects the ability to perceive an incomplete pattern or object as complete or whole. In other words, coherent perception of an image content occurs under circumstances when the visual information is incomplete (Grützner et al., 2010). Such a methodological approach allows assessing the degree to which the selectivity of each node is affected by perceptual rather than stimulus related factors, given the impoverished content of the image. This is because the impact of perceptual decision on dynamic selectivity provides a window to understand the nature of processing occurring before and after perceptual closure. Moreover, the assessment of each region-of-interest (ROI) beyond its categorical preference reveals into which extent dedicated processing indeed occurs in the visual cortex.

Previous studies addressing closure through impoverished images used pure noise images which change throughout time into a coherent object or face (Jiang et al., 2011; Ploran et al., 2007) or the popular alternative of Mooney images (Mooney, 1957). These latter binarized black−white versions of normal grayscale images can appear devoid of any meaning other than a simple set of blobs until holistic perception occurs. Accordingly, Mooney stimuli have been used to study face perception but not in the context of the impact of perceptual closure on response selectivity. McKeeff and Tong (2007) focused on the FFA to highlight its role in face perception while also showing an absence of decision-related activity in nonface-selective visual areas. In turn, a study by Andrews and Schluppeck (2004) found differential FFA activation when subjects reported seeing a face compared to perceiving the image as a collection of blobs, but found no difference in magnetic resonance response between face and no-face perceived events either in the superior temporal sulcus, a face selective area, or in the PPA and LOC. These studies are relevant and intriguing by studying these phenomena either at short time scales (Andrews & Schluppeck, 2004) or by focusing on a few pivotal regions (McKeeff & Tong, 2007), using faces or scrambled controls.

In this study we followed a different approach, because we were specifically interested in the temporal dynamics of selectivity before and after perceptual closure. We did therefore use long time scales, to dissect selectivity along time and its dependence on perceptual closure. We used 12 s trials of rotating Mooney images of faces and objects to assess the dynamics of activity and selectivity in category-preferring networks. In this manner we could investigate BOLD activity in selected regions of interest (ROIs) in response to different categories irrespective of their preference.

2. Materials and methods

2.1. Subjects

13 right-handed subjects (6 females, 7 males, ages 20–32, mean age 23.8 ± 3.5 years) participated in the study after providing informed consent. All had normal or corrected to normal vision.

The study followed the tenets of the Declaration of Helsinki, informed consent being obtained from all subjects for the protocol, which was approved by our local Ethics Committee.

2.2. Stimuli

The stimuli for our experiment were comprised of Mooney images. These images are simply impoverished black and white (two-value only, no grayscale) versions of regular images. Sixty Mooney faces were built from thresholding online images of faces, with a wide range in lighting, angle and face size properties, thus maximizing ambiguity. The same procedure was adopted for building 60 Mooney images of objects. Due to the broader span of the object category, images of objects were restricted to three sub-categories: utensils, means of transportation and musical instruments.

Mooney stimuli were chosen because they provide a classical way of generating ambiguous perception (which is enhanced if stimuli are viewed upside down). These stimuli may appear devoid of any recognizable content for several seconds until the observer suddenly becomes aware of the emergence of a holistic percept. Stimuli characteristics were thus suited to the research goal of uncoupling sensation from perception because the sudden global awareness of the content leads to temporally contained perceptual events (perceptual closure), separable from initial local sensory processing. Also, differential onset of activity on "early" and "late" detection trials is a distinguishing characteristic of a neural encoder of perceptual closure processes, a property which can advantageously be used in identifying the networks involved in this perceptual phenomenon. Finally, interpretation of the image content cannot be easily achieved through local visual analysis, and renders high-level processing impossible in the pre-perceptual period, which therefore serves as a sensory control/baseline.

The 120 Mooney images were converted into movies that consist of the rotation of such images. Starting from the inverted position, the image slowly rotates 20° per second until it reaches the upright position where it rests for 3 s. There were no repeated movies. Stimuli were presented in a black background and subtended approximately 12.40° of the visual field. Difficulty levels were adjusted in pilot experiments to guarantee variability in perception times.

2.3. Task: the dual categorical paradigm

Subjects performed two-tasks, each of which comprised a run with faces and a run with objects. Task choice was based on Rebola, Castelhano, Ferreira and Castelo-Branco (2012). In each experimental run subjects were requested to search for either faces or objects. In the case of objects runs, these were divided into three blocks, before which a cue was presented centrally for 4 s with the sub-category to search for. Since objects are a broader category than faces, implying more uncertainty in content, shapes and viewpoints, using this cue to specify the sub-category in the object runs allowed us to limit and equate this variability to the face runs, so that activity differences are not driven by different levels of expectancy.

In the first task, subjects were instructed to respond when they were confident they had perceived the content of the images. Response was achieved through a response box, by pressing of a button with a finger of the left hand. This task is referred to as the "Simultaneous Response Task".

In the second task, the image foreground (the white part of the Mooney image) changes color every TR (2 sec) in the following order (white, blue, yellow, pink, green, and light gray). Upon content perception, instead of responding immediately, subjects withheld their response until the end of the trial, when they were instructed to identify from a list the color of the foreground (in case of detection) that was present at the moment of perceptual closure. Thus, the selected color encoded the time of perception, which was decoupled from response processes. Selection was made by using two buttons in one hand to move a cursor up or down until the correct color was highlighted and then pressing a button with the other hand to confirm the choice. When the subject responded the color list disappeared, followed by fixation. A simplified timeline of this dual-task paradigm is shown in Fig. 1 (see also Rebola et al. (2012)).

In total, there were four runs: two for the "Response Task" and two for the "Color Task".

The order of the runs was counterbalanced across subjects. Given that both tasks lead to comparable modulation across visual areas (Rebola et al., 2012), activity in high-level visual ROIs was consequently pooled across tasks.

2.4. Localizer scans to map selective regions for ROI analysis

Localizer stimuli consisted of grayscale images of faces, places (buildings, landscapes, and skylines), objects (tools, cars, and chairs), and scrambled versions of objects. Stimuli were presented in a black background and subtended approximately 9.48° of the visual field.

Localizer scans consisted of two runs of alternately viewed blocks of stimuli from a given class (faces, places, objects, and scrambled images). Each run had 12 blocks and each block lasted 20 s (20 images, 800 ms each, 200 ms gap), separated by 10 s fixation baseline intervals. During each block subjects performed a 1-back task to keep stable attention levels. Three repetitions per block were employed. The definition of contrasts to identify distinct brain regions of interest (ROIs) is shown in Table 2.

ROIs were defined for each subject with conservative statistical criteria and without smoothing, thereby minimizing smearing and overlap issues. For illustration purposes, though, group location of the studied ROIs is depicted in Fig. 2.

2.5. Image acquisition parameters and pre-processing

Images were obtained on a Siemens Tim Trio 3T scanner using a 12 channel head coil. Structural images were collected using a T_1 weighted MPRAGE (magnetization-prepared rapid-acquisition gradient echo) (TR=2300 ms, TE=2.98 ms, flip angle=9°, matrix size=256 × 256, voxel size=1 mm³). Standard T_2^*-weighted gradient-echo echo planar imaging was used for the functional task runs (TR= 2000 ms; TE=47 ms; 2.5 mm × 2.5 mm in-plane resolution; 3.5 mm slice thickness with 0.7 gap; flip angle=90°; matrix size=102 × 102; number of slices=25; for faces, 455 measurements were acquired for the Color Task and 335 were acquired for the Simultaneous Response Task; for objects, due to the cue that signals the sub-categories, 476 measurements were acquired for the Color Task and 356 were acquired for the simultaneous Response Task; 186 measurements were acquired for the localizer runs). The slices were positioned parallel to the infero-temporal surface of the brain to obtain maximum coverage. Runs were acquired across two sessions. Image processing was performed using BrainVoyager QX v2.1 (Brain Innovation, Maastricht, The Netherlands) Pre-processing steps included motion correction, slice scan-time correction, linear trend removal and temporal high-pass filtering of 0.00980 Hz (3 cycles in time course).

2.6. Data analysis

2.6.1. Trial sorting: timing of perceptual closure

Perceptual closure, the moment when the subject makes sense out of a seemingly meaningless image, could occur anytime during the movies. It could also not occur at all. In this manner, trials were sorted into different post-hoc "perceptual closure conditions" according to the moment of the emerging percept. Responses within the same TR were lumped together, thus yielding seven conditions for each category, six "perceived" conditions (distinct according to the time of perceptual closure) plus one condition where the content was "unperceived". As an example, if the content was perceived in the first TR (0–2 s after movie onset), this is a different condition than if it was perceived on the second TR (perceptual closure 2–4 s after movie onset), and so on until the sixth "perceived" condition (10–12 s).

2.6.2. GLM contrasts

Due to the nature of our paradigm, and the different ROI's sensivity to sensory and perceptual processes, we opted for a deconvolution approach, which poses no constraints on the shape of the HRF.

For designs such as these which include several processes within a trial which can happen at any point of time, this is one of the appropriate forms of analysis. The principles for this kind of analysis (mixed effects analysis; separation of processes within trials) are described in Ollinger, Shulman, Corbetta, and Method (2001), Worsley et al. (2002) and Serences (2004). Practical applications of using segments
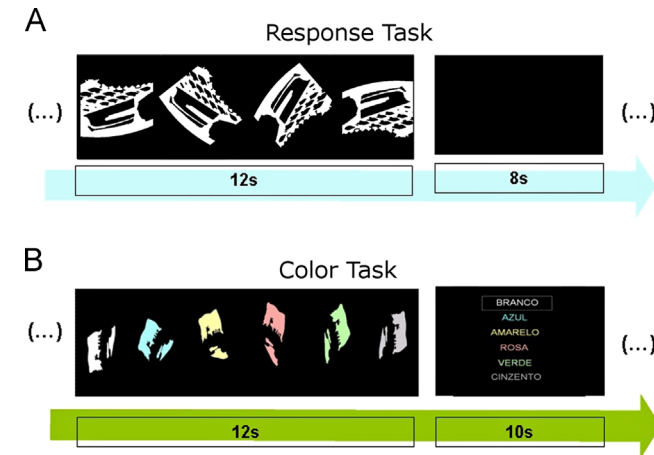

Fig. 1. Timeline of the perceptual closure paradigm using ambiguous Mooney stimuli; A – the image, rotates from inverted to upright and the subject presses a button when (and only if) the content is detected; B – the "white component" (foreground) of the Mooney image, changes color every TR (acquisition volume) and the subject indicates the moment of closure only at the end of the trial by selecting from a list the color that corresponds to perception time. This last task precludes simultaneous processes of closure and response. The two tasks were carried out using both Mooney faces and objects, in separate runs. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
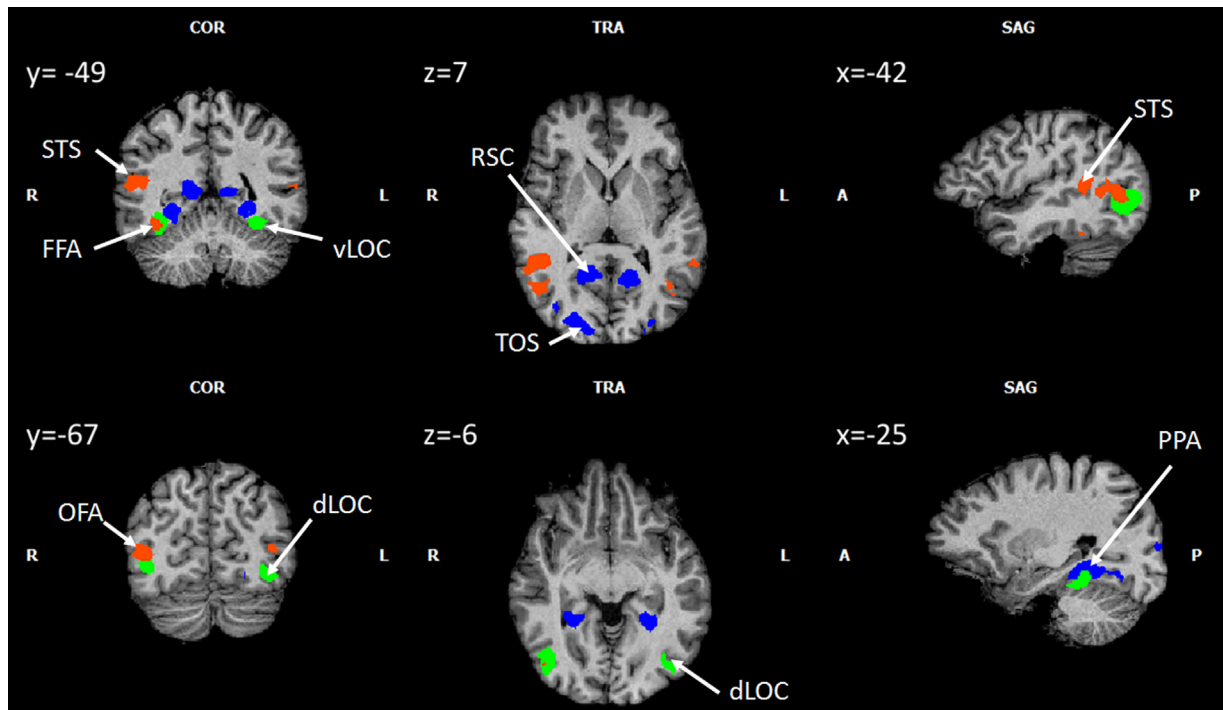

Fig. 2. Group average location of the identified ROIs for selected coronal, sagittal and axial slices. Face-selective patches (red) comprise the FFA, OFA and the STS. Object-selective areas (green) are identified as vLOC and dLOC. Finally, place-selective regions (blue) are labeled as PPA, RSC and TOS. The contrasts used to localize these areas are the same as described in Table 2 but here the statistical thresholds have been adjusted for visualization purposes. Place and object areas are thresholded at $p < 0.05$ (Bonferroni corrected), while face patches are thresholded at $p < 0.001$ (uncorrected). Note that individual subject maps do not suffer from the same amount of overlap between neighboring regions.

of a deconvoluted timecourse for contrasts and analysis can be found, for example, in Brown, Vilis, and Everling (2007), Brown, Vilis, and Everling (2008). For each ROI, this approach results in a succession of 10 beta values and its inherent statistics along the whole of the timecourse, starting from stimulus onset. In fact, due to the slow event-related design used, this representation of ROI activity is equivalent to an event-related average. However, the beta-value statistics for each point in the timecourse allow a flexible planning and use of contrasts focused either on categorical selectivity or perceptual dynamics. In this manner, two sets of contrasts were computed to reflect the impact of each of these factors.

The first one evaluates the impact of perceptual closure on ongoing BOLD activity.

To this end, the most straightforward procedure is to contrast, across the 'perceived' conditions, the moment of perception to its non perceptual predecessor (accounting for the haemodynamic lag). Graphical examples of these contrasts are shown in Fig. 3. The evaluation of this contrast for faces and objects within a given ROI, shows how much the BOLD response is shaped by perceptual closure of a given category. Furthermore, the difference between the values obtained for faces and objects reflects if the impact of perception is significantly different between categories.

The second type of contrasts assesses categorical selectivity dynamics. Thus, this time, the logic is in contrast with one category versus the other within each ROI.

By evaluating this contrast prior, during, and after perceptual closure (across the 'perceived' conditions), one can verify how the dynamics of selectivity change between and within the different category-preferring networks. Graphical examples of these contrasts are shown in Fig. 4. Note that these contrasts take the dynamics, activity and selectivity of each ROI as a whole. It is therefore beyond the scope of this study to look within the studied ROIs as to investigate the distributed coding of preferred and non-preferred categories putatively carried by multivoxel patterns and their stability (but see Haxby et al. (2001); Hanson, Matsuka, and Haxby (2004); Schurger, Pereira, Treisman, and Cohen (2010)).

It is important to point out that both sets of contrasts are calculated and collapsed across conditions 2–5 (which correspond to increasing delays in perceptual closure). This is because condition 1 (images perceived in the interval 0–2 s) does not have a pre-perceptual period and condition 6 (images perceived in the interval 10–12 s) does not have a post-perceptual period.

3. Results

3.1. Behavioral results

The behavioral results are shown in Table 1 for the overall data and for each category separately. Relative frequencies of detection were similar across categories (Independent Samples Mann– Whitney U-test, $p = 0.286$). The choice of difficulty levels for detection stimuli led to spread in decision times ($\sim 75\%$ of the stimuli requiring at least a few seconds for detection) and a sizeable number of trials where stimulus content was not perceived.

3.2. Localization of object, scene and face selective regions

The present study focused on three category-preferring networks: the face network, the object network and the place network. From the face network we focused on the core system: FFA, OFA and pSTS. The object network includes the LOC, partitioned into the segregate ventral and dorsal regions: vLOC and dLOC (Grill-Spector et al., 1999b). The analyzed scene-preferring areas comprise the PPA, RSC and TOS.

Table 2 shows mean Talairach coordinates and mean number of voxels for the localized regions.

3.3. Selectivity dynamics across the ventral stream

For each of the ROIs considered above, two sets of analyses were conducted that highlight different aspects of perceptual closure and selectivity dynamics within these regions.

3.3.1. The impact of perceptual closure on ongoing brain activity

We first analyzed the impact that perceptual closure of different image categories has on ongoing activity. Such activity, starting from stimulus onset, encompasses sensory processing of
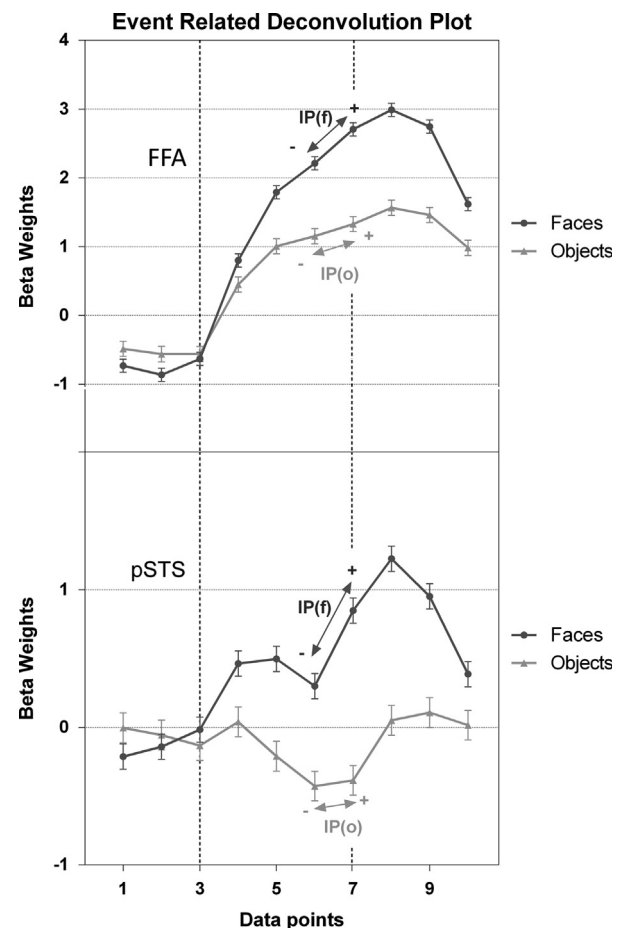

Fig. 3. Impact of perceptual closure on ongoing activity as measured by the first set of contrasts in the fMRI data (FFA and pSTS, respectively). Changes in BOLD activity (see arrows) reflected perceptual closure for both preferred and non-preferred categories. Though this effect was calculated and collapsed across conditions 2–5, these examples depict closure condition 4, where faces and objects are seen from 6 to 8 s. The left dashed line represents stimulus onset, after the hemodynamic lag, whereas the right dashed line represents time of perception for this condition, after the same lag. By contrasting, for each category, the moment of perception to its predecessor, one can statistically quantify the impact of perception of faces – IP(f) – and objects – IP (o). Graphs are shown for the FFA and the pSTS. The former (top) shows a significant impact for both categories (see Table 3) and the latter only for faces (bottom).

impoverished image content. Changes in activity when the subject finally forms a gestalt should therefore be accounted for by the perceptual closure process (see Fig. 3, arrows depict moment of closure, see Table 3 for statistical summary). We also tested whether neural modulation by such closure step differs significantly between categories.

Within the face-preferring network, we found the expected significant impact of perceiving faces (all p values < 0.001). Moreover, we also identified a highly significant impact of perceiving objects in the FFA ($p < 0.001$) and the OFA ($p = 0.003$). In other words, perceptual forming of a gestalt of the non preferred category changes brain activity for face responsive regions. Interestingly, we found that STS is a notable exception to this rule ($p = 0.800$). Hence, in the pSTS, only the perception of faces has a significant impact on ongoing activity ($p < 0.001$). It is noteworthy, that despite this rise in BOLD activity for closure of faces and objects in the FFA and OFA, the increase is significantly larger for faces.

Concerning functional modulation of LOC subdivisions, both the perception of objects and faces increments ongoing activity
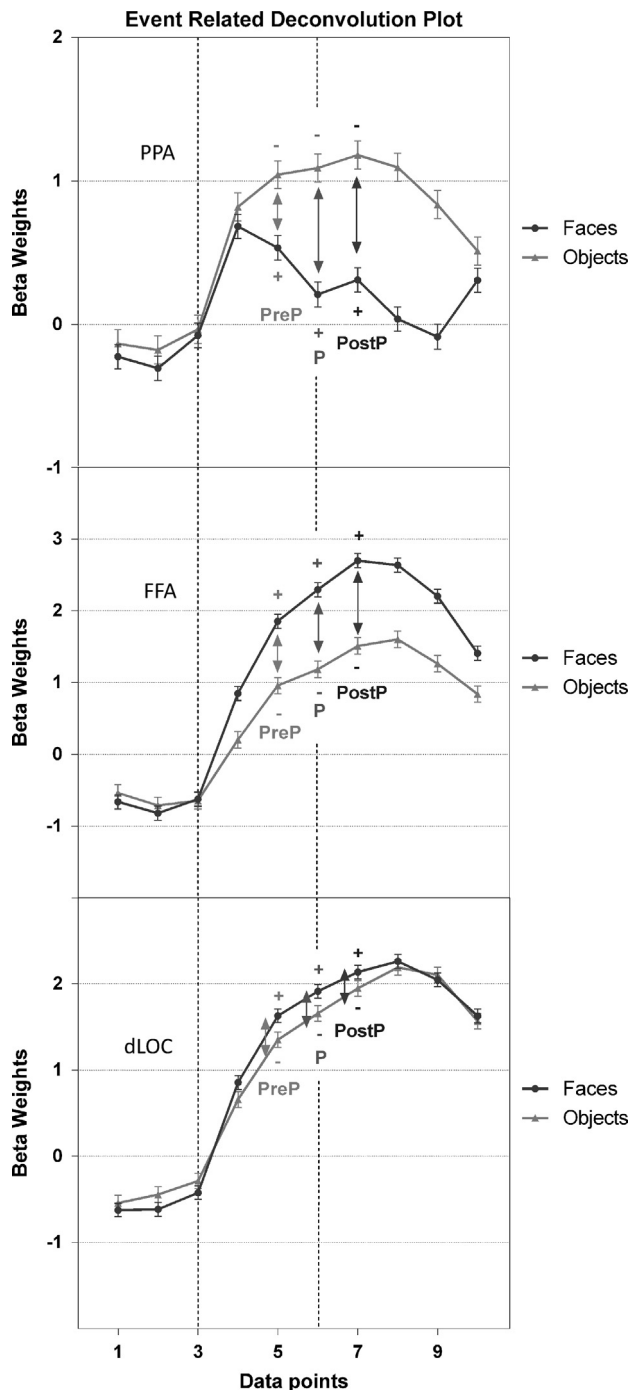
Fig. 4. Distinct dynamics of Category selectivity before, during and after perceptual closure, across ventral stream regions. The panels illustrate closure condition 3, i.e., faces and objects seen from 4 to 6 s. In this panel, the left dashed line represents stimulus onset, after the hemodynamic lag, whereas the right dashed line represents time of perception for this condition, after the same lag. As in Fig. 3, though only depicted for closure condition 3, contrasts are calculated and collapsed across conditions 2−5. Graphs are shown for the PPA, FFA and dLOC. Face selectivity increases over time, until after closure, for FFA. Object selectivity follows the same rule in ventral LOC (vLOC) and scene preferring regions but not in the dorsal part of LOC (dLOC, depicted). For PPA, a decrease of activity followed perceptual closure of faces, hence increasing selectivity for objects.

(p values < 0.001). Interestingly, there is not a significant difference in how much the activity rises with perception of the two different categories (p values > 0.3).

Scene-selective regions exhibited different activity patterns. The PPA is impacted by object perception but for faces this was not the case (see Table 3 for statistical summary). The RSC is

Table 1
Trial distribution, sorted by time of perceptual closure (absolute and relative frequencies), for faces and objects.

Time of perception (conditions)	Faces	%	Objects	%
0–2 s	117	15	147	19
2–4 s	132	17	162	21
4–6 s	166	21	125	16
6–8 s	168	22	126	16
8–10 s	92	12	80	10
10–12 s	21	3	27	3
Unperceived	84	11	113	14
Total	780		780	

Note: Bins are two seconds in length (matching the TR).

negatively impacted by perceiving faces (deactivation) but not by objects. Finally, activity in the TOS rises significantly with perceptual closure of both categories.

3.3.2. Changes in selectivity induced by perceptual closure

For each ROI, the differences in activity elicited by the two tested categories (faces and objects) were evaluated before, during and after perception. This analysis reveals how the selectivity is shaped by the perceptual closure processes, as illustrated in Fig. 4 (see arrows) and described in Table 4.

All face-preferring areas exhibit a large selectivity even in pre-perceptual periods. This selectivity is enhanced with perceptual closure, and increases in the post-perceptual period, suggesting that additional processing steps kick-in. Object-preferring regions show an intriguing dichotomy. In vLOC, the higher activity for objects than faces in the pre-perceptual period increases with perceptual closure but only reaches significance in the post-perceptual period ($p=0.028$). As for the dorsal part of the LOC, the already significantly higher activity for faces increases even further with perceptual closure (both p values < 0.001).

In sum, face selectivity increases over time, until after closure, for all regions of the core face network (OFA, FFA and STS). Object selectivity obeys the same rule in ventral LOC (vLOC) but not in the dorsal part of LOC (dLOC). Scene preferring regions also become more engaged by object in contrast with face images as the perceptual closure process progresses.

4. Discussion

We set out to study selectivity dynamics within the face, object and scene-preferring networks using a delayed perceptual closure paradigm. This design uses a gestalt rule whereby a percept is constructed from incomplete physical information. To this end, we first localized category selective ROIs. Then, we used long presentation trials of ambiguous faces and objects images, to assess activity and selectivity dynamics prior, during and after perceptual closure. We verified that significant modulation of activity occurs with the perception of both faces and objects, which corroborates the view that processing in these areas can be extended even to non-preferred categories. However, we found intriguing functional dissociations from this general rule in particular; dedicated face processing takes place in pSTS. Moreover, PPA also exhibits significant modulations to objects which were absent for faces.

4.1. The Impact of perceptual closure on ongoing brain activity

We addressed the impact of perceptual closure on ongoing BOLD activity, for each ROI, for preferred and non-preferred categories. All category-preferring ROIs, with the exception of

Table 2
Mean Talairach coordinates and mean number of voxels for the localized ROIs.

		X	Y	Z	No. of Voxels
Face-preferring		(Faces > Scrambled AND > Places AND > Objects) q(fdr) < 0.01			
FFA	L	−39 (3)	−48 (8)	−20 (4)	462
	R	37 (4)	−48 (6)	−21 (4)	621
OFA	L	−43 (9)	−73 (7)	−5 (8)	236
	R	44 (6)	−67 (2)	0 (5)	745
pSTS	L	−47 (8)	−56 (10)	9 (3)	392
	R	45 (5)	−48 (6)	8 (6)	300
Object-preferring		(Objects > Scrambled) q(fdr) < 0.01			
vLOC	L	−33 (7)	−54 (10)	−17 (4)	1052
	R	30 (7)	−51 (11)	−18 (4)	673
dLOC	L	−40 (6)	−79 (7)	−2 (7)	2926
	R	36 (5)	−79 (7)	−3 (9)	1376
Scene-preferring		(Places > Scrambled AND > Faces AND > Objects) q(fdr) < 0.01			
PPA	L	−25 (2)	−44 (3)	−10 (3)	710
	R	23 (5)	−42 (3)	−11 (4)	883
RSC	L	−16 (5)	−55 (5)	6 (5)	678
	R	16 (4)	−54 (3)	8 (6)	642
TOS	L	27 (7)	−86 (7)	13 (7)	1081
	R	−28 (7)	−87 (7)	11 (9)	1045

Note: The expression AND in the contrasts used for ROI localization denotes a conjunction of contrasts. Numbers in parenthesis represent standard deviations.

Table 3
Categorical dependence of the impact of closure on ongoing brain activity.

Area	Faces			Objects			Difference		
	t	p	d	t	p	d	t	p	d
FFA	8.624	< 0.001	2.490	4.538	< 0.001	1.310	2.586	0.009	0.747
OFA	6.042	< 0.001	1.744	2.957	0.003	0.854	1.969	0.048	0.568
pSTS	4.608	< 0.001	1.330	0.255	0.800	0.074	2.938	0.003	0.848
vLOC	4.422	< 0.001	1.277	5.359	< 0.001	1.547	−0.892	0.372	0.257
dLOC	6.185	< 0.001	1.785	5.146	< 0.001	1.486	0.469	0.638	0.135
PPA	1.337	0.181	0.386	4.490	< 0.001	1.296	−2.364	0.018	0.682
RSC	−2.456	0.014	0.709	−0.085	0.931	0.025	−1.616	0.106	0.466
TOS	2.406	0.016	0.695	3.630	< 0.001	1.048	−0.961	0.336	0.277

Note: t contrasts collapsed across closure conditions 2–5; for each closure condition the predictor corresponding to the moment of perception is contrasted against the last pre-closure predictor. Graphical interpretation of these contrasts is depicted in Fig. 2. d – Cohen's effect size.

RSC, show a significant closure-induced increase in activity when perceiving the preferred-category (FFA > OFA > pSTS; dLOC > vLOC). Furthermore, all these areas also show in their BOLD activity a significant increase with perceptual closure of the non-preferred category, with the notable exception of the pSTS when viewing objects (showing evidence for highly specific responses to faces). This also occurred in the PPA but only when viewing faces.

Apart from the two outstanding exceptions described above – the main finding of this study − our results do not corroborate the view of a modularized system for perceptual closure dependent on category. In fact, all the remaining high-level visual areas participate in the perceptual closure of faces AND objects, thus being category-preferring rather than truly category-selective. These findings favor the view that some of the computations of these specialized modules can be shared by the non-preferred categories (Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Ewbank, Schluppeck, & Andrews, 2005; O'Toole, Jiang, Abdi, & Haxby, 2005; Haxby et al., 2010; Mur et al., 2012).

As mentioned, the PPA shows a highly significant modulation when perceiving objects while being unaffected by the perception of faces. This PPA response to objects may arise from object landmarks being viewed as spatial cues relevant for navigation. Additionally, this might explain why processing taking place in the PPA is not homogenous and exclusive to places, as recently suggested by Baldassano, Beck, and Fei-Fei (2013) but cannot be extended to the processing of faces. It is worth noting that

we could separate PPA proper from mFUS-objects (Grill-Spector, 2003), thereby minimizing a potential overlap problem and allowing to validate the inference concerning reduced responses to faces as compared to other objects. However, because scenes were only used in the localizer approaches, we can only infer about reduced responses to faces as compared to other objects and not scenes, the preferred category of the PPA.

In turn, the failure of the pSTS to respond to object perception strengthens its hypothesized role of extracting social and emotional meaning from the stimuli (Allison, Puce, & McCarthy, 2000; Materna, Dicke, & Thier, 2008; Lahnakoski et al., 2012). The strict non responsiveness to perceptual closure in objects in contrast to faces points to an important position in the social cognition network. A previous study (Gschwind, Pourtois, Schwartz, Van De Ville, & Vuilleumier, 2012) that used DTI to assess connectivity patterns within the face-network had already suggested dissociation between the pSTS and the remaining face-processing core network. The data in this study brings novel functional evidence for this dissociation.

4.2. Dynamic changes in categorical selectivity induced by perceptual closure

We explicitly confirmed selectivity changes before, during and after the perceptual closure process. The prediction was that if brain activity within a ROI is modulated differently to the

Table 4
Dynamics of ROI selectivity along the perceptual closure process.

Area	Pre-Percept (f−o)			Percept (f−o)			PostPercept (f−o)		
	t	p	d	t	p	d	t	p	d
FFA	10.151	< 0.001	2.930	13.452	< 0.001	3.883	13.390	< 0.001	3.865
OFA	8.100	< 0.001	2.338	10.616	< 0.001	3.065	10.879	< 0.001	3.140
pSTS	8.164	< 0.001	2.357	11.911	< 0.001	3.438	12.691	< 0.001	3.664
vLOC	− 0.530	0.595	0.153	− 1.669	0.095	0.482	− 2.192	0.028	0.633
dLOC	3.684	< 0.001	1.063	4.283	< 0.001	1.236	3.170	0.001	0.915
PPA	− 7.772	< 0.001	2.244	− 10.793	< 0.001	3.116	− 13.033	< 0.001	3.762
RSC	− 1.647	0.099	0.475	− 3.712	< 0.001	1.072	− 4.969	< 0.001	1.434
TOS	− 5.285	< 0.001	1.526	− 6.514	< 0.001	1.880	− 8.500	< 0.001	2.454

Note: f−o=Faces − Objects; *t* contrasts collapsed across closure conditions 2–5; for each closure condition, the predictor corresponding to a given moment (relative to the perceptual closure process) for the activity elicited by the face category is contrasted against the same moment for its object category counterpart. Graphical interpretation of these contrasts is depicted in Fig. 3. *d* – Cohen's effect size.

perception of faces and objects, then an impact on selectivity should be found.

For all the face-preferring areas, the already highly significant selectivity in the pre-perceptual search period increases during the perceptual interval with a further boost in the post-closure period. A similar pattern, albeit with inverse selectivity (higher for objects than faces), is present in the scene-preferring areas.

As for the LOC, we found spatially distinct patterns. The fusiform part, vLOC, shows a moderate trend towards higher object-related activity during pre-closure search, extends this trend during perceptual closure of stimulus content but only reaches significance in the post-perceptual interval. In contrast, dLOC showed surprisingly significantly higher activity to faces than objects in the pre-perceptual period, and the effect size of this difference even widened with perception.

This apparent lack of selectivity may be explained by the standard criteria to define the LOC, which classically opposes objects to scrambled objects (Malach et al., 1995; Kim, Biederman, Lescroart, & Hayworth, 2009; Haist, Lee, & Stiles, 2010; Cichy, Chen, & Haynes, 2011; Macevoy & Yang, 2012), thus not constraining face-responsive subclusters. The subtle but important question whether faces can be considered as an integral subset of the object class should be therefore considered for the purpose of meta-analytic studies on the function of the LOC region.

The problem of how to operationally define visual areas such as LOC might explain previous apparent discrepancies in the literature. For instance, the study by Andrews and Schluppeck (2004) with Mooney images did not unveil an impact of perceived versus unperceived face images in the LOC when the contrast objects > faces were used for its definition. In turn, Nagy, Greenlee, and Kovács (2012) highlight an important role of the LO cortex in face perception, backed up by connectivity studies.

5. Conclusion

We found that categorical selectivity changes before, during and after perceptual closure, suggesting that the nature of visual computations changes across time in ventral regions as a function of perceptual demands. This dynamical view helped shed light on the relative functional properties of regions such as FFA, OFA, PPA, LOC and pSTS. Importantly, we found that pSTS is a notable exception to the general evidence for shared computations during perceptual closure. PPA is responsive to objects that may be potential landmarks in a scene but not to faces. Our findings corroborate the important notion of a link between the pSTS region, which cannot be engaged by object stimuli, and the social face cognition networks.

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