BELSPO RETURN GRANT FINAL REPORT Valérie Goffaux Start date : 1 May 2012 End date: 30 September 2013

This final report provides a description of my research accomplishments in the framework of the BELSPO return contract performed at the Laboratory of Biological Psychology at KU Leuven (start date: 01 May 2012).

1. Objectives

Faces are core visual stimuli. They reveal peers' identity and are intense social interfaces. Humans process faces very efficiently despite the fact that face information is conveyed via subtle physical variations and is often modulated by variations in pose and lighting.

Answering the question of how the brain represents face identity is timely to advance our understanding of visual perception in general.

I approached this question, starting from the information that is made explicit in the first stages of cortical processing, more specifically in the primary visual cortex (V1). V1 neurons are well-characterized by 2D-Fourier filters; i.e., they primarily decompose regions of the scene falling within their receptive fields along the dimensions of spatial frequency (SF) and orientation).

Recent psychophysical work indicates that considering primary visual information has the potential to advance the understanding of face identity processing. It was indeed shown that faces convey a disproportionate amount of information via their horizontal orientation structure and that human observers mainly use horizontal bands of face information in order to discriminate faces.

The privileged processing of horizontal bands of orientation seems to be at the core of high-level perceptual expertise for faces as the horizontal advantage for processing faces is lost when faces are turned upside-down, a manipulation impairing the perception of faces more than other visual stimuli. These findings indicate that human face identity coding relies on observer-dependent biases in encoding primary visual dimensions of face information.

How does the brain represent individual faces?

Once captured by the retina, visual information travels in several steps to primary visual cortex (V1). From V1, the so-called ventral pathway runs to secondary visual cortex (V2/V3) through area V4 and then into a series of further high-level visual processing stages along the ventral cortical surface of the temporal lobe . Neuroimaging techniques have addressed the question of how the human brain represents face identity. Among these, functional Magnetic Resonance Imaging (fMRI) measures hemodynamic modulation related to brain activity at millimeter resolution.

Human fMRI studies have demonstrated that the ventral visual cortex contains large cortical regions that show strong selectivity to faces, bodies, scenes and letter strings. In particular, the viewing of faces when compared with other visual categories activates a vast cortical network of high-level visual regions. In this network, a region localized in the middle fusiform gyrus (coined Fusiform Face Area or FFA) is thought to represent face identity as it responds stronger to face identity changes than to face identity repetition. These response modulations to face identity are thought to reflect high-level face-specific encoding as they are attenuated or eliminated by inversion.

The representation of face identity in FFA suggests the existence of distinct neuronal representations of individual faces in this region. Recently, a new approach was introduced using pattern-analysis methods that are well suited to study distinct neuronal representations in brain regions. Pattern-analysis methods allow detecting modulations of the activation pattern across the voxels within a specific region of interests (ROI). They contrast with conventional statistical analysis methods, which rely on spatial smoothing and averaging of activity in large regions of interest (ROI, such as the FFA in fMRI studies on face perception), and which are therefore mainly sensitive to macroscopic activation. In pattern analysis methods, small biases in individual voxel activation are taken to reflect the biases of underlying neuronal populations. This method has proven very powerful. For example, pattern-analysis methods applied to V1 could predict which of 8 angles of grating orientation a subject was viewing, while the averaged activity of V1 failed to carry very specific information about viewed orientation.

2. Methodology and results

In my proposal, I planned to conduct two fMRI studies in order to investigate the integration of orientation ranges during face perception.

The (preliminary) results of Study 1 have been presented at ECVP conference last year and the manuscript is under preparation. I have conducted the behavioral pilots related to Study 2. It is still in the preparation phase. I plan to collect the fMRI data this summer.

Study 1 Orientation coding in ventral visual cortex

Face identity processing is tuned to horizontally-oriented cues. Here we used fMRI to investigate the neural correlates of this horizontal-tuning in the Fusiform Face Area (FFA) and V1. Eight subjects viewed blocks of upright, inverted, and phase-scrambled faces filtered to preserve a 20°-orientation range centered either on horizontal, vertical, or oblique orientations (Figure 1).

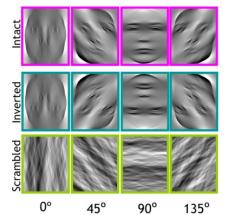


Figure 1. Stimuli used in the behavioral matching and main fMRI experiments were faces filtered in the Fourier domain to preserve energy in selective 20° -orientation ranges. Filters were centered on 0° , 45° , 90° or 135° to spare vertical, left oblique, horizontal or right oblique information, respectively. These face images were presented either in an intact, or inverted version in the behavioral experiment. In the fMRI experiment, filtered faces were additionally presented in a phase-randomized version (i.e., scrambled).

Univariate analysis revealed that the FFA responded most strongly to upright-horizontal faces whereas V1 showed no orientation preference (Figure 2).

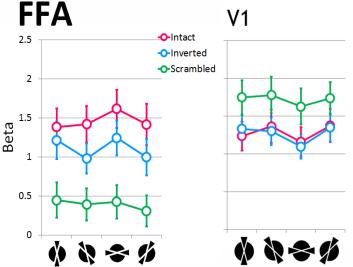


Figure 2. Univariate analyses (General Linear Model, GLM) of FFA and V1 ROI activation. Group-averaged of each bilateral ROI beta values are plotted for each orientation stimulus range and type separately. Error bars represent intersubject the variability (standard errors of the means).

Linear support vector machines were then used to decode stimulus category (upright, inverted, scrambled) or orientation content (horizontal, vertical, left-oblique, right-oblique) based on FFA and V1 activation patterns. In the FFA, classification of stimulus category was significantly better for upright-horizontal faces than upright-vertical faces. No orientation preference was found for inverted and scrambled faces. In contrast, category decoding was comparable across vertical and horizontal conditions in V1. When decoding orientation, high accuracies were obtained in V1 for upright and inverted faces whereas classification performance was close to chance for scrambled faces. In FFA, orientation decoding was close to chance level in all stimulus categories (Figure 3).

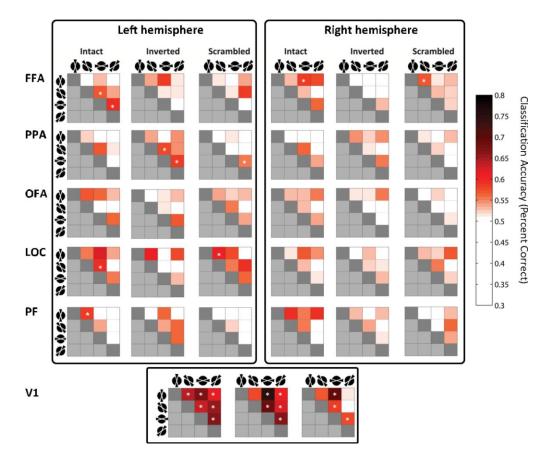


Figure 3. The accuracy of linear SVM classifiers when classifying all possible orientation pairs is shown for each stimulus condition and ROI, separately. Asterisks indicates orientation pairs that could be discriminated significantly above empirical chance level.

These results indicate that (1) FFA is tuned to horizontally-oriented information selectively when processing upright faces and that (2) this horizontal-tuning was not passively inherited from V1.

Study 2 Decoding of face identity in primary and ventral visual cortex

The decoding of face identity has recently proven to be possible based on patterns of activation in the FFA (Goesaert and Op de Beeck, 2012¹). Study 2 aims at exploring the visual information (in terms of orientation) building up the representations of face identity in the different face-selective regions of the human brain.

We scanned thirteen participants who were *a priori* familiarised with 2 easily discriminable face identities in an upright or inverted planar-orientation.

The selection of face identities was based on two separate datasets. First, we tested 5 subjects in a similarity rating task. Upright faces were presented in pairs, one at a time. They always differed and subjects had to rate on a 1 to 7 scale their similarity. We normalized the individual rating scores and averaged across pairs. We found two male faces that were rated as maximally dissimilar. Second, we cross-validated these results based on a different set of subjects 15 subjects in a same/different matching task. In this task, the same face pairs as in the rating task were viewed.

Based on d' and correct RT measures, we could determine the two faces that were best discriminable. Again, the two male faces that were found to be maximally dissimilar were those which induced the highest d' scores and fastest RT in the matching task, suggesting that these are the most discriminable faces in the face set tested (Figure 4). Importantly, the discrimination of this face pair was also found to be significantly impaired by inversion.

¹Goesaert E., Op de Beeck H. 2013. Representations of facial identity information in the ventral visual stream investigated with multivoxel pattern analyses. Journal of Neuroscience. nr.33 (19), pages 8549-8558, ISSN 0270-6474.

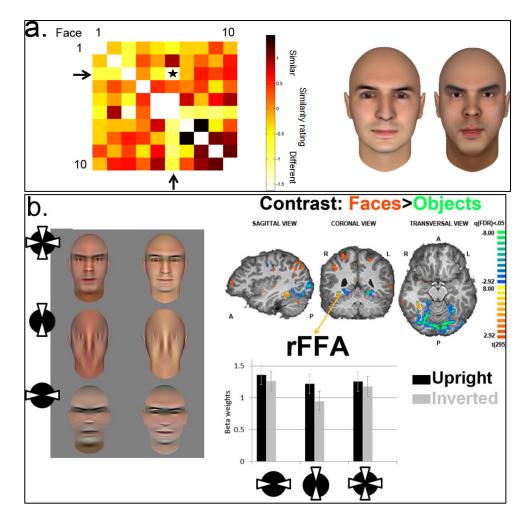


Figure 4.a. *left* Similarity rating for pairs of male faces. Arrows indicate the face that was rated as maximally different from all the other faces tested. As the second face, we selected the one of those that were rated as most dissimilar to the former one (see star) as confirmed with another task and subject sample. *right* The most discriminable face pair of the set. **b**. left Examples of face stimuli used during themain fMRI experiment. Animations of the two selected face identities contained either horizontal, vertical, or both orientation content. *right* Preliminary analyses of one example subject. The right-lateralized FFA was localized in each participant based on his/her brain preferential activation to faces (as compared to objects) in the face localizer fMRI runs. Univariate GLM analyses were applied to the ROI with Planar orientation by Orientation content conditions as predictors. We did not attempt to enter the face identity as a predictor as univariate analyses are not suited to distinguish brain activations related to individual identities. The output of this analysis for the present subject is expressed in terms of beta weights.

Before scanning, participants were familiarized with both face identities. Concretely they learned the respective fictional life stories of each identity, and were trained recognize them under different facial expressions and poses. After the familiarization phase, the participants' knowledge of the respective life stories was tested. They were further tested in an old/new paradigm testing their ability to discriminate the learned identities from other, unlearned identities.

In August-September 2013, thirteen participants performed two scanning sessions. In the first scanning session, participants were presented with short animations of each of the two identities (duration: 3 seconds). Animations were made up of face images filtered to only preserve horizontal, vertical, or both information. In a sixth of the trials, the animation was followed by a few words, and the task of the participant was to decide whether or not these words depicted a detail of the life story of the face identity just presented. This task maximized the chance that the participants actively attempted to process face identity at the finest precision level.

In the second scanning session, participants performed three different types of localizer runs. In two so-called retinotopic runs, participants were presented with colored and black and white vertical and horizontal wedge-

shaped stimuli to delineate at the individual level: face-selective cortical regions, V1, and regions being tuned to horizontal and vertical oriented bars.

So far we have explored the modulation of the right FFA of each of our scanned subjects using univariate analyses in order to verify the quality of the fMRI data (see figure 4b). However, our main hypotheses relate to the output of multivariate analyses, which have recently proven to be sensitive enough to dissociate between different face identities based on the activation pattern they elicit (e.g., Goesaert and Op de Beeck, 2012). We predict that the most successful face identity decoding will be obtained when pattern analyses only includes horizontally-tuned voxels within face-selective regions. Face inversion is known to dramatically hamper face recognition abilities while preserving most input properties (complexity, luminance, contrast, SF content). To ascertain that the distinct spatial patterns obtained for each individual face identity reflect activation dynamics genuinely involved in face identity coding, the success at decoding identity based on spatial patterns of voxel activation should be significantly higher for upright than inverted faces. In addition, we will perform the same analysis in V1. Also here we expect the most successful face identity decoding in horizontally-tuned voxels. However, it is less clear whether this effect should be different for upright and inverted faces, and the answer to this question depends on whether the responses in V1 are exclusively related to bottom-up processing or also involve feedback processing (see above). We still have to perform these analyses.

Study 3 Orientation processing in the perception of gaze

Other orientations likely play a significant role in processing emotional and intentional (via expression and gaze direction, respectively) face cues. We conducted a series of behavioral experiments to measure the sensitivity of human adults to gaze in horizontal and vertical orientation ranges (Figure 5). These findings indicate that:

(1) There is no horizontal tuning when processing gaze direction, i.e. when compared directly, there was no performance difference whether gaze was processed based on vertically- and horizontally-filtered face cues; this contrasts with the robust horizontal tuning reported for the processing of identity.

(2) Vertical face information allows for more distinct representations of different gaze directions than horizontal information. Hence, the performance difference when searching for direct vs. averted gaze in a crowd of faces was found for vertically- but not horizontally-filtered faces; moreover, gaze-cued attentional orienting is driven by vertical face information; it is absent with horizontally-filtered faces.

These results point to a dissociation between the processing of social cues being driven by vertically-oriented gaze cues and the processing of identity provided by horizontally-organized information.

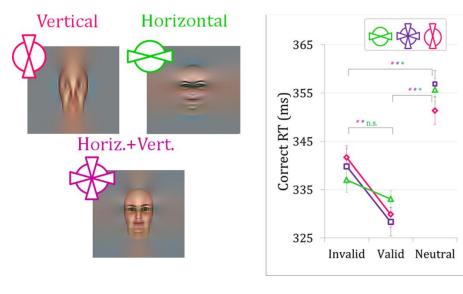


Figure 5. *left* Examples of the stimuli employed in the gaze attentional cueing experiment in study 3. Face displayed left, right, or direct gaze. They were filtered to only preserve horizontal, vertical or both ranges of information. *right* Results of the gaze cueing experiment. Subjects were significantly faster to detect a lateral target when cued by the gaze direction of a centrak filtered face, but only when the central face contained vertical information. There was no significant gaze attentional cueing of the target detection latency when the face only contained horizontal information.

3. Dissemination

3.1. Publications in the framework of the BELSPO return grant

Note: The manuscripts related to studies 1 and 3 are under preparation. These papers should be submitted within the next months. The submission of the manuscript related to study 2 is expected to take place in early January 2014.

• Goffaux Valérie, Sanae Okamoto-Barth (in preparation). Contribution of cardinal orientations to gaze perception.

• Goffaux Valérie, Duecker Felix, Hausfeld Lars, Schiltz Christine, Goebel Rainer (in preparation). Orientation tuning for faces in the Fusiform Face Area and Primary Visual Cortex.

3.2. Publications NOT related to the BELSPO return grant

• Goffaux Valérie (2012). The discriminability of local cues determines the strength of holistic face processing. Vision Research, 64, 17–22.

• Goffaux Valérie, Schiltz Christine, Mur Marieke, Goebel Rainer (2012). Local discriminability determines the strength of holistic processing for faces in the fusiform face area. Front Psychol. 2012;3:604. doi: 10.3389/fpsyg.2012.00604. Epub 2013 Jan 8.

• Goffaux Valérie, Martin Romain, Dormal Giulia, Goebel Rainer, Schiltz Christine (2012). Attentional shifts induced by uninformative number symbols modulate neural activity in human occipital cortex. Neuropsychologia, 50(14):3419-28.

3.3. Missions

3.3.1. International conferences

• Vision Science society Meeting, Naples, Florida.

Note: The VSS Annual Meeting offers attendees the opportunity to learn about the latest vision research, see recent advancements in technology.

- 2012: Goffaux Valérie, Duecker Felix, Schiltz Christine, Goebel Rainer (2012). Orientation tuning for faces in the Fusiform Face Area and Primary Visual Cortex. Journal of Vision August 13, 2012 vol. 12 no. 9 article 27.
- 2013: Valérie Goffaux and Sanae Okamoto-Barth (2012). Contribution of cardinal orientations to the "Stare-in-the-crowd" effect.

• European Conference of Visual Perception.

Note: The European Conference on Visual Perception is an annual meeting devoted to scientific study of human visual perception. ECVP has been held each year since 1978, and attracts a wide variety of participants from such fields as Psychology, Neuroscience and Cognitive Science.

- 2012: Goffaux Valérie and Okamoto-Barth Sanae (2012). Contribution of cardinal orientations to the "Stare-in-the-crowd" effect. Perception 41 ECVP Abstract Supplement, page 112.
- 2012 : Goffaux Valérie, Duecker Felix, Schiltz Christine, Goebel Rainer (2012). Orientation tuning for faces in the Fusiform Face Area and Primary Visual Cortex. Perception 41 ECVP Abstract Supplement, page 21.

3.3.2. Invited talks

- "The orientation selectivity of face perception". Talk invitation by Professor Rufin Vogels, at the Research Group Neurophysiology of the KU Leuven (14-01-2013).
- "Human face identity perception critically depends on horizontal information, gaze processing tells a different story...." Talk invitation Professor Boutheina Jemel, at the Research laboratory in neurosciences and cognitive electrophysiology of the University of Montreal (23-07-2013).

4. Accomplishments and perspectives

4.1. Career perspectives

At KU Leuven, I was proposed by the supervisor of my BELSPO grant (Professor Op de Beeck) to submit a grant application for Odysseus grant. I applied but received a negative answer. I really appreciated to work in the Laboratory of Biological Psychology during the BELSPO grant period. Unfortunately, apart from the Odysseus grant, my perspectives of permanent integration were very limited.

I will actually now develop my scientific career at UC Louvain as I obtained a permanent Researcher Associate position (F.N.R.S. funding) in that institution (UC Louvain). This is the reason why I resigned my BELSPO contract

sooner than the initial end-date.

4.2. Contributions to the host institution and for "Belgian" research in general

My research focuses on the study of human face perception, which is an extensive field of research in cognitive neurosciences. Nonetheless, the findings of my research challenge predominant serial-hierarchical models of vision, which posit that primary visual properties such as orientation and SF do not affect higher-level visual processing stages involved in the representation of complex stimuli such as faces. Thus, they have important implications not only for face perception, but for high-level vision in general. This is probably why they are influential in the domain of vision research as illustrated by their high number of citations.

I hope that my expertise in the field of face perception, and imaging techniques have been profitable to my host institution.