Title: Integration of identity and emotion information in faces: fMRI evidence

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Abstract

Separate neural systems have been implicated in the recognition of facial identity and emotional expression. A growing number of studies now provide evidence against this modular view by demonstrating that integration of identity and emotion information enhances face processing. Yet, the neural mechanisms that shape this integration remain largely unknown. We hypothesize that the presence of both personal and emotional expression target information triggers changes in functional connectivity between frontal and extrastriate areas in the brain. We report and discuss three important findings. First, the presence of target identity and emotional expression in the same face was associated with super capacity and violations of the independent processing of identity and expression cues. Second, activity in the orbitofrontal cortex (OFC) was associated with the presence of redundant targets and changes in functional connectivity between a particular region of the right OFC (BA11/47) and bilateral visual brain regions (the inferior occipital gyrus (IOG)). Third, these changes in connectivity showed a strong link to behavioural measures of capacity processing. We suggest that the changes in functional connectivity between the right OFC and IOG reduce variability of BOLD responses in the IOG, enhancing integration of identity and emotional expression cues in faces.

Key words: facilitation effect, face processing, OFC, workload capacity

Introduction

Rapid processing of information conveyed by faces is an essential skill

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in social interactions. Understanding the brain mechanisms underlying this ability has been a core issue since the inception of experimental psychology, but we are still far from developing a full account. Influential cognitive and neural models of face perception (Bruce & Young, 1986; Haxby, Hoffman, & Gobbini, 2000) have proposed independent, parallel routes for processing personal and emotional information in faces.

Although, mounting evidence against this view emerged since, the architecture of face processing is still open for debate. Of direct relevance here is work demonstrating facilitation effects between identity and emotion cues in faces (Bach, Schmidt-Daffy, & Dolan, 2014; D'Argembeau & Van der Linden, 2011; de Gelder, Frissen, Barton, & Hadjikhani, 2003; Duchaine & Yovel, 2015; Fisher, Towler, & Eimer, 2016; Fitousi, 2016; Johnson, Senju, & Tomalski, 2015; Li et al., 2010; Liu, Chen, & Ward, 2014; Martens, Leuthold, & Schweinberger, 2010; Soto, Vucovich, Musgrave, & Ashby, 2015; Van den Stock & de Gelder, 2012; Yankouskaya, Booth, & Humphreys, 2012). For example, clinical studies reported that emotional expression enhanced recognition of a person in patients with prosopagnosia (de Gelder et al., 2003). Studies with healthy individuals found that unfamiliar faces that had been learned with emotional expressions were recognized better compared to faces learned with a neutral expression (D'Argembeau & Van der Linden, 2011; Liu et al., 2014). Fitousi (2016) provided compelling evidence that the variant and invariant facial attributes of emotion and identity do interact in the binding process. Mutual facilitation between matching facial identity and facial expressions, in accuracy as well as in reaction times, was reported in a study that investigated the interactions between identity and expressions of

unfamiliar face (Levy & Bentin, 2008). Furthermore, it was demonstrated that observers can use personal information as a reference on which they can faster compute expressions and that they can also use unique expressions to facilitate computations of identity (Ganel, Goshen-Gottstein, & Ganel, 2004). Moreover, when participants were required to attend to both target identity and target emotion in faces, they responded faster to a face containing both targets compared to faces containing either single target (Yankouskaya et al., 2012).

A key question unanswered to this day is how the brain supports the facilitation effect in faces. Does the presence of both the identity and emotion targets enhance communication between brain areas, gaining processing capacity? Another possibility is that the facilitation effect in faces employs brain mechanisms similar to those supporting the redundant target effect in processing of multiple object attributes (Mooshagian, Kaplan, Zaidel, & Iacoboni, 2008). Answering these questions will inform current models of face processing and may have important implications for clinical studies (e.g., autism spectrum disorders, prosopagnosia). Here we aim to contribute toward understanding brain mechanisms of the facilitation effect between personal and emotional information in faces.

Behavioural evidence for the facilitation effect between identity and emotion in faces comes from studies employing a dual task (Miller, 1982) where, for example, participants are required to monitor two sources of information in a face simultaneously (target person and target emotion) to decide if any target is present or absent (Yankouskaya et al., 2012). The facilitation effect occurs for combinations of emotionally valenced expressions

with facial identity but not when identity is combined with a neutral expression (Yankouskaya et al., 2012). By asking individuals to attend to two sources of target information at the same time, this experimental paradigm overcomes some limitations of previous studies (Yankouskaya, Rotshtein, & Humphreys, 2014).

The above studies used mathematical tests of capacity measures (Eidels, Townsend, Hughes, & Perry, 2015a, 2015b; Townsend & Wenger, 2004) and the race model (Miller, 1982; Mordkoff & Miller, 1993) that enabled a precise estimation of the facilitation effect and the inference about cognitive mechanisms underlying the relationship between the processing of identity and emotional expression. For example, by varying the number of available sources of information in faces (e.g., target emotional expression, target personal information or both target emotion and target identity) it is possible to model and estimate the architecture of processing (Townsend & Eidels, 2011). If the identity and emotion cues are processed in stochastically independent fashion, varying workload of information will not change the efficiency processing of the system implying unlimited capacity (parallel architecture of processing). If the presence of both the identity and emotion target information benefits performance (i.e., faster response time), the processing is characterised as having co-active architecture indicating increased efficiency in processing (super capacity) (Townsend, Fific, & Neufeld, 2007; Townsend & Wenger, 2004). It has to be noted that the term 'co-activation' means that information about one target is added together with that from the other target in a subsequent pooled outlet (Eidels et al., 2015b).

Previous studies tested the facilitation effect in face processing which was operationalised in terms of a gain in response time (RT-gain) for a face containing both target identity and target emotion compared to faces with either single target (Yankouskaya et al., 2012; Yankouskaya, Humphreys, & Rotshtein, 2014). It was demonstrated that the presence of these two facial cues triggered co-active processing that led to increasing processing efficiency. Moreover, the capacity of the system was significantly superior to those predicted by independent processes (Yankouskaya, Humphreys, et al., 2014).

The dual task with faces generates behavioural effects of co-active processing (i.e., faster RT, large RT gain) similar to those observed in experiments with simple objects (Miller, 1982; Mordkoff & Miller, 1993; Murray, Foxe, Higgins, Javitt, & Schroeder, 2001). It is plausible to assume that although face and object processing employ different neural mechanisms (Haxby et al., 2001; Rolls, 2008), the brain may use a unified mechanism to facilitate processing of multiple visual signals. For example, electrophysiological (Miniussi, Girelli, & Marzi, 1998; Saron, Schroeder, Foxe, & Vaughan, 2001) and neuroimaging studies (Iacoboni & Zaidel, 2003; Roser & Corballis, 2003; Schulte et al., 2006) supporting the co-active processing with simple objects suggest that two neural mechanisms are involved in generating the redundancy gains – a posterior one associated with posterior callosal connectivity and extrastriate activation (BA 17, 18), and an anterior one that involves frontal areas (BA 44, 46, 47). The extrastriate activation was linked to attention-independent, automatic processes for efficient and fast transmission of redundant information at an early sensory processing stage,

whereas the frontal areas were associated with modulation and attenuation of response facilitation from redundant targets (Schulte et al., 2006) .

Recently, Shim and colleagues (2013) examined mechanisms of redundancy gain in complex objects (such as human faces, houses, scenes) by measuring BOLD responses to a single stimulus as a function of whether or not other stimuli are also presented simultaneously. The authors argued that the redundancy gain observed at early retinotopic cortex resulted from feedback from higher visual areas and might underlie perceptual averaging and other ensemble coding phenomena observed behaviorally (Shim, Jiang, & Kanwisher, 2013). Similar findings were reported in other studies on redundancy gains (Jiang, Kwon, Shim, & Won, 2010; Sweeny, Haroz, & Whitney, 2013).

The neuroimaging studies above provide clear evidence for neural communication between higher and lower cortical areas to efficiently integrate visual information from multiple sources. However, the majority of these studies on redundancy gains were looking at spatial localization of the effect in simple objects or employed pre-defined regions of interest to test hypotheses about an involvement of specific brain areas in complex object processing. This limits our understanding of whether the RT-gain in the processing of identity and emotion in faces may recruit different brain regions.

Neuropsychological studies report that individuals with occipito-temporal brain lesions who demonstrate an impaired ability to process facial configuration, show improved identity matching when faces display emotional expression, irrelevant to the task (de Gelder et al., 2003). In the study by de Gelder et al. (2003) participants were required to match a complete face to

two face parts (either mouth or eyes) displayed underneath. It was proposed that, as a consequence of brain damage, the relative speed of processing of the different, parallel routes involved in processing identity and emotion may be altered in a way that the slower route (i.e., emotional processing) can become the fast one or sometimes the only available route. Thus, the presence of an emotional expression would enhance the sensitivity to stimulus orientation and the ensuing configural processes. Interestingly, although the facilitation effect of emotional expression on identity recognition was specific to patients only, both patient's and control subject's neuroimaging data showed activation in the right orbitofrontal cortex (rOFC) – a region involved in top-down modulation of processing invariant facial features in the inferior occipital (IOC) and fusiform cortex (FFC) (Haxby et al., 2001; Li et al., 2010). This finding indicates that the OFC may play a role in reallocating processing resources between the streams for identity and emotion.

Taken together, the studies with patients and healthy individuals indicate that at least two areas may contribute to the facilitation effect when processing identity and emotion in faces – the frontal cortex (such as BA 44, 46, 47) and the extrastriate cortex (such as BA 17, 18). Here we tested this assumption. In addition, we hypothesise that the facilitation effect in faces may be associated with changes in the functional connectivity between higher and lower cortical areas. We collected fMRI data during a dual task with face stimuli that was reported previously (Yankouskaya et al., 2012) where the results indicated super capacity in processing of identity and emotional expression information in faces. This experiment included three types of

target faces: 1) target identity (I), 2) target emotional expression (E) and 3) faces displaying both identity and expression targets (IE), as well as, three faces containing no target (NT1, NT2, NT3). Participants were asked to indicate as quickly and accurately as possible whether a displayed face contained a target.

In the absence of a precise hypothesis regarding the brain areas involved, we adopted an exploratory approach in fMRI data analysis. First, we tested whether facilitation effects in faces containing both targets showed regional specificity in the brain (e.g., in OFC and extrastriate areas) by performing a whole-brain univariate analysis. To examine whether the facilitation effect in faces may be associated with changes in the functional connectivity between higher and lower cortical areas, we applied a multivariate, data-driven approach (Whitfield-Gabrieli & Nieto-Castanon, 2012) and analysed changes in functional connectivity across the brain that are dependent on the redundant (IE) condition. By adopting the multivariate approach, we eliminated an experimental disadvantage of a user selection bias in targeting brain regions involved in the processing of redundant information in faces. Furthermore, a data-driven approach may help to amplify inherent interactions between previously established areas in face processing networks.

Materials & Method

Participants

Seventeen right-handed participants (ten females; mean age 23.6 years) with normal or corrected-to-normal vision and no history of neurological

disorders participated in this study. The data of one participant were discarded due to extensive head movements and signal loss in the OFC/ITG (Supplementary Material, Figure S2, Participant 17, for details). The experiment was carried out in accord with the ethical guidelines of the British Psychological Society and approved by the Ethics Committee of the School of Psychology (University of Birmingham). An entry screening procedure and questionnaire ensured that participants were aware of all critical health and safety issues associated with fMRI. Each participant gave written informed consent at the start.

Stimuli

Three sets of 6 photographs were randomly assigned across participants. All face images were sourced from The NimStim Face Stimuli Set (Tottenham et al., 2009). The sets consisted of Caucasian actors (please, see the identity number of the models in the Supplementary Material). Recognition of facial expression in all the photographs was previously rated as 80% or more (Tottenham et al., 2009) (an example of a set consisted of female Caucasian faces, see Figure 1). The photographs were cropped around the hairline to eliminate the possibility of target judgments being based on hairstyle. Any visible background was coloured black. A detailed description of stimuli selection can be found in Yankouskaya, et al. (2012).

The presentation of the stimuli and data acquisition were controlled using Cogent 2000 and Cogent Graphics developed by the Cogent 2000 team at the FIL and the ICN (http://www.vislab.ucl.ac.uk/cogent_2000.php).
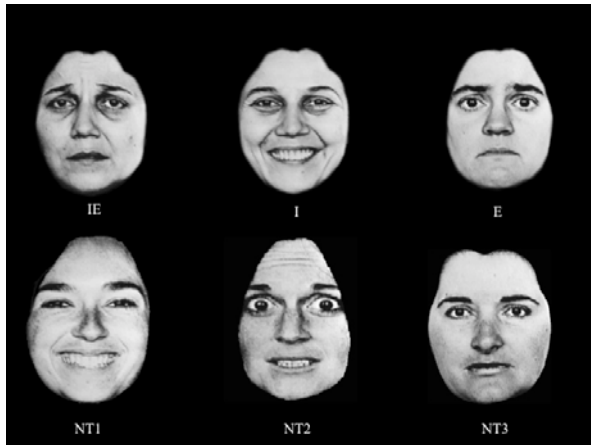
Figure 1. An example of the stimuli set. IE – a face containing both the target identity and the target emotional expression; I – a face containing the target identity but not the expression; E – a face containing target emotional expression; NT1-NT3 faces containing neither the target identity nor the target emotion. In this study, we used faces from the NimStim database, but due to publication restrictions, we present other faces here (Ekman & O'Sullivan, 1988) as examples only.

Design and procedure

A divided attention task was used, similar to that reported in Yankouskaya et al. (2012). Participants were presented with a set of selected photographs of faces that varied in identity and emotion, and they were instructed to respond "target present" as quickly and accurately as possible when they saw a target person and/or a target emotional expression. When they saw neither the target person nor the target emotional expression, participants were required to respond "target absent". Half of the trials used stimuli containing at least one target (target identity - person 1, target emotional expression - sad, or both targets). The targets were: Person 1 expressing a sad emotion (redundant targets); Person 1 with a happy expression (target identity and non-target expression); Person 2 with a sad

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expression (target expression and non-target identity). The other half of the trials used stimuli that did not convey any target attribute: Person 3 with a neutral expression, Person 4 with a surprised expression and Person 5 with an angry expression (all of them non-target-identity and non-target emotion). Prior to the scanner sessions, participants completed an initial practice block of 30 trials during which they were given feedback on their accuracy and reaction time (RT) after each trial.

The experiment was divided into six sessions. In each session, there were 60 trials (10 events per condition) in a random order. A trial started with a 500 ms fixation cross, followed by a 500 ms presentation of a face and ended with a blank screen of random duration (3.5-7 sec). Participants responded "target present" or "target absent" by pressing buttons with their index fingers using the response box.

Behavioural data analysis

To assess behavioural characteristics of the facilitation effect, three analyses were carried out. First, we examined the effect of target (IE, I, E) on accuracy and response time using repeated measures ANOVA. Second, we calculated individual's RT-gain using RTs for correct responses only. Previously, it has been shown that some observers might favour one dimension over another, and it was suggested to use more conservative estimation of RT-gain by subtracting the mean RT for redundant targets from the mean RT for the fastest single target (Biederman & Checkosky, 1970; Mordkoff & Yantis, 1991). Therefore, prior to computing RT-gain, we identified the fastest single target (I or E) and then defined RT-gain as follows: [mean RT fastest single target – mean RT for IE condition]. A one-sample t-test was

used to test whether the magnitude of RT-gains across participants was significantly greater than zero.

The third analysis tested architecture and workload capacity (efficiency) of processing identity and emotional expression. Workload capacity is defined by the rate or unit of work that can be accomplished in a given amount of time (Townsend & Eidels, 2011). The evaluation of workload capacity is a critical factor in determining the allocation of resources to optimise task performance – with more or less resources being allocated according to workload capacity and consequent effects on other ongoing processes (Maylor & Lavie, 1998).

If the processing speed of an individual target is not affected by an increase in workload, the information processing system is defined as having unlimited capacity (i.e., either single target is processed simultaneously in a stochastically independent way). This type of processing is referred to as being unlimited in capacity, independent, parallel (UCIP) and considered as a baseline for capacity measures (Silbert, Townsend, & Lentz, 2009; Townsend & Wenger, 2004). If, after increasing workload, the processing speed increases, the system is considered to have super-capacity relative to the unlimited capacity system. The super-capacity processing indicates that the two single targets interact, producing qualitative changes to the system because the two signals are summed together before a decision ('target present') is made. If the processing speed slows down (i.e., two processes interact negatively interfering with one another) the system is considered to have limited capacity relative to the unlimited capacity processing. In this case, the system can be described as having limited resources, serial processing or possessing inhibitory connections across the channels

(Townsend & Eidels, 2011; Altieri & Townsend, 2011; Townsend & Wenger, 2004).

For each condition, we calculated the empirical cumulative distribution function (CDF) using small time window bins (10ms). Then the empirical survivor function was computed for each condition at each time bin - this is simply the complement of the cumulative distribution (the proportion of trials that were slower than the specified RT). After averaging the CDFs for the redundant targets and each single target, the data were converted into survivor functions.

$$C_{OR}(t) = \frac{-\log[S_{IE}(t)]}{-\log[S_I(t) * S_E(t)]}, \quad (2)$$

C(t) reflects the capacity coefficient at a specific time point (t); S denotes the survival function at this time, i.e., the probability that a trial has not been completed.

For example, if responses for 10% of the trials were shorter than 400 ms than the survivor function for this time point indicates a 0.9 probability that a trial has not been completed by this time. The survival function of the redundant target condition is in the numerator, and the product of the survival functions for the two single target conditions is in the denominator. Therefore, C(t)=1 implies unlimited capacity; C(t) < 1 reflects limited capacity and C(t) >1 indicates super capacity. Thus, if identity and expression interact in a facilitatory fashion, we would expect the results to demonstrate that the system operates in super-capacity mode.

All computations were performed using Matlab codes (Townsend & Eidels, 2011). Subsequently the group capacity coefficient was generated by

creating a ratio of the averaged survivor functions at each time bin across participants (Hugenschmidt, Hayasaka, Peiffer, & Laurienti, 2010).

We also performed an additional analysis based on methodology proposed by Miller and colleagues (Miller, 1982) to obtain complementary evidence for interactive processing of identity and emotion information. This analysis is available in the Supplementary Material.

Image acquisition

MRI data were obtained using a Phillips 3T Achieva system with an eight-channel phased-array SENSE coil configuration (Birmingham University Imaging Centre). Six hundred and six T2*-weighted images were acquired from each participant (41 contiguous 3-mm axial slices with 30° tilt (Deichmann, Gottfried, Hutton, & Turner, 2003) with no gap, echo time = 35 ms, repetition time = 2.4 s, flip angle = 79.1°, field of view = 240 × 240 x 128). T1-weighted anatomical data were also collected (175 sagittal slices, 1 mm × 1 mm × 1 mm, flip angle = 8°; TE = 3.8 TR = 8.4). To remove spatial distortions caused by magnetic field inhomogeneity, we obtained a field map for each participant in the same space as functional images immediately after functional runs.

Neuroimaging data analysis

Functional images were analysed using SPM8 software (Wellcome Department of Imaging Neuroscience, London, UK; www.fil.ion.ucl. ac.uk/spm). The first four volumes were discarded to allow for T1 equilibration. After timing correction, functional volumes were spatially realigned to the first EPI volume. Unwarping was used to compensate for non-linear distortions caused by head movement and geometric distortions caused

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by susceptibility-induced field inhomogeneity (Hutton et al., 2002). Field maps were estimated from the phase difference between the images acquired at the short and long TE with the FieldMap toolbox for SPM8. The anatomical T1 image was then co-registered to the mean EPI which had been generated during the realignment step and spatially normalized to the Montreal Neurological Institute (MNI) space using the SPM8 unified segmentation routine. Normalization of all EPI volumes was performed by application of the deformation parameters estimated in the anatomical normalization step. The original resolution of the anatomical (1mmx1mmx1mm) and EPI (3mmx3mmx3mm) images were maintained during the normalization step. Normalized EPI images were smoothed using a 6 mm full-width at half-maximum Gaussian kernel. It has to be noted that to prevent removing crucial components of the task-related BOLD signal, the data were resampled only once after head motion correction (Swallow, Braver, Snyder, Speer, & Zacks, 2003).

Univariate voxel-based analysis. The data were modelled using the General Linear Model (GLM). First, individual fMRI time series for the six conditions were regressed onto a single fixed-effect general linear model. The single-subject hemodynamic responses were modeled by convolving delta-stick functions aligned to the onset of each condition with a first-order canonical hemodynamic response function. Stimulus onsets were defined relative to the acquisition of the middle slice. The six motion-correction parameters estimated from the realignment procedure, and two temporal derivatives (one controlling for the small shift in pick of HDR, the second controlling for duration dispersion for pick HDR) were entered as regressors of

no interest. To account for within subject correlation and the assumptions made about variance, the serial correlations were estimated with a ReML (restricted maximum likelihood) algorithm using an autoregressive AR(1) model during parameter estimation. This estimate assumes the same correlation structure for each voxel, within each run. The ReML estimates are then used to correct for non-sphericity during inference by adjusting the statistics and degrees of freedom appropriately. To accommodate between-run differences in the raw BOLD signal, data from each run were scaled to have a grand mean value of 100 across all voxels and volumes. Individual statistical parametric maps were then generated from linear contrasts between the different conditions and entered into random effect analysis (Friston, Holmes, Price, Buchel, & Worsley, 1999; Friston, Holmes, & Worsley, 1999) for the group statistical interference.

Functional connectivity analysis.

EPI images were preprocessed in a similar way as for the whole-brain univariate analysis with an additional preprocessing step - the component-based noise correction method (CompCor) (Whitfield-Gabrieli & Nieto-Castanon, 2012). Previous studies suggested that removing physiological and other noise sources increased the sensitivity and selectivity of functional connectivity MRI analysis. The CompCor method models the influence of noise as a voxel-specific linear combination of multiple empirically-estimated noise sources, eliminates head movements, performs temporal filtering and windowing of the residual blood oxygen level-dependent (BOLD) contrast signal. The waveform of each brain voxel was filtered using a bandpass filter (0.008-0.09 Hz) to reduce the effect of low-frequency drift and high-frequency

noise. Prior to submitting the data to the functional connectivity analyses, functional runs were scaled, concatenated and an additional regressor that indicated the runs' order was specified.

To test the assumption that the interaction between identity and emotional information in faces reflects changes in functional connectivity, we used a data-driven approach implemented in the "connectome-MVPA" CONN toolbox (Whitfield-Gabrieli & Nieto-Castanon, 2012). The idea of this approach is to define data-driven regions of interest (seeds) prior to performing a post hoc analysis on the seeds to analyse brain connectivity patterns (Beaty, Benedek, Kaufman, & Silvia, 2015; Thompson & Fransson, 2016; Whitfield-Gabrieli et al., 2016).

To define the data-driven seeds, we calculated global connectivity (connectome, based on voxel-to-voxel correlation) for three conditions of interest (IE – a face containing both the target identity and the target emotional expression; I – a face containing the target identity but not the expression; E – a face containing target emotional expression). For each voxel per condition and participant we obtained a vector of correlations between the voxel and the rest of the brain. To reduce the data, CONN performed Principal Component Analysis (PCA) of the variability in connectivity patterns between this voxel and the rest of the brain. This analysis resulted in c-dimensional (where c is the number of principal components) multivariate representations of the connectivity at each voxel. The representations were stored as connectome maps per principal component, condition and participant and entered into random effect analysis to examine the connectome differences between the conditions. We focused on the following contrasts: (i) redundant and single

targets: IE vs. I + E; (ii) single targets I vs. E. The changes in the magnitude

and the extent of spatial connectivity between the conditions (peak value p <

0.001, uncorrected, extent threshold of 50 contiguous voxels) were

thresholded using family-wise error (FWE) correction of pFWE < 0.05 for the

whole-brain volume. Voxels that survived FWE correction were entered as

seeds for the post-hoc analyses. It has to be noted that the connectome

analysis shows only whether the connectomes are different between

conditions, but it does not indicate what areas contributed to that connectivity

differences.

To elucidate which regions in the brain changed their connectivity in

relation to the face containing identity and emotion targets, we performed a

post-hoc analysis. The clusters showing significant differences between the

conditions at the connectome level were entered as seed points of interest

against all other voxels in the brain. The connectivity maps were computed for

each condition and participant and then entered into random effect analysis.

Results

Behavioural results

The overall percentage of correct responses was 97.6%. A one-way

repeated-measures ANOVA showed that the error rates did not differ across

the conditions ($F(5, 75) = 1.9$, $p > .05$, $p\eta2 = .11$).

A repeated measures ANOVA with face (target, nontarget) and stimulus

type (I, E, IE/NT1, NT2, NT3) as within-subject factors showed that participant

responded faster to faces containing targets compared to nontarget faces

($F(1, 15) = 34.75$, $p < .001$, $p\eta2 = .69$) (Figure 2). There was a main effect of

stimulus ($F(2, 30) = 9.34$, $p < .001$, $p\eta2 = .38$). The interaction between face

and stimulus did not reach significance (F(2, 30) = 3.08, p = 0.06, pη2 = .17).

Post Hoc paired sample t-tests using Bonferroni adjustment for multiple comparisons showed that responses for a face containing both the identity and the emotion targets were significantly faster compared to either single target faces (p < 0.001 and p = 0.015 for target identity and emotion respectively). There was no difference between the single target faces (p = .98). The differences in RT between faces containing no target information were not significant (all ps > 0.05).
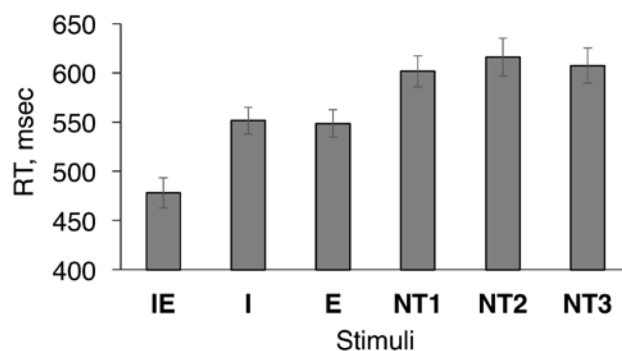

Figure 2. Mean RTs for responses to faces containing both the identity and emotional expression targets (IE), the identity target (I), the emotional expression target (E) and nontarget information (NT1, NT2, NT3). Error bars represent +/- 1SEM.

The facilitation effect (RT-gain) for the IE-condition compared to the fastest of the single target conditions (M = 60 msec, SD = 38.95) was significantly different from zero (t(15) = 6.24, p < .001, dz = 1.56).

The overall capacity coefficients across participants are presented in Figure 3. The result suggests super capacity for processing identity and emotional expression at bins 310 ms to 410 ms. Individual capacity coefficients are presented in the Supplementary Material (Table S2).
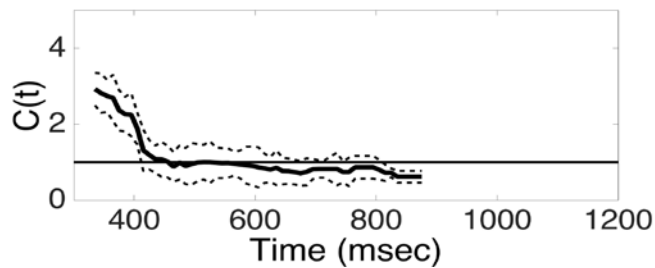
Figure 3. Capacity coefficient (C(t)) averages at each time bin across participants. The horizontal line at C(t) = 1 indicates the reference value for unlimited capacity. The capacity coefficients are depicted in solid line; the confidence interval for capacity coefficient in dash line.

The magnitude of RT-gain showed a strong relationship with capacity processing (*rho* = .54, p = .032, BCa 95% CI [- .22; .88]) suggesting that greater redundancy gains are associated with greater capacity in the processing of identity and emotional expression (individual capacity coefficients are presented in the Supplementary Material, Table S1).

The results of capacity analysis suggest that the presence of both personal and emotion information in faces increases processing efficiency. Importantly, increasing the load of information 'to-be-processed' reflects qualitative changes in the architecture of processing – the perceptual signals are pooled together facilitating the response 'target present'.

Univariate effects of redundant targets*.*

A one-way ANOVA was performed on the whole brain to explore the effects of stimuli containing targets (I, E, IE) (voxel-threshold p < 0.001, uncorrected; extend-threshold with k = 50 contiguous voxels). We did not observe a main effect of stimuli. Furthermore, we did not find any clusters above the height threshold even with smaller cluster size (k = 10). These

results do not support our hypothesis that facilitation effects in faces containing both targets yield regional specificity in the brain.

To test whether the absence of regionally specific changes in BOLD responses to any target condition was due to low sensitivity to target information in faces, we examined the effects of target versus nontarget using a repeated measures ANOVA with face (target, nontarget) and stimulus type (3 levels) as within-subject factors. The results revealed a main effect of face in the bilateral Supramarginal Gyrus SMG) and the right superior temporal sulcus (STS) (Figure 4). The stereotactic locations and statistical values for these clusters are shown in Table 1.
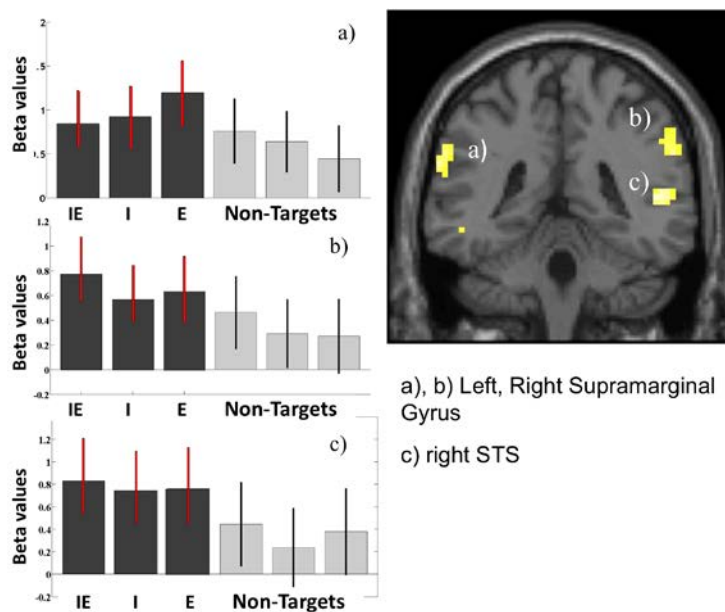

a), b) Left, Right Supramarginal Gyrus

c) right STS

Figure 4. Brain areas showing largeer BOLD responses for faces containing targets as compared to non-targets (voxel threshold $p < 0.001$, uncorrected; extend-threshold of 50 voxels; FWE-corrected $p < 0.05$,). IE – redundant targets, I – the identity target, E – the emotional expression target.

Table 1. *Clusters* showing large magnitude of BOLD response for faces containing targets as compared to non-target faces*

Anatomical labels	Z-scores	No of voxels	MNI-coordinated		
			x	y	z
r-Supramarginal gyrus	3.86	68	57	-34	37
l-Supramarginal gyrus	4.05	87	-60	-40	25
r-STS	4.26	92	54	-43	7

* All clusters reported here are significant at p < 0.05, FWE-corrected

Changes in whole-brain connectivity for redundant targets.

It has to be noted that PCA reported here was performed by retaining only the first principal component. Our choice was determined by the convention that the number of principal components is equal to 10–20% of the number of subjects (which here falls between 2 and 1). Although there is no agreement about the optimal sample-to-PC ratio for PCA, the majority of research suggests higher ratio scores such as 20:1 (Costello & Osborne, 2005; Hair, Anderson, Tatham, & Black, 1998). However, to ensure that we do not miss smaller variations in connectivity across the conditions, we initially performed PCA analyses with two principal components. Random effect analyses on the second principal component showed that no voxel survived FWE correction for the contrasts [IE vs. I+E; I vs. E] even when the extent threshold was dropped to 10 contiguous voxels. These results indicate that it is unlikely that the second principal component can explain the variations in connectivity across the conditions.

Connectome analysis. To obtain connectome maps, the whole brain connectivity matrix for each voxel and condition was reshaped into a row vector and subsequently concatenated over all participants into a matrix Np x V, where Np was the number of participants and V the number of voxels

within the brain mask. The dimensionality of the matrix was then reduced by PCA that resulted in Np rows of one component score volume that best represented the whole brain connectivity pattern per participant and per condition. These volumes were then entered into random effect analysis. The resulting map was thresholded (voxel threshold p < 0.001, extend-threshold k = 50) and FWE-corrected (p < 0.05).

The random effects analysis showed three clusters (Figure 5, Table 2) that represent the difference between connectomes for faces containing both targets compared to connectomes for single targets (i.e., IE > I + E). These three clusters located in the right and left OFC and in the right hippocampus were entered as seeds for follow up post-hoc analyses to examine what areas contributed to the connectome differences.
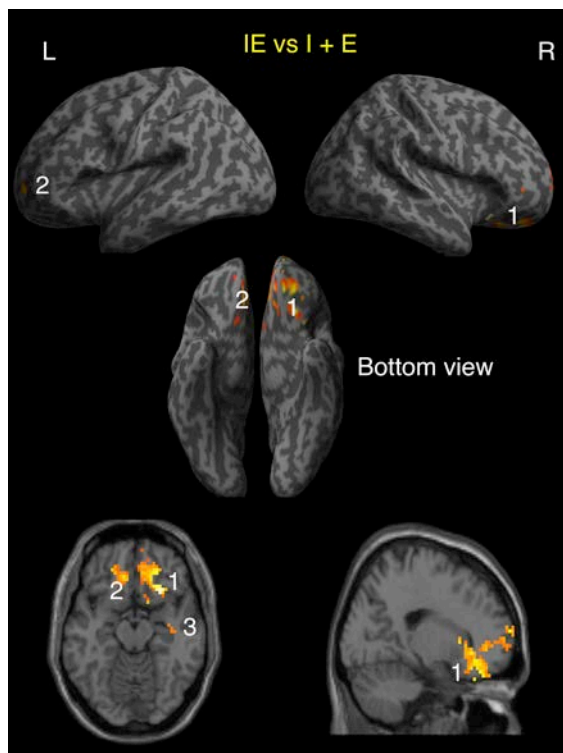

Figure 5. Clusters of voxels that showed different connectivity to the rest of the brain when redundant targets were presented compared to both single targets (FWE-corrected at the cluster level, with min of 50 voxels) rendered on

a SPM canonical cortical surface (upper row), overlaid on a SPM canonical

single subject T1 weighted image (middle row). These clusters include voxels

in the right Orbitofrontal Cortex (rOFC) (1), the left Orbitofrontal Cortex (lOFC)

(2) and the right hippocampus (rHp) (3).

Table 2. *Seed regions* derived from the connectome analysis and representing the differences in connectivity for redundant targets (IE) as compared to both single targets (I + E)*

Anatomical label	Hemisphere	Brodmann area	Z-scores	No of voxels	MNI coordinates**		
					x	y	z
OFC	r	47	4.49	227	27	20	-14
OFC	l	11/47	4.12	155	-21	38	-15
Hp	r	28	3.23	51	24	-28	-10

* All clusters reported here are significant at p < 0.05, FWE-corrected (extended threshold k = 50).
** Anatomical coordinates for the seed regions are given in the MNI space (Montreal Neurological Institute).

Post-hoc analysis. Using spherical seeds placed at the peak voxels at

the three suprathresholded clusters derived from the connectome analysis

(Table 2), we performed a post-hoc seed-to-voxel correlation analysis. For

each seed, we obtained three seed-to-voxel correlation maps (for IE, I, E

conditions) per participant. These individual correlation maps were entered

into random effect analysis (separately for each seed) to test the difference in

functional connectivity between the redundant target and the single target

conditions (IE versus I + E) across participants. Resulting contrast-maps were

thresholded at (p < 0.001, uncorrected) and then corrected with FEW (p <

0.05 with a minimum cluster of 50 contiguous voxels).

The results of the post-hoc seed-to-voxel analyses showed that the face containing both the identity and the emotional expression targets was associated with a significant increase in coupling between the right OFC and the bilateral inferior occipital gyrus (IOG) (contrast [IE>I+E]) (Figure 6, Table 3). No other seed regions (lOFC, rHp) showed significant changes in connectivity for the redundant target face. The reverse contrast ([I+E>IE]) did not show any significant differences in connectivity at cluster or at peak voxel levels for the seeds.
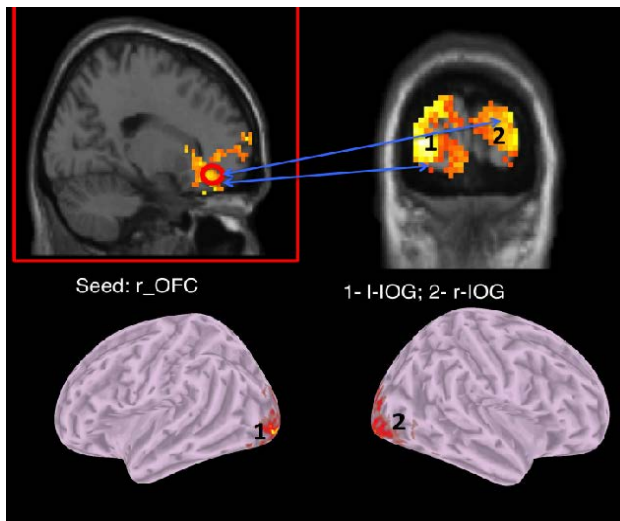

Figure 6. The results of the seed-to-voxel analysis (contrast [2]IE > [-1]I + [-1]E) (FWE-corrected SPMs at the cluster level with min of 50 voxels showing Z > 4.67) rendered on a SPM canonical cortical surface, and overlaid on a SPM canonical single subject T1 weighted image. The red circle outlines the center of the cluster in the r-OFC. The blue arrows show functional connectivity from the seed region to connected areas in the l-IOG (1) and the r-IOF (2)

Table 3. *Results of seed-to-voxels functional connectivity for the redundant targets (IE) as compared to both single targets (I + E) with the r-OFC as a seed*

Cluster*	Hemisphere	Brodmann area	Z-scores	No of voxels	MNI coordinates		
					x	Y	z
r-IOG	R	18	4.67	471	33	-94	-8
l-IOG	L	17/18	4.91	611	-21	-100	-8

*significant at cluster level ($p < 0.05$, FWE-corrected)

The relationship between changes in brain connectivity redundant targets and behavioural performance.

Taken together, the results of the functional connectivity analyses indicate that the face containing both the identity and emotional expression targets is associated with increased coupling between the r-OFC and bilateral IOG. We next assessed whether and how brain responses in these regions relate to the behavioural characteristics of the interaction between identity and emotion.

First, we correlated PCA scores representing the difference between connectomes for faces containing both targets compared to connectomes for single targets (i.e., [IE > I + E]) in the r-OFC with capacity and RT-gain measurements. We created a ROI (sphere, 7mm radius, 57 voxels) centered at peak voxels (x = 27, y = 20, z = -14) in the r-OFC (Table 2) and extracted PCA scores from the connectome map for the contrast [IE > I + E]. The PCA scores were averaged across all voxels for each participant and entered into a non-parametric correlation analyses with an accelerated bias-corrected (BCa) percentile method to obtain bootstrapped confidence intervals.

The analysis indicates that individual capacity coefficients positively correlated with PCA scores for the IE condition in the r-OFC (*rho* = .55, *p* = .028; BCa, bootstrapped 95% CI [-.01; .88]) (Figure 7, a). The correlation

between these PCA scores and the RT-gain measure was not significant (*rho* = .25, *p* = 0.35).
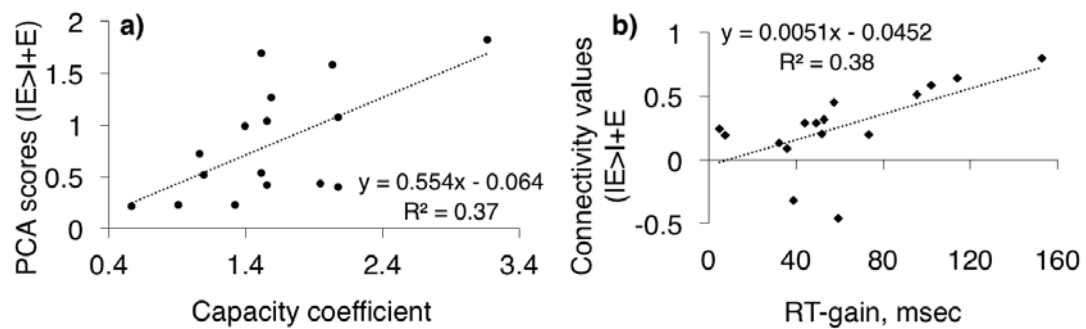

Figure 7. The relationship between a) PCA scores for IE condition in the r-OFC (defined by contrast [IE > I + E]) and individual capacity coefficients; b) changes in functional connectivity for IE condition in the r-IOG and the magnitude of RT-gain. The values of changes in connectivity were obtained by contrasting the seed-to-voxel connectivity map (IE > I + E) with the seed placed in the r-OFC.

Second, we examined the relationship between changes in functional connectivity for the IE-condition in the bilateral IOG with capacity and RT-gain measures. We created two ROIs (sphere, 7 mm radius, 57 voxels) centered at peak voxel in the r-IOG (x = 33, y = -94, x = -8) and the l-IOG (x = -21, y = -100, z = -8) (Table 3) and extracted values representing the changes in functional connectivity for the IE condition (defined by contrast [IE > I + E]) from seed-to-voxel connectivity maps. The values were averaged across voxels in each ROI for each participant and entered into a non-parametric correlation analyses with an accelerated bias-corrected (BCa) percentile method.

The changes in functional connectivity for the IE condition showed a significant positive correlation with the magnitude of RT-gain in the r-IOG (rho = .61, p = .013, BCa, bootstrapped 95% CI [.06; .94]) (Figure 7, b), but not with capacity coefficient (rho = .26, p = .32). We also did not find any significant correlation between the behavioural measures and changes in functional connectivity for the IE condition (IE > I + E) in the l-IOG (rho=.2, p = .43; rho = .18, p = .49 respectively for RT-gain and capacity coefficient).

Discussion

To the best of our knowledge, this is the first report of functional neuroimaging data regarding the facilitation effect for the processing of facial identity and emotion in healthy subjects. We employed a divided attention task that required participants to monitor two sources of information in faces (target identity and target emotional expression) simultaneously – a situation that closely resembles daily life. Behavioural studies demonstrated that this task generates robust facilitation effects for faces containing both targets compared to faces with either single target (Yankouskaya et al., 2012; Yankouskaya, Humphreys, et al., 2014; Yankouskaya, Rotshtein, et al., 2014). The main question that we addressed here is how the brain supports this facilitation effect.

Our behavioural data replicate previous findings with the same experimental paradigm by showing faster responses to faces containing both personal and emotion targets. Using the System Factorial Technology (Townsend & Eidels, 2011; Townsend & Wenger, 2004) that provides a theoretical and methodological framework to examine the properties of

cognitive processes, we found evidence for a co-active architecture and supercapacity in the processing of identity and emotion information, which explains the facilitation effect. As mentioned in the Methods section, supercapacity implies that processing of dual targets in faces requires less resources compared to single targets. This finding is in line with results of previous studies reporting the facilitation effect between personal and emotional expression information in faces (Eidels, Houpt, Altieri, Pei, & Townsend, 2011; Eidels et al., 2015b).

Here we found that the facilitation effect for dual targets was associated with increased functional connectivity between the right orbitofrontal cortex (BA 11/47) and the bilateral inferior occipital cortex (BA 17/18). The lateral part of the OFC (BA 47) and the IOG are functionally (Zald et al., 2014) and anatomically (Martino, Brogna, Robles, Vergani, & Duffau, 2010) interconnected regions and they both are involved in processing of different aspects of faces(Haxby et al., 2001; Hoffman & Haxby, 2000; Ishai, 2008; Ishai, Schmidt, & Boesiger, 2005; Rotshtein, Henson, Treves, Driver, & Dolan, 2005) . For example, the OFC shows differential responses when observers encode facial expressions (Rolls, Critchley, Browning, & Inoue, 2006) or judge facial attractiveness (Ishai, 2008). Recent studies report face-selective (BA11) and domain-general responses to faces (BA 47) in the OFC (Troiani, Dougherty, Michael, & Olson, 2016). The IOG is part of an extended system for face recognition (Haxby et al., 2001; Ishai, 2008; Zhen, Fang, & Liu, 2013) and plays a crucial role in the visual analysis of face images (Haxby et al., 2001).

Our data provide evidence that changes in functional connectivity for dual target faces (compared to either single target) in the OFC showed a strong correlation with capacity measures. The results suggest that the OFC may play a crucial role in integrating complex visual information from faces to facilitate face processing. The changes in functional connectivity as a function of processing demands can be triggered in a bottom-up or a top-down manner (Wu et al., 2015). Sensory integration between the dual information in faces may enhance bottom-up signals to the OFC, increasing activity there along with changing functional connectivity between the IOG and the OFC. Furthermore, the dual signals may modulate the role of the OFC in a top-down manner. For example, electrophysiological and neuroimaging studies provide evidence that the OFC generates predictions about upcoming signals, sending feedback to sensory areas to promote recognition. It was demonstrated that in visual object recognition, top-down feedback from the OFC gates activity in the ventral visual pathway, biasing low level visual processing towards the signals registered in the OFC (Bar, 2003; Bar et al., 2006; Chaumon, Kveraga, Barrett, & Bar, 2014; O'Callaghan, Kveraga, Shine, Adams, & Bar, 2017; Summerfield et al., 2006).

Interestingly, the idea that the OFC may be involved in predictive coding in face processing and an indeterminate facial input increases the top-down connectivity from the OFC to higher visual areas was mentioned ten years ago (Ishai, 2008). Here we suggest that the OFC registers processing demands in faces by changing its functional connectivity with the IOG. In relation to this suggestion, it is important to note that Chaumon and colleagues (Chaumon et al., 2014) argue that only a specific subregion of the

OFC is involved in predicting upcoming signals and plays a crucial role in facilitating the recognition of sensory signals via top-down feedback to visual areas– namely BA47. Our finding that BA47 alters its functional connectivity with early visual areas when dual facial information is present fits with this account.

The results of the functional connectivity analysis showed that the magnitude of the facilitation effect (RT-gain) correlated with changes in connectivity for dual target faces in the r-IOG, but not in the l-IOG. A particular role of the r-IOG in face processing is well established. For example, the earlier proposition that higher-level face areas receive direct input from the r-IOG (Haxby, et al., 2000) has been supported by many recent studies (Nagy, Greenlee, & Kovacs, 2012; Pitcher, Walsh, & Duchaine, 2011; Weiner & Grill-Spector, 2013). Moreover, patient studies suggest that face-sensitive regions in the right hemisphere are critical for normal face discrimination (Rossion et al., 2003). We speculate here that the interplay between the r-OFC and the r-IOG increases the efficiency of perceptual processes for faces containing both personal and emotional expression targets by generating saliency signals that modulate perceptual and motor processes, and thus in turn facilitate the RT-gain. Although this explanation is plausible, we are careful in inferring direct connections between the r-OFC and the r-IOG. There is a possibility that functional connectivity between these areas may be mediated by the fusiform face area which has been shown to have feedback connections to the IOG and direct connections to the OFC (Rossion et al., 2003) .

The data here showed no significant univariate effect for faces containing target identity and target emotion, compared to faces containing

single target information. There are two possible reasons for this result. First, the weak effect in the voxel-based analyses may reflect between-subject variability which is often large in face processing; not only behaviorally but also in the magnitude of activation in medial prefrontal cortex(Doty, Japee, Ingvar, & Ungerleider, 2014). Second, repeated exposure to a stimulus may lead to the attenuation of the functional magnetic resonance imaging signal resulting in decreased regional neural responses, but enhanced interactions between brain regions, which facilitates performance and reduces processing demands on the regions (Ghuman, Bar, Dobbins, & Schnyer, 2008).

Finally, it is important to discuss factors that may affect the facilitation effect between facial identity and emotional expression. A previous study using the same experimental paradigm demonstrated that the facilitation effect was diminished for other race faces (Yankouskaya, Humphreys, et al., 2014). It was suggested that the effect of expertise in processing faces from different races facilitates the pooling of information from the face – for example to form stronger facial configurations for face identification and to facilitate the integration of identity and emotion. In the present study, all participants were born in the UK (15 participants were Caucasian, one participant was born in a mixed-race family (Caucasian-Asian)). Therefore, we cannot account for the effect of different experience with faces here. However, we cannot exclude the possibility that if our sample would consist of different race individuals, we would find diminished changes in functional connectivity between the OFC and the IOG.

Here we used face stimuli that were tested prior to the dual target task to ensure that the basic dimensions were processed with roughly equal

efficiency (Yankouskaya et al., 2012). The discriminability of emotional

expression and identity information of faces was assessed by measuring RTs

for judgements, whether pairs of faces varying in identity and emotional

expression were physically identical or not. Using the tested stimuli set allows

for tight control of experimental variables. However, whether the facilitation

effect will be preserved in faces with different discriminability of personal and

emotional cues is largely unknown. Although our pilot data with 18

participants and untested stimuli sets indicate that the facilitation effect occurs

in 15 participants, a within-subject design is required to make a conclusion.

Conclusion

The facilitation effect for processing identity and emotion in faces is

supported by increased functional connectivity between the right OFC (BA

11/47) and extrastriate cortex (the IOG, BA 17/18). The OFC plays a crucial

role in integrating target identity and emotional cues in faces by registering

processing demands and changing functional connectivity with the IOG.

Directions for further research

The results of the present study raise two important questions. First, it

is still unclear whether the facilitation effect between identity and emotion in

faces in patients is supported by the same neural mechanisms as in healthy

individuals. For example, whether reducing bottom-up input to the OFC due to

lesions in extrastriate cortex results in increased top-down modulation from

the OFC. Second, it would be interesting to know to what extend the

facilitation effects for faces and objects are supported by the same neural

mechanisms. The results of the current study suggest that there are at least

two functional differences. First, previous imaging studies on the RT-gain in

simple objects reported that extrastriate BOLD responses occurred regardless

of the magnitude of RT-gain, but recruitment of premotor and frontal brain

areas was associated with an attenuated RT-gain (Schulte et al., 2006). Here,

PCA connectivity scores in the r-OFC were positively correlated with

processing efficiency, whereas the r-IOG showed a positive correlation with

the magnitude of RT-gain. Second, our data showed that the enhanced

processing of dual signals is supported by changes in functional connectivity

between frontal and visual areas. In contrast, multidimentional information in

object processing showed a regional specificity (e.g., the TPJ). This may

indicate different mechanisms employed by the brain for the integration of the

multidimensional information present in human faces compared to more

simple objects. Further examination of this issue will contribute to the debate

about modularity in face recognition.

References

Altieri, N., & Townsend, J.T. (2011). An Assessment of behavioural dynamic
information processing measures in audiovisual speech perception.
Frontiers in Psychology, 2, 238, doi: 10.3389/fpsyg.2011.00238

Bach, D. R., Schmidt-Daffy, M., & Dolan, R. J. (2014). Facial expression
influences face identity recognition during the attentional blink.
Emotion, 14(6), 1007-1013. doi:10.1037/a0037945

Bar, M. (2003). A cortical mechanism for triggering top-down facilitation in
visual object recognition. *Journal of Cognitive Neuroscience, 15*(4),
600-609. doi:10.1162/089892903321662976

Bar, M., Kassam, K. S., Ghuman, A. S., Boshyan, J., Schmid, A. M., Dale, A.
M., . . . Halgren, E. (2006). Top-down facilitation of visual recognition.
*Proceedings of the National Academy of Sciences of the United States
of America, 103*(2), 449-454. doi:10.1073/pnas.0507062103

Beaty, R. E., Benedek, M., Kaufman, S. B., & Silvia, P. J. (2015). Default and Executive Network Coupling Supports Creative Idea Production. *Scientific Report, 5*, 10964. doi:10.1038/srep10964

Biederman, & Checkosky. (1970). Processing redundant information. *Journal of Experimental Psychology: General, 83*, 486–490.

Bruce, V., & Young, A. (1986). Understanding face recognition. *British journal of Psychology, 77 (Pt 3)*, 305-327.

Chaumon, M., Kveraga, K., Barrett, L. F., & Bar, M. (2014). Visual predictions in the orbitofrontal cortex rely on associative content. *Cerebral Cortex, 24*(11), 2899-2907. doi:10.1093/cercor/bht146

Costello, A. B., & Osborne, J. W. (2005). Best Practices in Exploratory Factor Analysis: Four Recommendations for Getting the Most From Your Analysis. 🗑️🗑️*Practical Assessment, Research & Evaluation, 10*(7).

D'Argembeau, A., & Van der Linden, M. (2011). Influence of facial expression on memory for facial identity: effects of visual features or emotional meaning? *Emotion, 11*(1), 199-202. doi:10.1037/a0022592

de Gelder, B., Frissen, I., Barton, J., & Hadjikhani, N. (2003). A modulatory role for facial expressions in prosopagnosia. *Proceedings of the National Academy of Sciences of the United States of America, 100*(22), 13105-13110. doi:10.1073/pnas.1735530100

Deichmann, R., Gottfried, J. A., Hutton, C., & Turner, R. (2003). Optimized EPI for fMRI studies of the orbitofrontal cortex. *Neuroimage, 19*(2 Pt 1), 430-441.

Doty, T. J., Japee, S., Ingvar, M., & Ungerleider, L. G. (2014). Intersubject variability in fearful face processing: the link between behavior and neural activation. *Cognitive and Affective Behavioural Neuroscience, 14*(4), 1438-1453. doi:10.3758/s13415-014-0290-y

Duchaine, B., & Yovel, G. (2015). A Revised Neural Framework for Face Processing. *The Annual Review of Vision Science, 1*, 393–416. doi:10.1146/annurev-vision-082114-035518

Eidels, A., Houpt, J. W., Altieri, N., Pei, L., & Townsend, J. T. (2011). Nice Guys Finish Fast and Bad Guys Finish Last: Facilitatory vs. Inhibitory Interaction in Parallel Systems. *J Math Psychol, 55*(2), 176-190. doi:10.1016/j.jmp.2010.11.003

Eidels, A., Townsend, J. T., Hughes, H. C., & Perry, L. A. (2015a). Erratum to: Evaluating perceptual integration: uniting response-time and accuracy-based methodologies. *Attention, Perception & Psychophysics, 77*(1), 369. doi:10.3758/s13414-014-0808-y

Eidels, A., Townsend, J. T., Hughes, H. C., & Perry, L. A. (2015b). Evaluating perceptual integration: uniting response-time- and accuracy-based methodologies. *Attention, Perception & Psychophysics, 77*(2), 659-680. doi:10.3758/s13414-014-0788-y

Ekman, P., & O'Sullivan, M. (1988). The role of context in interpreting facial expression: comment on Russell and Fehr (1987). *Journal of Experimental Psychology: General, 117*(1), 86-90.

Fisher, K., Towler, J., & Eimer, M. (2016). Facial identity and facial expression are initially integrated at visual perceptual stages of face processing. *Neuropsychologia, 80*, 115-125. doi:10.1016/j.neuropsychologia.2015.11.011

Fitousi, D. (2016). What's in a "face file"? Feature binding with facial identity, emotion, and gaze direction. *Psychological Research*, 1-18. doi:10.1007/s00426-016-0783-0

Friston, K. J., Holmes, A. P., Price, C. J., Buchel, C., & Worsley, K. J. (1999). Multisubject fMRI studies and conjunction analyses. *Neuroimage, 10*(4), 385-396. doi:10.1006/nimg.1999.0484

Friston, K. J., Holmes, A. P., & Worsley, K. J. (1999). How many subjects constitute a study? *Neuroimage, 10*(1), 1-5. doi:10.1006/nimg.1999.0439

Ganel, T., Goshen-Gottstein, Y., & Ganel, T. (2004). Effects of familiarity on the perceptual integrality of the identity and expression of faces: the parallel-route hypothesis revisited. *Journal of Experimenta Psychology: Human Perception & Performance, 30*(3), 583-597. doi:10.1037/0096-1523.30.3.583

Ghuman, A. S., Bar, M., Dobbins, I. G., & Schnyer, D. M. (2008). The effects of priming on frontal-temporal communication. *Proceedings of the National Academy of Sciences of the United States of America, 105*(24), 8405-8409. doi:10.1073/pnas.0710674105

Hair, J. F. J., Anderson, R. E., Tatham, R. L., & Black, W. C. (1998). *Multivariate Data Analysis*: Upper Saddle River, NJ: Prentice Hall.

Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., & Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science, 293*(5539), 2425-2430. doi:10.1126/science.1063736

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Science, 4*(6), 223-233.

Hoffman, E. A., & Haxby, J. V. (2000). Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nature Neuroscience, 3*(1), 80-84. doi:10.1038/71152

Hugenschmidt, C. E., Hayasaka, S., Peiffer, A. M., & Laurienti, P. J. (2010). Applying capacity analyses to psychophysical evaluation of multisensory interactions. *Information Fusion, 11*(1), 12-20. doi:10.1016/j.inffus.2009.04.004

Hutton, C., Bork, A., Josephs, O., Deichmann, R., Ashburner, J., & Turner, R. (2002). Image distortion correction in fMRI: A quantitative evaluation. *Neuroimage, 16*, 217–240.

Iacoboni, M., & Zaidel, E. (2003). Interhemispheric visuo-motor integration in humans: the effect of redundant targets. *Eur J Neurosci, 17*(9), 1981-1986.

Ishai, A. (2008). Let's face it: it's a cortical network. *Neuroimage, 40*(2), 415-419. doi:10.1016/j.neuroimage.2007.10.040

Ishai, A., Schmidt, C. F., & Boesiger, P. (2005). Face perception is mediated by a distributed cortical network. *Brain Research Bulletin, 67*(1-2), 87-93. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/16140166 doi:10.1016/j.brainresbull.2005.05.027

Jiang, Y. V., Kwon, M. Y., Shim, W. M., & Won, B. Y. (2010). Redundancy effects in the perception and memory of visual objects. *Visual Cognititon, 18*, 1233-1252. doi:http://dx.doi.org/10.1080/13506281003791074

Johnson, M. H., Senju, A., & Tomalski, P. (2015). The two-process theory of face processing: modifications based on two decades of data from infants and adults. *Neuroscience & Biobehavioural Review, 50*, 169-179. doi:10.1016/j.neubiorev.2014.10.009

Levy, Y., & Bentin, S. (2008). Interactive processes in matching identity and expressions of unfamiliar faces: evidence for mutual facilitation effects. *Perception, 37*(6), 915-930.

Li, J., Liu, J., Liang, J., Zhang, H., Zhao, J., Rieth, C. A., . . . Lee, K. (2010). Effective connectivities of cortical regions for top-down face processing: a dynamic causal modeling study. *Brain Research, 1340*, 40-51. doi:10.1016/j.brainres.2010.04.044

Liu, C. H., Chen, W., & Ward, J. (2014). Remembering faces with emotional expressions. *Frontiers in Psycholology, 5*, 1439. doi:10.3389/fpsyg.2014.01439

Martens, U., Leuthold, H., & Schweinberger, S. R. (2010). Parallel processing in face perception. *Journal of Experimental Psychology: Human Perception & Performance, 36*(1), 103-121. doi:10.1037/a0017167

Martino, J., Brogna, C., Robles, S. G., Vergani, F., & Duffau, H. (2010). Anatomic dissection of the inferior fronto-occipital fasciculus revisited in the lights of brain stimulation data. *Cortex, 46*(5), 691-699. doi:10.1016/j.cortex.2009.07.015

Maylor, E. A., & Lavie, N. (1998). The influence of perceptual load on age differences in selective attention. *Psychology of Aging, 13*(4), 563-573.

Miller, J. (1982). Divided attention: evidence for coactivation with redundant signals. *Cognitive Psychology, 14*(2), 247-279. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/7083803

Miniussi, C., Girelli, M., & Marzi, C. A. (1998). Neural site of the redundant target effect electrophysiological evidence. *J Cogn Neurosci, 10*(2), 216-230.

Mooshagian, E., Kaplan, J., Zaidel, E., & Iacoboni, M. (2008). Fast visuomotor processing of redundant targets: the role of the right temporo-parietal junction. *PLoS One, 3*(6), e2348. doi:10.1371/journal.pone.0002348

Mordkoff, J. T., & Miller, J. (1993). Redundancy gains and coactivation with two different targets: the problem of target preferences and the effects of display frequency. *Perception & Psychophysics, 53*(5), 527-535. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/8332422

Mordkoff, J. T., & Yantis, S. (1991). An interactive race model of divided attention. *J Exp Psychol Hum Percept Perform, 17*(2), 520-538. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/1830090

Murray, M. M., Foxe, J. J., Higgins, B. A., Javitt, D. C., & Schroeder, C. E. (2001). Visuo-spatial neural response interactions in early cortical processing during a simple reaction time task: a high-density electrical mapping study. *Neuropsychologia, 39*(8), 828-844.

Nagy, K., Greenlee, M. W., & Kovacs, G. (2012). The lateral occipital cortex in the face perception network: an effective connectivity study. *Frontiers in Psychology, 3*, 141. doi:10.3389/fpsyg.2012.00141

O'Callaghan, C., Kveraga, K., Shine, J. M., Adams, R. B., Jr., & Bar, M. (2017). Predictions penetrate perception: Converging insights from brain, behaviour and disorder. *Consciousness and Cognition, 47*, 63-74. doi:10.1016/j.concog.2016.05.003

Pitcher, D., Walsh, V., & Duchaine, B. (2011). The role of the occipital face area in the cortical face perception network. *Experimental Brain Research, 209*(4), 481-493. doi:10.1007/s00221-011-2579-1

Rolls, E. T. (2008). Face processing in different brain areas, and critical band masking. *Journal of Neuropsychology, 2*(Pt 2), 325-360.

Rolls, E. T., Critchley, H. D., Browning, A. S., & Inoue, K. (2006). Face-selective and auditory neurons in the primate orbitofrontal cortex. *Experimental Brain Research, 170*(1), 74-87. doi:10.1007/s00221-005-0191-y

Roser, M., & Corballis, M. C. (2003). Interhemispheric neural summation in the split brain: effects of stimulus colour and task. *Neuropsychologia, 41*(7), 830-846.

Rossion, B., Caldara, R., Seghier, M., Schuller, A. M., Lazeyras, F., & Mayer, E. (2003). A network of occipito-temporal face-sensitive areas besides the right middle fusiform gyrus is necessary for normal face processing. *Brain, 126*(Pt 11), 2381-2395. doi:10.1093/brain/awg241

Rotshtein, P., Henson, R. N., Treves, A., Driver, J., & Dolan, R. J. (2005). Morphing Marilyn into Maggie dissociates physical and identity face representations in the brain. *Nature Neuroscience, 8*(1), 107-113. doi:10.1038/nn1370

Saron, C. D., Schroeder, C. E., Foxe, J. J., & Vaughan, H. G., Jr. (2001). Visual activation of frontal cortex: segregation from occipital activity. *Brain Research. Cognitive Brain Research, 12*(1), 75-88.

Schulte, T., Chen, S. H., Muller-Oehring, E. M., Adalsteinsson, E., Pfefferbaum, A., & Sullivan, E. V. (2006). fMRI evidence for individual differences in premotor modulation of extrastriatal visual-perceptual processing of redundant targets. *Neuroimage, 30*(3), 973-982. doi:10.1016/j.neuroimage.2005.10.023

Shim, W. M., Jiang, Y. V., & Kanwisher, N. (2013). Redundancy gains in retinotopic cortex. *Journal of Neurophysiology, 110*(9), 2227-2235. doi:10.1152/jn.00175.2013

Silbert, N. H., Townsend, J. T., & Lentz, J. J. (2009). Independence and separability in the perception of complex nonspeech sounds. *Attention, Perception, & Psychophysics, 71*(8), 1900-1915. doi:10.3758/APP.71.8.1900

Soto, F. A., Vucovich, L., Musgrave, R., & Ashby, F. G. (2015). General recognition theory with individual differences: a new method for examining perceptual and decisional interactions with an application to face perception. *Psychonomic Bulletin and Review, 22*(1), 88-111. doi:10.3758/s13423-014-0661-y

Summerfield, C., Greene, M., Wager, T., Egner, T., Hirsch, J., & Mangels, J. (2006). Neocortical connectivity during episodic memory formation. *PLoS Biol, 4*(5), e128. doi:10.1371/journal.pbio.0040128

Swallow, K. M., Braver, T. S., Snyder, A. Z., Speer, N. K., & Zacks, J. M. (2003). Reliability of functional localization using fMRI. *Neuroimage, 20*(3), 1561-1577.

Sweeny, T. D., Haroz, S., & Whitney, D. (2013). Perceiving group behavior: sensitive ensemble coding mechanisms for biological motion of human crowds. *Journal of Experimental Psychology. Human Perception & Performance, 39*(2), 329-337. doi:10.1037/a0028712

Thompson, W. H., & Fransson, P. (2016). On Stabilizing the Variance of Dynamic Functional Brain Connectivity Time Series. *Brain Connectivity, 6*(10), 735-746. doi:10.1089/brain.2016.0454

Tottenham, N., Tanaka, J. W., Leon, A. C., McCarry, T., Nurse, M., Hare, T. A., . . . Nelson, C. (2009). The NimStim set of facial expressions: judgments from untrained research participants. *Psychiatry Research, 168*(3), 242-249. doi:10.1016/j.psychres.2008.05.006

Townsend, J. T., & Eidels, A. (2011). Workload capacity spaces: a unified methodology for response time measures of efficiency as workload is varied. *Psychon Bul & Rev, 18*(4), 659-681. doi:10.3758/s13423-011-0106-9

Townsend, J. T., Fific, M., & Neufeld, R. W. J. (2007). Assessment of mental architecture in clinical/cognitive research. In R. R. B. T. A. Treat, & T. B. Baker (Ed.), *Psychological clinical science: papers in honor of richard m. mcfall* (pp. 223–258). New York: Psychology Press.

Townsend, J. T., & Wenger, M. J. (2004). A theory of interactive parallel processing: new capacity measures and predictions for a response time inequality series. *Psychological Review, 111*(4), 1003-1035. doi:10.1037/0033-295X.111.4.1003

Troiani, V., Dougherty, C. C., Michael, A. M., & Olson, I. R. (2016). Characterization of Face-Selective Patches in Orbitofrontal Cortex. *Frontiers in Human Neuroscience, 10*, 279. doi:10.3389/fnhum.2016.00279

Van den Stock, J., & de Gelder, B. (2012). Emotional information in body and background hampers recognition memory for faces. *Neurobiology of Learning and Memory, 97*(3), 321-325. doi:10.1016/j.nlm.2012.01.007

Weiner, K. S., & Grill-Spector, K. (2013). Neural representations of faces and limbs neighbor in human high-level visual cortex: evidence for a new organization principle. *Psychological Research, 77*(1), 74-97. doi:10.1007/s00426-011-0392-x

Whitfield-Gabrieli, S., Ghosh, S. S., Nieto-Castanon, A., Saygin, Z., Doehrmann, O., Chai, X. J., . . . Gabrieli, J. D. (2016). Brain connectomics predict response to treatment in social anxiety disorder. *Molecular Psychiatry, 21*(5), 680-685. doi:10.1038/mp.2015.109

Whitfield-Gabrieli, S., & Nieto-Castanon, A. (2012). Conn: a functional connectivity toolbox for correlated and anticorrelated brain networks. *Brain Connectivity, 2*(3), 125-141. doi:10.1089/brain.2012.0073

Wu, Q., Chang, C. F., Xi, S., Huang, I. W., Liu, Z., Juan, C. H., . . . Fan, J. (2015). A critical role of temporoparietal junction in the integration of top-down and bottom-up attentional control. *Human Brain Mapping, 36*(11), 4317-4333. doi:10.1002/hbm.22919

Yankouskaya, A., Booth, D. A., & Humphreys, G. (2012). Interactions between facial emotion and identity in face processing: Evidence based on redundancy gains. *Attention, Perception & Psychophysics*. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/22814949 doi:10.3758/s13414-012-0345-5

Yankouskaya, A., Humphreys, G. W., & Rotshtein, P. (2014). Differential interactions between identity and emotional expression in own and other-race faces: effects of familiarity revealed through redundancy

gains. *J Exp Psychol Learn Mem Cogn, 40*(4), 1025-1038. doi:10.1037/a0036259

Yankouskaya, A., Rotshtein, P., & Humphreys, G. W. (2014). Interactions between Identity and Emotional Expression in Face Processing across the Lifespan: Evidence from Redundancy Gains. *J Aging Res, 2014*, 136073. doi:10.1155/2014/136073

Zald, D. H., McHugo, M., Ray, K. L., Glahn, D. C., Eickhoff, S. B., & Laird, A. R. (2014). Meta-analytic connectivity modeling reveals differential functional connectivity of the medial and lateral orbitofrontal cortex. *Cerebral Cortex, 24*(1), 232-248. doi:10.1093/cercor/bhs308

Zhen, Z., Fang, H., & Liu, J. (2013). The hierarchical brain network for face recognition. *PLoS One, 8*(3), e59886. doi:10.1371/journal.pone.0059886