

Self-face enhances processing of immediately preceding invisible faces

Alessia Pannese^{a,b,e,*}, Joy Hirsch^{a,b,c,d}

^a Functional MRI Research Center, Columbia University, Neurological Institute B41, 710 W. 168th Street, New York, NY 10032, United States

^b Department of Neuroscience, Columbia University, New York, NY 10032, United States

^c Department of Radiology, Columbia University, New York, NY 10032, United States

^d Department of Psychology, Columbia University, New York, NY 10032, United States

^e Italian Academy for Advanced Studies in America, Columbia University, 1161 Amsterdam Ave, New York, NY 10027, United States

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ABSTRACT

The self-face is thought to be an especially salient stimulus. Behavioral evidence suggests that self-face processing advantage is associated with enhanced processing of temporally adjacent subliminal stimuli. However, the neural basis of this self-related processing modulation has not been investigated.

We studied self-face induced signal amplification through masked priming and repetition suppression (fMRI adaptation). Subjects performed a gender-categorization task on self- and non-self target faces preceded by subliminal (17 ms) prime faces. The relationship between prime and target was varied between task-incongruent (when prime and target belonged to a different gender) and task-congruent (when prime and target belonged to the same gender) pairs.

We found that, in the presence of the visible self-face (but not of other non-self faces), a bilateral fronto-parietal network exhibited repetition suppression to subliminal prime faces belonging to the same gender (task-congruent) as the target, consistent with the notion that, in the presence of the self-face, subliminal stimuli access high-level processing systems. These results are in agreement with the notion of self-specific top-down amplification of subliminal task-relevant information, and suggest that the self-face, through its high salience, is particularly efficacious in focusing attention.

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1. Introduction

The recognition of one's own face is among the most fundamental and sophisticated cognitive abilities. Self face's special salience has lately become largely agreed upon (Brédart, Delchambre, & Laureys, 2006; Gray, Ambady, Lowenthal, & Deldin, 2004; Lavie, Ro, & Russell, 2003), and may explain why one's own face is identified faster (Tong & Nakayama, 1999), is sensitive to cross-modal facilitation with other self-related stimuli (Platek, Thomson, & Gallup, 2004), and interferes more with ongoing tasks (Brédart et al., 2006) compared to non-self faces. Overall, the available experimental evidence points to a self-specific processing advantage (Brédart et al., 2006; Platek, Thomson, et al., 2004), although the neural bases underlying this advantage remain debated.

Based on the ideas that self-face recognition reflects self-consciousness (Gallup, 1977), and that self-consciousness requires language (Singer, 2001), it was first hypothesized that, like language, self-face recognition would predominantly involve activity in the left-hemisphere. Consistent with this view, Turk et al.

(2002) found self-face recognition to be associated with left-hemisphere activation. However, several lines of evidence have argued in favor of right-hemisphere superiority in self-face recognition. In commissurotomed subjects, Preilowski (1977) found significantly higher skin conductance following presentation of self (but not familiar or unknown) faces to the right hemisphere versus the left hemisphere, while Keenan, Gallup, and Falk (2003) reported faster left-hand (versus right-hand) responses to self- (but not to non-self) faces. Failure to recognize the self-face was reported following intracarotid amobarbital (WADA) anaesthesia of the right hemisphere (but not of the left hemisphere) (Keenan, Nelson, O'Connor, & Pascual-Leone, 2001). In studies involving healthy subjects, Keenan et al. (1999), Keenan, Freund, Hamilton, Ganis, and Pascual-Leone (2000) found self-face recognition to be associated with faster left-hand responses, consistent with right-hemisphere activation. Further evidence for right-hemisphere involvement in self-recognition comes from case studies of mirror self-misidentification in patients suffering from right-hemisphere damage (Breen, Caine, & Coltheart, 2001), as well as from reports of higher error rates in self-identification in schizophrenic patients, when the self face was presented to the left hemisphere (i.e.: right visual field), compared to when it was presented to the right hemisphere (i.e.: left visual field) (Kircher, Seiferth, Plewnia, Baar, & Schwabe, 2007).

* Corresponding author at: Italian Academy for Advanced Studies in America, Columbia University, 1161 Amsterdam Ave, New York, NY 10027, United States.
E-mail address: ap2215@columbia.edu (A. Pannese).

While behavioral and lesion data argue for right-hemisphere superiority in self-processing, imaging studies have yielded contradictory results. Kircher et al. (2001) found greater bilateral (right limbic, left prefrontal and superior temporal) activation during self versus familiar face viewing, while Kelley, Macrae, Wyland, Caglar, and Inati (2002) observed selective activity in medial prefrontal cortex involved in self-referential processing. Conversely, Uddin, Kaplan, Molnar-Szakacs, Zaidel, & Iacoboni (2005) found medial prefrontal areas to be predominantly active during non-self familiar processing. In a positron emission tomography (PET) study, Sugiura et al. (2000) found left fusiform gyrus and putamen, as well as right supramarginal gyrus and hypothalamus to be more active during self versus non-self face viewing. Platek, Keenan, Gallup, and Mohamed (2004) detected stronger BOLD signal in right superior, middle, and inferior frontal gyri during self- versus famous-face processing, while Uddin, Kaplan, et al. (2005) reported evidence for a right-hemisphere network, including inferior frontal and occipital gyri, as well as inferior and superior parietal lobules, activated by recognition of morphed self-faces. In a different study published shortly thereafter, Platek et al. (2006) reported that both right (superior and medial frontal, and inferior parietal), and left (middle temporal) brain regions were differentially activated during self- versus familiar-face viewing, pointing to the existence of a bilateral network for self-face processing. This finding is consistent with another report by Uddin, Rayman, and Zaidel (2005), where both hemispheres of a commissurotomy patient independently and equally possessed the ability to self-recognize (although only the right hemisphere could successfully recognize familiar others). Although Platek's and Uddin's findings seemed to support a modular concept of self-recognition, as a cognitive function separately present in each cerebral hemisphere, several subsequently published fMRI studies (Devue et al., 2007; Sui & Han, 2007) pointed back to right-hemisphere predominance in self-face processing.

In summary, there is little agreement about the spatial characterization of the neural networks involved in self-face recognition, and although compelling behavioral evidence argues for a self-face processing advantage, the neural bases of this phenomenon remain largely unexplored.

The recently discovered self-specific priming effect (Pannese & Hirsch, 2010) provides an opportunity to explore such neural bases. In self-specific priming, subjects' response to their own (but not to others') face is modulated by immediately preceding invisible faces. This behavioral phenomenon is consistent with models of target-related signal amplification (Dehaene & Naccache, 2001), whereby, in the presence of the self face, neighboring stimuli would benefit from increased perceptual resources. This model raises the possibility that invisible stimuli presented immediately prior to the self face may involve semantic processing. However, since response time is the net outcome of multiple processing stages, based on behavioral measures alone it is not possible to establish whether the self-specific signal amplification occurs at low level visual perception (e.g.: in V1), or whether it engages high level processing (e.g.: in fronto-parietal associative areas). Furthermore, it is not known whether this signal amplification involves the ventral (e.g.: fusiform face area) or the dorsal (e.g.: posterior parietal cortex) visual stream. To answer this question, we investigated self-induced signal amplification by exploiting the psychological tool of masked priming and the neurophysiological phenomenon of repetition suppression (fMRI adaptation).

1.1. Masked priming

The term "priming" refers to a change in the speed, bias or accuracy of the processing of a stimulus, following prior exposure to the same or to a related stimulus (Henson & Rugg, 2003). In a priming experiment subjects are exposed, in each trial, to a first stimu-

lus (the 'prime'), then to a second stimulus (the 'target'), while performing a constant task on the target. The relation between prime and target is varied between congruent and incongruent trials, based on whether or not prime and target belong to the same conceptual category relative to the task (e.g.: if the task is gender categorization, in congruent trials prime and target belong to the same gender). Priming is indexed by the difference between the responses to a congruent prime, and to an incongruent prime.

Unlike conventional priming, where both prime and target are clearly visible, in "masked priming", the first stimulus (prime) is flashed for a few tens of milliseconds, and is immediately followed by a second stimulus (mask), which "backwardly masks" the prime, reducing (or abolishing) its conscious visibility (Dehaene et al., 2001). In the present study we employed "target masked priming", a particular version of masked priming in which the target itself acts as a backward mask on the prime. By avoiding intervening stimuli between the prime and the target, this approach is thought to maximize detectability of the often subtle priming effect (e.g.: Grill-Spector, Henson, & Martin, 2006).

1.2. Repetition suppression

Repetition suppression has been described as a general mechanism reflecting neural coding specificity (Naccache & Dehaene, 2001) and able to characterize the functional properties of neural populations at subvoxel resolutions (Grill-Spector & Malach, 2001). Detecting repetition suppression in trials in which prime and target share a given feature (e.g.: gender), is thought to provide evidence for processing of that feature. Furthermore, the spatial distribution of brain areas exhibiting repetition suppression for certain prime-target pairs indicates the level of processing (along the stimulus – response pathway) reached by the prime.

At a neural level, priming is typically associated with a reduced response – repetition suppression (RS) – for primed versus unprimed stimuli (Naccache & Dehaene, 2001). This reduced response is thought to reflect faster (more efficient) processing of the primed stimulus, owing to recent processing of a related stimulus (prime) (Grill-Spector et al., 1999; Wiggs & Martin, 1998). At the cellular level, the processing of the prime is thought to induce synaptic changes in a given stimulus response pathway, which can facilitate subsequent responses when that same pathway is re-used for the primed stimulus. The exact mechanism by which this priming-induced neural plasticity occurs is debated: proposed models include "sharpening" of the stimulus representation, allowing recruitment of fewer neurons (Wiggs & Martin, 1998); increased representation efficiency, whereby neurons become able to perform the same processing through activity of lower intensity (Grill-Spector et al., 1999) or shorter duration (Henson & Rugg, 2003); and fatigue (Grill-Spector et al., 2006). Importantly, not all processes taking place between stimulus and response are facilitated by repetition. Previous studies have reported repetition suppression for faces and other stimuli in inferior temporal and inferior frontal cortices in both humans (Reber, Gitelman, Parrish, & Mesulam, 2005; Sayres & Grill-Spector, 2006; Simons, Koutstaal, Prince, Wagner, & Schacter, 2003; Vuilleumier et al., 2002) and monkeys (Sobotka & Ringo, 1994), whereas RS is generally not observed in early visual areas or late motor regions.

In the present study we applied this logic to probe whether and where the self face modulates the processing of immediately preceding masked primes. Subjects responded to the gender of the visible target face ignoring the preceding prime, which could be either a face of different gender (task-incongruent), or a face of same gender (task-congruent) (Fig. 1b). For each type of target face (self-, very familiar, moderately familiar, less familiar, famous, and unknown), we measured the difference in response time and brain activity (BOLD% signal change) between trials in which the target

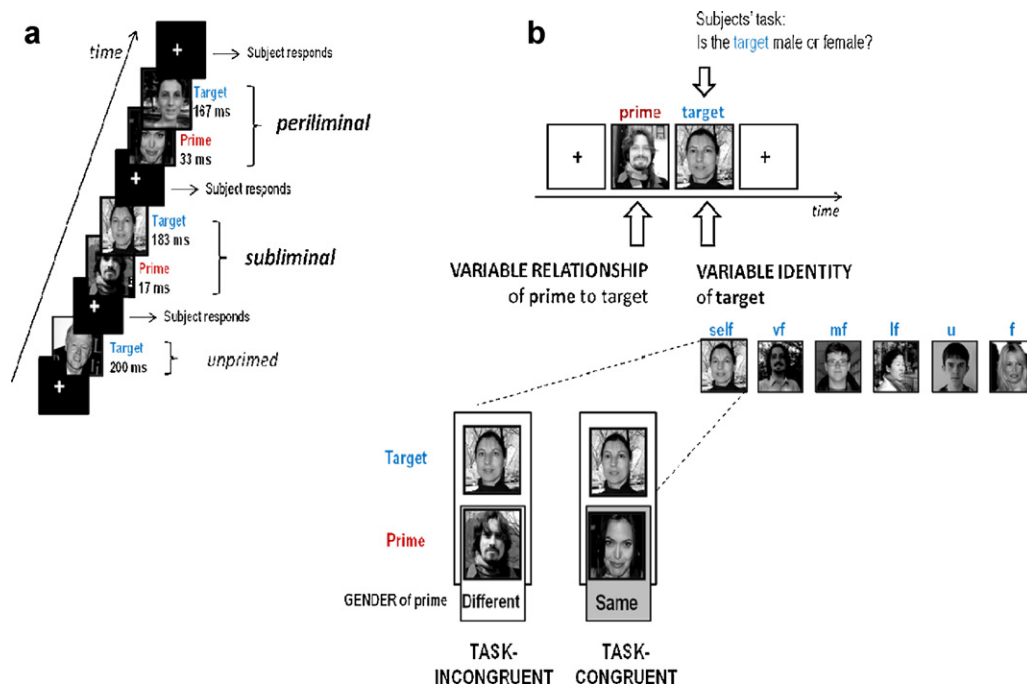


Fig. 1. Experimental design. (a) Each trial consisted of a 200 ms stimulus presentation (200 ms for the unprimed; 17 ms + 183 ms, and 33 ms + 167 ms respectively for the subliminal and periliminal primed conditions), followed by a blank screen with a central crosshair, at jittered intervals spanning from 2.2 to 6.6 s. (b) Subjects responded to the gender of the visible target face, ignoring the preceding prime, which could be either a face of different gender (task-incongruent), or a face of same identity (task-congruent/non-repeated), or a face of same identity (repeated). *Response priming* was measured as the difference in response time and brain activity between trials in which the target was preceded by a prime of different gender (task-incongruent, interfering with task response) and trials in which the target was preceded by a prime of same gender (task-congruent, not interfering with task response) and different identity (non-repeated). Vf = very familiar; mf = moderately familiar; lf = less familiar; f = famous; u = unknown.

was preceded by a prime of different gender (task-incongruent, interfering with task response) and trials in which the visible target was preceded by a prime of same gender (task-congruent, not interfering with task response). In order to capture neural adaptation relative to the repetition of the task-relevant dimension of the face (gender), excluding effects due to intrinsic pre-existing associations, we excluded from the analysis trials in which prime and target faces belonged to the same person.

2. Materials and methods

2.1. Subjects

Twelve healthy volunteers participated in the study (7 males, mean age 30, age range 20–49) after giving written informed consent according to IRB approved procedures. Eleven of them were right-handed, all had normal or corrected vision, all declared not to have had any neurological or psychiatric history. Upon recruitment, each volunteer was asked to bring three individuals from their social entourage who were willing to be photographed by the experimenter: one close friend (or domestic partner), one friend of medium familiarity, and one acquaintance.

2.2. Stimuli

Prior to the experiment, close-up digital photographs were taken of each participant as well as of each of their three friends, with different backgrounds, clothing, lighting conditions and natural (neutral or positive) facial expressions. These photographs served as stimuli for the “self” and for three (very-, moderately-, and less-) familiar conditions. Photographs of famous individuals (actors, singers, politicians, and models) drawn from the internet served as stimuli for the “famous” condition. Anonymous photographs drawn from publicly available face databases served as stimuli for the “unknown” condition. All photographs portrayed the individual the way they normally appear (e.g.: with usual hairdo, spectacles etc.). All images were cropped into a 500 by 500 pixel square and converted into black and white format using Adobe Photoshop (San Jose, CA). Self-face photographs were presented mirror-reversed (i.e.: as they appear in a mirror). Two hundred and eight photographs were selected for each condition, totalling 1248 photographs (208 × 6 conditions, fifty percent males) shown throughout each subject’s session. Throughout the experiment, each photograph was only shown once. In the “self” and in each of the “friend” conditions, the same individuals were shown in 208 different poses. In both “famous” and

“unknown” conditions 208 different individuals were portrayed. Although introducing a difference in stimulus variability, this approach is preferable in that it allows minimising any specific reactions to individual celebrities (in the “famous” condition), and prevents familiarisation with strangers’ faces over the course of the experiment (in the “unknown” condition). In order to ensure proper labelling of the “famous” faces, upon completion of the experiment subjects were asked to identify each of the 208 celebrities in a paper questionnaire. Unrecognised celebrities were subsequently treated as “unknown” in the individual subject’s data analysis.

2.3. Experimental design and task

2.3.1. Main fMRI scan

Self-, familiar-, famous-, and unknown target faces were presented either in isolation (unprimed), or preceded by either periliminal (33 ms) or subliminal (17 ms) primes. Subjects were instructed to identify the gender of the target face as “male” or “female” by pressing one of two buttons on a response pad. The existence of primes was not mentioned to the subjects until after the study was completed. The choice of the gender discrimination task was motivated by its orthogonality to our conditions of interest (i.e.: males and females were represented both in self- and non-self faces, as well as in congruent and incongruent trials), and by its suitability to keep subjects naïve about the main purpose of the study, thereby reducing the likelihood of conscious, top-down modulations of attention. Each trial consisted of a 200 ms stimulus presentation (200 ms for the unprimed; 17 ms + 183 ms, and 33 ms + 167 ms respectively for the subliminal and periliminal primed conditions), followed by a blank screen with a central crosshair, at jittered intervals spanning from 2.2 to 6.6 s (Fig. 1a). Four fifteen-minute runs were carried out, in which a total of 1248 photographs were shown in 672 trials (576 primed, of which 288 subliminal, 288 periliminal, and 96 unprimed). Photographs were presented in a pseudo randomised order, counterbalanced for gender (fifty percent males) and identity. Relative to the target face, primes could portray either an individual of different gender, or of different identity and same gender, or of same identity (i.e.: the same individual as in the immediately following target). In the present report, in order to ensure that any effects were due to response priming, we excluded trials in which the target was preceded by a prime face belonging to the same individual (see Introduction). The spatio-temporal arrangement of the stimuli was symmetrical: each and every face type (i.e.: self-, very-, moderately-, less familiar, famous, and unknown) appeared an equal number of times in combination with each and every other face type, both as target and as prime, but always in different poses (each photograph appeared only once in the entire experiment). The experimental paradigm was developed using Matlab (Mathworks). All visual stimuli were administered to the subjects through fMRI-compatible LCD goggles. All fMRI images

were acquired on a General Electric Signa Twin Speed 1.5 Tesla scanner, using a T2* weighted gradient echo sequence: TE = 40 ms, TR = 2 s, flip angle = 60 degrees, in plane resolution = 64 × 64, voxel size = 3 mm × 3 mm × 4.5 mm, FOV = 190 mm, slice separation = 0 mm.

2.3.2. Face localizer scan

Prior to the main experiment, subjects performed a standard localizer scan during which they viewed sequences of anonymous faces and houses, presented in alternating blocks of 16 s, interleaved with rest periods of equal duration. Each block consisted of 16 stimuli, each presented for 750 ms, followed by a fixation cross for 250 ms. The entire run included 12 blocks (6 face-blocks and 6 house-blocks). The localizer scan provided an independent set of data to be used for the region of interest analysis of the main scan.

2.4. Discriminability test

Although the threshold for visual awareness has often been reported to lie at approximately 30 ms (e.g.: Esteves & Ohman, 1993; Etkin et al., 2004), individual differences exist, and claims of unconscious processing may only be made after careful case-by-case assessment. Since we did not want to alert the subjects to the presence of subliminal primes prior to the experiment, we used the two stimulus durations thought to cover most individuals' threshold for awareness: 33 ms, and 17 ms, and we performed the case-by-case assessment of the individual threshold for visual awareness after the experiment was completed. Primes visibility to the subjects was individually assessed through a forced-choice test. A subset of non-self (familiar-, famous-, and unknown) target faces from the main experiment was presented in combination with 17 ms or 33 ms, self- or non-self primes. The self face never appeared as target, whereas its rate of occurrence as prime was fifty percent. Subjects were instructed to press a key whenever they saw their own face (self). Each subject's performance was measured in terms of discriminability score (d'), representing the standardized difference between the means of the Signal Present (self) and Signal Absent (non self) distributions. This score was calculated according to the formula: $d' = z(H) - z(FA)$, where $z(H)$ and $z(FA)$ represent the transformation of the hit and false alarm rates to z -scores. A discriminability score of "0" corresponds to 50% accuracy. In our study we found that discriminability score for 33 ms primes was significantly higher than 0 ($t_{(11)} = 4.07, p = 0.002$), indicating that 33 ms primes were visible, whereas discriminability scores for 17 ms primes was not significantly higher than 0 ($t_{(11)} = 2.2, p = 0.05$). Consequently, since our intent was to investigate subliminal effects, we restricted our analysis to the 17 ms trials.

The above reported results from the discriminability test warrant a further clarification with regard to prime duration, visibility, and attention. Increasing evidence indicates that, in the absence of attention, even clearly visible stimuli may not be consciously perceived. Behavioral (e.g., Simons & Rensink, 2005), imaging (e.g., Kanwisher, 2001), and neuropsychological (e.g., Driver & Vuilleumier, 2001) evidence suggests that attention may be necessary (although not sufficient) for conscious perception. Under conditions of inattention, even a salient visual stimulus may not be consciously detected, as evident in the phenomena of "inattention blindness", "attentional blink" (Raymond, Shapiro, & Arnell, 1992), and "change blindness" (O'Regan, Rensink, & Clark, 1999). Therefore, a potentially visible stimulus can still fail to be consciously seen when attention is drawn away from it.

This consideration bears relevance to the interpretation of our visibility test results (reported above), based on which we took 17 ms primes to be subliminal. Although the d' -score associated with 17 ms primes was only barely ($p = 0.05$) not significantly different from 0, it is important to realize that the conditions under which participants performed the main task differed from those under which they performed the visibility test. During the main task, subjects were instructed to respond to the visible target, and not to pay attention to the primes. On the contrary, during the forced-choice visibility test they were instructed to focus on the prime. The results of the visibility test are therefore likely to overestimate the visibility of the primes during the main experiment (where primes were neither expected nor attended to by the subjects). For this reason, the 17 ms stimuli, which were below the threshold for awareness during the discriminability test, are likely to have been even less visible during the actual experiment, making it reasonable to treat them as unconscious.

2.5. Calibration

In order to ensure that stimuli were actually displayed for the desired duration, we carried out a calibration on the goggles used during the experiment. A battery-alimented photodiode was placed against the goggle's right field lens. A foam lid was inserted in the goggles around the photodiode's head in order to filter out ambient light. The photodiode was then connected to a circuit, and plugged into an oscilloscope. 500 × 500 pixel white and gray squares were displayed in the goggles (and, simultaneously, in an external monitor) for different durations: 17 ms, 33 ms, 167 ms, 183 ms, and 200 ms, interleaved with a black background. The photodiode excitation occurring when the bright squares were displayed in the goggles was detected and displayed in the monitor of the oscilloscope. 1024 × 768 photographs were taken of the oscilloscope monitor for a sample of trials of each duration using a Sony MpegMovie digital camera DSC-S50. The photographs were subsequently printed at high resolution, and the distance between the onset and the peak of

excitation was manually calculated for each individual sample. This distance corresponds to the duration of the photodiode excitation, and therefore, to the duration of display of the squares. Means and standard deviations were obtained for each duration of display. The results indicate that the measured stimulus duration matched the desired duration as follows: desired 17 ms, measured 17.5 ms (± 2.1); desired 33 ms, measured 32.5 ms (± 2.3); desired 167 ms, measured 164.5 (± 4.2); desired 183 ms, measured 180.2 (± 4.1); desired 200 ms, measured 192 (± 4). A schematic illustration of the calibration procedure is provided in [Supplementary Material](#).

2.6. Data analysis

2.6.1. Behavioral data

Response times and accuracy data were analysed with Microsoft Office Excel and the Statistical Package for the Social Sciences (SPSS 15) software. Error trials and correct trials were analysed separately in order to detect any speed-accuracy trade-off. Mean response times were calculated for each subject and each condition of interest. Planned paired t -tests were performed on these means.

2.6.2. fMRI data

Magnetic Resonance Imaging data were analysed using the Statistical Parametric Mapping (SPM5) software (Wellcome Department of Cognitive Neurology, London, UK). Functional data were slice-time and motion corrected to the median image, high pass-filtered and spatially smoothed. The median functional and anatomical volumes were coregistered and normalized into a standard anatomical space (T1 Montreal Neurological Institute template) in order to allow for cross-subject comparison. Subject-level statistical analyses were performed using the general linear model in SPM5. The conditions in each run were modeled using a canonical hemodynamic response function (HRF). Two separate analyses were carried out: one for the localizer scan, and one for the main scan.

2.6.2.1. Localizer. For the localizer scan we constructed two regressors coding for the hemodynamic response function based on onset and duration of face and house blocks. These regressors were convolved with the HRF and regressed against the BOLD data. In order to define face-responsive clusters, we contrasted activity associated with face blocks with that associated with house blocks within each of our regions of interest (ROIs). The boundaries of these ROIs were anatomically defined using the WFU-PickAtlas function in SPM5. The BOLD% signal change from functionally identified face-related activation clusters within each structurally delimited ROIs was subsequently extracted from the analysis of the main scan using Marsbar (<http://marsbar.sourceforge.net>).

2.6.2.2. Main effect. We constructed a total of 46 regressors. 38 coded for the onset of each condition of interest: 6 regressors coded for each of the unprimed conditions (corresponding to each face type: self, very familiar, moderately familiar, less familiar, famous, and unknown); 32 regressors coded for the primed conditions, 16 for the subliminal (17 ms), and the other 16 for the perliminal. Within subliminal and perliminal conditions, each regressor corresponded to a target (self, very familiar, moderately familiar, less familiar, famous, or unknown) and a prime (different gender or same gender/different identity, or same identity). Note that the identities of famous and unknown faces were never repeated, therefore no same identity regressors existed for them. In addition to the 38 regressors of interest we included in the model 8 regressors of no interest in order to maximize detection of true condition-related signal in our data. These included a response regressor (coding for trial duration and motor activity related to the button press, serving as a control for the overall task-related, but not condition-specific activity, an error regressor (coding for error trials), and the 6 movement parameters computed by SPM during preprocessing (2 for each axis).

Contrast maps were obtained by linearly contrasting different conditions. Group-level analyses were carried out using the random effect model: for each contrast type, the corresponding maps previously obtained from all subjects were entered into a one-sample- T -test. The resulting SPM{T} maps were transformed to unit normal distribution SPM{Z} maps, a threshold of significance was applied and surviving voxels were retained.

In each subject we extracted the mean BOLD% signal change associated with each of the 38 conditions of interest from the previously identified face-responsive clusters within each structurally delimited ROIs. Statistical analyses on the mean% signal change were performed with SPSS software.

3. Results

3.1. Behavioral results

Compared to task-congruent primes, task-incongruent primes displayed for 17 ms (subliminal) induced significantly slower responses in the gender-categorization of the immediately following visible target, in trials whose visible target was the self-face ($t_{(11)} = -4.27, p = 0.001$, two-tailed), and not in trials in which the

Table 1
Neural activity in subliminal trials. Mean ($n=12$) BOLD percent signal change (arbitrary units) extracted from each region of interest (ROI) during trials in which self- and non-self visible target faces were preceded by subliminal (17 ms) primes of same (task-congruent) or different (task-incongruent) gender. Task-congruent primes are associated with significant repetition suppression in bilateral fronto-parietal regions exclusively in trials in which they were immediately followed by a visible self-face target. Con. = Task-congruent; Inc. = Task-incongruent; VF = very familiar; MF = moderately familiar; LF = less familiar; F = famous; U = unknown.

ROI	MNI coordinates				Prime (17 ms)	Target											
	x	y	z	Side		Self		VF		MF		LF		F		U	
						Inc.	Con.	Inc.	Con.	Inc.	Con.	Inc.	Con.	Inc.	Con.	Inc.	Con.
V1	16	-84	-6		0.24	0.19	0.19	0.18	0.22	0.27	0.2	0.19	0.17	0.2	0.16	0.2	
FFA	-38	-40	-22	L	0	0.01	-0.05	0.02	-0.01	0.01	-0.02	-0.04	-0.02	-0.01	-0.05	-0.04	
	46	-58	-22	R	0.16	0.1	0.05	0.06	0.06	0.13	0.06	0.04	0.06	0.12	0.04	0.09	
Posterior Parietal	-48	-72	36	L	-0.05	-0.15**	-0.18	-0.11	-0.1	-0.01	-0.11	-0.14	-0.16	-0.16	-0.19	-0.22	
	52	-64	32	R	-0.09	-0.19**	-0.13	-0.09	-0.15	-0.03	-0.16	-0.13	-0.22	-0.17	-0.2	-0.2	
Middle Frontal	-46	18	48	L	-0.08	-0.25**	-0.16	-0.19	-0.13	-0.07	-0.17	-0.14	-0.26	-0.23	-0.22	-0.17	
	40	16	42	R	-0.06	-0.16**	-0.13	-0.09	-0.07	-0.03	-0.14	-0.12	-0.2	-0.17	-0.16	-0.15	
M1	-36	-20	54	L	0.09	0.07	0.1	0.05	0.06	0.14	0.08	0.05	0.06	0.05	0.08	0.08	
	40	-16	52	R	-0.05	-0.04	-0.04	-0.06	0.01	-0.04	-0.05	-0.06	-0.06	-0.06	-0.05	0.06	

** $p < .02$.

visible target was any of the non-self faces. These behavioral results show that the self-specific priming described in Pannese and Hirsch (2010), observed by comparing task-incongruent prime faces with task-congruent prime faces, regardless of whether they have different identity (i.e.: same gender, but different person), or same identity (i.e.: same person) as the target face, holds true also if we eliminate from the analysis those trials in which the task-congruent prime faces have the same identity (i.e.: same person as the target) as the visible target face. This allows qualifying this effect as self-specific response priming.

3.2. Imaging results

3.2.1. Region of interest (ROI) analysis

In order to address the question of which visual stream is involved in self-specific priming, we measured the mean BOLD% signal change in face-responsive clusters within the main nodes of the ventral and dorsal visual streams: (1) Fusiform gyrus (FFA, in the ventral stream); and (2) Posterior parietal cortex (PP) (Brodmann areas 39 and 40, in the dorsal stream). Additionally, in order to test the involvement of early-visual and late-motor processing, we examined the primary visual (V1, Brodmann area 17), and motor (M1, Brodmann area 4) cortices. Importantly, all these regions of interest were obtained from the contrast [Face > House] in a separate fMRI localizer scan. This approach ensured complete independence between the two steps of the analysis (ROI definition, and signal extraction), as each involved distinct data.

Mean BOLD percent signal change was extracted from each subject's scan for each ROI and for each conditions of interest, and was then entered in a series of planned pairwise t-tests comparing congruent versus incongruent conditions across self- and (each of the) non-self targets. Mean BOLD values for each region of interest and each condition are reported (along with BOLD values from middle frontal clusters obtained through whole-brain analysis) in Table 1.

The results show that significant repetition suppression for task-congruent (compared to task-incongruent) subliminal primes occurred exclusively in trials in which primes were presented in combination with visible self-face targets, and that this effect involved bilateral posterior parietal cortex (left: $t_{(11)} = 2.79$, $p = 0.009$; right: $t_{(11)} = 2.79$, $p = 0.008$, one-tailed) (Table 1). BOLD results from the FFA (ventral stream) and posterior parietal region (dorsal stream) are also illustrated more synthetically (representing the five non-self trial types, for which individual data are reported in Table 1, in a single "other" category) in Fig. 2. The self-specific repetition suppression found in the posterior parietal

regions, but not in the FFA, is consistent with dorsal stream engagement in self-specific priming.

3.2.2. Whole-brain analysis

In order to test whether, in addition to our regions of interest (ROI), other brain areas were sensitive to subliminal or perili-minal primes, we supplemented the ROI-analysis with a whole-brain analysis. We interrogated brain images for areas exhibiting repetition suppression to congruent primes presented in combination with self- or non-self targets. Group-level statistical maps were thresholded at $p = 0.001$, uncorrected.

The results from the whole-brain analysis were compatible with those of the region of interest (ROI) analysis. The contrast [task-incongruent > task-congruent] on trials in which subliminal primes were presented in combination with visible self-face targets yielded three clusters (Fig. 3): one was located in the right posterior parietal cortex/temporo-parietal junction, largely overlapping with the posterior parietal cluster obtained in the localizer scan and reported in the ROI analysis. Two additional clusters were located in left and right prefrontal cortex, a region that had not been included in our ROI analysis because beyond its scope (testing repetition effects along visual pathways). Overall, results from the whole brain analysis show that 17 ms primes immediately followed by visible self targets engage a bilateral fronto-parietal network.

Performing the same contrast [task-incongruent > task-congruent] on trials in which subliminal primes were presented in combination with visible non-self targets yielded (with the exception of a small cluster in the premotor cortex for very-familiar targets) no suprathreshold voxels.

4. Discussion

We found that subliminal congruent primes immediately followed by a visible self-face (but not by non-self faces) were associated with repetition suppression in bilateral fronto-parietal regions. These results address important topics related to hemispheric laterality in self-face processing, the role of the dorsal visual stream in self-specific priming, and the ability of self-faces to modulate attention.

4.1. Self-face processing and the issue of hemispheric laterality

Although some evidence for bilateral hemispheric involvement in self-recognition has been reported (e.g.: Platak et al., 2006; Uddin, Rayman, et al., 2005), numerous other studies (e.g.: Breen

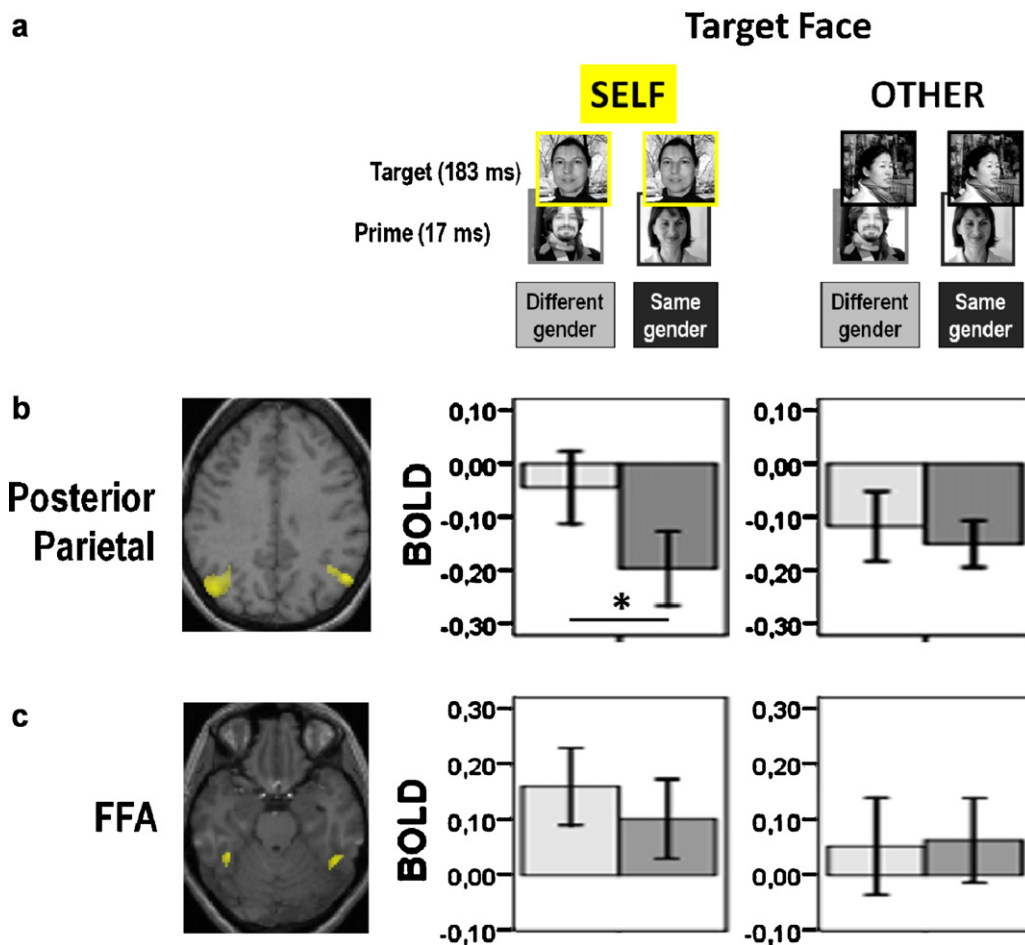


Fig. 2. Self-specific repetition suppression in the dorsal stream. (a) Subjects responded to the gender of the visible target face, which could be their own (self) or someone else's (other). Target faces were preceded by subliminal (17 ms) prime faces, which could depict either an individual of the same gender as the following target face, or of a different gender. (b and c) Blood oxygen level dependent (BOLD) percent signal change (in arbitrary units) extracted from independently identified clusters within the posterior parietal cortex (b) and the fusiform face area (FFA) (c). The posterior parietal cortex exhibits repetition suppression for congruent (same gender, dark bars), compared to incongruent (different gender, light bars) subliminal primes only when the visible target is the self-face. No effect was detected within the fusiform face area. Error bars represent the standard error of the mean. Statistical values are reported in the text. BOLD values for "other" trials correspond to the values we found for "very familiar" faces, and are meant to synthetically represent all five non-self trial types employed in the experiment, whose individual values are reported in Table 1, and none of which showed any effect.

et al., 2001; Keenan et al., 1999, 2000, 2001, 2003; Kircher et al., 2007; Preilowski, 1977) have argued for a predominantly right-lateralized neural engagement in response to self-face processing. In the imaging literature, despite bilateral hemispheric activation associated with self-face processing has been observed, evidence for a consistent self-specific pattern of neural activity has been sparse.

An important consideration that may account for the discrepancies found in the literature about self-face processing is that most fMRI studies have reported self-related brain activity in terms of statistical "contrasts", where, in order to eliminate unspecific activation, a statistical subtraction is implemented between the "self-" and the "non-self" conditions. Reporting self-related activity in terms of self/non-self contrast introduces a possible source of non-self-related variability in the results, meaning that different patterns of brain activity reported by different studies as being "self-related" may reflect the different "non-self" controls employed. For example, some investigators contrasted the self-face with familiar faces (Platek et al., 2006; Sugiura et al., 2005), others with unknown faces (Kircher et al., 2001; Sugiura et al., 2000), others with famous ones (Platek, Keenan, et al., 2004; Platek, Thomson, et al., 2004). The type of "non-self" face employed as control may profoundly affect contrast-based imaging results in consideration

of the fact that the issue of hemispheric laterality seems to apply to the processing of non-self faces as well (compare, for example, Barbeau et al., 2008; Bourne & Hole, 2006; Elfgren et al., 2006; Megreya & Burton, 2006).

Based on these considerations, in the present study self-related activity was not obtained through a self/non-self subtraction, but rather through direct measurement of "self-" or "non-self" conditions, as each contained both terms of the contrast of interest (i.e.: congruent versus incongruent). Therefore, the bilateral frontoparietal engagement we found in association with self-face trials is likely to reflect self-specificity, in line with the previously discussed reports by Uddin et al. (2005b) and Platek et al. (2006).

4.2. The fronto-parietal network and conscious perception

Neural activity in fronto-parietal association cortices has often been associated with phenomenal consciousness (Beck, Rees, Frith, & Lavie, 2001; Gross et al., 2004; Koivisto & Revonsuo, 2003), and has been proposed as the neuronal mechanism of access to conscious perception (Dehaene & Naccache, 2001; Dehaene, Kerszberg, & Changeux, 1998; Desimone & Duncan, 1995; Miller & Cohen, 2001; Posner, 1994; Rees, Kreiman, & Koch, 2002).

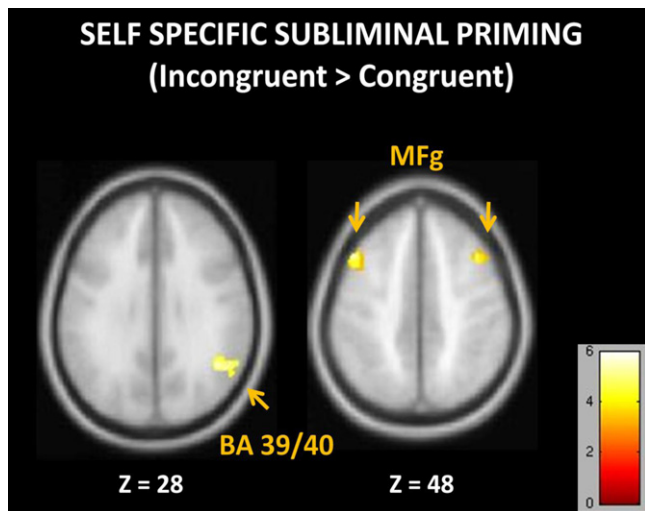


Fig. 3. Results from whole-brain analysis. Subliminal primes immediately followed by visible self-face targets engage a fronto-parietal network. The contrast [task-incongruent > task-congruent] on trials in which subliminal (17 ms) primes were presented in combination with visible self-face targets yielded three clusters exhibiting repetition suppression. The cluster in the right posterior parietal cortex/temporo-parietal junction (Brodmann areas 39/40) largely overlaps with the posterior parietal cluster obtained in the localizer scan and reported in the ROI analysis. Two additional clusters were located in left and right prefrontal cortex (Middle Frontal gyri). Clusters are displayed at a threshold of $p = 0.001$, uncorrected. MNI coordinates and BOLD% signal change are reported in Table 1. MFg = Middle Frontal gyrus. Colored bar indicates T-value.

An alternative account holds that fronto-parietal activation might be attributed to the additional cognitive processes afforded by conscious access rather than to conscious perception per se. According to this view, conscious perception is associated with a narrower set of brain regions, possibly limited to those at the sensory encoding level of processing. In Zeki's "microconsciousness" (2003) or Lamme's "recurrent loop" (2003) accounts, early and focal stimulus-specific activation is sufficient to generate conscious perception. However, although low-level correlates of conscious visual perception have been reported in several studies (Bar et al., 2001; Grill-Spector, Kushnir, Hendler, & Malach, 2000; Koivisto & Revonsuo, 2003; Moutoussis & Zeki, 2002; Ress & Heeger, 2003), in most cases they were accompanied by distributed parieto-frontal activity, making it difficult to evaluate their specific contribution to phenomenal perception. At all events, whether expressing conscious perception per se, or additional cognitive processes afforded by it, activity in fronto-parietal networks remains largely regarded as a neural correlate of perceptual awareness.

In our design, the prime was masked by the target itself (target masked priming), an approach thought to maximize detectability of (generally subtle) subliminal priming effects. The immediate temporal proximity between prime and target leaves open the possibility of target related modulation of prime processing. This notion is consistent with the repetition suppression we detected in self-trials, under conditions that did not yield any repetition suppression in non-self trials, indicating that masking may be modulated by the nature (self versus non-self) of the target. A possible interpretation of our finding is that whereas non-self targets interrupted the propagation of prime-related visual activity into anterior cortical areas, self targets did not, allowing for response-priming (in the form of neural repetition suppression) to occur in fronto-parietal association regions. Although it is impossible to ascertain whether subjects were differentially aware of "17 ms primes followed by self targets" as opposed to "17 ms primes followed by non-self targets", based on our finding it is conceivable that primes followed by self targets benefited from

enhanced processing compared to primes followed by non-self targets, as suggested by the self-specific repetition suppression in the fronto-parietal network. This enhanced processing could result from globally increased perceptual resources in the presence of the target self face.

Target-related signal amplification of unconscious primes has been described in the context of the global neuronal workspace (GNW) theory (Dehaene & Naccache, 2001), proposing that conscious stimuli induce a reorganization of the GNW, which in turn affects the processing of unconscious information. Based on this account, it is conceivable that, in self-trials, our subliminal (and otherwise unprocessed) primes became more visible thanks to their becoming beneficiaries of extra processing resources afforded by the presence of the temporally adjacent visible self face.

4.3. Alternative accounts for prefrontal activity

The left and right prefrontal areas exhibiting self-specific repetition suppression for subliminal primes of same gender partially overlap with the frontal eye field (FEF, Brodmann area 8), a region known to be involved in saccadic eye and attention movements (Schall, 2004). In spite of its anterior localization, the FEF is increasingly thought of as an early visual processing area, connected to visual cortex (Schmolecky et al., 1998) and responsive to subliminal visual stimuli (Thompson & Schall, 1999). Based on these notions, it is conceivable that the repetition suppression we found in prefrontal areas in association with subliminal primes may (at least partially) originate at early processing stages. However the concurrent activation of posterior parietal regions, known to send abundant projections to prefrontal association cortex, suggests that at least part of the effect found in the prefrontal clusters is likely to involve high-level processing.

Prefrontal brain regions have also been shown to play an important role in the development and maintenance of autoegetic awareness, the ability to bind together the awareness of oneself as a continuous entity through time (Tulving, 1985; Wheeler, Stuss, & Tulving, 1997). From a phylogenetical perspective, frontal lobes are more developed in species exhibiting self-recognition (Semendeferi, Damasio, & Frank, 1997). Similarly, the rapid frontal lobe growth in children occurs synchronously with the acquisition of self-recognition (between the ages of one and three) (Amsterdam, 1972; Lewis, Sullivan, Stanger, & Weiss, 1989). Further support for frontal lobe involvement in self awareness comes from empirical reports describing disruption of self-mentaling ability following frontal lobe damage (Luria, 1969; Weinberger, 1993). Our finding of prefrontal engagement only in self-face trials (in which subjects responded to their own face) fits well with existing knowledge about frontal lobe function, and contributes further evidence for frontal lobe involvement in the processing of self-related information.

4.4. Self-specific priming and the posterior parietal cortex

The parietal cortex has long been thought to play an important role in spatial attention. Electrophysiological studies have shown that, in non-human primates, the lateral intraparietal area (LIP) is implicated not only in attention-based guidance of the oculomotor system (Gottlieb, Kusunoki, & Goldberg, 1998), but also in the generation of a salience map for attentional modulation in the ventral visual stream (Goldberg, Bisley, Powell, & Gottlieb, 2006). Further support for the implication of parietal areas in attention modulation comes from clinical observations in humans, where damage to posterior parietal cortex has been associated with a variety of cognitive deficits implicating visuo-spatial impairment (Damasio & Benton, 1979; Kolb & Whishaw, 2003 for review). Therefore, our finding of self-specific subliminal response priming

effect (repetition suppression for trials in which the self face was preceded by a subliminal prime of same gender, compared to trials in which it was preceded by a prime of different gender) fits well in the light of existing knowledge about attention-related parietal function.

A further consideration is that the observed signal change in the posterior parietal cortex in response to self-related congruent trials was below baseline. This strong repetition-related self-specific deactivation bears relevance to current debates about other functions involving parietal engagement, such as self-specific processing, and the resting state.

Activity within the right lateral parietal cortex has been reported in association with a variety of self-related conditions, including visual self-face recognition (Kircher et al., 2001), self-description (Kircher et al., 2002), autobiographical memory (Maguire & Mummery, 1999), Theory of Mind (Vogeley et al., 2001), asomatognosia (Feinberg, 2001), and violation of the sense of agency in both healthy (Ruby & Decety, 2001) and schizophrenic individuals (Spence et al., 1997). This implication of posterior parietal cortex in the representation of both physical and mental aspects of the “self” has been taken to suggest a parietal role in self-representation “in general” (Lou et al., 2004, p. 6831). Interestingly, the posterior parietal regions reported in self-related processing closely overlap with the lateral parietal nodes of the so-called “default network”, implicated in brain’s resting state (Raichle, MacLeod, Snyder, Powers, & Shulman, 2001). Although the functions of this network are still unclear, it has been hypothesized that these may include keeping the brain in a responsive state (Raichle et al., 2001), reviewing past experience, planning future behavior, and supporting self-consciousness (Cavanna & Trimble, 2006). Based on the overlap between the regions (including posterior parietal cortex) found in the self-related literature and those found during resting state, Ruby and Legrand (2008) suggested an interesting model whereby these regions are not “self-specific”, but rather respond more in self- than in non-self conditions by virtue of the greater salience and pathways to memory that stimuli related to the subject’s own person afford.

Our finding of a self-specific deactivation in congruent trials provides evidence for self-specific processing in the parietal cortex, and suggests that the specific self-responsive clusters we found are not involved in the default state (if this were the case, we would expect them to show decreased activity during incongruent – i.e.: harder – trials). The combination between our results and the well documented involvement of parietal regions in the default state, suggests an integrated model, whereby the posterior parietal cortex contributes to both resting state and self-processing.

4.5. Self-specific priming and attention

Several previous studies (e.g.: Bennett, Lleras, Oriet, & Enns, 2007; Henson, Mouchlianitis, Matthews, & Kouider, 2008; Kouider, Eger, Dolan, & Henson, 2009) have reported masked congruency effects with faces. Importantly, in all these studies, the face stimuli employed were non-self, and were temporally attended, a condition often regarded as necessary for masked priming to occur (Naccache, Blandin, & Dehaene, 2002). In the present study, attention could not be reliably focused on the prime, as the jittered inter-trial-interval made it difficult for the subjects to predict at which moment the prime-target sequence would appear. Under these conditions, based on the previous literature one would expect not to observe any masked priming effects. Consistent with this prediction, we did not find any priming effect for non-self faces. However, contrary to this prediction, we did find priming effect and repetition suppression when the target was a self-face. This self-specific result identifies a previously unreported property of

self-face processing, and is consistent with the notion that self-faces are uniquely efficacious in focusing temporal attention.

5. Conclusions

In summary, we found that subliminal face primes immediately followed by a visible self-face engaged fronto-parietal regions, consistent with dorsal stream involvement in self-specific priming, and suggestive that, despite their being masked and unreportable, invisible primes accessed high-level associative areas. Crucially, this fronto-parietal responsiveness to subliminal primes was exclusively observed in the presence of visible self-faces. This finding fits well with theories of top-down signal amplification, and indicates that the self-face, through its special salience, is particularly efficient in focusing attention and enhancing processing of temporally adjacent stimuli.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuropsychologia.2010.12.019.

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