

Category expectations: A differential modulation of the N170 potential for faces and words

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ABSTRACT

The goal of the present study was to explore whether endogenous attention can be oriented to different perceptual categories and to examine how these expectations modulate visual stimulus processing. We designed a cueing paradigm that prepared participants, on a trial-by-trial basis, for the most likely stimulus category of the target, which could be either a face or a word. Participants were asked to discriminate the gender of the stimuli, regardless of their category. We measured participants' brain activity by means of a high-density electroencephalographic recording system to investigate the neural correlates of orienting attention to faces and words. As expected, we observed a behavioural facilitation for valid compared to invalid trials. In addition, target expectations influenced stimulus processing at several points in time. Most importantly, attention modulated the lateralized N170 component in a category-specific fashion. These results show that, at least under certain circumstances, orienting endogenous attention to different categories can influence the perceptual stages of face and word visual processing.

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1. Introduction

Voluntary attention has been mainly investigated in the context of spatial locations (e.g. Posner, 1980), simple perceptual features (e.g. Anllo-Vento & Hillyard, 1996) and objects (e.g. Duncan, 1984). This body of research has repeatedly shown that attended attributes are processed more efficiently than unattended ones. However, attention can also be directed to more complex or abstract features (see Scholl, 2001) such as specific motor responses (Rushworth, Johansen-Berg, Göbel, & Devlin, 2003), instants of time (Correa, Sanabria, Spence, Tudela, & Lupiáñez, 2006; Nobre, 2001), representations held in memory (Lepsien & Nobre, 2007) or different aspects of linguistic processing (Cristescu & Nobre, 2008; Ruz & Nobre, 2008a, 2008b). However, the effects of expectations of different stimulus categories have been scarcely studied (Esterman & Yantis, 2009; Puri & Wojciulik, 2008; Puri, Wojciulik, & Ranganath, 2009), and none of the published investigations have approached this subject by means of event-related potential recordings (ERPs). Therefore, the goal of the present study was to explore the electrophysiological correlates of category expectations to investigate whether they are able to influence initial stages of visual stimulus processing.

Converging evidence in neuroscience has revealed that our brain sustains a high degree of specialization. There are regions that respond specifically to the visual presentation of different categories such as human faces (Allison, McCarthy, Nobre, Puce, & Belger, 1994; Kanwisher, McDermott, & Chun, 1997), words (Cohen et al., 2000; Nobre, Allison, & McCarthy, 1994), body parts (Downing, Jiang, Shuman, & Kanwisher, 2001), buildings (Aguirre, Zarahn, & D'Esposito, 1998), tools (Chao, Haxby, & Martin, 1999) or animals (Chao, Martin, & Haxby, 1999). Among them, faces and words are the perceptual categories that have boosted more interest. These stimuli are identified faster and more accurately than other types of objects, which suggests that humans process them in a highly efficient manner (e.g. McCandliss, Cohen, & Dehaene, 2003; Rayner & Pollatsek, 1989; Yin, 1969). On the one hand, face processing is severely disrupted by stimuli inversion, which has been taken as evidence of holistic analysis of up-right faces (e.g. Hochberg & Galper, 1967). On the other hand, several authors have suggested that letters are grouped together, resulting in individual units that are perceived as a whole (Riesenhuber & Poggio, 1999; Warrington & Shallice, 1980). As a result, it has been proposed that the efficient processing of faces and words reflects configurational perceptual analysis.

Regarding the particular neural substrates of face and word processing, fMRI studies have shown that the visual presentation of faces evokes activation in the lateral fusiform gyri, which is generally greater on the right hemisphere (Kanwisher et al., 1997; McCarthy, Puce, Gore, & Allison, 1997), while words recruit a specific area of the left fusiform gyrus (Cohen et al., 2000; Dehaene,

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Le Clec'h, Poline, Le Bihan, & Cohen, 2002; Polk & Farah, 2002; for a review, see McCandliss et al., 2003; although see Price & Devlin, 2003). These regions have been labelled as the face fusiform area (FFA) and the visual word form area (VWFA), respectively. Neuropsychological cases support these claims by showing deficits in face processing after right occipito-temporal damage (prosopagnosia; e.g. Damasio, Damasio, & Van Hoesen, 1982; Farah, 1995; although see Gauthier, Behrmann, & Tarr, 2004) and deficits in word processing after left occipital damage (pure alexia; Binder & Mohr, 1992; Warrington & Shallice, 1980).

Crucially, electroencephalographic studies have also identified specific potentials that reflect the distinct processing of face and word stimuli. Faces evoke a negative event-related peak over occipito-temporal regions, named N170, which shows a bilateral pattern, although it is more pronounced in the right hemisphere (e.g. Bentin, Allison, Puce, Perez, & McCarthy, 1996; Eimer, 2000; Lueschow et al., 2004; Watanabe, Kakigi, Koyama, & Kirino, 1999). On the other hand, words evoke an analogous negative potential, which is also observed over occipito-temporal regions and presents a strongly left-lateralized pattern (e.g. Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999; Maurer, Brandeis, & McCandliss, 2005; Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999). It is important to note that source localization analyses and correlation studies support the view that the face and word N170 originate mainly from right and left inferior occipito-temporal regions, respectively (e.g. Brem et al., 2005; Henson et al., 2003; Herrmann, Ehlis, Muehlberger, & Fallgatter, 2005; Itier, Herdman, George, Cheyne, & Taylor, 2006), which is in agreement with previously mentioned fMRI findings. Taking these findings together, the N170 seems to be a satisfactory index of categorical stimulus processing (although see Dering, Martin, & Thierry, 2009; Thierry, Martin, Downing, & Pegna, 2007).

The attentional modulation of the N170 potential has evoked notable controversy. Numerous studies have reported that orienting attention to faces or words does not exert an influence on the N170 amplitude (e.g. Carmel & Bentin, 2002; Cauquil, Edmonds, & Taylor, 2000; Lueschow et al., 2004; Thierry et al., 2007; see also Nobre, Allison, & McCarthy, 1998), which has led some authors to claim that the initial stages of categorical processing are *cognitively impenetrable* (Cauquil et al., 2000; see Fodor, 1983 to understand “cognitive impenetrability” from a Fodorian perspective). However, recent findings indicate that face and word N170 potentials can be modulated by top-down factors, at least under certain circumstances.

Working memory (WM) demands seem to play a critical role in observing amplitude modulations on the face N170. Several studies have reported such modulations as a result of the particular requirements related to different phases of a WM task: increased N170 amplitudes during face encoding and reduced N170 amplitudes during retrieval, in response to face distractors or target stimuli (e.g. Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005; Morgan, Klein, Boehm, Shapiro, & Linden, 2008; Sreenivasan & Jha, 2007). These opposite patterns emphasized the role of attention during encoding, which optimizes target processing, and during retrieval, which preserves the maintenance of face representations by restraining current stimulus processing. In contrast, classic attentional manipulations have rarely induced a modulation on the face N170 amplitude (e.g. Carmel & Bentin, 2002; Cauquil et al., 2000). As an exception, we can cite three studies: two of spatial visual attention and a recently published study of selective attention (Crist, Wu, Karp, & Woldorff, 2008; Holmes, Vuilleumier, & Eimer, 2003; Sreenivasan, Goldstein, Lustig, Rivas, & Jha, 2009). These studies reported attentional N170 modulations to attended in contrast to unattended faces, while using complex visual arrays within a spatial paradigm (Crist et al., 2008; Holmes et al., 2003) or under deprived perceptual conditions (Sreenivasan et al., 2009).

Overall, these data show that the face N170 is susceptible to attentional modulation in certain circumstances, although most of the time faces appear to be processed in a highly automatic fashion (e.g. Lavie, Ro, & Russell, 2003; Liu, Harris, & Kanwisher, 2002).

In contrast to the high number of publications related to the face N170, the attentional modulation of the word N170 has been scarcely explored. However, a recent study that manipulated task instructions reported an attentional modulation of the word N170 potential (Ruz & Nobre, 2008a). In this study, focusing attention on the orthographic nature of the letters within words as compared to their phonology or semantics enhanced the amplitude of the N170. This outcome was at odds with previous results that failed to find an attentional influence on early visual stages of word processing (e.g. Nobre et al., 1998).

The main goal of the present study was to explore whether expectations about different perceptual categories, i.e. faces and words, optimize the visual processing of an upcoming stimulus belonging to one of these categories. In addition, we investigated whether these expectations modulate early stages of processing by focusing specifically on the N170, which is thought to reflect categorical perceptual analysis of the stimuli.

We used an attentional cueing paradigm to create expectations about the most likely category of the target stimulus, which could be either a face or a word. Our hypotheses were the following. First, we expected that attention to a perceptual category would enhance the processing of the exemplars belonging to it and as a consequence, participants' responses would be faster for valid than for invalid trials. In addition, we predicted that expectations would modulate the category-related N170 potentials to faces and words. In order to assess these two hypotheses, we recorded high-density electrophysiological recordings (EEG) while participants performed a gender evaluation task on cued face and word target stimuli.

2. Methods

2.1. Participants

Twenty-four right-handed students (14 females, mean age: 24, age range: 18–46) from the University of Granada participated in the study in exchange for course credits. All participants reported normal or corrected to normal vision and had no history of neurological disorders. They all signed a consent form approved by the Ethics Committee of the University of Granada.

2.2. Experimental task

Participants were asked to discriminate the gender of visually presented faces or words as fast and accurately as possible. To help them perform this task, a symbolic cue that predicted the most likely category of the upcoming stimulus was presented prior to target onset. Cues were valid in 75% of the trials and were invalid in the remaining 25%. Note that the gender discrimination task was independent of the dimension signalled by the cue (Target category), which avoided confounding factors related to the preparation of specific motor responses.

We used 80 first-names, displayed in black, and 80 human faces, displayed in black and white, as targets. Half of the names and faces were female and the other half were male. The words had 3–7 letters (5.48 in average, matched across genders) and were collected from a Spanish word database. The faces were obtained from the Max-Planck-Institute for Biological Cybernetics database (Tuebingen, Germany). All of them had the hair removed and were equated in terms of size and luminance. The cue was a star coloured in blue or red. Each colour was associated with one stimulus category in a counterbalanced manner across participants. All stimuli were presented centrally in a 17 in. monitor controlled by Biological E-prime software (Schneider, Eschman, & Zuccolotto, 2002).

Each trial comprised a fixation point (1.5°), a cue (3.48°) and a target, all displayed on a grey background, as can be seen in Fig. 1. After a fixation point of 750 ms of duration, the cue was flashed for 200 ms, followed by a blank inter-stimulus-interval (ISI of a random duration between 1300–2300 ms). Then, the target stimulus, either a word (5.22°/2.73° on average) or a face (4.38°/4.80° on average), was presented for 1200 ms. Participants had 1200 ms to give a response and afterwards, they received visual feedback of their performance for 500 ms (correct, incorrect or missing response). The feedback helped to keep participants engaged on the task during the experiment.



Fig. 1. Sequence of events in a trial.

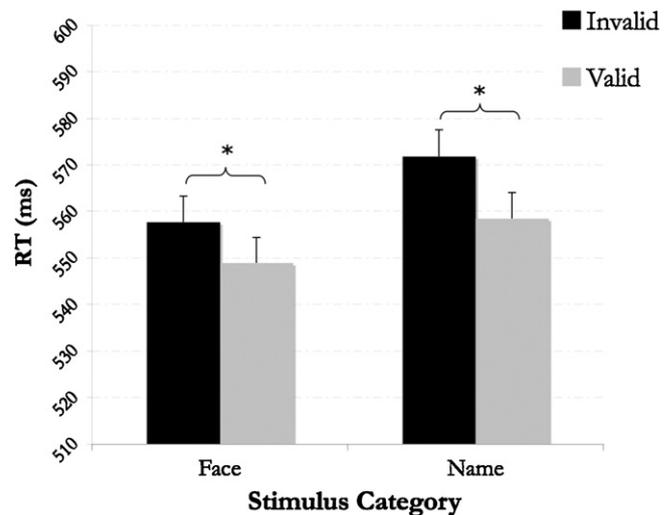


Fig. 2. Validity effect on reaction times.

2.3. Procedure

Participants sat in a dimly illuminated and electrically shielded room facing a computer screen placed 50 cm in front of them. At the beginning of the experiment, they read the instructions that explained the task and the relationship between the coloured cues and the predicted target categories. Participants were asked to keep their eyes fixated on the centre of the screen and to avoid eye movements and blinks during the presentation of the stimuli. Responses were given by pressing one of two buttons with the left and right index fingers. The association between hand and response was counterbalanced across participants.

The experiment was composed of three blocks of 160 trials each (480 trials in total), with brief breaks between them. The assignment of the validity conditions across individual stimuli was achieved by creating lists with different validity-item associations, which were counterbalanced across blocks and participants. This controlled assignment made sure that each stimulus (i.e. a specific face) was associated to each validity condition (invalid, valid) an equal number of trials, as well as presented in a different order between blocks. In addition, the presentation of stimuli within each block was randomized. At the beginning of the session, participants performed a training block of 100 trials to familiarize themselves with the task and the electrophysiological recording set-up. The whole EEG recording session lasted for about 50 min.

EEG was collected with a high-density EEG system [Geodesics Sensor Net with 128 electrodes from *Electrical Geodesics, Inc. (EGI)*], referenced to the vertex channel. The electrodes located above, beneath and to the left and right of the external canthi of the eyes were used as electrooculograph leads to detect eye movements. The EEG net was connected to an AC-coupled, high-input impedance amplifier (200 M Ω); impedances were kept below 50 k Ω , as recommended for the Electrical Geodesics high-input impedance amplifiers. The signal was amplified (0.1–100-Hz band pass) and digitized at a sampling rate of 250 Hz (16 bits A/D converter). Data were filtered off-line with a 30 Hz low-pass filter.

The EEG continuous recording was segmented into epochs, 200 ms before and 500 ms after target onset, and subsequently submitted to software processing for identification of artefacts. Epochs showing an excessively noisy EEG ($\pm 100 \mu\text{V}$ from one sample to the next), eye-movements artefacts (blinks or saccades: $\pm 70 \mu\text{V}$ on EOG channels) or incorrect behavioural responses were rejected. Data from individual channels that were consistently bad for a specific subject (>20% of trials) were replaced using a spherical interpolation algorithm (Pernier, Bertrand, & Echallier, 1989). Trials with reaction times (RTs) faster than 300 ms or slower than 800 ms were regarded as anticipations or late responses, and were also excluded from the analyses (9.25%). Finally, we established a minimum criterion of 30 artefact-free trials per subject and condition to maintain an acceptable signal-to-noise ratio.

Four group-averaged ERPs waveforms were constructed according to the Target category (face, name) and cue Validity (valid, invalid trials). ERPs were re-referenced to the average to eliminate the effects of reference-site activity and to generate an accurate estimation of the scalp topography of the recorded electrical fields (Dien, 1998; Tucker, Liotti, Potts, Russell, & Posner, 1994). The 200-ms pre-stimulus epoch served as baseline.

2.4. Electrophysiological analysis

We analyzed the voltage of specific ERP potentials to study the effect of cue validity on the processing of target stimuli across categories. The factors tested were Target category (face, name), Validity (valid, invalid) and Hemisphere (right, left), where relevant.

Prior to voltage analyses, we performed a topographical analysis of the ERP data. This analysis shows how the distribution of scalp voltage (i.e. topographies) evolves over time for each experimental condition. Topographical maps represent stable periods of electrical field patterns that correspond to dissociable functional states of the brain, which usually match identifiable ERPs on the grand-averaged waveforms (see Pascual-Marqui, Michel, & Lehmann, 1995). Therefore, a sequence of different maps is thought to reflect a succession of different stages of information processing (Murray et al., 2004; Thierry et al., 2007). In accordance, we used the topographical analysis to explore different brain states during face and word processing and to guide the selection of optimal spatio-temporal windows for voltage comparisons. To obtain the topographical maps on a group-average level, we used a *Segmentation-into-microstates procedure* implemented in Cartool software (developed by Denis Brunet: <http://brainmapping.unige.ch/Cartool.php>). This procedure was applied with several constraints: the maps had to remain stable for 20 ms and the maximum correlation between different topographies should not exceed 92%. The finding of distinct maps for different conditions was tested by a *Fitting procedure*, which provides information about the percentage of times that the different maps are found in the data from individual participants (see Murray et al., 2002 for a detailed description of these procedures). These values, susceptible to statistic analyses, were then introduced into multifactorial analyses of variance (ANOVAs). A significant interaction between Map and Experimental condition suggests that the conditions involve distinct neural configurations (Brandeis, Lehmann, Michel, & Mingrone, 1995; Lehmann & Skrandies, 1980).

We carried out the voltage analyses on selected spatio-temporal windows that captured the grand-average peaks of the P1, N170 and P300 potentials. The selected electrodes were those where the components of interest were maximally distributed. The temporal windows chosen were centred in the peak of the potentials in the grand-averaged waveforms, within the time-interval of the corresponding ERP topographical map. Mean amplitude values were computed with reference to the 200 ms pre-stimulus baseline.

3. Results

3.1. Behavioural results

Reaction times shorter than 300 ms and longer than 800 ms (9.91%), and errors (3.98%) were excluded from the analysis. Participants' mean response time (RT) and accuracy were submitted to a within-subjects repeated-measures ANOVA with the factors of Target category (face, name) and Validity (valid, invalid).

The mean accuracy on the task was 95.5% with no significant differences between valid and invalid trials ($F < 1$). Participant's accuracy was numerically higher for faces (95.9%) than for names (95.2%), although the effect only approached statistical significance, $F(1,23) = 3.36$; $p = .08$.

The RT analysis showed that participants were faster for valid (553 ms) than for invalid targets (564 ms), resulting in a significant main effect of Validity, $F(1,23) = 17.81$, $p < .001$ (see Fig. 2). The main effect of Target category also reached significance: responses to faces were faster than responses to words (551 ms and 561 ms,

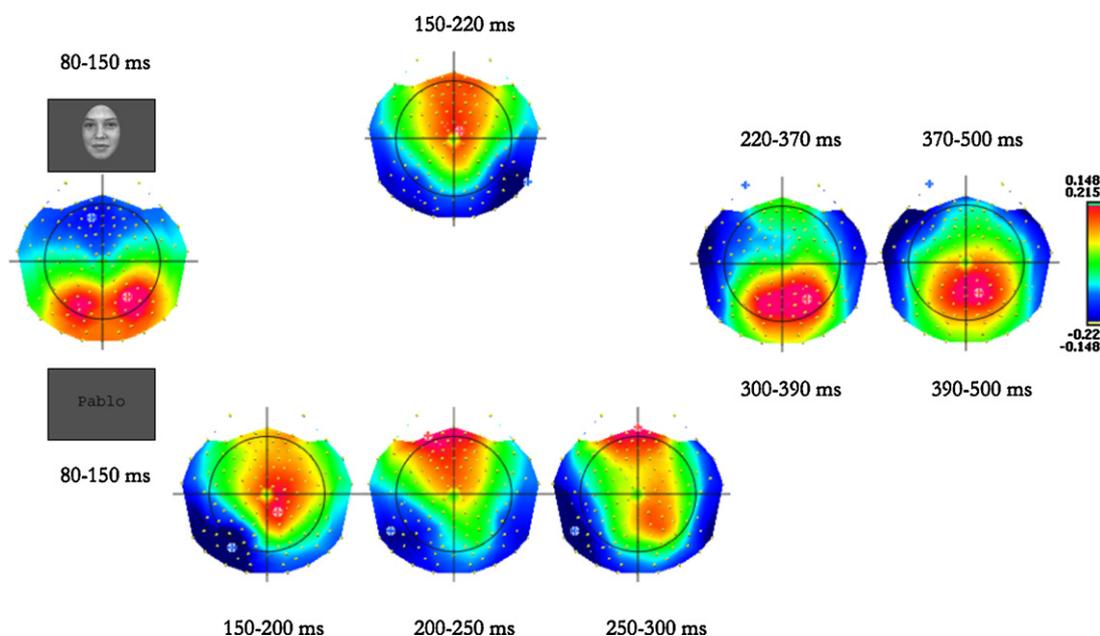


Fig. 3. Sequence of topographies associated with face and word processing.

respectively, $F(1,23) = 16.27, p = .001$). The interaction between Target category and Validity was not significant, $F < 1$.

3.2. ERP results

3.2.1. Topographical analyses

After data pre-processing, the average number of trials retained for target analyses was 140 in both valid conditions (out of a possible maximum of 180) and 46 in both invalid conditions (out of a possible maximum of 60).

The segmentation analysis yielded seven different maps explaining 95.5% of the variance in the ERPs associated to word and face processing, which are displayed in Fig. 3.¹ The first map was common for both types of stimuli and corresponded to the P1 component: it showed a bilateral distribution of positive voltages at posterior regions and negative values at frontal regions. At 150 ms, however, face and word topographies became different from each other. Although both maps showed negative voltages over occipito-parietal regions, this negativity presented a differential hemispheric pattern: it was highly left-lateralized for word stimuli and bilateral but slightly right-lateralized for face stimuli. These topographies encompassed from 150 to 220 ms in the case of faces and from 150 to 200 ms in the case of words. A fitting procedure was carried out on these two maps to test the differences at a statistical level (temporal interval: 152–192 ms). The ANOVA revealed a significant Map \times Target category interaction, $F(1,23) = 16.3, p < .001$, which supported the predominance of right and left lateralized topographies on face and word processing, respectively.

Faces generated a different topography at 220 ms, which had a positive polarity in central channels and negative voltages over lateral frontal areas. The topographies for words, in contrast, remained negative in posterior channels until 300 ms. We performed two additional fitting analyses to corroborate that face and word topographies were actually different also during those temporal windows (intervals: 200–250 ms and 250–300 ms). Both

ANOVAs showed significant interactions between Map and Target category, $F(1,23) = 13.8, p < 0.01$ and $F(1,23) = 6.05, p < 0.05$, respectively. These findings suggest that the distinct sequence of maps for face and word processing resulted from the activation of different neural generators. However, after 300 ms both perceptual categories shared again the same topographical distributions, as can be seen in Fig. 3.

3.2.2. Voltage analyses

Voltage comparisons were performed on three temporal windows that encompassed the peaks of the P1, N170 and P3 potentials. Although we specifically focused on the attentional modulation of the category-specific N170, we also found relevant to investigate the influence of endogenous attention on earlier and later stages of processing. Mean amplitude voltages over the selected electrodes and time windows were submitted to repeated measures ANOVAs with the factors Target category (face/word), Validity (valid/invalid) and Hemisphere (left/right).²

Latency ranges across subjects were 116–135 ms for the P1 (mean: 125, SD = 5.4), 172–185 ms for the N170 (mean: 176, SD = 6.6) and 478–498 for the P3 (mean: 490, SD = 4.2). Those ranges were comparable across experimental conditions and subjects for all the potentials analyzed, except for the word-N170 that reached its maximum amplitude later on the left than on the right hemisphere [$F(1,23) = 9.7, p = .004$; Faces: $F < 1$], as it can be observed in Fig. A.1 of Appendix A. Crucially, we did not find any significant effect of validity on the ERP's latency.

The P1 peaked at 126 ms in the grand-average waveforms. The effect of attention on this component was analyzed from 116 to 136 ms, over 10 occipito-parietal electrodes on both hemispheres. The analysis yielded a significant main effect of Target category, $F(1,23) = 11.47; p < 0.01$, as the P1 amplitudes for faces were larger than for words. In addition, we observed a significant main effect of Hemisphere, $F(1,23) = 4.4; p < 0.05$, which revealed larger ampli-

¹ An additional analysis showed that invalid and valid conditions did not generate dissociable topographies.

² A supplementary analysis showed that similar results were achieved for the N170 and P3 potentials when using only a random subset of valid trials to match trial numbers across conditions. Unexpectedly, the matched-trials numbers analysis revealed a significant effect of Validity on the word-P1: Invalid trials elicited a larger P1 than valid trials for word stimuli on the left hemisphere, $F(1,23) = 6.69, p = .01$.

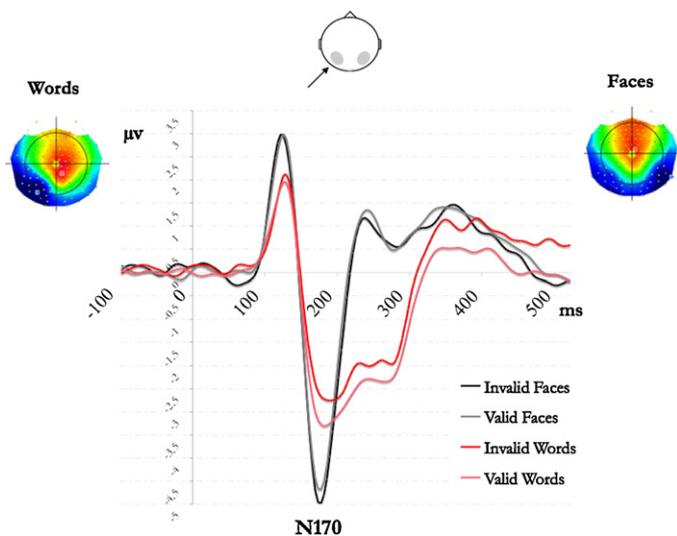


Fig. 4. Attentional modulations on the face- and word-related N170. The display presents the location of the electrodes used for the voltage analyses, the topographies for face and word processing during the N170 time-window and the ERPs of a representative electrode on the left hemisphere.

tudes for both stimuli on the right than the left hemisphere. Neither the main effect of Validity nor any of the interactions reached statistical significance.

The N170 potential peaked at 176 ms in the grand-average waveforms. The effect of attention was analyzed from 164 to 188 ms, over 18 occipito-temporal electrodes on both hemispheres. The ANOVA revealed a significant Target category \times Validity interaction, $F(1,23)=6.7$, $p<0.05$. Subsequent analyses showed that Validity significantly influenced the N170 amplitude for both faces, $F(1,23)=4.36$, $p<0.05$, and words, $F(1,23)=4.86$, $p<0.05$. The significant two-way interaction emerged as a result of a reversed pattern of modulation, as can be seen in Fig. 4. For words, valid trials elicited a larger N170 than invalid trials ($-3.71 \mu\text{V}$ vs. $-3.24 \mu\text{V}$) while for faces, invalid trials showed an enhanced amplitude as compared to valid trials ($-5.13 \mu\text{V}$ vs. $-4.68 \mu\text{V}$). Given our a-priori hypotheses, we used planned comparisons to explore further the lateralization of the validity effect, although the Target category \times Validity \times Hemisphere interaction did not reach statistical significance, $p=.4$. The results showed that the validity modulation was only significant on the right hemisphere for faces, $F(1,23)=10.23$, $p<.01$ [left hemisphere: $F(1,23)=1.131$, $p=0.29$]. In a similar way, the attentional effect on the word N170 was statistically significant on the left hemisphere, $F(1,23)=4.64$, $p<0.05$, while it only approached significance on the right hemisphere, $F(1,23)=3.47$, $p=.075$.

Finally, we analyzed the influence of endogenous attention on the P3 potential, which peaked at 492 ms in the grand-average waveforms. The voltages of 8 central electrodes from 480 ms to 500 ms were submitted to a repeated measures ANOVA. We found a significant main effect of validity, $F(1,23)=5.01$, $p<0.05$, with the P3 amplitude significantly larger for valid as compared to invalid stimuli. None of the rest of the terms in the analysis reached statistical significance.

4. Discussion

The present study investigated whether expectations about different categories were able to influence the perceptual stages of stimulus visual processing, by focusing specifically on the attentional modulation of the category-related N170. Although category expectations had been previously studied (Esterman & Yantis,

2009; Puri & Wojciulik, 2008; Puri et al., 2009), the current investigation was the first to assess the topic from an electrophysiological approach to explore whether these expectations modulate perceptual and/or post-perceptual stages of visual processing. To this end, we selected faces and words and focused on the N170 potential, which is considered a reliable index of categorical perceptual processing for these categories (although see Dering et al., 2009; Thierry et al., 2007). As attention was focused on perceptual categories, we hypothesized that the N170 would be likely to be modulated by attentional expectations.

Our behavioural results showed shorter RTs for valid as compared to invalid trials for both faces and words. These findings suggest that participants could use the symbolic cues to prepare efficiently to respond to stimuli belonging to the expected category. These results are at odds with a previous study by Puri and Wojciulik (2008), which failed to show such category expectation effects on behavioural measures. This study explored the effects of expectations about categories and specific exemplars but found a behavioural benefit exclusively for the latter, which led the authors to conclude that category expectations were not able to induce a facilitation of stimulus processing. In contrast, two recent neuroimaging studies have provided divergent results (Esterman & Yantis, 2009; Puri et al., 2009) by showing that house and face expectations influenced behavioural indexes of performance. In addition, brain activation analysis revealed that these expectations led to a strong activation of category-specific visual areas prior to stimulus presentation (FFA for faces and PPA for houses). These findings are in line with our results, which have confirmed that expectations regarding complex stimuli are able to influence target stimulus processing.

The results of the topographical analysis showed that both categories shared a similar topography on the P1 temporal window. However, by 150 ms the topographical results suggested that faces and words were processed by separable neural generators. The significantly different maps corresponded to the category-specific N170 component (e.g. Bentin et al., 1996, 1999). This finding is in accordance with previous studies that suggest that these electrophysiological indexes might reflect activity within the fusiform gyri (e.g. Brem et al., 2005; Henson et al., 2003; Herrmann et al., 2005; Itier et al., 2006), which are thought to be differentially activated during face and word processing (e.g. Cohen et al., 2000; Kanwisher et al., 1997). These topographies showed a bilateral but slightly right lateralized negativity for faces and a left lateralized negativity for words on posterior sites. From 200 to 300 ms, face and word processing still had different topographies. After 300 ms, the maps for both categories were again indistinguishable, which may represent common stages of response decision-making and motor preparation.

Voltage analyses were carried out on the P1, N170 and P3 to investigate the effect of attention along different stages of stimulus visual processing. We found a dissociable attentional modulation of the N170 for both categories. This finding lends further support to the susceptibility of the face and word N170 potentials to top-down modulations. But crucially, it shows for the first time that category expectations influence perceptual stages of stimulus processing. Nevertheless, our results do not necessarily preclude the existence of previous perceptual stages of categorical processing that might not be susceptible to attentional manipulations (e.g. P1, see Thierry et al., 2007). Note, however, that in contrast to Thierry et al. (2007) our topographical analysis did not yield different topographies during the P1 potential.

The N170 attentional modulation revealed a category-specific pattern. In the first place, the attentional effect on the face N170 was exclusively significant on the right hemisphere, while the word N170 modulation was observed on both hemispheres: statistically and marginally significant on the left and right regions of

the scalp, respectively. But crucially, the category-specific pattern was not restricted to laterality, but showed an opposed attentional effect on the N170 as a function of Target category. In response to faces, invalid trials elicited an enhanced negative peak compared to valid trials, while in response to words, valid trials evoked a larger negativity as compared to invalid trials. At the behavioural level, however, both categories showed a comparable and positive validity effect.

Previous literature has claimed the automatic nature and cognitive impenetrability of initial face processing (e.g. Carmel & Bentin, 2002; Cauquil et al., 2000; Lueschow et al., 2004). Nevertheless, our results lend support to recent findings that have reported top-down effects on the face N170 potential. Most of those findings arise from working memory research (Gazzaley et al., 2005; Morgan et al., 2008; Sreenivasan & Jha, 2007) or attentional paradigms where visual perception is boosted by spatial attention (Crist et al., 2008; Holmes et al., 2003) or compromised by deprived stimulus presentation (Sreenivasan et al., 2009). It is important to note that these studies share a particular characteristic: high cognitive or perceptual demands. By contrast, lower demands, just as those frequently observed in selective attention paradigms, usually lead to no differences in the N170 for attended and unattended faces (e.g. Carmel & Bentin, 2002; Cauquil et al., 2000). The present study provides novel data about the way that initial face processing can be modulated by attention under normal perceptual conditions. Our results revealed a reversed pattern of the attentional modulation, as previous findings reported larger N170 amplitudes for valid compared to invalid trials (Crist et al., 2008; Holmes et al., 2003; Sreenivasan et al., 2009). In our view, it could be the case that face valid trials within the simple design used in the current study may have not benefited from attentional orienting, just in the same way as in earlier studies (e.g. Carmel & Bentin, 2002; Cauquil et al., 2000; Lueschow et al., 2004). However, it seems possible that the unexpected appearance of a face on invalid trials may have induced the reallocation of attentional resources, which would have induced a greater N170 potential for invalid trials. Note that this result closely resembles the face inversion effect, which is characterized by a larger N170 in response to inverted stimulus presentation (e.g. Bentin et al., 1996; Itier et al., 2006; Itier & Taylor, 2004; Jacques & Rossion, 2007; Rossion et al., 2000). Although delayed latencies usually associated to the inversion of faces were not identified in our current data, this may be explained because invalid trials in our study did not compromise configural face processing (while see e.g. Freire, Lee, & Symons, 2000 for upside-down faces). However, it seems likely that both cases require the reallocation of attention, as the N170 amplitude effect to inverted face-stimuli has been also explained in terms of effortful processing on several occasions (e.g. Haxby et al., 1999; Rossion et al., 1999).

The attentional modulation found for the word N170 potential is in accordance with previous findings (Ruz & Nobre, 2008a), which showed an enhanced negativity to orthography task instructions compared to phonology or semantic instructions. Previous studies investigating the effects of attention on language perception had failed to find a similar effect on early stages of processing (e.g. Bentin, Kutas, & Hillyard, 1995; Cristescu & Nobre, 2008; Holcomb, 1993; Nobre et al., 1998). Nevertheless, our results extend Ruz and Nobre's by showing the modulation of the word-N170 as a result of focusing attention on the category of word stimuli rather than on their orthographic features (like in Ruz and Nobre's study). This suggests that both tasks may tap into similar processes of "word form" perception. Interestingly, the direction of the category-specific attentional modulation of the N170 suggests the existence of differences in the nature of word and face visual processing, despite the previously remarked similarity in speed and accuracy behavioural indices, which might be based on the ecological relevance of the stimuli.

It is not clear, however, to what extent spatial attention may have contributed to our findings. Faces and words in our experiment had a different spatial arrangement and hence, it could be argued that the reported effects are partially due to an adjustment of the focus of spatial attention. However, there are several factors that make this hypothesis unlikely. An explanation in terms of spatial attention would leave the reverted attentional effect found for faces unexplained, as the studies that have actually manipulated spatial attention to faces have found larger amplitude for valid than invalid stimuli (Crist et al., 2008; Holmes et al., 2003). Also, fMRI findings show that category-expectations induce selective activation on specialized brain areas, which suggests that anticipatory states rely on category-related information rather than on the spatial configuration of stimuli (Esterman & Yantis, 2009; Puri et al., 2009). Hence, although our current data cannot completely rule out the potential contribution of spatial attention, they suggest that additional factors are at play. Further studies that avoid spatial confounding factors (e.g. keeping the stimulus category constant) will be needed to clarify this issue.

We also found later attentional modulations for faces and words. The P3 showed an increased positivity for valid in contrast to invalid stimuli for both types of categories, a result that has been observed in previous studies (e.g. Donchin, 1981; Hopfinger & Mangun, 1998; Lueschow et al., 2004; McCarthy & Nobre, 1993). This probably reflects post-lexical evaluation and decision-making processes related to the behavioural responses (e.g. Kramer & Strayer, 1988). It is important to note that faces and words present the same topographical distribution during the P3 time window, which suggests that attention modulates response-related processes through similar neural generators for both categories.

In conclusion, our results indicate that expectations about different perceptual categories are able to modulate both perceptual and later stages related to stimulus processing. Crucially, we show that face and word expectations influence the N170 in a category-specific fashion, during the time interval associated to differential

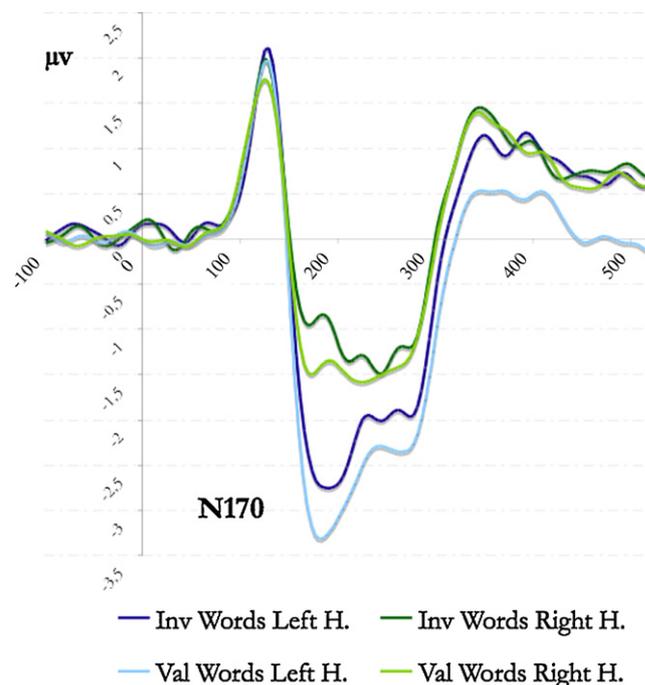


Fig. A.1. Hemisphere effects on the word-N170's latency. The figure presents the ERP waveforms associated to valid (light colours) and invalid trials (dark colours) of word stimuli recorded from a right channel (green) and a left channel (blue) from occipito-temporal areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

topographies for both types of stimuli. These novel findings extend previous research by showing that endogenous attention can be focused on complex perceptual categories, and that this influences perceptual stages of categorical processing. Further research would be desirable to clarify the role of space-based and identity-based information. Additional studies could explore whether specific items belonging to the same category, which share a common spatial arrangement, can also be modulated by top-down attention.

Appendix A.

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