Differential Lateralization for Words and Faces: Category or Psychophysics?

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Abstract

■ This set of three experiments assessed the influence of different psychophysical factors on the lateralization of the N170 event-related potential (ERP) component to words and faces. In all experiments, words elicited a left-lateralized N170, whereas faces elicited a right-lateralized or nonlateralized N170 depending on presentation conditions. Experiment 1 showed that lateralization for words (but not for faces) was influenced by spatial frequency. Experiment 2 showed that stimulus presentation time influenced N170 lateralization independently of spatial frequency composition. Finally, Experiment 3 showed that stimulus size and resolution did not influence N170 lateralization, but did influence N170 amplitude, albeit differentially for words and faces. These findings suggest that differential lateralization for words and faces, at least as measured by the N170, is influenced by spatial frequency (words), stimulus presentation time, and category. ■

INTRODUCTION

It is now well accepted that the two cerebral hemispheres are functionally different. However, there is still no agreement about the processes underlying brain lateralization. Specifically, it remains unclear how to explain the differences in lateralization observed between some stimulus categories (e.g., words and faces), and to what extent this pattern reflects the co-occurring psychophysical differences between these categories. Traditionally, patterns of lateralization were described in terms of the verbal/visuospatial dichotomy, a pattern that emerged from the clinical observation of patients with unilateral brain lesions. On this view, patients with lesions of the left hemisphere (LH) are more likely to show language deficits, whereas right hemisphere (RH) lesions result more often in visuospatial deficits, including prosopagnosia (Gazzaniga, Ivry, & Mangun, 2002; De Renzi, Perani, Carlesimo, Silveri, & Fazio, 1994; Hellige, 1993; Springer & Deutsch, 1993). This pattern has been observed using several empirical techniques such as the divided visual field paradigm, electroencephalography (EEG), and imaging techniques. Nonetheless, there are several important caveats to this proposed general hemispheric "division of labor."

Firstly, there does not appear to be a strict lateralization of visual and language functions. For example, it has become clear that the RH has an important (and even maybe dominant) role in some aspects of verbal communication, including the comprehension and production of prosody, lexicosemantics, discourse, and pragmatics (Tompkins, 1995; Joanette, Goulet, & Hannequin, 1990). Similarly, although face processing is generally known to drive an RH advantage, this visuospatial task can also elicit an LH advantage in some circumstances, for example, when the faces are familiar, when the task emphasizes processing of features, or when the presentation time is longer (Gazzaniga et al., 2002; Rossion et al., 2000; Sergent, 1982a). In sum, simple domain dichotomies cannot account for the complexity of the pattern observed and asymmetries should be described in terms of how information is represented and processed by each hemisphere (Robertson & Ivry, 2000; Ivry & Robertson, 1998). Second, as Sergent (1983) points out, verbal and visuospatial stimuli are often tested in different experiments, and task differences or other differences in experimental procedure (including stimulus size and presentation time) could influence hemispheric lateralization. Differences in task can imply the use of different cognitive or computational processes that can, in turn, influence lateralization (Hellige, 1993). For example, differences in lateralization were widely demonstrated for global versus local processing (Moses et al., 2002; Martínez et al., 1997; Sergent, 1982b) and for coordinate versus categorical spatial relations (Okubo & Michimata, 2002, 2004; Kosslyn, Chabris, Marsolek, & Koenig, 1992). Thus, a true test of hemispheric differences in verbal and visuospatial processing should ideally match task and experimental procedure for both types of stimuli. Third, low-level perceptual differences in the verbal and visuospatial stimuli themselves might have profound effects on

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the pattern of lateralization. For instance, the distribution of spatial frequencies in a visual scene may influence the pattern of lateralization evoked by that stimulus (Peyrin, Chauvin, Chokron, & Marendaz, 2003; Martínez, Di Russo, Anllo-Vento, & Hillyard, 2001; Grabowska & Nowicka, 1996; Zani & Proverbio, 1995; Sergent, 1983).

These issues raise the following more global question: To what extent can the differential pattern of lateralization for verbal and visuospatial stimuli be explained by differences in stimulus properties and experimental procedure? We address this question in the present study by systematically varying basic stimulus and timing parameters that may drive the patterns of differential lateralization reported for verbal and visuospatial information. We used written words and human faces as canonical exemplars of verbal and visuospatial categories.[1] Words and faces are ideal for comparing across the two domains, in that (1) they can be presented in the same modality using the same experimental paradigm; (2) there is an ample literature on these stimulus classes that generally reports opposite patterns of lateralization (left for words and right for faces) (Maurer, Brandeis, & McCandliss, 2005; Caldara, Rossion, Bovet, & Hauert, 2004; Rossion, Joyce, Cottrell, & Tarr, 2003; de Haan, Pascalis, & Johnson, 2002; Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999; Gerschlager et al., 1998; Schweinberger & Sommer, 1991); and (3) perception of both classes of stimuli is highly overpracticed and is thought to rely on ''expert'' systems (Johnson, 2005; Maurer et al., 2005; Caldara, Rossion, et al., 2004; Cohen & Dehaene, 2004; Caldara et al., 2003).

Here, we report the results of three experiments that use the same task, stimuli, and experimental paradigm to systematically probe the psychophysical, temporal, and informational factors influencing the hemispheric lateralization of visual word and face processing. Using event-related potentials (ERPs), we assessed the relative lateralization of face and word processing using a sensitive electrophysiological index of complex visual processing, namely, the amplitude of the N170 component. This ERP component is of particular interest in that previous research has suggested that this component is left lateralized when elicited by words (Simon, Petit, Bernard, & Rebai, 2007; Maurer et al., 2005; Caldara, Jermann, Lopez Arango, & Van der Linden, 2004; Rossion et al., 2003; Bentin et al., 1999; Gerschlager et al., 1998), and right lateralized when elicited by faces (Caldara, Rossion, et al., 2004; Rossion et al., 2003; de Haan et al., 2002; Schweinberger & Sommer, 1991).

Experiment 1 targets the effect of varying a fundamental psychophysical property—spatial frequency—on hemispheric lateralization and tests the hypothesis that lateralization of the N170 to words and faces is influenced by the spatial frequency composition of the stimulus. Experiment 2 probes the interaction of spatial frequency composition and stimulus timing, testing the hypothesis that the hemispheric asymmetries driven by spatial frequency composition are stronger when stimuli are presented for brief periods of time. Finally, Experiment 3 investigates the role of stimulus size and resolution in driving lateralization on the hypothesis that larger word and face stimuli should elicit a more right lateralized N170, whereas smaller stimuli should elicit a more left lateralized N170. In short, we examine the influence of five factors on hemispheric lateralization for face and word processing: stimulus category (words versus faces), spatial frequency composition, presentation time, stimulus size, and stimulus resolution.

EXPERIMENT 1

As noted above, words and faces differ along some basic psychophysical characteristics—such as spatial frequency—that might influence the pattern of lateralization observed for these two categories (Sergent, 1982b).

Spatial Frequency

Spatial frequency can be defined as the change in luminance as a function of space (Viggiano, Costantini, Vannucci, & Righi, 2004), and it is generally measured in cycles/degree of visual angle, or in cycles/image. High spatial frequencies (HSFs) result from sudden luminance changes (i.e., fine edges) and supports perceptual extraction of local features. Low spatial frequencies (LSFs) result from gradual luminance changes, and are generally more informative about the overall configuration of an image (Goffaux & Rossion, 2006; Goffaux, Hault, Michel, Vuong, & Rossion, 2005). Object recognition requires decomposition of the image in terms of its component spatial frequencies (Sekular & Blake, 2002). In V1, different clusters of cells are selectively activated by different spatial frequencies (Issa, Trepel, & Stryker, 2000). Each of these clusters comprises an ''information channel'' that encodes the information carried by a specific spatial frequency band (Sekular & Blake, 2002).

Hemispheric Asymmetries in Processing Spatial Frequency

A hemispheric bias for processing certain spatial frequencies was initially proposed by Sergent (1982a, 1982b, 1983). This hypothesis states that, in a decision-making task, the LH shows an advantage in the processing of HSF, whereas the RH shows an advantage to process LSF. Sergent's hypothesis has been tested using varied experimental techniques and different kinds of stimuli. Using a divided visual field paradigm, Peyrin et al. (2003) showed subjects normal or spatially filtered pictures of natural scenes. Subjects demonstrated no hemispheric dominance in judging whether the scene represented a city or a highway when the pictures were composed of the whole spectrum of spatial frequencies. However, when the pictures were filtered to keep only HSF, a right visual field (RVF/LH) advantage emerged in this task. Conversely, when the pictures were filtered to conserve only LSF, a left visual field (LVF/RH) advantage was observed.

Electrophysiology and neuroimaging have also provided evidence for the spatial frequency hypothesis. Using ERPs, Martínez et al. (2001) found that attending to HSF or LSF checkerboards elicited an increased negativity relative to the corresponding unattended condition. This "selection negativity" was asymmetrically distributed between the two hemispheres in the 220–300 msec range: It was larger at ventrolateral electrodes of the LH for HSF checkerboards, and larger at the ventrolateral electrodes of the RH for LSF checkerboards. A negative component peaking around 100 to 140 msec (named ND120) was also found to be left lateralized for HSF and nonlateralized for LSF, a finding that was also observed by Zani and Proverbio (1995). Comparable results were found using functional magnetic resonance imaging (Iidaka, Yamashita, Kashikura, & Yonekura, 2004; Vuilleumier, Armony, Driver, & Dolan, 2003).

In a thorough literature review, Grabowska and Nowicka (1996) found that spatial-frequency-driven lateralization was contingent upon the experimental task. Almost all studies using an active paradigm (such as a recognition task) found hemispheric asymmetries similar to those reported above. In contrast, when a lower-level perceptual task was employed, either no hemispheric asymmetry was observed, or a more general RH bias for processing a wide variety of visuospatial patterns, regardless of spatial frequency content.

Spatial Frequency in Words and Faces

Faces and words typically differ radically in their spatial frequency content, and in the spatial frequency bands used to process these stimuli. In both the reading and face processing literature, spatial frequency is typically defined in terms of cycles per "object" (e.g., cycles/letter, or cycles/face). In order to directly compare different stimulus types, it is necessary to convert these measurements into cycles per degree of visual angle, a measure that is dependent upon the position of the viewer relative to the object, and the size of the object itself. In that respect, one cycle/letter is generally much higher in spatial frequency than one cycle/face when measured in cycles/degree of visual angle.

For words and letters, sharp edges (and thus HSF) are of primary importance. It is estimated that the maximum of energy present in a letter is at 2 to 3 cycles/letter (Põder, 2003), and that a letter can be identified based on any spatial frequency band from 1.5 to 10 cycles/letter (Majaj, Pelli, Kurshan, & Palomares, 2002). On the other hand, faces can be identified using a wide range of spatial frequency, with each spatial frequency band carrying a different level of information. Spatial frequencies above 32 cycles/face support the extraction of local features in a face, such as the shape of the eyes or the wrinkliness of the skin. Spatial frequencies lower than 8 cycles/face are more informative about the configural aspects of the face, such as the metric distance between the eyes (Goffaux & Rossion, 2006; Goffaux et al., 2005). Interestingly, selective elimination of the spatial frequency information between 8 and 16 cycles/face is particularly disruptive to face processing (Ruiz-Soler & Beltran, 2006; Gold, Bennett, & Sekular, 1999; Costen, Parker, & Craw, 1996). ERP studies also demonstrated the importance of LSF in face processing: An N170 of reduced amplitude has been observed for high-pass (HP) face stimuli compared to low-pass (LP) face stimuli in gender discrimination task (Goffaux, Jemel, Jacques, Rossion, & Schyns, 2003) and in face detection task (Halit, de Haan, Schyns, & Johnson, 2006).

It is possible that the difference in the spatial frequency content and informativeness over the two classes of stimuli could account for some of the hemispheric asymmetries noted above. However, relatively few experiments have explored the influence of spatial frequency on hemispheric asymmetries for faces or words. More to the point, no published study has directly compared spatial frequency effects for both faces and words in a single experiment. This raises the question of whether the lateralization pattern for faces and for words could be entirely explained by differences in spatial frequency. Further, is the influence of spatial frequency on lateralization similar for both faces and words? Experiment 1 directly addresses these questions by measuring the changes in hemispheric lateralization caused by manipulating the spatial frequency content of words and faces. Based on previous literature, we hypothesized that the N170 elicited by HP-filtered words and faces would be left lateralized, whereas the N170 to LP-filtered words and faces would be right lateralized.

Methods

Participants

Thirteen right-handed participants (21–39 years old, mean age = 28 years; 9 women) were recruited from the University of London and were paid for their participation. All were native English speakers with normal or corrected-to-normal vision; none reported language, reading, learning, or hearing disorders, and none reported current use of psychoactive drugs.

Stimuli

Stimuli were gray-scale pictures of faces, words, and abstract patterns (data from abstract patterns will not be reported in this article) on a rectangle background. All stimuli were 280 × 364 pixels, and occupied 5° of horizontal and 6.5° of vertical angle from a viewing distance of 57 cm. Of this stimulus dimensions, the face itself occupied approximately 4° × 6° and words approximately

4.75° × 1°. Each category was composed of 60 exemplars, with an additional 8 per category as practice items. Faces all depicted Caucasian women with a direct gaze and a neutral facial expression, displayed on a white background with the eyes occupying the center of the picture. Stimuli were adapted from the face databases of the Centre for Brain and Cognitive Development, the Nim Stim Face Stimulus Set[2] (Tottenham et al., in press), and the CVL Face Database (Solina, Peer, Batagelj, Juvan, & Kovae, 2003). Word stimuli were presented in uppercase black Arial capital font on a gray background, and were five-letter nouns with four to five phonemes, one to two syllables, and one morpheme. Words were rated between 200 and 600 for familiarity, concreteness, and imageability (on a rating ranging from 100 to 700), had eight or fewer orthographic neighbors (MRC Psycholinguistic Database: Wilson, 1987), and had a written frequency of occurrence between 20 and 150 per million words (Kucera & Francis, 1967).

Word and face stimuli were spatially filtered using Matlab by applying a 2-D Gaussian filter to the Fourier-transformed image data to create a LP-filtered (<1 cycle/degree or 5 cycles/image width) and HP-filtered version (>4 cycles/degree or 20 cycles/image width) (see Figure 1). Spatial frequency cutoff points were chosen based on similarity with literature using spatially filtered stimuli (Halit et al., 2006; Hsiao, Hsieh, Lin, & Chang, 2005; Vuilleumier et al., 2003). Even if words and faces differ in terms of spatial frequency and especially in terms of diagnostic spatial frequency, the same cutoff points were used for both categories, as the aim of the study was to analyze the effect of spatial frequency independent of category. Brightness was equated over all stimulus categories; equivalence in luminance was confirmed using a Sekonic luminance meter, positioned at participants' eye level and pointed to the center of the image (57 cm from a 21-in. monitor), with the whole image being incorporated in the visor.

Design

A 2 × 3 within-subject design crossed stimulus category (face, word) with spatial frequency composition (full-spectrum [FS], high-pass [HP] and low-pass [LP]). Behavioral dependent variables were response time (RT) and accuracy; electrophysiological dependent variables were P1 and N170 amplitude averaged over electrodes of the RH and the LH (see below).

Procedure

EEG signal was recorded using a Geodesic Sensor Net with 128 electrodes (Tucker, 1993), with vertex as reference; horizontal and vertical electrooculograms were used to monitor eye movements. EGI NetAmps 200 was used (gain = 1000), and data were digitized with sampling rate of 250 Hz, and band-pass filtered between 0.1 and 100 Hz.

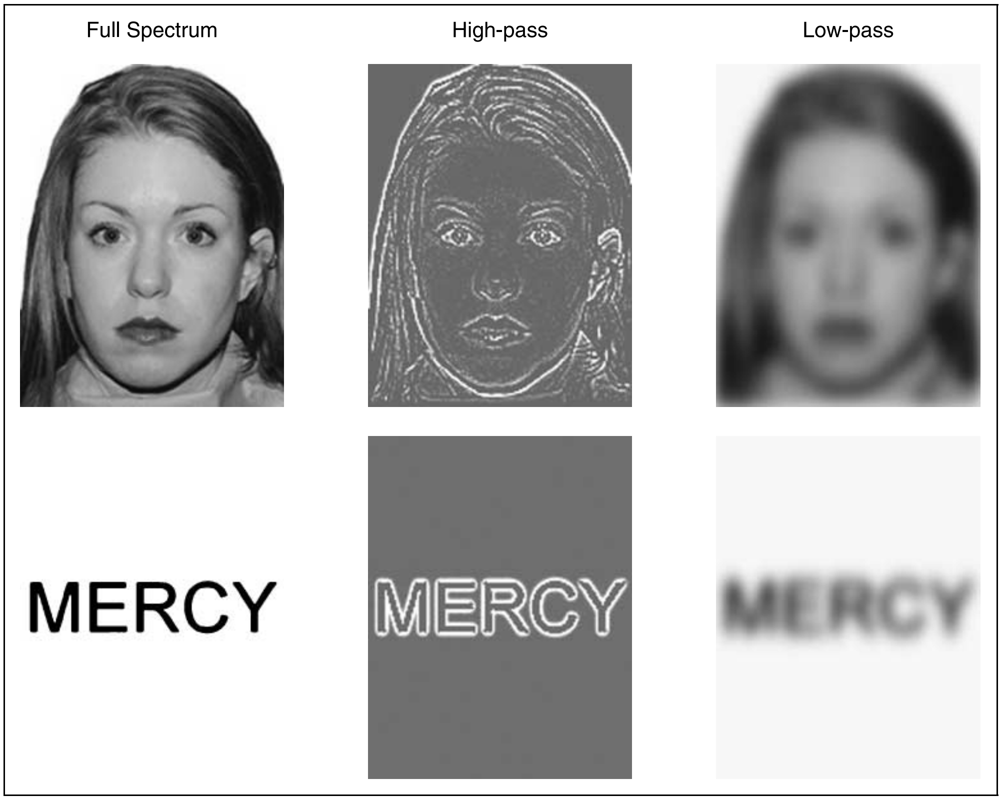


Figure 1. Sample of stimuli for Experiment 1.

Task

Participants performed a "one-back" memory task, pressing a joystick key every time they thought that a stimulus had been presented twice in a row.[3] Each cell of the experimental design was presented in a separate block (FS Faces, HP Faces, LP Faces, FS Words, HP Words, LP Words), with 10 practice items (8 stimuli, 2 targets/repetitions) beginning each block. Participants repeated practice blocks if their button-press accuracy was <90% (including false alarms). Experimental blocks were composed of 70 trials (60 stimuli, 10 repetitions/targets). Each trial began with a 700-msec presentation of a stimulus in the middle of the screen, followed by a 1350-msec response window. Trials that represented a repetition of stimuli (targets) and those where subjects responded incorrectly (e.g., false alarms) were eliminated from analyses, leaving only response-free trials for analyses.

ERP Waveform Analysis

Each trial was segmented from the continuous EEG data (windowed from 200 msec prestimulus onset to 600 msec poststimulus onset). Segments were individually inspected for artifacts; signal from rejected electrodes was replaced using the "bad channel replacement" algorithm in Nestation 4.0. If more than 10 of 128 channels were rejected, the trial was not included in the condition average. Participants with >50% rejected trials in one or more conditions were eliminated from all subsequent analyses (1 participant eliminated, final $n = 12$). Statistics regarding the number of trials included on each stimulus category are available in the supplementary material on www.cbcd.bbk.ac.uk/people/scientificstaff/evelyne.

Waveforms were baseline-corrected using the 200-msec prestimulus interval. Averages were computed for each participant in each experimental condition, and data were re-referenced to the average of channels. Based on visual inspection of the grand average, a montage of electrodes was created where the N170 and P1 components were maximal in the right and left occipito-temporal regions (left: 57, 58, 59, 60, 63, 64, 65, 66, 67, 69, 70, 71, 72, 74, 75; right: 77, 78, 83, 84, 85, 86, 89, 90, 91, 92, 95, 96, 97, 100, 101). The time window was based on the previous literature (Halit et al., 2006; Maurer et al., 2005; Rossion et al., 2003; Halit, 2002; Bentin et al., 1999) and visual inspection, and was set to 99–247 msec poststimulus for the N170, and to 67–159 msec poststimulus for the P1. The component peak amplitude within this time window was extracted for each participant, in each condition, for the average of all channels in the LH and in the RH montages. Analyses were concentrated on amplitudes rather than latencies because previous literature indicates that lateralization effects for words and faces (which was the main focus of this study) could be mainly observed in terms of amplitude of the N170 (see, for example, Simon et al., 2007; Maurer et al., 2005; Caldara, Jermann, et al., 2004; Rossion et al., 2003; de Haan et al., 2002; Bentin et al., 1999). Figure 2 illustrates the morphology of the grand-average waveform for FS stimuli (grand-average waveforms for other conditions are included in the supplementary material on www.cbcd.bbk.ac.uk/people/scientificstaff/evelyne).

Results

Behavioral Results

A 2 × 3 (Category × Spatial Frequency) within-subjects analyses of variance (ANOVAs) on RT and accuracy measures showed no significant ($p < .05$) main effects and second- or third-order interactions (see Table 1 for cell

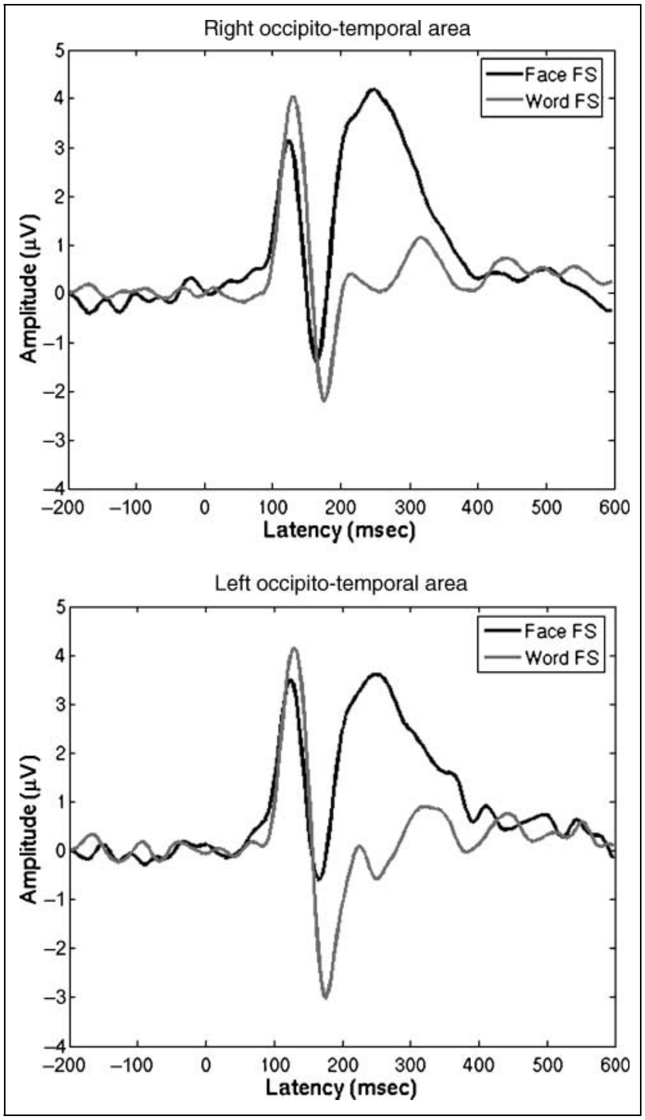


Figure 2. Grand-averaged waveform for full-spectrum faces and words in Experiment 1.

Table 1. Summary of Behavioral Data in Experiment 1

	Misses (%)	*False Alarms (%)*	*Response Time (msec)*
Faces			
Full-spectrum	2	<1	805
High-pass	4	<1	827
Low-pass	9	2	840
Words			
Full-spectrum	3	<1	842
High-pass	0	<1	872
Low-pass	2	<1	841

means). This suggests that the level of difficulty was approximately equal over the different conditions.

ERP Results

P1. We performed a 2 × 3 × 2 (Category × Spatial Frequency × Hemisphere) ANOVA on the peak amplitude of the P1. No effect or interaction of effects was found significant.

N170. The same ANOVA was also performed on the peak amplitude of the N170 followed by post hoc t tests on individual contrasts (see Table 2 for statistics main effects and interactions, and Figure 3). ANOVAs revealed that there was an overall modulation of the N170 amplitude by spatial frequency, where HP > FS > LP [HP vs. FS: $t(47) = 3.8$, $p < .001$; HP vs. LP: $t(47) = 6.9$, $p < .001$; FS vs. LP: $t(47) = 3.4$, $p = .001$]. Overall N170 peak amplitude was also modulated by stimulus category, where words > faces. There was no global effect of lateralization of the N170; however, a significant Category × Hemisphere interaction suggested that words and faces showed different profiles of lateralization. Post hoc t tests showed that N170 amplitude for words was greater in the LH than in the RH [$t(35) = 4.6$, $p < .001$], with a weak converse trend for faces [$t(35) = 1.5$, $p = .139$]. Within-hemisphere comparisons across category showed that the N170 was larger for words than for faces in the LH [$t(35) = 5.5$, $p < .001$], whereas no difference was found in the RH [$t(35) = 1.1$, $p = .263$].

Table 2. Summary of Statistics for the N170 Peak Amplitude in Experiment 1

	F	*p*
Category	(1, 11) = 5.7	.036*
Spatial frequency	(2, 10) = 7.8	.009*
Hemisphere	(1, 11) = 1.2	.297
Category × Spatial frequency	(2, 10) = 1.6	.240
Category × Hemisphere	(1, 11) = 12.1	.005*
Spatial frequency × Hemisphere	(2, 10) = 0.3	.753
Category × Spatial frequency × Hemisphere	(2, 10) = 14.0	.001*

*Indicates a p value lower than .05.

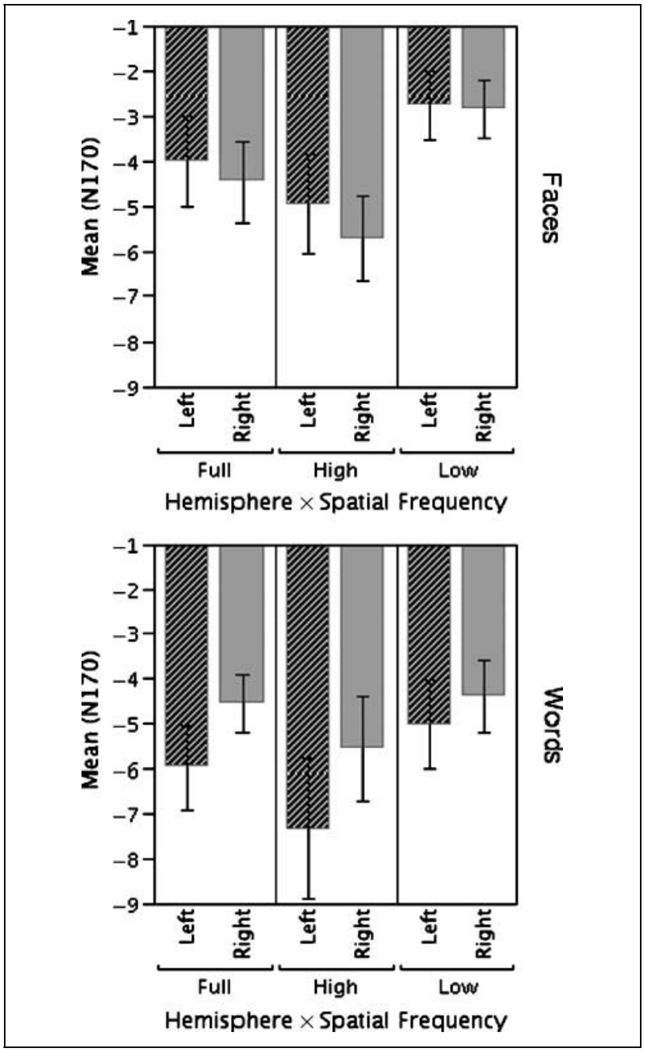


Figure 3. Average of individual peak amplitude for the N170 in Experiment 1.

Spatial frequency had a complex effect on the lateralization of the N170, in that there was no simple Spatial frequency × Hemisphere interaction, but a significant three-way interaction of Spatial frequency × Hemisphere × Category. Here, post hoc t tests revealed that spatial frequency did not modulate lateralization of faces [FS: $t(11) = 0.8$, $p = .412$; HP: $t(11) = 1.4$, $p = .196$; LP: $t(11) = 0.2$, $p = .835$]; the three-way interaction was driven entirely by the fact that for HP and FS words, N170 amplitude was greater in the LH than in the RH [FS: $t(11) = 3.2$, $p = .008$; HP: $t(11) = 3.1$, $p = .011$], whereas for LP words, this lateralization was severely attenuated [$t(11) = 1.7, p = .113$].[4]

Discussion

Influences on the Lateralization of the N170

The most straightforward effect on N170 lateralization was that of stimulus category, with a significantly left-lateralized N170 for words, and a trend for a right-lateralized N170 for faces. Contrary to our hypothesis, spatial frequency did not significantly influence lateralization. However, spatial frequency did interact with stimulus category to modulate N170 lateralization. Here, N170 lateralization for words was seriously attenuated with LP filtering, whereas there was no significant effect of spatial frequency filtering on N170 lateralization for faces. These results suggest that the oft-observed left lateralization for words may be driven to some degree by the *information* conveyed by frequencies above 4 cycles/degree, a result consistent with the predictions of Sergent (1982a). The lack of significant spatial frequency effects on N170 face lateralization shows that simple differences in spatial frequency content over faces and words are unlikely to account for lateralization differences. It could be argued that this lack of influence of spatial frequency on lateralization can be due to the fact that the different spatial frequency conditions were blocked rather than mixed. However, the same result was obtained in an unpublished study from our laboratory, where the HP and LP conditions were mixed in the same experimental block.

Influences on the Amplitude of the N170

Rather unexpectedly, the N170 amplitude was greater overall for words than for faces, an effect primarily driven by signal in the LH. Changes in spatial frequency also modulated N170 amplitude regardless of stimulus category. Here, the N170 was greater for HP than for FS stimuli, which was, in turn, greater than for LP stimuli. On the contrary, previous ERP studies on spatially filtered faces found a smaller N170 for HP faces than for FS faces (Halit et al., 2006; Goffaux et al., 2003). This discrepancy in the results will be investigated further in Experiment 2. Because this effect did not differ over words and faces, it likely does not reflect the stimulus-specific information carried by different spatial frequency bands.

EXPERIMENT 2

The results of Experiment 1 strongly suggest that category-specific profiles of lateralization are not driven solely by spatial frequency content. However, it is possible that the kinds of spatial frequency effects reported in the literature summarized above may only emerge under specific temporal conditions, as suggested by experimental data (Peyrin, Mermillod, Chokron, & Marendaz, 2006; Evert & Kmen, 2003; Peyrin, 2003; Blanca, Zalabardo, García-Criado, & Siles, 1994). These studies suggest that stimulus duration might be a key factor in the emergence of hemispheric asymmetries for different parts of the spatial frequency spectrum. A divided visual field study by Peyrin et al. (2006) showed that when spatially filtered stimuli were presented for 30 msec, the classic hemispheric specialization pattern could be observed (LVF/RH superiority for LP stimuli and RVF/LH superiority for HP stimuli). However, when the same stimuli were presented for 150 msec, a general trend to an RH advantage appeared, irrespective of the SF content of the stimuli. These results suggest that hemispheric biases for particular spatial frequency bands only emerge under short stimulus duration—a hypothesis that may, in part, explain the relative lack of overall spatial frequency effects on lateralization in our first experiment. In Experiment 1, stimulus presentation time was considerably longer (700 msec) than in studies reporting the full or partial pattern of lateralization for spatial frequencies (presentation time rarely exceeding 150 msec; Iidaka et al., 2004; Peyrin et al., 2003; Martínez et al., 2001; Kenemans, Baas, Mangun, Lijffijt, & Verbaten, 2000; Zani & Proverbio, 1995). It is therefore possible that the discrepancy between the results from Experiment 1 and those of previous studies might be driven by differences in stimulus presentation time. Experiment 2 tests the hypothesis that the changes in hemispheric asymmetry associated with high and low spatial frequencies would be more pronounced with brief stimulus presentation times, compared with the longer stimulus presentation time used in Experiment 1.

Methods

The present experiment differed from Experiment 1 only in the stimulus presentation times: Stimuli were presented for either 30 msec (as in Peyrin, 2003) or 700 msec (as in Experiment 1).

Participants

Nineteen participants (21 to 38 years old, mean age = 26 years; 11 women) were recruited using the same inclusion and exclusion criteria as in Experiment 1.

Stimuli

FS stimuli were those used in Experiment 1, as were HSF and LSF cutoffs; however, the spatial frequency filtering method differed somewhat from the Experiment 1 (see Figure 4 for example of HP stimuli in Experiments 1 and 2).[5] All pictures were equated in luminance using average image brightness in Photoshop. Measurement with a Sekonic luminance meter revealed no significant difference in luminance between the six stimulus categories.

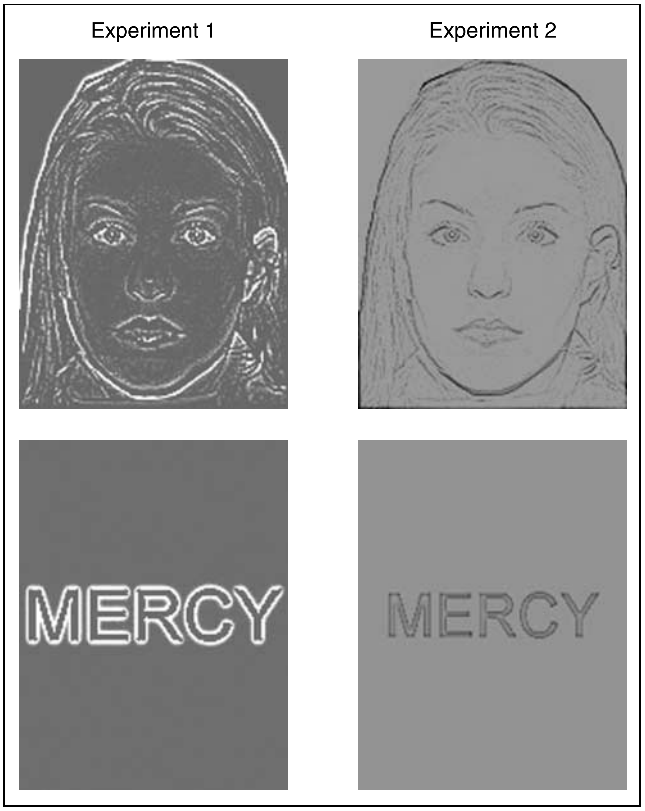


Figure 4. Sample of high-pass stimuli used in Experiments 1 and 2.

Design

A 2 × 3 × 2 within-subject design crossed stimulus category (faces and words), spatial frequency composition (FS, HP, and LP), and presentation time (brief: 30 msec and long: 700 msec). As previously, behavioral dependent variables were RT and accuracy in the one-back task. The electrophysiological dependent variables were the P1 and N170 peak amplitude in the occipito-temporal region of the LH and RH.

Procedure

The procedure was identical to Experiment 1, with the exception that there were 12 randomly presented blocks, with stimulus durations of either 700 msec or 30 msec.

ERP Analysis

ERP analysis was identical to Experiment 1. Data from one participant were rejected due to a high frequency of eye movements; data from three further participants were lost due to technical problems. The final sample was $n = 15$. It was impossible to select a single N170 time window because of considerable latency differences in peak amplitude across conditions. Time windows in each condition were selected to encompass each subject's peak amplitude, and were set to the following: FS faces, 119–219 msec; FS words, 119–227 msec; HP words/faces, 155–263 msec; LP words/faces, 115–230 msec. (Note that the same results were obtained using peak amplitude in a single window from 115 to 263 msec). For P1, the time window was set to 59–147 msec.

Results

Behavioral Results

We performed 2 × 3 × 2 (Category × Spatial frequency × Presentation time) within-subjects ANOVAs on RT and accuracy, followed by post hoc *t* tests on individual contrasts (see Table 3 for cell means and Table 4 for statistical main effects and interactions). RTs were modulated by spatial frequency (where FS < HP = LP) [FS vs. HP: $t(59) = 3.6, p < .001$; FS vs. LP: $t(59) = 2.6, p = .012$; HP vs. LP: $t(59) = 1.8, p = .081$] and by presentation time, with subjects responding faster when the stimulus was presented for a shorter time. Subjects' accuracy was modulated by stimulus category (words > faces), and by presentation time (long presentation time > brief presentation time). The latter was especially true for face stimuli, as revealed by a significant Category × Presentation time interaction. Spatial frequency also modulated overall accuracy (FS = LP > HP) [FS vs. LP: $t(59) = 1.0, p = .318$; FS vs. HP: $t(59) = 3.9, p < .001$; HP vs. LP: $t(59) = 3.2,$

Table 3. Summary of Behavioral Data in Experiment 2

	Misses (%)	*False Alarms (%)*	*Response Time (msec)*
Faces			
Brief presentation			
Full-spectrum	9	3	755
High-pass	30	5	861
Low-pass	12	4	813
Long presentation			
Full-spectrum	0	2	866
High-pass	6	2	931
Low-pass	3	1	892
Words			
Brief presentation			
Full-spectrum	2	1	771
High-pass	12	2	838
Low-pass	4	1	818
Long presentation			
Full-spectrum	1	1	854
High-pass	3	1	891
Low-pass	7	1	883

Table 4. Summary of Behavioral Statistics for Experiment 2

	Response Time		*Accuracy*	
	F	*p*	*F*	*p*
Category	(1, 14) = 0.6	.461	(1, 14) = 16.6	.001*
Spatial frequency	(2, 13) = 8.0	.005*	(2, 13) = 11.5	.001*
Presentation time	(1, 14) = 7.6	.015*	(1, 14) = 8.0	.014*
Category × Spatial frequency	(2, 13) = 0.5	.610	(2, 13) = 5.0	.024*
Category × Presentation time	(1, 14) = 0.8	.387	(1, 14) = 9.3	.009*
Spatial frequency × Presentation time	(2, 13) = 0.7	.519	(2, 13) = 6.6	.010*
Category × Spatial frequency × Presentation time	(2, 13) < 0.1	.960	(2, 13) = 1.1	.357

*Indicates a p value lower than .05.

$p = .002$]. This spatial frequency effect on subjects' accuracy also significantly interacted with stimulus category (Faces: FS = LP > HP; Words: FS > HP = LP) [Faces FS vs. LP: $t(29) = 0.1, p = .939$; Faces FS vs. HP: $t(29) = 3.0$, $p = .006$; Faces LP vs. HP: $t(29) = 2.8$, $p = .008$; Words FS vs. HP: $t(29) = 2.5, p = .017$; Words FS vs. LP: $t(29) = 2.2, p = .039$; Words HP vs. LP: $t(29) = 1.5$, $p = .139$] as well as with presentation time (brief presentation time < long presentation time for HP and LP, but not for FS) [HP: $t(29) = 2.8, p = .010$; LP: $t(29) = 3.4$, $p = .002$; FS: $t(29) = 1.6, p = .114$].

ERP Results

P1. We performed a 2 × 3 × 2 × 2 (Category × Spatial frequency × Presentation time × Hemisphere) within-subjects ANOVA on P1 peak amplitude followed by post hoc t tests (see Table 5 and Figure 5A for main effects and interactions). The spatial frequency composition of the stimulus significantly influenced the P1 peak amplitude, where HP > LP > FS [HP vs. LP: $t(119) = 3.1, p = .002$; HP vs. FS: $t(119) = 4.5, p < .001$; LP vs. FS: $t(119) = 2.4$, $p = .017$]. P1 amplitude was also larger for long presentation times. Finally, the P1 peak amplitude was greater in the RH compared to the LH, regardless of conditions.

N170. The same ANOVA was also performed on the peak amplitude of the N170 followed by post hoc t tests (see Table 6 and Figure 5B for main effects and interactions). As in Experiment 1, N170 amplitude was larger for words than for faces. The N170 was also greater for brief presentation time than for long presentation time. In addition, this words > faces N170 difference was larger for long, than for brief presentation times, as revealed by a Category × Presentation time interaction and post hoc t tests [average words–faces difference in long presentation time = 1.49 μV in favor of words; average words–faces difference in short presentation time = 0.73 μV in favor of words; $t(89) = 3.32$, $p = .001$]. Again, as in Experiment 1, there were no global effects of N170 lateralization ($p > .2$). Furthermore, a significant Category × Hemisphere interaction revealed that words and faces were differentially lateralized, where N170 peak amplitude for words was LH > RH [$t(89) = 4.0$, $p < .001$], and for faces was RH > LH [$t(89) = 2.2$, $p = .031$]. Presentation time also influenced relative N170 lateralization, in that the N170 to long presentation times was significantly left lateralized

Table 5. Summary of Statistics for the Peak Amplitude of P1 in Experiment 2

	F	*p*
Category	(1, 14) = 0.4	.521
Spatial frequency	(2, 13) = 4.4	.034*
Presentation time	(1, 14) = 7.3	.017*
Hemisphere	(1, 14) = 11.1	.005*
Category × Spatial frequency	(2, 13) = 2.8	.094
Category × Presentation time	(1, 14) = 0.2	.630
Category × Hemisphere	(1, 14) = 3.3	.092
Spatial frequency × Presentation time	(2, 13) = 0.1	.912
Spatial frequency × Hemisphere	(2, 13) = 0.3	.734
Presentation time × Hemisphere	(1, 14) = 4.0	.065
Category × Spatial frequency × Presentation time	(2, 13) = 0.2	.843
Category × Spatial frequency × Hemisphere	(2, 13) = 0.1	.958
Category × Presentation time × Hemisphere	(1, 14) = 0.3	.584
Spatial frequency × Presentation time × Hemisphere	(2, 13) = 1.2	.323
Category × Spatial frequency × Presentation time × Hemisphere	(2, 13) = 1.5	.257

*Indicates a p value lower than .05.

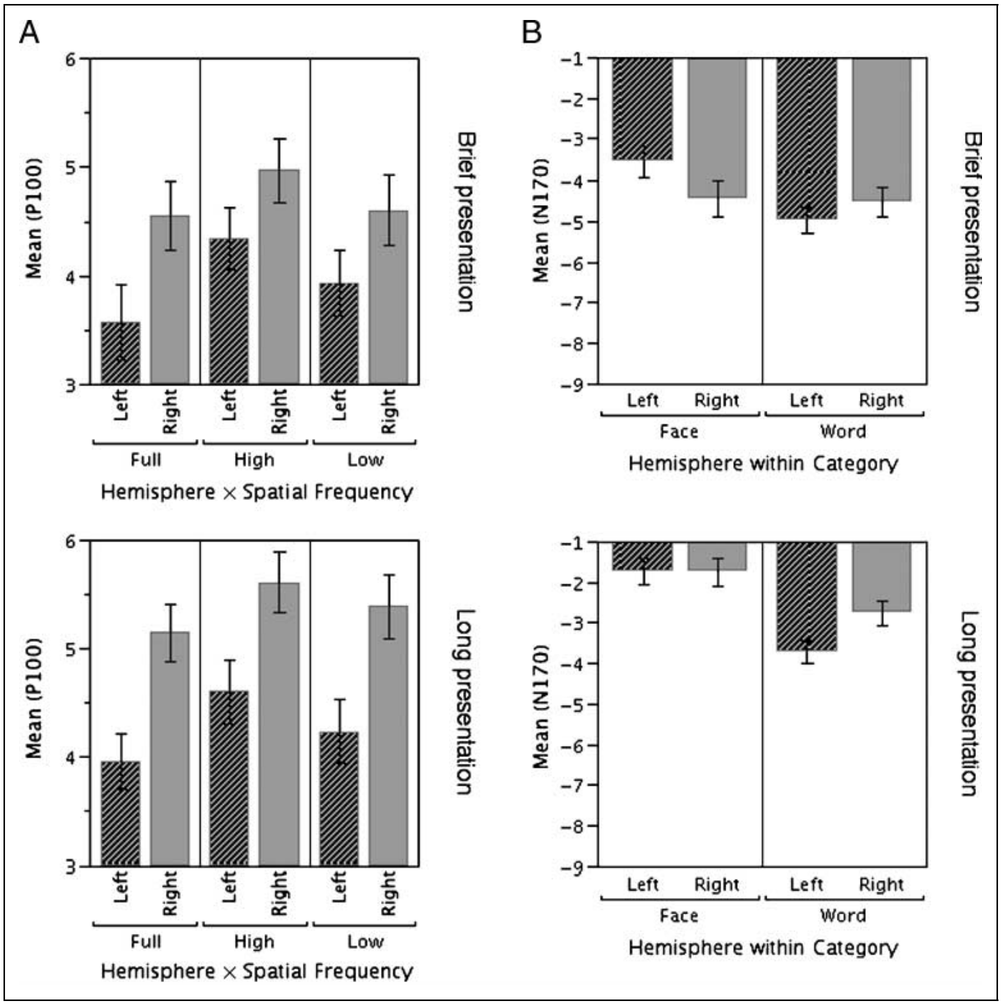


Figure 5. Average of individual peak amplitude (A) for P1 and (B) for N170 in Experiment 2.

[$t(89) = 2.6, p = .011$], with the N170 to brief presentation times showing no significant lateralization (although there was a nonsignificant numerical trend for right lateralization) [$t(89) = 1.1$, $p = .288$]. As with Experiment 1, there was no Hemisphere × Spatial frequency interaction (indeed, the numerical trend was opposite that predicted for Experiment 1); however, we did not find the predicted three-way interaction of Hemisphere × Spatial frequency × Presentation time. Substantially, the same results were found with an analysis of the peak-to-peak difference between the P1 and N170.[6]

Discussion

Influences on the Lateralization of the N170

As observed in Experiment 1, stimulus category influenced N170 lateralization, with a significant left-lateralized N170 to words and right-lateralized N170 to faces. The right-lateralized N170 to faces appeared to be driven by responses during short presentation times, in that there was no significant RH > LH N170 in the long presentation time condition. This result replicates and clarifies the findings of Experiment 1. Also as in Experiment 1, there was no overall effect of spatial frequency on N170 lateralization.

Contrary to our hypothesis, decreasing presentation time did not reveal any spatial-frequency-dependent N170 asymmetries. Indeed, a novel finding of Experiment 2 was that the length of time a stimulus was presented influenced N170 lateralization regardless of spatial frequency content or stimulus category: For long presentation times, the N170 was LH > RH, whereas for brief presentation times, the N170 was not strongly lateralized (albeit with a very weak RH > LH trend). This is consistent with the experimental results of Sergent (1982a), who observed an RH advantage for briefly presented faces (40 msec) but an LH advantage for faces presented for a longer period (200 msec). This is also consistent with results from a positron emission tomography study of silent reading (Price, Moore, & Frackowiak, 1996) that demonstrated an increase in regional cerebral blood flow (rCBF) with short (150 msec) versus long (1000 msec) presentation time in several RH, but not LH, regions (including the middle temporal gyrus, temporo-parietal junction, inferior parietal sulcus, frontal operculum, and inferior frontal gyrus). Conversely, rCBF increases related to greater stimulus duration (1000 msec > 150 msec)

Table 6. Summary of Statistics for the Peak Amplitude of the N170 in Experiment 2

	F	*p*
Category	(1, 14) = 11.3	.005*
Spatial frequency	(2, 13) = 1.5	.250
Presentation time	(1, 14) = 30.5	<.001*
Hemisphere	(1, 14) = 0.1	.742
Category × Spatial frequency	(2, 13) = 3.4	.064
Category × Presentation time	(1, 14) = 8.1	.013*
Category × Hemisphere	(1, 14) = 17.1	.001*
Spatial frequency × Presentation time	(2, 13) = 1.9	.193
Spatial frequency × Hemisphere	(2, 13) = 3.5	.062
Presentation time × Hemisphere	(1, 14) = 15.2	.002*
Category × Spatial frequency × Presentation time	(2, 13) = 0.9	.444
Category × Spatial frequency × Hemisphere	(2, 13) = 0.3	.771
Category × Presentation time × Hemisphere	(1, 14) = 4.0	.066
Spatial frequency × Presentation time × Hemisphere	(2, 13) = 0.2	.830
Category × Spatial frequency × Presentation time × Hemisphere	(2, 13) = 1.6	.247

*Indicates a *p* value lower than .05.

were primarily found in LH regions, including the fusiform gyrus, the sensorimotor cortex, and the dorsolateral prefrontal cortex. This pattern of results is consistent with the effects of duration observed in the present study, where left lateralization was found for long stimulus presentations and bilateral activity for shorter stimulus presentation. It is possible that these differences in presentation time might have influenced the types of processing strategies subjects used. For example, longer presentation time might allow for a more featural processing of face and word stimuli, but when briefly presented, the same stimuli might be processed more globally. Because the LH/RH are thought to be more engaged by local/global processing (Moses et al., 2002; Martínez et al., 1997; Hellige, 1993; Delis et al., 1986), such potential differences in processing strategies might explain the differences in the lateralization pattern observed for different presentation times.

Influences on the Amplitude of the N170

As in Experiment 1, N170 amplitude was generally larger for words than for faces, a difference driven primarily by the LH. This words > faces N170 difference was further augmented under longer presentation times.

Unlike in Experiment 1, where HP stimuli elicited a larger N170 amplitude relative to their LP and FS counterparts, in Experiment 2, spatial frequency did not appear to influence the amplitude of the N170.[7]

Finally, Experiment 2 suggested that longer presentation times are associated with a larger P1 and smaller N170 relative to shorter presentation times. This finding relates to those of Price et al. (1996), who reported rCBF increases to longer presentation times in regions involved in early visual processing; this may correspond to the larger P1 associated with longer presentations in the present study. As noted above, Price et al. also observed that, in RH higher-order regions involved in word processing, rCBF increased as stimulus duration decreased. These "negative duration" effects, which may reflect increased attention to short lived stimuli, may possibly relate to the negative effect of presentation time on the N170 component we observed in Experiment 2.

EXPERIMENT 3

Although it is possible to match face and word stimuli on certain dimensions such as spatial frequency and luminance, stimulus dimensions are difficult to equate over the two categories. For instance, in Experiment 1 and Experiment 2, although both face and word stimuli were presented in rectangles of the same size (with words and faces having approximately the same width), it might be argued that word stimuli were "smaller," as the meaningful part of the stimulus occupied fewer degrees of visual angle on the vertical axis relative to face stimuli. In this regard, it is almost impossible to morph word stimuli into face-equivalent dimensions without affecting the naturalistic quality of the font. Indeed, one might argue that faces and words do truly differ in size in the natural world; single words in newspapers or even in road signs tend to subtend less than one degree of visual angle (for instance, the words in this article), whereas single faces can often occupy up to tens of degrees of visual angle in both dimensions.

Because of these intrinsic face–word differences, it would seem particularly important to determine if stimulus size influences brain lateralization. It is, however, important to consider that any modification of size is accompanied by a modification of spatial frequency. Reducing the size of an image will increase its spatial frequency as measured in cycles/degree: The same cycles are compressed in less degrees of visual angle in the smallest picture. On the other hand, reducing the size of an image will slightly diminish its spatial frequency in cycles/image because some of the high SF details will be lost (Sowden & Schyns, 2006). Keeping these considerations in mind, Pederson and Polich (2001) presented matrices of different sizes that held spatial frequency in cycles/degree constant across all sizes (larger matrices simply contained more cells than smaller ones, and thus, were the same cell "resolution"). Using the divided visual field paradigm, they found that stimulus size did influence the pattern of lateralization even when spatial frequency was kept constant. When subjects judged whether the number of filled cells was even or odd, an RVF (LH) advantage was found for small matrices, with an LVF (RH) advantage for larger matrices. Further data to support an influence of size on lateralization come from divided visual field and neuroimaging studies of hierarchical form perception—such as a large A made of B's. However, these studies have usually been interpreted as a difference in the local/global level of processing (Moses et al., 2002; Martínez et al., 1997; Sergent, 1982b).

Pilot results from our laboratory are also consistent with these reports of size effects on lateralization. In a previous unpublished experiment, we presented stimuli that were twice the size of those used in Experiment 1 and Experiment 2, but that were otherwise identical. N170 responses to these larger face stimuli were significantly right lateralized, whereas the N170 response to larger words was generally nonlateralized. Thus, it may be that this RH "shift" is driven by stimulus size alone.

Our third experiment tests the hypothesis that smaller face and word stimuli should elicit a left-lateralized N170, whereas larger stimuli should elicit a right-lateralized N170. In this experiment, we systematically varied stimulus size and resolution to disentangle the effects of size from those of spatial frequency modifications that inevitably accompany any size modification. Variation of resolution was chosen over LP spatial frequency filtering because the variation of resolution affects the whole spatial frequency spectrum (with an emphasis on HSF), like a variation of size or distance whereas LP filtering only affects a specific band of the spectrum.

Methods

Participants

Thirteen participants (20–40 years old, mean age = 30 years; 7 women) were recruited using the same inclusion and exclusion criteria as in Experiments 1 and 2.

Stimuli

The stimuli used in this experiment were similar to the FS stimuli used in Experiments 1 and 2, but were presented in two different sizes and in two different resolution levels per size: (1) small pictures with high resolution (Small-HiRes)—identical to those presented in Experiment 1 and Experiment 2, with 5° × 6.5° of visual angle from a viewing distance of 57 cm, and a resolution of 28 pixels/cm (140 pixels × 182 pixels); (2) large stimuli with high resolution (Large-HiRes), with 10° × 13° of visual angle, and a resolution of 28 pixels/cm (280 pixels × 364 pixels); (3) small stimuli with low resolution (Small-LoRes), with 5° × 6.5° of visual angle, and a resolution of 14 pixels/cm (70 pixels × 91 pixels); and (4) large stimuli with low resolution (Large-LoRes), with 10° × 13° of visual angle, and a resolution of 14 pixels/cm (140 pixels × 182 pixels).

Spatial frequency in cycles/degree increased proportionally to the decrease of size, but decreased with a decrease of resolution. In sum, spatial frequency in cycles/degree increased in the following order: Large-LoRes < Large-HiRes < Small-LoRes < Small-HiRes. When spatial frequency was measured in *cycles/image*, spatial frequency decreased with the decrease of size and with the decrease of resolution. Interestingly, small pictures with high resolution presented the same spatial frequency composition in cycles/image as large pictures with low resolution. In other words, spatial frequency in cycles/image increased as follows: Small-LoRes < Small-HiRes = Large-LoRes < Large-HiRes.

Design

This 2 × 2 × 2 within-subjects design crossed stimulus category (faces/words), size (small/large), and resolution (HiRes/LoRes). Behavioral dependent variables were RT and accuracy on the one-back task; electrophysiological dependent variables were the amplitude of the N170 and P1 component on the LH and RH montages.

Procedure

Eight blocks of stimuli were presented in random order, according to the procedure described for Experiment 1.

ERP Analysis

ERPs were analyzed as in Experiments 1 and 2. One participant was eliminated from analyses due to a high concentration of eye movements; the data presented are based on 12 participants. The time window for the N170 was determined as in Experiments 1 and 2 and was 99–199 msec; time window for the P1 component was set to 67–147 msec.

Results

Behavioral Results

2 × 2 × 2 (Category × Size × Resolution) Within-subjects ANOVAs were performed on RT and accuracy (see Table 7 for cell means). For RT, neither main effects nor interaction of factors was significant. For accuracy, only stimulus category had a significant effect [$F(1, 11) = 9.0; p = .010$], where accuracy for faces was slightly lower than for words.

ERP Results

P1. We performed a 2 × 2 × 2 × 2 (Category × Size × Resolution × Hemisphere) within-subject ANOVA on P1

Table 7. Summary of Behavioral Data in Experiment 3

	Misses (%)	*False Alarms (%)*	*Response Time (msec)*
Faces			
Large-HiRes	6	1	757
Large-LoRes	8	<1	750
Small-HiRes	12	<1	759
Small-LoRes	5	1	775
Words			
Large-HiRes	2	<1	782
Large-LoRes	2	<1	768
Small-HiRes	3	<1	790
Small-LoRes	4	0	785

peak amplitude. Only the main effect of hemisphere was significant [$F(1, 11) = 8.0$; $p = .017$], where LH > RH—a pattern opposite that of Experiment 2.

N170. The same ANOVA was also performed on N170 peak amplitude, followed by post hoc t tests on individual contrasts (see Table 8 and Figure 6 for statistics main effects and interactions). As in Experiment 1 and Experiment 2, the peak amplitude of the N170 was not globally lateralized, but a Category × Hemisphere significant interaction suggested that faces and words elicited a different pattern of lateralization. Post hoc t tests revealed that, for words, the N170 was larger in the LH than in the RH [$t(47) = 4.8, p < .001$], whereas for faces, the N170 was nonlateralized [$t(47) = 1.7, p = .094$]. Interestingly, there was no significant Size × Hemisphere interaction ($p > .2$). Stimulus size did interact with resolution, where N170 amplitude was Small-LoRes > Large-HiRes = Small-HiRes = Large-LoRes [Small-LoRes vs. Large-HiRes: $t(47) = 1.2$, $p = .238$; Small-LoRes vs. Small-HiRes: $t(47) = 2.5, p = .015$; Small-LoRes vs. Large-LoRes: $t(47) = 2.1$, $p = .042$; Large-HiRes vs. Small-HiRes: $t(47) = 0.9, p = .347$; Large-HiRes vs. Large-LoRes: $t(47) = 1.3$, $p = .192$; Small-HiRes vs. Large-LoRes: $t(47) = 0.1$, $p = .892$]. However, this overall pattern was quite different when broken down by stimulus category, as shown by a significant interaction of Size × Category × Resolution. Separate ANOVAs on faces and words revealed quite category-specific effects: For faces, there was a significant Size × Resolution interaction [$F(1, 11) = 0.511, p = .011$]. Post hoc t tests showed that for HiRes stimuli, N170 amplitude was greater for large-sized versions [$t(23) = 5.3$, $p < .001$], whereas for LoRes stimuli, the pattern was the opposite, for instance, small > large [$t(23) = 2.6, p = .015$]. In contrast, for words, there were no significant modulations of N170 amplitude by size [$F(1, 11) = 0.4$, $p = .523$] or resolution [$F(1, 11) = 2.2, p = .165$], nor did the two interact [$F(1, 11) = 1.6, p = .227$]. Substantially, the same results were found with an analysis of the peak-to-peak difference between P1 and N170.[8]

Discussion

Influences on the Lateralization of the N170

As in Experiments 1 and 2, stimulus category had a significant influence on N170 lateralization. In the present experiment, the N170 to words was larger in the LH than in the RH, whereas the N170 to faces was nonlateralized. Contrary to our hypothesis, stimulus size and resolution did not modulate N170 lateralization, suggesting that the differential N170 lateralization for words and faces is not due to differences in the "meaningful size" of these stimuli.

Influences on the Amplitude of the N170

In contrast to N170 *lateralization*, N170 *amplitude* was modulated by stimulus size and resolution—and this effect was highly category-specific. The N170 elicited by words was of comparable amplitude regardless of size or resolution. For faces, the pattern was more complex, with Small-HiRes and Large-LoRes stimuli evoking a smaller N170 than Large-HiRes and Small-LoRes stimuli.

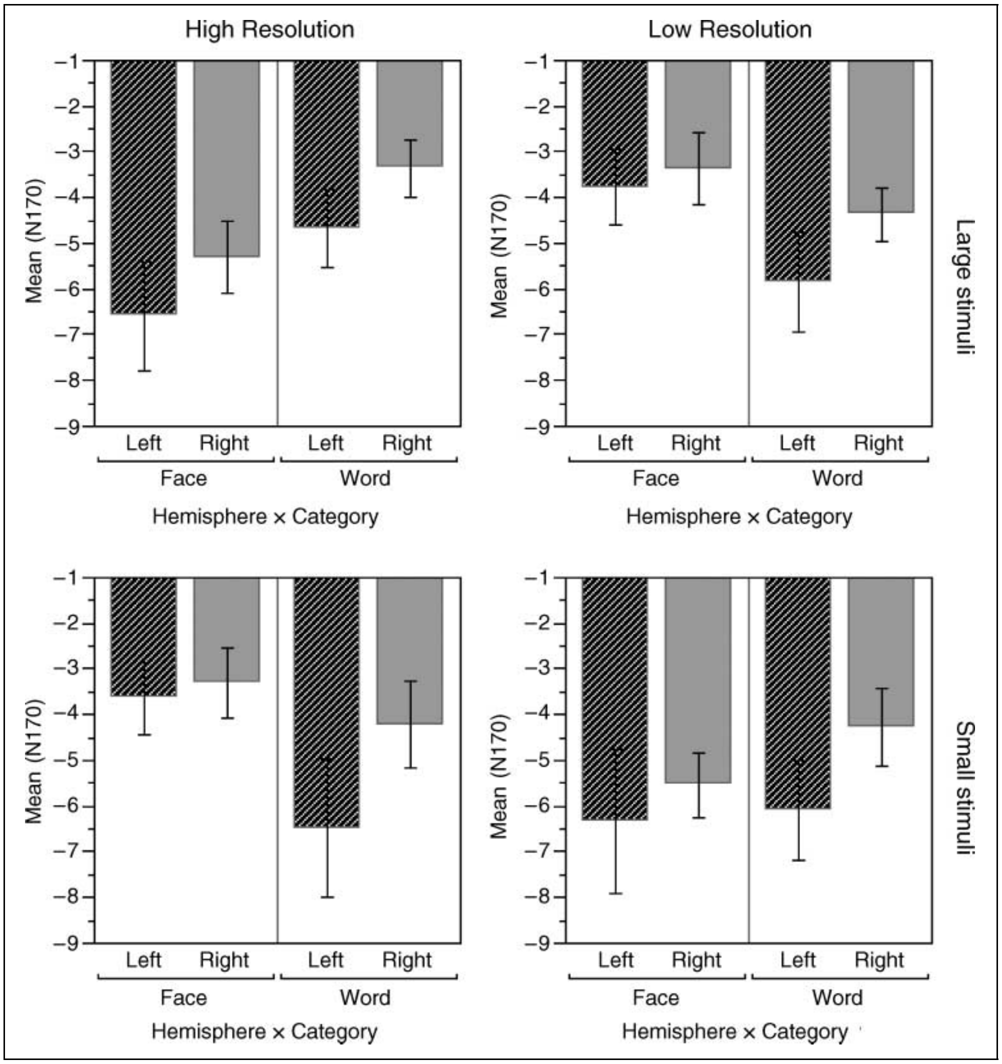
We hypothesize that the Small-HiRes and Large-LoRes stimuli may represent an "optimal" level of detail for

Table 8. Summary of Statistics for the Peak Amplitude of the N170 in Experiment 3

	F	*p*
Category	(1, 11) = 0.1	.733
Site	(1, 11) = 0.3	.613
Resolution	(1, 11) = 0.7	.435
Hemisphere	(1, 11) = 3.3	.096
Category × Size	(1, 11) = 0.4	.528
Category × Resolution	(1, 11) = 0.4	.531
Category × Hemisphere	(1, 11) = 8.6	.014*
Size × Resolution	(1, 11) = 5.0	.047*
Size × Hemisphere	(1, 11) = 0.2	.680
Resolution × Hemisphere	(1, 11) = 0.3	.606
Category × Size × Resolution	(1, 11) = 8.6	.014*
Category × Size × Hemisphere	(1, 11) = 2.4	.149
Category × Resolution × Hemisphere	(1, 11) < 0.1	.910
Size × Resolution × Hemisphere	(1, 11) = 0.5	.492
Category × Size × Resolution × Hemisphere	(1, 11) = 1.8	.203

*Indicates a p value lower than .05.

Figure 6. Average of individual peak amplitude for the N170 in Experiment 3.



efficient face processing, in that they share the same spatial frequency in cycles/image. The nonoptimal Large-HiRes and Small-LoRes stimuli may present an additional challenge to visual processing mechanisms by presenting too much or too little information, thereby generating a larger N170 amplitude. This result might be similar to the well-known face-inversion effect, where N170 amplitude for the nonoptimal inverted faces is increased relative to upright faces.

Recall that in Experiments 1 and 2, there was a somewhat unexpectedly greater N170 amplitude for words relative to faces. This result was replicated here in Experiment 3, in that the stimuli of the same size and resolution as in Experiment 1 and Experiment 2 (Small-HiRes) again evoked a greater N170 to words than to faces ($p = .067$). However, the results of Experiment 3 also showed that this words > faces N170 difference was strongly influenced by image size and resolution. For example, the opposite pattern (e.g., N170 amplitude for faces > words, $p < .05$) was found for Large-HiRes stimuli; the relative N170 amplitudes for words and faces in Large-LoRes and Small-LoRes conditions fell somewhere in between. From these results, it could be suggested that words elicit larger N170 amplitudes when they are small-sized, and faces when they are larger, as these are their ''natural'' sizes in the visual environment. However, low-resolution stimuli show the opposite trend, thereby ruling out a simple size-based explanation. In reality, both size and resolution influence the relative amplitude of the N170 for words and faces.

GENERAL DISCUSSION

In this set of experiments, we tested three hypotheses concerning the possible influences on N170 lateralization for words and faces. Our first hypothesis was that N170 lateralization would be influenced by the spatial frequency composition of the stimulus. The results of Experiment 1 showed that spatial frequency composition did not have a domain-general effect on lateralization. Rather, for word stimuli, the degree of left lateralization was modulated by spatial frequency content—indeed, a left-lateralized N170 response to written words seemed to depend upon the presence of spatial information above

4 cycles/degree. In contrast, spatial frequency composition did not appear to affect N170 lateralization to faces.

Our second hypothesis was that spatial-frequency-related hemispheric asymmetries would increase with shorter stimulus presentation times. The results of Experiment 2 suggested that stimulus duration can influence N170 lateralization, and that the relative shift in asymmetries is not modulated by spatial frequency composition. For example, face stimuli elicited a more robustly right-lateralized N170 when presented for 30 msec than when presented for 700 msec, regardless of spatial frequency content. In general, stimuli presented for a longer period of time tended to evoke a more left-lateralized N170, whereas briefly presented stimuli evoked a more bilateral or somewhat right-lateralized N170. Finally, our third hypothesis suggested that stimulus size would also influence N170 lateralization, a hypothesis that was refuted by the results of Experiment 3, where neither size nor resolution manipulations had any effect on N170 lateralization.

Over these three experiments, we showed that the relative amplitude and lateralization of the N170 component—an oft-used index of ''higher-level'' visual characteristics—may be modulated by varying lower-level psychophysical properties, such as spatial frequency, size, resolution, and stimulus duration. In terms of N170 lateralization, our results showed that words and faces did indeed differ in this regard, but that this difference might be driven not only by stimulus category (e.g., verbal versus visuospatial) but also by the underlying physical and temporal characteristics of the stimuli themselves. In other words, differential lateralization for words and faces is modulated by the psychophysical properties and presentation parameters of the stimuli, but is not wholly explained by these factors.

Our results also suggested that words and faces do not clearly differ in the overall amplitude of their N170. Although numerous studies have systematically demonstrated a larger N170 to faces than to objects (Bentin, Allison, Puce, Perez, & McCarthy, 1996), the evidence presented in these three experiments suggest that the N170 could be as ''word-sensitive'' as it is ''face-sensitive.'' Indeed, the relative N170 amplitude to both word and face stimuli is strongly contingent on stimulus duration, size, and resolution parameters—to the extent that under some conditions, word stimuli can elicit an N170 of larger amplitude than similarly presented face stimuli. In particular, the results of Experiment 3 suggest that stimulus size and resolution have a tremendous effect in varying the relative amplitude of the N170 to faces and words. In the three experiments presented, the N170 was systematically larger for words than for faces when the dimensions were 5° × 6.5° and the resolution was high. However, when stimulus size was doubled (and resolution kept high), the N170 was significantly larger for faces than for words. Stimuli with low resolution fell somewhere between these two patterns. This suggests that any study that did not use the same size or resolution could have found a different pattern of results. In Rossion et al. (2003) and Joyce and Rossion's (2005) study, in particular, face stimuli subtended 4.19° × 5.08°, whereas word stimuli were presented in a rectangle of 6.96° × 3.01°. The dimensions of the word itself inside the background are not mentioned, but based on the stimulus provided, they probably approximated 3° × 1.30°. These dimensions in degrees of visual angle are not massively different from the small stimuli in our studies, but viewing distance was almost twice as high (so actual metric stimulus size was almost double). Because size in degrees of visual angle and resolution influences the amplitude of the N170, it follows logically that viewing distance could also influence the amplitude of the N170. A stimulus of 5° viewed at a distance of 57 cm could differ from a stimulus of 5° viewed at a distance of 100 cm. The results of Experiment 3 suggest that even a small difference like this one could explain the opposite pattern of results obtained between Rossion et al. and the present studies. An alternative explanation is that, in the present studies, unlike in the Rossion et al. study, faces were presented in their natural background, with neck, shoulder, and hair. A study by Bentin, DeGutis, D'Esposito, and Robertson (2007) showed that, in normal participants, the N170 was larger to faces when the face contour was missing than when they were presented naturally with neck, shoulder, and hair. Thierry, Martin, Downing, and Pegna (2007) also found that the N170 could be sensitive to interstimulus perceptual variance (ISPV) in that stimuli that were perceptually more homogeneous drove a larger N170 compared to stimuli that were perceptually more varied. It is reasonable to infer that the faces presented by Rossion et al. had a lower ISPV compared to the faces presented in the present studies because of the absence of neck, shoulder, and especially hair. This could be another reason why the N170 in Rossion's study was larger for faces than for words, whereas this was not always the case in our studies.

More generally, our results force the conclusion that the N170 ERP component is a complex brain response, one that can be modulated by multiple low- and high-level factors. When interpreting studies from the literature, one should keep in mind that the experimental procedure can strongly influence the pattern of results. Although it is tempting to state that face processing elicits a right lateralized N170 or that the N170 to faces is larger relative to the N170 to words, our results show that this component reflects more a complex, and ultimately, more interesting set of perceptual and neural influences.

Acknowledgments

This work was supported by MRC grant PG97 15587 to M. J. and G0400341 to F. D., as well as by the Canadian Institutes of Health Research and Birkbeck, University of London to E. M.

We thank the participants who took part in these studies; Agnes Volein, Sarah Fox, and Sara Bernardelli for their help with testing participants; Matthew Morley and Robert Leech for their help with computer programming.

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Notes

1. In adults, processing of upright faces is based primarily upon the analysis of spacing among features (e.g., distance between the eyes, or the distance between the mouth and the chin; Mondloch, Le Grand, & Maurer, 2002), and thus involves multiple types of visuospatial processing.
2. Development of the MacBrain Face Stimulus Set was overseen by Nim Tottenham and supported by the John D. and Catherine T. MacArthur Foundation Research Network on Early Experience and Brain Development. Please contact Nim Tottenham at tott0006@tc.umn.edu for more information concerning the stimulus set.
3. It could be argued that the task differed between words and faces in that words were familiar stimuli, whereas faces were not. It was decided in this study not to use famous faces as these could elicit a name and that was not desirable in a study comparing words and faces. However, there is evidence in the literature that familiarity of a face does not influence early components such as the P1 and N170, but only later components (Bentin & Deouell, 2000; Eimer, 2000). Because only the P1 and N170 were analyzed in this study, it can be assumed that the results would not be influenced by familiarity of one class of stimuli.
4. The same effects were observed when the N170 was extracted from lateral channels concentrated around the mastoid area (left = 57, 58, 59, 64, 65; right = 91, 92, 96, 97, 101), except that the stimulus effect did not reach significance level (Word > Face; $p = .064$).
5. As any filter, the filter used in Experiment 1 first transformed the image in the frequency domain using a Fourier transform, multiplied with a Gaussian filter and then retransformed into the spatial domain. In this filter, the HP image was created by subtracting an LP image using an identical cutoff to the original image. This operation set the mathematically arbitrary zero values to black. (In black-and-white spatial filtering, a zero value is arbitrarily chosen to be either black or white, meaning that if the filter encounters no cycles of spatial frequency, as if the image is uniform, it will return a black or white image depending on the color of the zero value. The filter then depicts the edges in the opposite color to the zero value.) We realized that, in the literature, the HP image is more often created by directly applying a HP filter rather than by subtraction (for example, the filter used by Peyrin et al., 2003) and that the polarity of the zero value is consequently white (Iidaka et al., 2004; Peyrin, 2003; Peyrin et al., 2003; Halit, 2002; Okubo & Michimata, 2002). In Experiment 2, to make our HP stimuli more similar to the ones presented in the literature, the polarity of the image was inverted before and after filtering. This procedure returns a stimulus equivalent to a simple HP filter and sets the zero value to white. Besides making the HP stimuli more similar to the ones used in the literature, this procedure had a few advantages. First, black-edged face images are more "naturalistic" and they require less brightness modification in order to equilibrate them to their FS and LP counterparts. Finally, by inverting edge polarity, we are able to ascertain whether previous findings were driven solely by spatial frequency, and not by modifications of other visual parameters (such as brightness and contrast) that invariably accompanies any spatial filtering. Nevertheless, these two types of HP stimuli have the same spatial frequency composition, both showing an attenuation of spatial frequencies lower than 4 cycles/degree.
6. To take into account any potential differences in the P1 preceding the N170, the same ANOVA was also performed on the P1 to N170 *peak-to-peak* difference. The results were the same as for the N170 peak amplitude, except that this peak-to-peak difference was greater in the RH compared to the LH *regardless* of category, as revealed by a main effect of hemisphere and no Hemisphere × Category interaction. Note that for peak-to-peak difference, the interaction of presentation time and hemisphere showed only a trend at $p = .08$.
7. Indeed, in Experiment 2, there was a tendency for the N170 amplitude to be *smaller* for HP faces relative to LP and FS faces. We suggest that this difference is driven by the differences in edge polarity, as discussed in the introduction to Experiment 2. As noted, a double polarity inversion does not change the spatial frequency of the image and both types of HP-filtered images had a similar power spectrum. Nevertheless, N170 amplitude to the HP-filtered images from Experiment 1 and Experiment 2 differed greatly, in that the Experiment 1 HP-filtered images drove the largest N170 amplitude, whereas the Experiment 2 HP-filtered images drove the smallest N170. This pattern of results suggests that changes in N170 amplitude that were associated with spatial frequency bands in Experiment 1 might not be the effect of the spatial frequency itself, but instead might be due to variation in other psychophysical parameters that invariably accompany spatial filtering, such as specific patterns of contrast. Furthermore, it is interesting to note that the stimuli used in Experiment 2, which were made more similar to the ones used in the literature, elicited the same results generally found in the literature (Halit et al., 2006; Goffaux et al., 2003): a smaller N170 to HP faces compared to FS and LP.
8. The same ANOVA on the P1–N170 peak-to-peak difference revealed that this amplitude was larger in the LH compared to the RH regardless of stimulus category, as revealed by a main effect of hemisphere. Also, the Size × Resolution significant interaction only appeared as a weak trend in the peak-to-peak difference ($p = .116$). The other results were the same as the results on peak amplitude of the N170.

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