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# The effects of face spatial frequencies on cortical processing revealed by magnetoencephalography

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**Abstract**

To study the spatial frequency (SF) effects on cortical face processing, we recorded magnetoencephalographic responses in seven healthy subjects to upright and inverted human faces. Four face types were used, including original (broad-band SF, BSF), low SF (LSF, <5 cycles/face), middle SF (MSF, 5–15 cycles/face), and high SF (HSF, >15 cycles/face) face images. Using equivalent current dipole (ECD) modeling, neuromagnetic M170 responses peaking around 160–185 ms were localized in right occipitotemporal region across subjects to BSF faces. M170 responses to LSF faces showed longer latency and smaller amplitude compared with those to BSF faces. We found no significant difference between BSF, MSF, and HSF conditions in M170 amplitude or latency. ECD locations for the four upright face conditions were close to one another, although the mean locations for MSF or HSF seemed more medial than those for BSF or LSF. Longer latencies for inverted than upright faces were observed in BSF (183.4 ± 8.5 ms versus 168 ± 6.9 ms, $P < 0.001$) and LSF face conditions (223.6 ± 13.1 ms versus 207.3 ± 16.3 ms, $P < 0.01$). M170 ECDs were located more medial for inverted than upright images in either BSF or LSF condition. In conclusion, the less M170 activation to LSF faces suggests that face parts information is important for early face processing. The cortical representations in right occipitotemporal region for configural and face feature processing are overlapping. Our findings on the face inversion effect suggest that inverted BSF and LSF faces may be processed as objects.


*Keywords:* Spatial frequency; Filtered face; Occipitotemporal; Face inversion; Magnetoencephalography; Human; M170

Spatial frequency (SF) information of faces is important for one to identify and discriminate individuals [3]. High SF (HSF) information in a face represents the fine scale cues such as contours or shapes of face parts [5,8,15,27], whereas low SF (LSF) conveys configural information [3,5,27]. Human face perception depends on the physiognomic evaluation of local features and global configuration [4]. Previous behavior studies suggest that face recognition preferentially relies on SF between 8 and 16 cycles/face, as subjects feel easier to recognize faces with than those without that SF information [5,21]. However, there remain controversies on how SF affects cortical face processing. For example, one event-related potential (ERP) study has suggested a salient role of LSF (below 8 cycles/face) in eliciting N170 responses [10]. In contrast, an important role of HSF (above 24 cycles/face) in fusiform gyrus activation has been shown in one recent functional magnetic resonance imaging (fMRI) study [28]. Thus, it is worthy further clarifying the SF effects on face processing.

Neuropsychological and neuroimaging investigations suggest that upright and inverted faces are processed by anatomically different systems [1,7,13,20]. Earlier ERP

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studies have identified latency delay and sometimes amplitude increase of N170 responses to inverted faces [6,10,14,18,24,25]. In contrast, no significant latency delay was observed for inverted non-face objects [6,16,24]. Thus, face inversion has been useful to evaluate face-specific processing [20,22].

Magnetoencephalography (MEG) records the magnetic fields produced by electric currents during neuronal activation [12]. Unlike scalp electric potentials, MEG activity is not smeared or attenuated by the intervening cerebral and extracerebral tissues. Therefore, the spatial resolution for MEG is better than that for scalp electroencephalography. The temporal resolution for MEG is much better than that for fMRI or positron emission tomography. MEG has been used to study face-related cerebral activation [11,16,26,29].

In this study, using MEG recordings and equivalent current dipole (ECD) modeling, we analyzed the temporal and spatial characteristics of cortical activity elicited by human face images in various face SF (<5, 5–15, and >15 cycles/face) and orientation conditions (upright, inverted). The aims of the present study were: (1) to clarify the systematic effect of SF on human face processing in terms of peak latencies, amplitudes, and locations of ECDs, and (2) to examine the inversion effect on face-activated responses with respect to various SF conditions.

We studied seven healthy, right-handed volunteers (5 men and 2 women; age 24–28 years), with normal or corrected-to-normal vision. None had neurological or psychiatric deficits. Informed consent was obtained from each participant.

Twenty-three gray-scale pictures of male ($n = 21$) and female ($n = 2$) Chinese faces with neutral expressions were used. All faces were without jewelry, or glasses. The face pictures were trimmed to remove background, clothing and hairlines. All faces were unfamiliar to our subjects.

With Gaussian filtering, original faces (broad-band, BSF) were filtered to produce LSF (<5 cycles/face), MSF (5–15 cycles/face), and HSF (>15 cycles/face) face images. We measured the screen luminance by a photometer (Minolta, LS-100, Osaka, Japan) at all 256 gray levels. The result was then used to obtain a linearized table for converting the pixel values of the scaled images to luminance values [15] and for matching equal luminance for all face stimuli.

The original and filtered faces were also turned upside down, resulting in eight stimulus conditions including upright BSF (uBSF), uLSF, uMSF, uHSF, inverted BSF (iBSF), iLSF, iMSF, and iHSF.

We delivered visual face stimuli (Fig. 1) by Presentation 0.52 NBS (Neurobehavioral Systems, Inc., CA, USA) with random order and equal probability. Stimuli with an average 12 cd/m$^2$ in brightness were centered on the screen at 120 cm in front of the subject and subtended a visual angle of 9.5° × 9.5° (vertical × horizontal).

Via a personal computer (Acer Veriton) and LCD projector (Electrohome Electronics, 38-DMD001-EXP, Canada), stimuli were randomly delivered with an interstimulus interval of 1 s. The duration of each stimulus was 500 ms. One

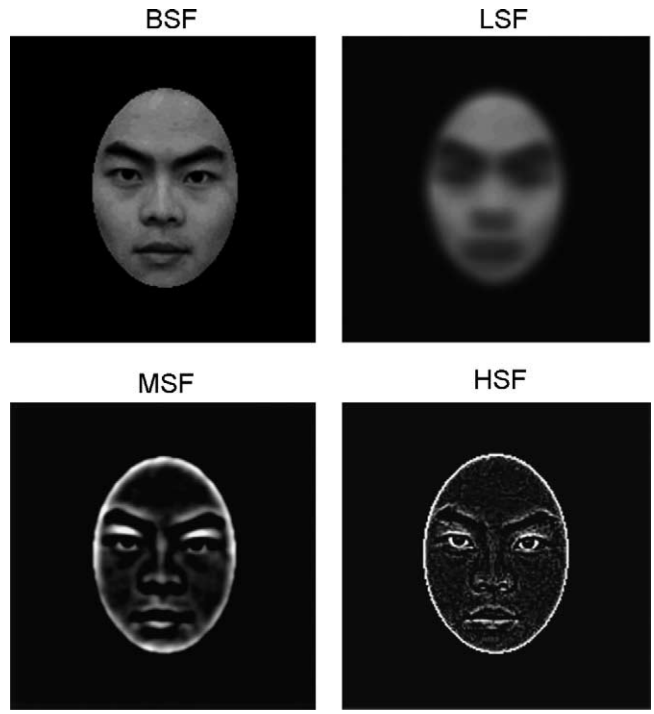


Fig. 1. Examples of upright face stimuli with respect to four spatial frequency (SF) conditions. B, broad-band; L, low (<5 cycles/face); M, middle (5–15 cycles/face); and H, high (>15 cycles/face).

stimulus block consisted of 184 trials (23 face pictures × 8 stimulus conditions). Five stimulus blocks were conducted in each subject, and on average 90–100 responses were obtained for each stimulus condition. Subjects were asked to fixate on the image center, and were required to respond to inverted or upright faces in separate blocks by lifting the right index finger.

MEG recordings were conducted in a shielded room with a whole-scalp 306-channel neuromagnetometer (Vectorview$^{TM}$, Elekta Neuromag, Helsinki, Finland), which comprises 102 identical triple sensor elements. Each sensor element consists of two orthogonal planar gradiometers and one magnetometer. During the recordings, the subject was sitting comfortably with the head supported against the helmet of the magnetometer. The MEG signals were digitized at 600 Hz, and the length of each recorded epoch was 1000 ms including a pre-stimulus baseline of 100 ms. Responses coincident with prominent vertical electro-oculogram signals (>300 uV) were automatically rejected from averaging. Before source analysis, the average responses were further band-pass filtered at 0.1–40 Hz.

The magnetometers have relatively poor signal-to-noise ratio (SNR) in comparison with the planar gradiometers, which may be related to the high sensitivity of magnetometers to both cerebral and extracerebral magnetic fields [12]. Thus, in this study we present MEG data from planar gradiometers, because of relatively poor SNR for magnetometer signals.

The exact location of the head with respect to the sensors was found by measuring magnetic signals produced by currents led to four head indicator coils, placed at known sites on the scalp. The locations of the coils with respect to anatomical landmarks on the head were determined with a three-dimensional (3D) digitizer to allow alignment of the MEG and magnetic resonance (MR) image coordinate systems [12]. MR images of the subject's brain were acquired with a 3 T Bruker Medspec300 scanner or 1.5 T Siemens Magnetom Sonata system (Germany).

Evoked magnetic responses to varying types of faces (uBSF, uLSF, uMSF, uHSF, iBSF, iLSF, iMSF, and iHSF) were individually analyzed. The length of analysis epoch was 350 ms including a pre-stimulus baseline of 50 ms. Within the post-stimulus 300-ms epoch, clear deflections were visually identified to select the time windows and cortical areas of interest for further analysis. During these time windows (from the beginning of the response deflection to its return to the baseline level) the magnetic field patterns were first visually surveyed in 2 ms steps to create the initial estimation of the number of active sources within that time period and to estimate the stability of the magnetic field pattern. Then the ECD that best described a local source current at the response peak was found by a least-squares search using a subset of 20–30 channels around the response area. These calculations resulted in the 3D location, orientation, and strength of the ECD in a spherical conductor, which were based on the subject's own MR images. The positive *x*-, *y*-, and *z*-axes in our head-coordinate system go towards the right preauricular point, the nasion, and the head vertex, respectively.

The goodness-of-fit ($g$) of the ECD model was also calculated to see what percentage of the measured signal variance was accounted for by the ECD. Only ECDs with $g$ value >80%, confidence volume $\leqq 1\,cm^3$, and source amplitude $\geqq 5$ nAm at selected periods of time in the subset of channels were used for the subsequent analysis.

In this paper, our statistic analysis was focused on the ECD (M170) identified at 150–200 ms after stimulus onset, as this response has been accepted as early face-evoked activity in earlier MEG studies [11,16,26,29]. Peak latencies, dipole strengths and ECD locations of M170 responses between different stimulus conditions were tested with face types (BSF, LSF, MSF, and HSF) and face orientations (upright and inverted) as factors by repeated measure analyses of variance (ANOVA) and post hoc statistics tests with Bonferroni corrections. $P < 0.05$ was taken as the significance threshold.

Fig. 2 shows the topographic distribution of MEG signals of Subject 1 in response to BSF faces. Clear deflections peaking around 182 ms were observed over the right posterior head region. The ECD was localized in the right occipitotemporal region, corresponding to N170 in ERP [2,6,9,10,14,18,24,25] or M170 in MEG recordings [11,16,26,29]. This M170 activity on the right occipitotemporal area was obtained from each subject. The left occipitotemporal activation was found in only one of our subjects.

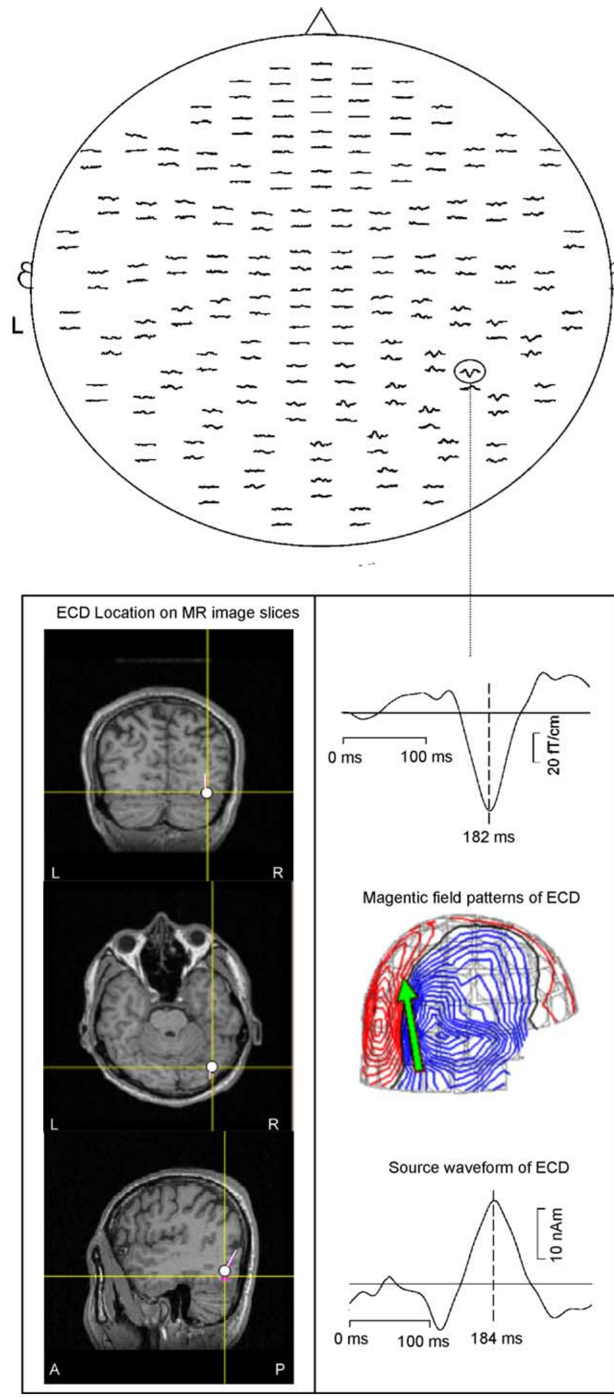


Fig. 2. *Upper panel*: Topographic distribution of evoked magnetic signals from Subject 1 in response to upright unfiltered faces. The head is flatten to a plane and viewed from above with the subject's nose pointing upward. Faces evoked responses are clearly seen on the lateral–posterior region in the right hemisphere, and the encircled signal was enlarged in the lower panel. *Lower right panel*: The enlarged response, its magnetic field pattern, and source waveform fitted by single dipole modeling at the 182-ms peak. *Lower left panel*: The dipole localization (white dots) superimposed over the subject's own MR images. R, right; L, left; A, anterior; and P, posterior.

The ANOVA showed a significant effect of SF on dipole strength ($F_{3,24} = 7.83$, $P < 0.001$). Post hoc analysis revealed that M170 dipole strength was clearly smaller for uLSF (14.4 ± 5.0 nAm) than for uBSF (20.6 ± 6.2 nAm), uMSF (20.4 ± 5.3 nAm), and uHSF (22.4 ± 7.1 nAm) faces ($P < 0.01$). The interaction between SF types and face orientations ($F_{3,48} = 5.536, P < 0.001$) revealed a significant increase in dipole strength for iBSF faces.

An ANOVA with SF showed a significant effect on latencies ($F_{3,24} = 16.6$, $P < 0.001$). As shown in Fig. 3, a significant latency delay was noted for uLSF (207 ± 16.9 ms) faces in comparison with uBSF (168 ± 6.9 ms), uMSF (175.1 ± 9.9 ms), and uHSF (172 ± 6.7 ms) faces ($P < 0.0001$). A significant interaction between SF and face orientation for latencies was found ($F_{3,48} = 13.57$, $P < 0.001$). M170 latencies to iBSF (183.4 ± 8.5 ms) and iLSF (223.6 ± 13.1 ms) were longer than those to uBSF and uLSF, respectively. On average, face inversion caused ∼15 ms latency delay for the BSF and LSF faces. No significant inversion effect was found for MSF and HSF faces ($P > 0.05$).

We did not identify a clear SF effect on cortical localization of M170 responses (*x*-axis: $F_{3,24} = 1.12$, *y*-axis: $F_{3,24} = 0.261$, *z*-axis: $F_{3,24} = 0.984$, all $P > 0.05$), although ECD location for uBSF and uLSF seemed to be more lateral that for uMSF and uHSF. As for the significant interaction effect of SF and orientation (*x*-axis: $F_{3,48} = 3.247, P < 0.005$), we observed smaller *x*-axis values of M170 ECDs for iBSF (40.1 ± 6.4 mm) than uBSF (48.8 ± 3.7 mm, $P < 0.05$). Similarly, *x*-axis values were smaller for iLSF (38.8 ± 3.2 mm) than uLSF (47.6 ± 4.8 mm, $P < 0.005$). However, we did not see significant difference in the *y*-axis and *z*-axis coordinates between inverted and upright faces.

We identified M170 responses to BSF faces in each subject, in line with earlier intracranial [18] and scalp ERP [2,6,9,10,14,24,25], and MEG recordings [11,16,26,29]. We further found that stable M170 responses can be obtained by spatially filtered face images, in agreement with previous monkey studies showing neural activity in face-sensitive brain regions in response to faces with partial SF content [23]. In the present study, moreover, the dipole strength and peak latency of M170 responses for HSF faces (>15 cycles/face) did not significantly differ from those for BSF faces, in line with one earlier fMRI study by Vuilleumier et al. [28] demonstrating similar activation in the fusiform gyrus for filtered faces (>24 cycles/face) and unfiltered faces. McCarthy and coworkers have also obtained equivalent N200 responses for normal faces and line-drawing faces approximating the high-pass filtered images (>12 cycles/face) [18].

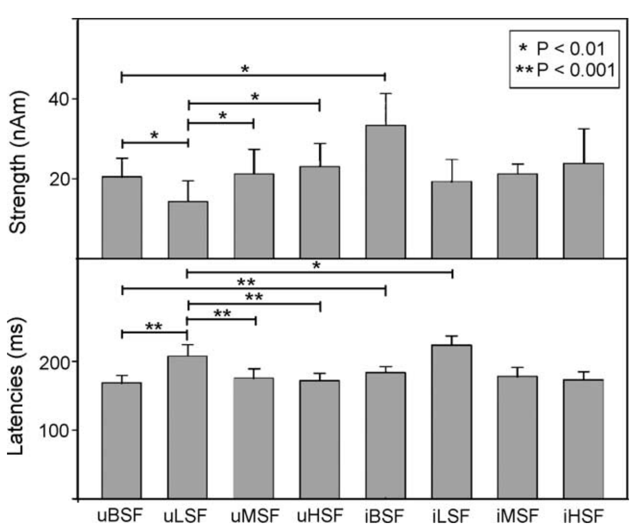


Fig. 3. Mean dipole strengths and peak latencies of face-evoked M170 responses across all subjects with respect to varying spatial frequency conditions. B, broad-band; L, low; M, middle; H, high; u, upright; and i, inverted.

Earlier psychophysical studies have indicated differential roles of distinct SF ranges in face processing [5,15,21,27]. The larger M170 activation for HSF than for LSF faces in our study supported earlier observation of a predominant fusiform activation for HSF than LSF information [28]. HSF components carry fine-grained information that is essential for delicate recognition of identity [8,15,27], whereas LSF components provide only poor information for detailed identification [5,27]. This distinction between HSF and LSF components may explain for the different M170 activation size between both face types in our study. The smaller strength and longer peak latency of the M170 by LSF than BSF faces might be due to removal of local face features and subsequent less processing of face components, although global face configuration was relatively preserved [5,27]. Moreover, the processing difference between LSF and HSF face information has also been proposed in earlier monkey or fMRI studies. LSF faces projects chiefly to the dorsal visual stream via magnocellular channels [17,19], and therefore, less activation for LSF faces (<6 cycles/face) than unfiltered faces in fusiform gyrus was found [28].

Our present observation of reduced M170 for LSF faces and normal M170 for HSF faces seems different from the ERP findings by Goffaux et al. [10] showing attenuated N170 responses for HSF faces. The discrepancy may be related to some methodological differences. First, adding low SF texture background to HSF face images by Goffaux et al. may blur face components in their HSF faces (please see Fig. 1 of the paper by Goffaux et al. [10]). Thus, the reduced N170 activation for HSF faces in their study may be at least partly related to the less clear presentation of face components, because N170 is associated primarily with the face component processing [2,25]. Second, the setting of SF ranges in filtered faces was obviously different. We defined LSF and HSF as <5 and >15 cycles/face, respectively, whereas LSF and HSF by Goffaux et al. were <8 and >32 cycles/face, respectively. Although recent publications have demonstrated the SF effect on face-evoked cortical activation [10,28], the SF range for modulating early face processing has not been well specified. Previous psychophysical studies have shown that subjects had recognition difficulty for faces of <5 cycles/face but not for those of 8 cycles/face [8], which agreed with the normal

N170 for LSF <8 cycles/face reported by Goffaux et al. [10]. The poor recognition performance for faces <5 cycles/face in psychophysical evaluation [8] is in line with the reduced M170 for LSF <5 cycles/face in our present study. In agreement with our good M170 for MSF (5–15 cycles/face), previous psychobehavior studies have shown good recognition for faces with SF at 8–16 cycles/face [5] or 8–13 cycles/face [21].

Face-inversion related latency prolongation for our BSF faces was in line with earlier ERP [6,14,18,24,25] and MEG studies [16,29]. Previous behavior evaluation also reported a longer reaction time for inverted than upright face recognition [3,22,30]. Disruption of configural information consequent to face inversion may be one of the reasons for the latency delay in early cortical processing of faces [20,22,30], because inversion affects the identification of the spatial configuration among face components more than the perception of individual components themselves [3,20,22]. Interestingly, face-inversion effect on M170 latency was found for LSF faces rather than MSF or HSF faces. Our face-inversion latency delay for BSF and LSF may suggest that recognition of BSF and LSF faces relies as much or more on identification of spatial relationship between face components, whereas MSF and HSF faces may be processed by component-based mechanisms.

In addition, our results showed a larger OT activation for inverted than upright BSF faces. The finding is consistent with earlier ERP studies suggesting that inversion of original faces may activate both face and non-face object processing [24,25]. One more explanation for the increased amplitude would be the superimposition of a relatively long-lasting temporal activation associated with difficulty for subjects to recognize inverted than normal faces [9]. However, the effects of face inversion on OT activities remain controversies as some other studies show no clear enhancement by inversing faces [18,29].

In neuropsychological studies, patients with occipitotemporal cortex lesions are unable to recognize upright faces, but they preserve the recognition function for inverted ones [7]. Conversely, patients with object agnosia could normally recognize upright faces, but they are unable to recognize inverted faces or upright objects [20]. Previous fMRI studies have shown that the "inferior temporal object area" is located medial to the "inferior temporal face area" [1,13], but few MEG studies have demonstrated such location differences. In our present study, the ECD locations for iBSF and iLSF faces were more medial than those for uBSF and uLSF faces (see Fig. 4), suggesting that the inverted face is processed as an object.

No inversion effect for MSF and LSF faces may be related to component-based processing mechanisms [3,20,22]. This idea might partly agree with the slightly, although not significantly, longer peak latency for MSF (175.1 ms) and HSF (172 ms) than that for BSF (168.9 ms). However, the locations for MSF and HSF showed no statistically significant difference from those for BSF and LSF, although the former

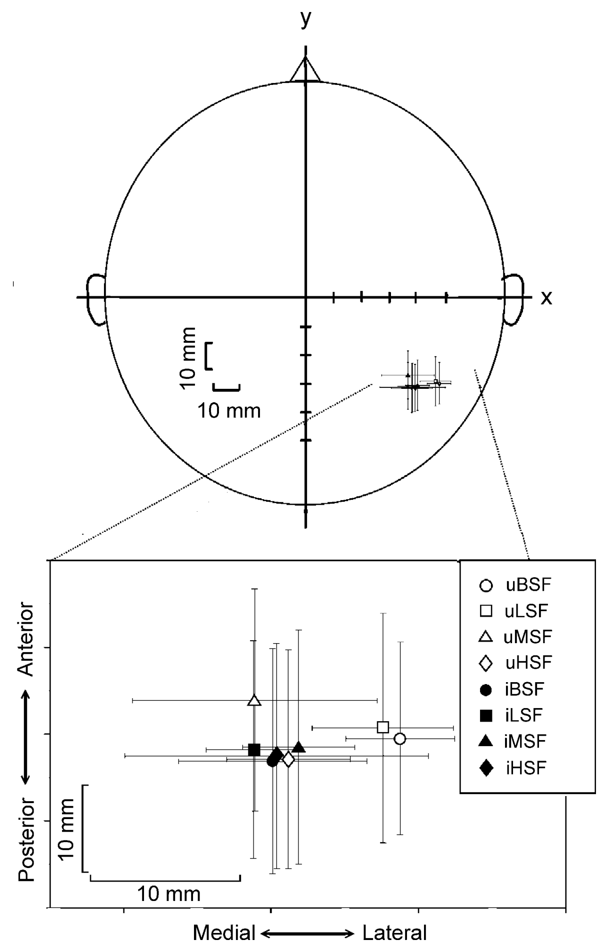


Fig. 4. Mean M170 locations (mean ± standard deviations) displayed in the schematic *x*–*y* coordinate system of a spherical head model with respect to different face conditions. The positive *x*- and *y*-axes go toward the right preauricular point and the nasion, respectively. SF, spatial frequency; B, broad-band; L, low; M, middle; H, high; u, upright; and i, inverted.

seemed located more medial than the latter (see Fig. 4). Further studies in more subjects are warranted to clarify whether MSF and HSF are processed by part-based mechanisms.

In conclusion, the less M170 activation to LSF faces suggests that face parts information is important for early face processing. The cortical representations in right occipitotemporal region for configural and face feature processing are overlapping. Moreover, our findings on the face inversion effect suggest that inverted BSF and LSF faces may be processed as an object.

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