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Research report

Neural organization for recognition of grammatical and emotional facial expressions in deaf ASL signers and hearing nonsigners

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Abstract

Recognition of emotional facial expressions is universal for all humans, but signed language users must also recognize certain non-affective facial expressions as linguistic markers. fMRI was used to investigate the neural systems underlying recognition of these functionally distinct expressions, comparing deaf ASL signers and hearing nonsigners. Within the superior temporal sulcus (STS), activation for emotional expressions was right lateralized for the hearing group and bilateral for the deaf group. In contrast, activation within STS for linguistic facial expressions was left lateralized only for signers and only when linguistic facial expressions co-occurred with verbs. Within the fusiform gyrus (FG), activation was left lateralized for ASL signers for both expression types, whereas activation was bilateral for both expression types for nonsigners. We propose that left lateralization in FG may be due to continuous analysis of local facial features during on-line sign language processing. The results indicate that function in part drives the lateralization of neural systems that process human facial expressions.

Theme: Neural basis of behavior
Topic: Cognition

Keywords: fMRI; Facial expression; Language

1. Introduction

Recognition of facial expressions of emotion is a crucial communication skill relevant for both human and non-human primates. Sensitivity to emotional facial expressions occurs very early in development, and the neural circuitry underlying facial affect recognition is partially independent of neural systems that underlie recognition of other information from faces, such as person identity or gender [13,17,34]. Humans have clearly evolved an ability to quickly recognize emotional and socially relevant facial expressions, and this ability appears to be processed by a distributed neural circuitry, generally lateralized to the right hemisphere [8,24,31]. We investigate the plasticity and functional organization of this neural circuitry by studying facial expressions that do not convey emotional or social-regulatory information, namely the linguistic facial expressions produced by users of American Sign Language (ASL).

A unique and modality specific aspect of the grammar of ASL and other signed languages is the use of the face as a linguistic marker. Distinct facial expressions serve to signal different lexical and syntactic structures, such as relative clauses, questions, conditionals, adverbials, and topics [4,29]. Linguistic facial expressions differ from emotional expressions in their scope and timing and in the facial muscles that are used [28]. Linguistic facial expressions have a clear onset and offset, and are coordinated with specific parts of the signed sentence. These expressions are critical for interpreting the syntactic structure of many ASL

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sentences. For example, restrictive relative clauses are indicated by raised eyebrows, a slightly lifted upper lip, and a backward tilt of the head. When this combination of head and facial features occurs, the co-occurring lexical items are interpreted as constituting a relative clause [22]. Facial behaviors also constitute adverbials that appear in predicates and carry various specific meanings. For example, the facial expression glossed as MM (lips pressed together and protruded) indicates an action done effortlessly, whereas the facial expression TH (tongue protrudes slightly) means "carelessly" (see Fig. 1A). These two facial expressions accompanying the same verb (e.g., DRIVE) convey quite different meanings ("drive effortlessly" or "drive carelessly").

Of course, deaf signers also use their face to convey emotional information. When perceiving visual linguistic input, ASL signers must be able to quickly identify and discriminate between different linguistic and affective facial expressions in order to process and interpret signed sentences. Thus, signers have a very different perceptual and cognitive experience with the human face compared to nonsigners. This experience appears to result in specific enhancements in face processing. Several studies have found that both hearing and deaf signers perform significantly better than nonsigners in distinguishing among similar faces (e.g., the Benton Faces Test), in identifying emotional facial expressions, and in discriminating local facial features [2,7,15,16,23]. It is possible that ASL signers exhibit a somewhat different neural representation for face perception due to their unique experience with human faces.

Recently, it has been argued that cognitively distinct aspects of face perception are mediated by distinct neural representations [17]. We hypothesize that the laterality of these representations can be influenced by the function of the expression conveyed by the face. Linguistic facial expressions are predicted to robustly engage left hemisphere structures only for deaf signers, whereas perception of emotional expressions is predicted to be lateralized to the right hemisphere for both signers and nonsigners.

An early hemifield study by Corina [10] found distinct visual field asymmetries for deaf ASL signers when recognizing linguistic and emotional facial expressions, compared to hearing nonsigners. The visual field effects were contingent upon the order of stimulus presentation. Both emotional and linguistic facial expressions produced significant left visual field (right hemisphere) asymmetries when emotional facial expressions were presented first. In contrast, when deaf signers viewed the linguistic expressions first, no significant visual field asymmetries were observed. Although suggestive, the results do not provide support for a dominant role of the left hemisphere in recognizing linguistic facial expressions. A right visual field (left hemisphere) advantage was not observed for linguistic facial expressions.

Nonetheless, data from lesion studies indicate that damage to the left hemisphere impairs signers' ability to produce ASL linguistic facial expressions [11,21]. In contrast, damage to the right hemisphere impairs the ability to produce emotional facial expressions, but leaves intact the ability to produce linguistic facial expressions [11]. With respect to perception, a recent study by Atkinson et al. [3] examined the comprehension of non-manual markers of negation in British Sign Language (BSL) by signers with left- or right-hemisphere damage. Non-manual negation in BSL is marked by a linguistic facial expression and an accompanying headshake. Right-hemisphere-damaged signers were impaired in comprehending non-manual negation, in contrast to left-hemisphere-damaged signers who were unimpaired. However, a negative headshake is obligatory for grammatical negation in BSL, and recognition of a headshake is distinct from the recognition of the linguistic facial expressions because (1) a headshake can be used non-linguistically to signal a negative response and (2) a headshake can occur without signing, unlike grammatical facial expressions which are bound to the

Fig. 1. Illustration of (A) ASL linguistic facial expressions and (B) emotional facial expressions used in the 'face only' condition. The labels under the linguistic expressions identify distinct facial adverbials (see text for details).

manual signs and do not occur in isolation. Thus, the neural organization for the recognition of linguistic facial expressions may differ from that for the recognition of headshakes marking negation. With the advent of functional neural imaging, we can now study the brain regions involved in the perception of linguistic and emotional facial expressions in intact deaf signers with much greater anatomical precision than is possible with lesion studies.

Neuroimaging results with hearing subjects indicate that the superior temporal sulcus (STS) is critically involved in processing changeable aspects of the face, such as eye gaze [19], mouth configuration [27], and facial expression [17]. Furthermore, attention to emotional facial expression can modulate activity within the right superior temporal sulcus [24]. We predict that attention to linguistic facial expressions will produce greater activity within the left STS for deaf signers than for hearing nonsigners.

In addition, recognition of facial expressions may modulate activity within the face-responsive areas within inferior temporal cortex. In particular, the fusiform gyrus (FG) has been identified as crucial to the perception of faces and as particularly critical to perceiving invariant properties of faces, such as gender or identity [17,20]. Activation within the fusiform gyrus in response to faces may be bilateral but is often lateralized to the right hemisphere. We hypothesize that the linguistic content of ASL facial expressions for deaf signers will modulate activity within the fusiform gyrus, shifting activation to the left hemisphere. In contrast, we hypothesize that hearing nonsigners will treat the unfamiliar ASL linguistic expressions as conveying social or affective information, even though these expressions are unique and non-identical to canonical affective expressions [28]. Thus, activation in the fusiform gyrus is expected to be bilateral or more lateralized to the right hemisphere for hearing subjects with no knowledge of ASL.

In our study, subjects viewed static facial expressions performed by different models who produced either emotional expressions or linguistic expressions (adverbials indicating manner and/or aspect) with or without accompanying ASL verbs. Subjects made same/different judgments to two sequentially presented facial expressions, blocked by expression type. This target task alternated with a control task in which subjects made same/different judgments regarding gender (the models produced neutral expressions with or without verbs). Fig. 1 provides examples of the ‘face only’ condition, and Fig. 2 provides examples from the ‘face with verb’ condition. In this latter condition, models produced ASL verbs with either linguistic, neutral, or emotional facial expression. The ‘face only’ condition was included because most previous face processing studies presented isolated face stimuli. Although emotional facial expressions can be produced without an accompanying manual sign, ASL linguistic facial expressions are bound morphemes (like *–ing* in English) that must co-occur with a manually produced sign. Therefore, we included a second ‘face with verb’ condition in order to present the linguistic facial expressions in a more natural linguistic context.

2. Materials and methods

2.1. Participants

Ten deaf native signers (five male, five female, mean age=29.4±6 years) and 10 hearing nonsigners (five male, five female, mean age=24.2±6 years) participated in the experiment. All of the deaf native signers had deaf parents and learned ASL from birth. All were prelingually deaf with severe to profound hearing loss (90 db or greater) and used ASL as their preferred means of communication. Hearing nonsigners had never been exposed to ASL. All subjects had attended college (an average of 5.1 and 3.8 years of college education for deaf and hearing subjects, respectively). No subject had a history of neurological or psychiatric illness, and none had taken any psychotropic medication within six months prior to the study. All subjects were right-handed and had normal or corrected-to-normal vision. All subjects signed an informed written consent approved by the Salk Institute Institutional Review Board.

2.2. Materials

The static facial expression stimuli used in the study were selected from digital videos of facial expressions generated

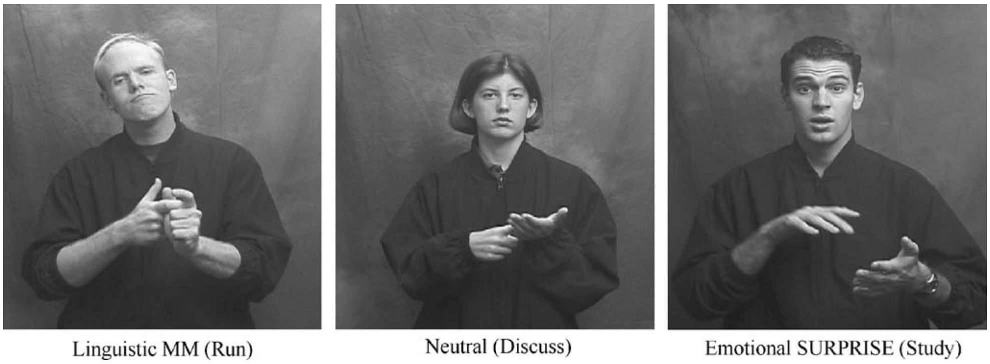
Linguistic MM (Run) Neutral (Discuss) Emotional SURPRISE (Study)

Fig. 2. Illustration of facial expressions produced with ASL verbs, used in the ‘face with verb’ condition.

by sign models who were certified ASL interpreters or ASL interpreters in training. None of the sign models were later found to be familiar to the subjects. All sign models were videotaped wearing the same dark clothing with a light blue background. During the videotaping, the sign models were instructed to generate a neutral facial expression, six emotional, and six adverbial facial expressions while signing ten different verbs: WRITE, DRIVE, READ, BICYCLE, SIGN, STUDY, RUN, CARRY, DISCUSS, and OPEN. These verbs were selected because they can be used naturally in conjunction with all of the emotional and linguistic facial expressions. The adverbial facial expressions were: MM (meaning "effortlessly"), CS ("recently"), TH ("carelessly"), INTENSE, PUFF ("a great deal" or "a large amount"), and PS ("smoothly") (see Fig. 1A). The emotional facial expressions were: happy, sad, anger, disgust, surprise, and fear (see Fig. 1B). Eye gaze was generally straight ahead, but occasionally gaze was directed to the side or downward. However, direction of gaze was balanced across conditions.

All static facial expressions were selected from digital videos using the following criteria. A still image for an emotional facial expression was selected if the image frame was at the peak of the expression and if the expression met the appropriate Facial Action Coding System (FACS) criteria, as assessed by a certified FACS coder [14]. Static images of linguistic facial expressions were screened and selected by a native ASL signer based on how accurately and clearly each expression conveyed the ASL facial adverb.

These emotional, linguistic, and neutral facial expression images were cropped to show only the head of sign model for the 'face only' condition. For the 'face with verb' condition, the stimuli were cropped to show the head and upper body of the sign model producing an ASL verb (see Fig. 2). All of the verbs were instantly recognizable from these still images.

An LCD video projector and PsyScope software [9] running on an Apple PowerBook were used to back-project the stimuli onto a translucent screen placed inside the scanner. The stimuli were viewed at a visual angle subtending 10° horizontally and vertically with an adjustable 45° mirror.

2.3. Procedure

The experimental task was to decide whether two sequentially presented facial expressions (produced by different sign models) were the same or different. The control (baseline) task was to decide whether two sequentially presented sign models (producing neutral facial expressions) were the same or different gender. For all tasks, subjects pressed a "yes" response button for same judgments and a "no" response button for different judgments. Response accuracy during the fMRI sessions was recorded using PsyScope software [9]. The 'face only' and 'face with verb' conditions were blocked and counterbalanced across subjects.

For each condition, subjects participated in two repeated sets of three runs: emotional-control, linguistic-control, and alternating blocks of emotional and linguistic expressions. Both sets contained the same run order, but the stimuli in each run were presented in a different order. Each run consisted of eight 32-s blocks alternating between experimental and control blocks. Each trial in the experimental block presented a pair of facial expression stimuli, each presented for 850 ms with a 500-ms ISI. At the start of each block, either the words 'facial expression' or the word 'gender' was presented for one second to inform subjects of the upcoming task. Each run lasted four minutes and sixteen seconds. All stimuli pairs in the experimental blocks showed different individuals expressing either the same or different facial expressions. Each trial in the control block showed different individuals with neutral facial expressions only. All blocks were approximately equal in the number of males/females and experimental blocks contained approximately equal numbers of facial expressions in each of the six categories.

2.4. Data acquisition, processing, and analysis

Both structural MRI and fMRI scans were performed using a 1.5-T Siemens MRI scanner with a whole head coil. Head movement was minimized by using cushioned supports placed around subject's head and neck within the whole head coil. Two structural MR images were acquired for each subject prior to the fMRI scans (T1-weighted MPRAGE with TR=11.4, TE=4.4, FOV 256, and 10° flip angle; voxel dimensions: 1×1×1 mm). These T1-weighted images were averaged post hoc using AFNI (Analysis of Functional NeuroImages) [12] to create a single high quality anatomical data set for registration and spatial normalization to the atlas of Talairach and Tournoux [32]. Each subject's anatomical data set in the Talairach atlas was used to delineate the region of interest (ROI) boundaries for the STS and the FG in both hemispheres. We defined the superior temporal sulcus ROI as the area encompassing the upper and lower bank of STS, extending from the temporo-occipital line to the posterior part of temporal pole. The fusiform gyrus was defined as the area bounded by the anterior and posterior transverse collateral sulci, medial occipito-temporal sulcus, and the lateral occipito-temporal sulcus.

For all functional scans, T2*-weighted interleaved multislice gradient-echo echo-planar imaging (TR=4 s, TE=44 ms, FOV 192, flip angle 90°, 64×64 matrix) was used to acquire 24 contiguous, 5-mm-thick coronal slices extending from occipital lobe to mid-frontal lobe with voxel dimension of 3×3×5 (mm). The fMRI time-series data were preprocessed and analyzed with AFNI in several steps in order to acquire voxel numbers from the ROIs for analysis. The first two volumes (acquired prior to equilibrium magnetization) from each scan were discarded. All scans were corrected for head motion using an iterative least-squares procedure that aligns all volumes to the reference volume (the third volume of the first functional scan acquired immediately after the last structural MRI scan). All volumes were then spatially smoothed with a 5-mm FWHM Gaussian kernel prior to the analysis.

The significance level for each voxel was calculated using Pearson product–moment correlation coefficient for cross-correlation of hemodynamically convolved reference waveform with the measured fMRI time-series for each voxel. A combination of AlphaSim [33] and AFNI's *3dclust* was used to derive numbers of statistically significant activated voxels from the regions of interest (superior temporal sulcus and fusiform gyrus) for subsequent ROI analyses, while minimizing the probability of random Type-1 errors due to large number of comparisons and spatial correlations resulting from gaussian smoothing. AlphaSim calculates the probability of occurrence of a cluster made up of specific number of smoothed neighboring voxels with a given P value through Monte Carlo simulations (see Ref. [33] for details). Based on AlphaSim calculations, only clusters of seven voxels (315 mm^3) or greater with voxel-wise significance level of $p \leq 0.001$ *within* the ROIs were used for statistical analysis of extent of activation.

In addition to the ROI analysis using individual data, we acquired group-level z-maps for each condition. This was done by normalizing all raw individual functional scans, which were then spatially converted into the Talairach atlas. The talairached individual scans were then concatenated before analysis with 3dDeconvolve (part of the AFNI package). For clarity, only neural activations within the ROI being discussed are shown in the figures.

3. Results

3.1. Behavioral results

All subjects performed the tasks without difficulty. Separate two-factor ANOVAs (2 (subject group)×2 (facial expression type)) were conducted on the accuracy data for the 'face only' and the 'face with verb' conditions. For the 'face only' condition, there were no significant main effects of group or facial expression type and no interaction between subject group and facial expression (F<1). For the emotional expressions, deaf and hearing subjects were equally accurate (81.8% and 80.6%, respectively). Importantly, deaf and hearing subjects were also equally accurate with the linguistic facial expressions (79.6% and 79.1%. respectively). Thus, any group differences in activation are unlikely to be due to differences in task difficulty for the two groups. Similarly, for the 'face with verb' condition,

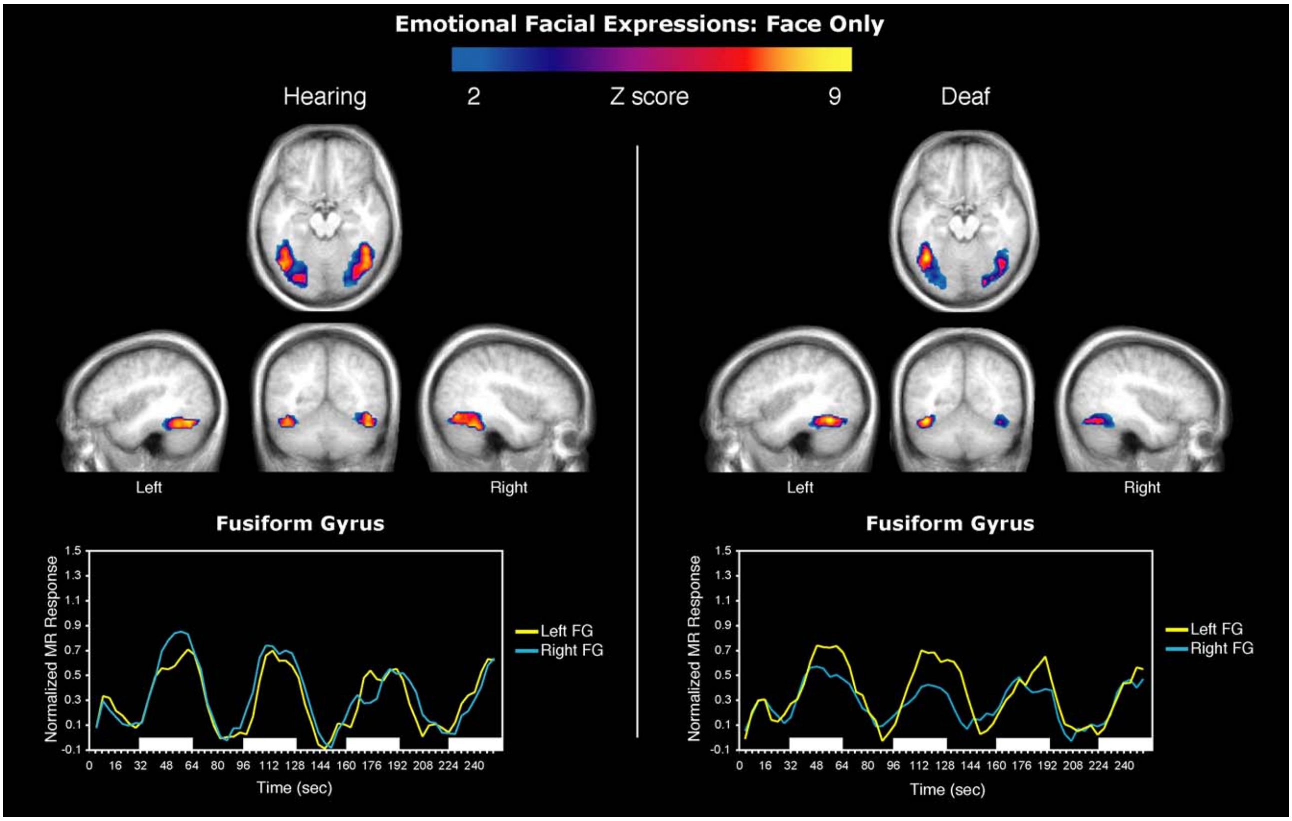

Fig. 3. Illustration of activation in the fusiform gyrus for emotional facial expressions in the 'face only' condition. The bottom graphs show normalized MR response from left (yellow) and right (cyan) ROIs averaged across subjects. For graph clarity, the final ROI time-series were smoothed using three-step moving average.

there were no main effects of group or facial expression type, and no interaction ($F<1$). For the emotional expressions, hearing subjects were slightly more accurate than deaf subjects (85.3% and 83.8%, respectively), but this difference was not significant. For the linguistic expressions, deaf subjects were slightly more accurate than hearing subjects (85.4% and 81.6%, respectively), but again, this difference was not significant. Thus, the behavioral data indicate that task difficulty did not contribute to the differences in neural activity observed between the groups.

3.2. Imaging results

A mixed-design ANOVA was conducted separately for each ROI for each stimulus condition, using extent of activation with voxel-wise probability ≥ 0.001 as the dependent measure. The mixed-design ANOVA consisted of one between group factor (subject group: deaf, hearing) and two within group factors: hemisphere (left, right) and facial expression type (emotional, linguistic). Activation patterns for the 'face only' and 'face with verb' conditions were analyzed separately. These analyses were based on results from the runs in which facial expressions alternated with the control condition. In the final section, we report on the results from the runs in which alternating emotional and linguistic facial expressions were presented.

3.2.1. Face only condition

3.2.1.1. Superior temporal sulcus. The pattern of neural activation in STS did not differ significantly for deaf and hearing subjects in the 'face only' condition. There were no main effects of subject group ($F<1$) or of facial expression type ($F<1$). Activation was bilateral, with no significant main effect of hemisphere ($F<1$). Although no interactions were significant, planned comparisons revealed significantly greater right- than left-hemisphere activation for emotional facial expressions for the hearing subjects ($F(1,9)=8.90$, $p<0.02$). No other hemispheric differences were significant.

3.2.1.2. Fusiform gyrus. There were no significant main effects of subject group or of facial expression type. However, the ANOVA revealed a significant interaction between subject group and cerebral hemisphere ($F(1,18)=5.45$, $p<0.05$). For deaf signers, activation within the fusiform gyrus was significantly left lateralized for emotional facial expressions ($F(1,9)=5.38$, $p<0.05$), but the pattern of left lateralization did not reach significance for linguistic facial expressions. For hearing subjects, activation in FG was consistently bilateral. There were no significant differences between activation in the left versus right hemisphere ($F<1$ for both linguistic and emotional facial expressions).

To demonstrate the correspondence between the MR response and task performance and to illustrate the strength of the left–right hemispheric differences in Blood Oxygen Level Dependent (BOLD) signal, we calculated the percent signal change in MR response across time in the left and right hemispheres for each group. This calculation was performed using the following steps: (1) For each individual, all MR response time-series within an ROI were normalized and averaged into an ROI time-series for each condition. (2) All ROI time-series were then averaged for each group for each condition and for each ROI. Fig. 3 illustrates the group difference in neural activation and percent signal change across time-series in the fusiform gyrus for the emotional facial expressions in the 'face only' condition.

Finally, Table 1 provides the Talairach coordinates, the mean volumes of activation, and the maximum z scores for activation extents for each ROI for the 'face only' condition.

3.2.2. Face with verb condition

3.2.2.1. Superior temporal sulcus. As in the 'face only' condition, there were no main effects of subject group ($F<1$) or of facial expression type ($F<1$). However, the interaction between hemisphere and group approached significance ($F(1,18)=4.86$, $p=0.059$). Planned comparisons showed that when presented with linguistic facial expressions produced with a verb, deaf subjects exhibited significantly more activation in the left than right hemisphere ($F(1,9)=6.82$, $p<0.05$). In contrast, hearing subjects exhibited no differences in hemispheric activation for linguistic expressions ($F(1,9)=2.12$, $p=0.187$). Fig. 4

Table 1
Brain regions activated in the 'face only' condition

		BA	Talairach coordinates			Volume (mm^3)	Maximum z score
			x	y	z		
Emotional facial expressions							
Deaf							
Fusiform gyrus	L	37	−36	−59	−14	1849	4.6
	R	37	34	−58	−13	661	4.4
STS	L	22/21	−54	−36	8	1740	4.9
	R	22/21	50	−44	10	2430	4.9
Hearing							
Fusiform gyrus	L	37	−37	−56	−13.8	2173	4.5
	R	37	39	−53	−14.5	2970	4.7
STS	L	22/21	−53	−43	5	954	4.5
	R	22/21	53	−36	4	2146	5
Linguistic facial expressions							
Deaf							
Fusiform gyrus	L	37	−37	−58	−13	1962	4.8
	R	37	32	−61	−11	1323	4.6
STS	L	22/21	−54	−41	8	1129	4.6
	R	22/21	51	−42	9	1462	4.7
Hearing							
Fusiform gyrus	L	37	−39	−57	−14	2290	5.17
	R	37	39	−54	−14	2560	4.84
STS	L	22/21	−55	−45	7	882	5.1
	R	22/21	53	−47	7	1674	5.5

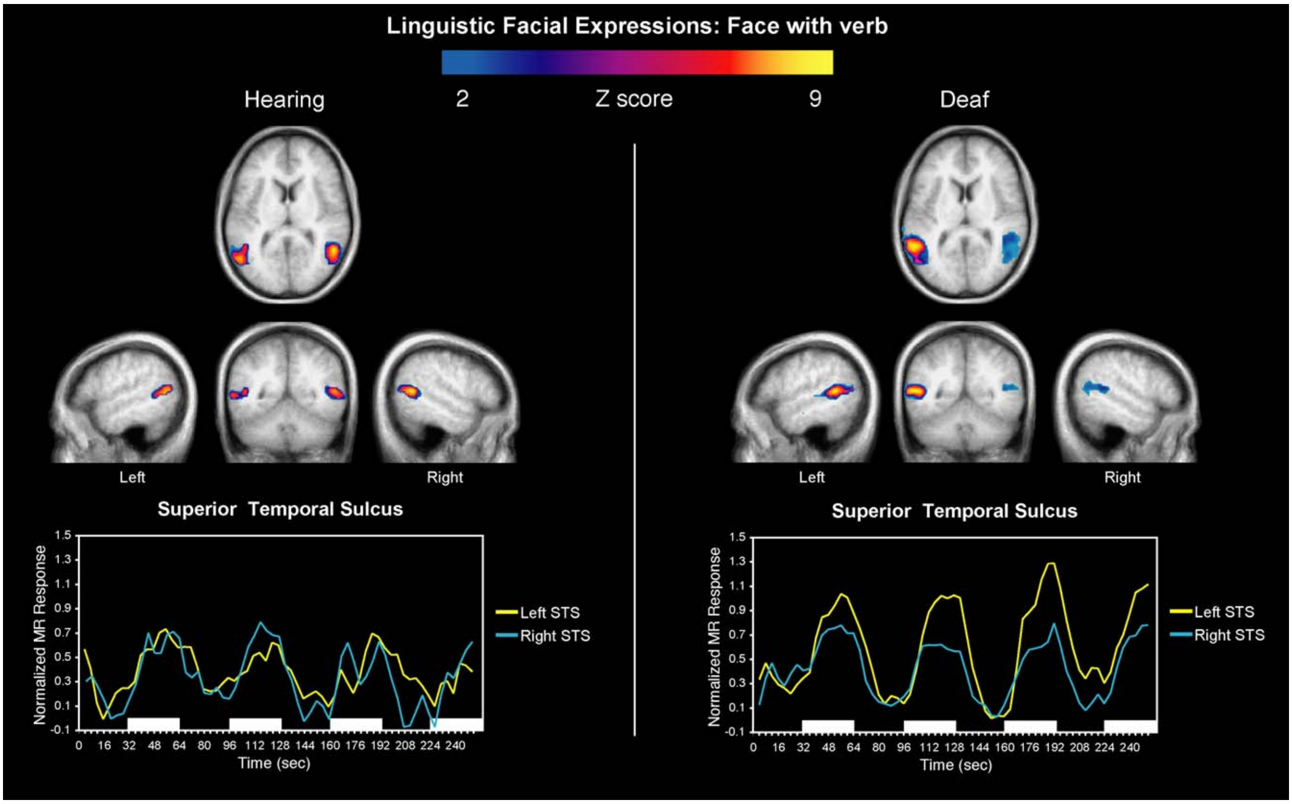

Fig. 4. Illustration of activation in the superior temporal sulcus for linguistic facial expressions in the ‘face with verb’ condition. The bottom graphs show normalized MR response from left (yellow) and right (cyan) ROIs averaged across subjects. For graph clarity, the final ROI time-series were smoothed using three-step moving average.

illustrates the group difference in neural activation and percent signal change in STS for the linguistic facial expressions in the ‘face with verb’ condition.

For emotional facial expressions produced with an ASL verb, deaf subjects exhibited bilateral activation ($F<1$); whereas, hearing subjects exhibited a trend for more right-lateralized activation ($F(1,9)=3.70$, $p=0.08$).

3.2.2.2. Fusiform gyrus. The pattern of results for the ‘face with verb’ condition was similar to the ‘face only’ condition. There were no significant main effects of group, facial expression, or hemisphere. Planned comparisons revealed that deaf subjects exhibited a strong trend for more activation in the left than right fusiform gyrus for both linguistic facial expressions ($F(1,9)=3.97$, $p=0.07$) and emotional facial expressions ($F(1,9)=4.67$, $p=0.05$). In contrast, activation was bilateral for hearing subjects for both types of facial expressions ($F<1$ for all contrasts).

Table 2 provides the Talairach coordinates, the mean volumes of activation, and the maximum z scores for activation extents for each ROI for the ‘face with verb’ condition.

Finally, to more clearly illustrate the pattern of hemispheric differences, we calculated a lateralization index based on the group means for the number of activated voxels thresholded above $p<0.001$ in the STS and FG ROIs in each hemisphere. A lateralization index (LI) for each ROI was computed according to the formula $LI=(Vol_R-Vol_L)/(Vol_R+Vol_L)$, where Vol_L and Vol_R represent the mean numbers of activated voxels in the left and right hemispheres. The laterality indices are graphed in Fig. 5 and are based on the mean volumes of activation shown in Tables 1 and 2. Fig. 5 thus provides a visual illustration of the group differences in hemispheric bias across tasks and conditions. Positive and negative index values represent rightward and leftward bias, respectively.

3.2.3. Alternating blocks of emotional and linguistic facial expressions

For runs consisting of alternating emotional and linguistic blocks, the percentage of signal change in the individual data sets was found to be weak. The partial correlation coefficient calculated for the ROIs from each run failed to rise above the pre-determined threshold required to prevent false positives. Thus, we could not perform ANOVA analyses for those data sets. However, z-maps acquired from the correlation coefficient analysis of concatenated data sets from the ‘face with verb’ condition across subjects in each group showed neural activity in the right middle temporal gyrus in both groups for emotional facial

Table 2
Brain regions activated in the 'face with verb' condition

		BA	Talairach coordinates			Volume (mm^3)	Maximum *z* score
			x	*y*	*z*		
Emotional facial expressions							
Deaf							
Fusiform gyrus	L	37	−34	−57	−13	2277	5
	R	37	31	−58	−13	936	4.6
STS	L	22/21	−54	−39	8	1975	4.9
	R	22/21	48	−41	10	2070	5
Hearing							
Fusiform gyrus	L	37	−42	−50	−14	2142	4.7
	R	37	39	−61	−14	2250	5
STS	L	22/21	−55	−40	6	837	4.5
	R	22/21	52	−40	6	1989	5
Linguistic facial expressions							
Deaf							
Fusiform gyrus	L	37	−36	−62	−12	2169	5.37
	R	37	35	−65	−13	814	4.9
STS	L	22/21	−54	−42	7.5	2389	5
	R	22/21	51	−42	8.5	823	4.6
Hearing							
Fusiform gyrus	L	37	−39	−55	−14	1467	4.98
	R	37	39	−54	−14	1789	4.8
STS	L	22/21	−53	−46	9	585	5
	R	22/21	54	−36	5	2083	5.3

expressions block. Activation in the left STS and lateral occipital temporal gyrus was found for linguistic facial expressions in deaf subjects only.

4. Discussion

Overall, our results revealed consistent activation in face-related neural regions for the recognition of both emotional and linguistic facial expressions for deaf and hearing subjects. Thus, the neural organization underlying facial expression recognition is relatively robust since these regions are engaged in processing all types of facial information, including linguistic facial expressions. However, the lateralization of activation within these face-related neural regions appears to be functionally driven and malleable.

4.1. Superior temporal sulcus

Presentation of emotional facial expressions resulted in right-lateralized activation within the STS for the hearing group (see Fig. 5A). This result is consistent with previous research indicating greater right hemisphere involvement in processing emotional information [17,24]. In addition, the pattern of right hemisphere lateralization was relatively unchanged when emotional expressions were presented with non-meaningful manual postures, i.e., ASL verbs (see Fig. 2). Thus, for hearing subjects, simply viewing the hands and arm does not modulate the pattern of right-lateralized activity within STS when perceiving emotional facial expressions.

For the deaf group, activation in STS was bilateral for emotional facial expressions in both the 'face only' and the 'face with verb' conditions. A possible explanation for bilateral processing of emotional facial expressions by deaf signers is that emotional facial expressions can occur as non-manual components of lexical signs denoting emotional states, e.g., the signs ANGRY, SAD, DISGUST, and HAPPY are most often (but not always) produced with the corresponding emotional facial expression. In addition, emotional facial expressions are often produced during "role shifted" discourse in which the affect of someone other than the signer is depicted. Deaf signers may show bilateral activation for emotional expressions within STS because for this group, linguistic processing involves the detection of emotional facial expressions during narrative discourse, as well as during lexical processing.

However, when linguistic facial expressions were accompanied by an ASL verb, deaf signers exhibited significant left-lateralized activation within STS (see Figs. 4 and 5A). The control condition also presented still images of models producing ASL verbs but with neutral facial expressions. Thus, activation associated with the verbs themselves was factored out. It was the combination of

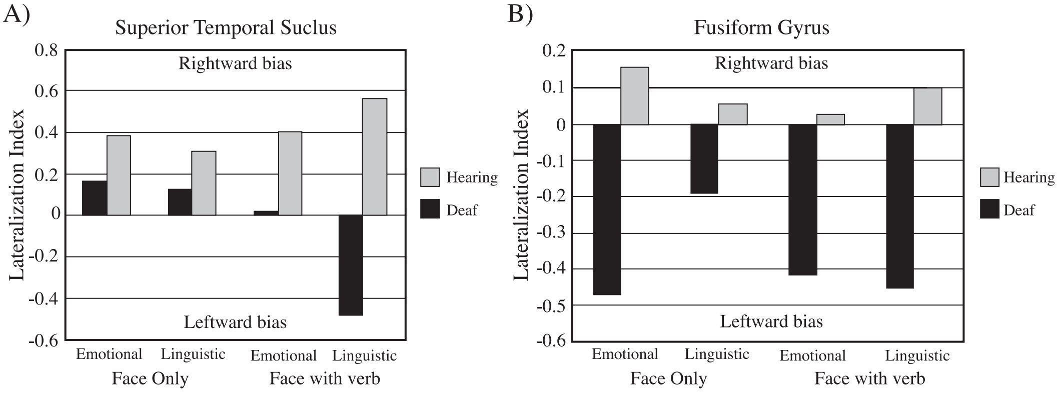

Fig. 5. Lateralization index for total number of voxels in left versus right in the STS (A) and in the fusiform gyrus (B). The index is calculated using the group means from Tables 1 and 2.

adverbial facial expressions with ASL verbs that shifted processing to the left hemisphere for deaf signers. Furthermore, this shift in hemispheric lateralization did not occur when linguistic facial expressions were presented in isolation (the ‘face only’ condition). For deaf signers, adverbial facial expressions presented without a manual verb are recognizable but incomplete because these expressions constitute bound morphemes. An English analogy would be presenting speakers with bound suffixes such as *-ing* or *-ness*. Thus, linguistic facial expressions significantly engage left STS only when these expressions occur within their obligatory linguistic context.

Unlike the deaf group, hearing signers exhibited bilateral activation within STS for ASL facial expressions in both the ‘face only’ and in the ‘face with verb’ conditions. Although the hearing group means suggest right-lateralized activation for ASL facial expressions (see Fig. 5A and Tables 1 and 2), there was a large variance in laterality patterns across hearing subjects, which led to the lack of statistical significance. The variability might be due to some hearing subjects interpreting ASL expressions as conveying affective or socially relevant information, while other subjects may have treated the expressions as unfamiliar facial gestures.

4.2. Fusiform gyrus

The fact that any activation within the fusiform gyrus was observed at all is significant because neutral faces were used as the control condition. Thus, the observed activation within the fusiform is not due to the processing of faces per se. Apparently, the fusiform remains part of the distributed neural circuitry mediating the recognition of facial expressions, despite its hypothesized role in processing invariant aspects of faces [17]. Whether the observed fusiform activation reflects top-down modulation of face processing or early visual face processing will require further investigation.

For hearing subjects, activation within the fusiform gyrus was bilateral for all conditions (see Figs. 3 and 5B). In contrast, activation within the fusiform gyrus was left lateralized or biased toward the left hemisphere for deaf subjects for all conditions (see Figs. 3 and 5B). Unlike activation within the STS, activation within the fusiform gyrus was unaffected by the presence of an ASL verb for deaf signers. This result indicates that activation within the fusiform gyrus is not modulated by the recognition of the linguistic content of the stimulus. For both subject groups, fusiform activation may primarily reflect the early analysis of facial features, regardless of the function of the facial expression (emotional vs. linguistic) or the linguistic/gesture context (i.e., ‘face only’ vs. ‘face with verb’).

The fact that deaf subjects exhibited left-lateralized activation within the fusiform gyrus for *emotional* expressions is somewhat surprising. One possible explanation is that the nature of the processing required for linguistic facial expressions shifts the activation to the left hemisphere for emotional expressions as well. Several studies have suggested that local and global face processing are mediated in the left and right fusiform gyrus respectively [18,30]. Recognition of linguistic facial expressions requires identification of *local* facial features, and we propose that left lateralization within the fusiform may arise from the lifelong and constant neural activity associated with local facial feature processing for deaf signers.

In contrast to linguistic facial expressions, emotional facial expression categories are determined by global and configurational processing of facial features—with the possible exception of the ‘happy’ facial expression [1]. Categories of linguistic facial expressions, on the other hand, are differentiated only by local changes to a single feature (e.g., mouth) or to specific groups of facial features (e.g., the two eyebrows). In the case of adverbial facial expressions, specific meanings are carried solely by different configurations of the mouth feature. That is, any changes associated with other individual facial features or the global configuration of facial features will not affect the adverbial meaning expressed by the mouth alone. Unlike emotional facial expressions which can be differently combined to create subordinate categories of specific emotional facial expressions (e.g., fearful surprise or happy surprise), linguistic facial expressions articulated with the same facial feature (e.g., mouth) cannot be combined and do not have any subordinate categories. In addition, emotional facial expressions can vary in strength, conveying different meanings (e.g., ‘rage’ versus ‘irritation’, with respect to the emotional category “angry”). In contrast, a difference in strength or intensity of the adverbial expression ‘MM’ does not convey any additional information. Variation in the intensity of adverbial expressions across individuals is not interpreted as variation in the intensity of the verbal modification; rather, such variation in expression is treated as phonetic variation that does not convey meaningful information. Thus, processing linguistic facial expressions requires categorical identification and detection of local facial feature configurations.

Crucially, behavioral evidence indicates that ASL signers (both deaf and hearing) excel at discriminating local facial features compared to nonsigners. McCullough and Emmorey [23] found that ASL signers were significantly more accurate than hearing nonsigners in discriminating between faces that were identical except for a change in a single facial feature. These behavioral data indicate that extended experience with featural processing of facial expressions affects how ASL signers process faces in general.

We propose that monitoring and processing both linguistic and emotional facial expressions during everyday sign language conversation may induce a constant competition between local and global processing for attentional resources. Perception of emotional facial expressions is nearly automatic but is still not spared from attentional competition [26]. Furthermore, since linguistic facial expressions are very brief and change frequently compared to emotional facial expressions, we suggest that processing linguistic facial expressions draws more attentional resources to local facial feature processing and keeps these processes engaged constantly. The continual difference in the attentional resources allocated to local versus global processing during life-long exposure to ASL may lead to changes in the efficiency and lateralization of activity within the fusiform gyrus for native signers.

Indeed, such changes in hemispheric lateralization of neural activation have been observed for perception of non-linguistic visual motion in deaf and hearing native signers [5,6,25]. MT/MST activation in response to peripheral visual motion stimuli was found to be left lateralized for native signers when compared to hearing non-signer controls [6]. This lateralization pattern is also argued to result from life-long exposure to sign language [6,25].

In conclusion, our study has shown that the neural regions associated with general facial expression recognition are consistent, predictable, and robust. Neural activation was consistently found in the STS and FG regions across both deaf and hearing subjects. In addition, the results support the hypothesis that the right hemisphere is dominant for recognition of emotional facial expressions. The results also show that the neural representation underlying facial expression recognition can be modulated. The leftward asymmetry observed in the STS region for facial expressions presented within a linguistic context implies a strong language dominance for left hemisphere processing regardless of the form in which that linguistic information is encoded. In addition, the left FG activation observed in signers when viewing either emotional or linguistic facial expressions suggests that long-term experience with sign language may affect the neural representation underlying early visual processing of faces. Future research with hearing native signers exposed to ASL from birth by their deaf parents will help determine whether the changes in neural organization for facial expression recognition are due to auditory deprivation or to linguistic experience, as we propose. In addition, research with signers who acquired ASL in adulthood or late childhood will determine the developmental plasticity of face-related neural regions within the brain.

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References

[1] R. Adolphs, Recognizing emotion from facial expressions: psychological and neurological mechanisms, Behavioral and Cognitive Neuroscience Reviews 1 (2002) 21–61.

[2] P. Arnold, C. Murray, Memory for faces and objects by deaf and hearing signers and hearing nonsigners, Journal of Psycholinguistic Research 27 (1998) 481–497.

[3] J. Atkinson, R. Campbell, J. Marshall, A. Thacker, B. Woll, Understanding 'not': neuropsychological dissociations between hand and head markers of negation in BSL, Neuropsychologia 42 (2004) 214–229.

[4] C. Baker, D. Cokley, ASL: A Teacher's Resource Text on Grammar and Culture, TJ Publishers, Silver Spring, 1980.

[5] D. Bavelier, A. Tomann, C. Hutton, T. Mitchell, G. Liu, D. Corina, H. Neville, Visual attention to the periphery is enhanced in congenitally deaf individuals, Journal of Neuroscience 20 (17) (2000) 1–6 (RC 93).

[6] D. Bavelier, C. Brozinsky, A. Tomann, T. Mitchell, H. Neville, G. Lui, Impact of early deafness and early exposure to sign language on the cerebral organization for motion processing, Journal of Neuroscience 21 (2001) 8931–8942.

[7] J. Bettger, K. Emmorey, S. McCullough, U. Bellugi, Enhanced facial discrimination: effects of experience with American Sign Language, Journal of Deaf Studies and Deaf Education 2 (1997) 223–233.

[8] J.C. Borod, J. Kent, E. Koff, C. Martin, Facial asymmetry while posing positive and negative emotions: support for the right hemisphere hypothesis, Neuropsychologia 26 (1988) 759–764.

[9] J.D. Cohen, B. MacWhinney, M. Flatt, J. Provost, PsyScope. A new graphic interactive environment for designing psychology experiments, Behavioral Research Methods, Instruments, and Computers 25 (1993) 257–271.

[10] D.P. Corina, Recognition of affective and noncanonical linguistic facial expressions in hearing and deaf subjects, Brain and Cognition 9 (1989) 227–237.

[11] D. Corina, U. Bellugi, J.S. Reilly, Neuropsychological studies of linguistic and affective facial expressions in deaf signers, Language and Speech 42 (1999) 307–331.

[12] R. Cox, AFNI: software for analysis and visualization of functional magnetic resonance neuroimages, Computers and Biomedical Research 29 (1996) 162–173.

[13] A. Damasio, H. Damasio, Cortical systems for retrieval of concrete knowledge: the convergence zone framework, in: C. Koch, J.L. Davis (Eds.), Large-Scale Neuronal Theories of the Brain, MIT Press, Cambridge, 1994, pp. 61–74.

[14] P. Ekman, W. Friesen, Facial Action Coding System: a Technique for the Measurement of Facial Movement, Consulting Psychologists Press, Palo Alto, 1978.

[15] N.S. Goldstein, R.S. Feldman, Knowledge of American Sign Language and the ability of hearing individuals to decode facial expressions of emotion, Journal of Nonverbal Behavior 20 (1996) 111–122.

[16] N.S. Goldstein, J. Sexton, R.S. Feldman, Encoding of facial expressions of emotion and knowledge of American Sign Language, Journal of Applied Social Psychology 30 (2000) 67–76.

[17] J.V. Haxby, E.A. Hoffman, M.I. Gobbini, The distributed human neural system for face perception, Trends in Cognitive Sciences 4 (2000) 223–233.

[18] L.A. Hillger, O. Koenig, Separable mechanisms in face processing: evidence from hemispheric specialization, Journal of Cognitive Neuroscience 3 (1991) 42–58.

[19] E.A. Hoffman, J.V. Haxby, Distinct representations of eye gaze and identity in the distributed human neural system for face perception, Nature Neuroscience 3 (2002) 80–84.

[20] N. Kanwisher, J. McDermott, M.M. Chun, The fusiform face area: a module in human extrastriate cortex specialized for face perception, Journal of Neuroscience 17 (1997) 4302–4311.

[21] J. Kegl, H. Poizner, Crosslinguistic/crossmodal syntactic consequences of left-hemisphere damage: evidence from an aphasic signer and his identical twin, Aphasiology 11 (1997) 1–37.

[22] S. Liddell, American Sign Language syntax, Mouton, Hague, 1980.

[23] S. McCullough, K. Emmorey, Face processing by deaf ASL signers: evidence for expertise in distinguishing local features, Journal of Deaf Studies and Deaf Education 2 (1997) 212–222.

[24] J. Narumoto, T. Okada, N. Sadato, K. Fukui, Y. Yonekura, Attention to emotion modulates fMRI activity in human right superior temporal sulcus, Cognitive Brain Research 12 (2001) 225–231.

[25] H. Neville, D. Lawson, Attention to central and peripheral visual space in a movement detection task: an event-related potential and behavioral study: III. Separate effects of auditory deprivation and acquisition of a visual language, Brain Research 405 (1987) 284–294.

[26] L. Pessoa, M. McKenna, E. Gutierrez, L.G. Ungerleider, Neural processing of emotional faces requires attention, Proceedings of the National Academy of Sciences 99 (2002) 11458–11463.

[27] A. Puce, T. Allison, S. Bentin, J.C. Gore, G. McCarthy, Temporal cortex activation in humans viewing eye and mouth movements, The Journal of Neuroscience 18 (1998) 2188–2199.

[28] J.S. Reilly, M. McIntire, U. Bellugi, The acquisition of conditionals in American Sign Language: grammaticized facial expressions, Applied Psycholinguistics 11 (1990) 369–392.

[29] J.S. Reilly, M. McIntire, U. Bellugi, Faces: the relationship between language and affect, in: V. Volterra, C.J. Erting (Eds.), From Gesture to Language in Hearing and Deaf Children, Springer-Verlag, New York, 1990.

[30] B. Rossion, L. Dricot, A. Devolder, J. Bodart, M. Crommelinck, Hemispheric asymmetries for whole-based and part-based face processing in the human fusiform gyrus, Journal of Cognitive Neuroscience 12 (2000) 793–802.

[31] J.J. Schmitt, W. Hartje, K. Willmes, Hemispheric asymmetry in the recognition of emotional attitude conveyed by facial expression prosody and propositional speech, Cortex 33 (1997) 65–81.

[32] J. Talairach, P. Tournoux, Co-Planar Stereotaxic Atlas of the Human Brain, Thieme, New York, 1988.

[33] B.D. Ward, Simultaneous Inference for fMRI Data, 2000. [On-line] Available: http://afni.nimh.nih.gov/afni/docpdf/AlphaSim.pdf.

[34] A.W. Young, Face and Mind, Oxford University Press, Oxford, 1998.