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Cortical Multisensory Connectivity is Present Near Birth in Humans

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Abstract

How the newborn brain adapts to its new multisensory environment has been a subject of debate. Although an early theory proposed that the brain acquires multisensory features as a result of postnatal experience, recent studies have demonstrated that the neonatal brain is already capable of processing multisensory information. For multisensory processing to be functional, it is a prerequisite that multisensory convergence among neural connections occur. However, multisensory connectivity has not been examined in human neonates nor are its location(s) or afferent sources understood. We used resting state functional MRI (fMRI) in two independent cohorts of infants to examine the functional connectivity of two cortical areas known to be multisensory in adults: the intraparietal sulcus (IPS) and the superior temporal sulcus (STS). In the neonate, the IPS was found to demonstrate significant functional connectivity with visual association and somatosensory association areas, while the STS showed significant functional connectivity with the visual association areas, primary auditory cortex, and somatosensory association areas. Our findings establish that each of these areas displays functional communication with cortical regions representing various sensory modalities. This demonstrates the presence of cortical areas with converging sensory inputs, representing that the functional architecture needed for multisensory processing is already present within the first weeks of life.

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Keywords

neonates; resting state functional MRI; multi-sensory connectivity; intraparietal sulcus; superior temporal sulcus

INTRODUCTION

The physical environment around us is complex, and the nervous system monitors this complex environment with multiple, different sensors that sample various “bandwidths” of energy or events. When an event is detected by more than one sensory modality, a redundancy in neural signaling occurs; this underlies multisensory processing. Multisensory processing is of substantial adaptive value, is ubiquitous across species, and has been extensively examined in the superior colliculus/optic tectum across the animal kingdom as well as in the cerebral cortex of mammals. Studies have revealed fundamental principles governing the convergence of sensory information and its processing leading to effects of multisensory integration (reviewed in (Stein and M. A. Meredith, 1993; Stein et al., 2014)). Although a great deal is understood about multisensory processing and its behavioral or cognitive effects in adults (for reviews, see (Stein et al., 2014)), substantially less information is available about how this fundamental feature of the brain develops in neonates.

Some of the initial theories on the development of multisensory processing held that the newborn brain initially segregated information from the different sensory modalities and developed multisensory features later through association and experience (Piaget, 1952) . In support of this notion, a developmental study of the multisensory region of the cat anterior ectosylvian cortex revealed that only unisensory somatosensory neurons were observed at 4 weeks postnatal, followed by unisensory auditory (and a few multisensory auditory-somatosensory) neurons by 8 weeks (Wallace et al., 2006) . An alternate view has also been proposed, whereby the brain is born multisensory and unisensory processing features result from pruning of connections directed by sensory experience. Human infants as young as 2 weeks can match visual cues with their own tactile/proprioceptive sensations to imitate facial expressions (Meltzoff and M. K. Moore, 1977) , can make visual-tactile transfers between pictures and objects (Streri and M. Molina, 1993) , and are capable of binding auditory and visual inputs when they are temporally synchronous (Lewkowicz et al., 2010) . This early-multisensory view has recently been modified by the “perceptual narrowing” model of multisensory development (Lewkowicz and A. A. Ghazanfar, 2009) . According to this model, in the first months after birth, infants present a very broad multisensory perceptual tuning that progressively narrows with age (Pascalis et al., 2005) . The data that support the “perceptual narrowing” model implies that multisensory cortical areas are already present in the first months of life in humans. However, it is not known whether cortical areas that are typically multisensory in adults are multisensory in early infancy, or if they receive inputs from sources representing different sensory modalities.

One well-studied multisensory area in the adult cortex of humans and monkeys is the intraparietal sulcus (IPS), which receives convergent inputs from visual and somatosensory

areas (Seltzer and D. N. Pandya, 1980) to signal the position of the body in space, eye movement, and the geometrical properties of objects such as shape, size, and orientation (Grefkes and G. R. Fink, 2005). Moreover, connectivity of the IPS with the frontal, temporal, and occipital cortices, as well as subcortical regions, has been demonstrated using non-invasive imaging techniques such as functional MRI (fMRI) and Diffusion Tensor Imaging (DTI) (Bray et al., 2013; Uddin et al., 2010). Another well-examined adult multisensory region is the cortex of the STS, which receives convergent inputs from visual, auditory, and somatosensory areas (Seltzer and D. N. Pandya, 1994) and has been documented in humans using fMRI (Beauchamp et al., 2008). The STS has been implicated in face and voice perception, processing of complex visual stimuli, and visuo-auditory processing (Hein and R. T. Knight, 2008). Thus, robust lines of evidence indicate that multisensory convergence and processing occurs within the adult IPS and the STS.

Although multisensory processing occurs in neonates, evidence for the convergence of connections from representations of different sensory modalities in the newborn brain is lacking as well as knowledge of the regions and sources of those convergent effects. Such connectional information is now accessible in humans, given recent advances in neuroimaging. Through resting state fMRI (rs-fMRI), it is now possible to non-invasively probe connections between different neural networks (Biswal et al., 1995) by measuring the strength of functional interactions between brain regions. These area-to-area interactions are based on the temporal correlations between small fluctuations in the blood oxygen level dependent (BOLD) signal which acts as an indirect measure of neuronal activation (Friston et al., 1993). This procedure is particularly effective in subjects who are unable to perform required behaviors for task-based fMRI, such as infants. Here we use rs-fMRI to examine the functional connectivity of IPS and STS cortices in order to evaluate whether these regions in neonates demonstrate connections with representations of different sensory modalities.

MATERIALS AND METHODS

Recruitment

Imaging data was obtained from two independent cohorts. The infants in the University of North Carolina (UNC) cohort (n=10; 5 male, 5 female) were prospectively recruited as part of a large study on brain development (Gilmore et al., 2007). The 10 infants were imaged within 6 weeks of birth (mean=3.5 weeks; range=1.3-5.9 weeks). Informed consent was obtained from parents of the infants and the study was approved by the University of North Carolina at Chapel Hill Internal Review Committee. The University of Maryland (UMD) cohort was comprised of 6 term infants (3 male/3 female) who were imaged within 4 weeks after birth (mean=2 weeks; range=1-4 weeks) for suspected neurological abnormalities based on clinical presentation. One infant was determined to have a small right germinal matrix hemorrhage, while the other 5 infants demonstrated no structural abnormalities using conventional brain imaging techniques. The retrospective data used as part of this study was approved by the University of Maryland Baltimore Internal Review Board. All infants were scanned un-sedated during natural sleep. See Table 1 for demographic data.

MR Data Acquisition

All images for the UNC cohort were acquired using a Siemens Allegra 3T scanner. Both a structural T1 weighted 3D magnetization prepared rapid gradient echo (T1-MPRAGE) sequence and a resting state BOLD sequence were obtained. The imaging parameters for the T1-MPRAGE included a repetition time (TR) = 1820 ms, echo time (TE) = 4.38ms, inversion time = 1100ms, flip angle 7° and 144 slices with a voxel size of $1 \times 1 \times 1 \text{ mm}^3$. The resting state sequence was obtained using a T2* weighted EPI sequence with the parameters TR = 2s, TE = 32 ms, 33 slices, and voxel size of $4 \times 4 \times 4 \text{ mm}^3$ with 150 time points.

All images for the UMD cohort were acquired using a Siemens Tim Trio 3.0T scanner. The imaging parameters for the T1-MPRAGE included were TR = 1900 ms, TE = 3.8ms, inversion time = 1100ms, flip angle = 15° , and 112 slices with a voxel size of $1 \times 1 \times 1 \text{ mm}^3$. The resting state sequence was obtained using a T2* weighted EPI sequence with the parameters TR = 1.72s, TE = 30 ms, 24 slices, flip angle = 80° , and voxel size of $2.8 \times 2.8 \times 4 \text{ mm}^3$ with 250 time points.

Resting State Data Pre-processing and Analysis

Processing of the resting state imaging data was performed using a combination of AFNI (Cox, 1996) and SPM 8 (SPM8,). Preprocessing included slice timing correction, registration of all volumes to the first volume of the time series, spatial smoothing (6mm FWHM), bandpass filtering ($0.005\text{Hz} < f < 0.1\text{Hz}$), and normalization to percent signal change. Resting state data was spatially normalized to a common template (the UNC infant atlas for neonates (Shi et al., 2011)). The global signal from the mean BOLD time series from the whole brain mask and the 6 motion correction parameters were included in the model as regressors to remove the variance related to non-neuronal contributions and motion. Resting state BOLD data was spatially resampled to 2mm isotropic resolution.

Seed based resting state functional connectivity analysis was performed on the rs-fMRI data by extracting the mean BOLD time series from anatomically defined regions of interest (ROIs). ROIs consisted of 4mm spherical ROIs centered in cortical regions associated with primary sensory processing, sensory association areas, and attentional control areas. ROIs included visual, somatosensory, auditory, motor, frontal attention areas as well as cortical multisensory areas. See Table 2 for specific ROIs. ROIs were selected from the UNC neonate template and the location of each ROI was verified by a board certified neuro-radiologist (PR). See Figure 1 for location of ROIs. Pair-wise correlations between the mean BOLD time series of selected ROIs were determined to create functional connectivity matrices for primary sensory, sensory association, and attention areas. All correlations were converted to normalized z-scores using the Fisher transformation for group comparisons. In addition, due to our specific interest in cortical regions associated with multisensory integration, whole brain functional connectivity maps were created by correlating the mean BOLD time series from the bilateral STS and bilateral IPS with the time series of each voxel of the entire brain. Whole brain functional connectivity maps were thresholded at a voxel wise threshold of $p < 0.001$ (FDR corrected for multiple comparisons) and a cluster extent threshold of 100 voxels. All correlations were converted to normalized z-scores using the Fisher transformation for group comparisons.

Statistical Analysis

Significant functional connectivity between the IPS or STS and other cortical ROIs was determined using one-sample t-tests to determine if the mean z-score for each pair of connections was significantly different than zero. Results were corrected for multiple comparisons using the Bonferroni correction assuming 9 comparisons for each ROI ($0.05/9=0.0056$).

RESULTS

The results of the seed based functional connectivity of the IPS (Figure 2a) and the pairwise connectivity matrix (Figure 2b) show the pattern of connectivity of the IPS in neonates from the UNC cohort. The IPS demonstrates the highest functional connectivity in visual association (MT, V3) and somatosensory association (S3) areas. Quantification of the functional connectivity demonstrates that there is significant connectivity between the IPS and the visual and somatosensory association areas (Figure 2c). A similar pattern of connectivity was observed in the independent UMD cohort as shown in Figure 2d. Furthermore, as anticipated, greater connectivity was observed within regions within specific sensory systems than between sensory systems as demonstrated by clusters of increased connectivity associated with each sensory system (Figure 2b and 3b). This observed pattern of connectivity in infants is similar to the functional and structural connectivity of the adult IPS (Bray et al., 2013; Uddin et al., 2010) .

Seed based functional connectivity maps (Figure 3a) and the pairwise connectivity matrix (Figure 3b) show the pattern of connectivity of the STS in neonates from the UNC cohort. The STS shows robust functional connectivity with the visual association areas (MT, V4), primary auditory cortex (A1), and somatosensory association areas (S2 and S3). Quantification of the functional connectivity demonstrates that there is significant functional connectivity between the STS and these areas (Figure 3c). While the overall magnitude of connectivity is lower, our findings using the UMB cohort show a similar pattern of connectivity as the analysis of the UNC cohort as shown in Figure 3d. The multiple sensory areas that show functional communication with the STS in term infants within weeks of birth are similar to those that project to the STS in adults (Beauchamp et al., 2008) . Taken together, these findings indicate that convergence of multiple sensory inputs to the IPS and STS is already present at birth.

DISCUSSION

These results demonstrate that regions of the neonate brain exhibit functional connections with cortical representations of different sensory modalities, thereby providing evidence that the functional architecture for the possibility of multisensory integration is already present at these early stages of development. Specifically, rs-fMRI shows that the IPS in infants connects with both visual (MT, V3) and somatosensory (S3) areas, while the neonatal STS connects with both the visual (MT, V4), auditory (A1) and somatosensory (S2, S3) cortical regions. Furthermore, this convergent pattern of connectivity is similar to that observed for the multisensory IPS and STS regions of adults. While the minimal functional connectivity between V1 and the STS may seem surprising, recent results by Biagi et al. which

investigated functional connectivity in human babies (approximately 7 weeks), found comparable results showing minimal functional connectivity between V1 and temporal areas (Biagi et al., 2015) . Consequently, the present results demonstrate that the connectional substrate for multisensory processing is present in neonates, which is supportive of current theories (e.g., “perceptual narrowing;” (Lewkowicz and A. A. Ghazanfar, 2009)) of multisensory development. These results are also consistent with the onset of cortico-cortical connectivity at birth in other altricial animals (Callaway and L. C. Katz, 1990; Katz and E. M. Callaway, 1992) .

Based on correlations of the BOLD signal from co-active regions representing different sensory modalities, the present observations establish that the neonatal areas of IPS and STS exhibit multisensory activity. One limitation of this methodology, however, is that due to the limited spatial resolution of fMRI, it is not possible to differentiate between the activity of populations of different unisensory neurons from that of multisensory neurons. Stated another way, the present results establish multisensory convergence within a neural area, but not for individual neurons. Such an arrangement could be similar to that reported for the anterior ectosylvian cortex of the 8-week old cat using single-unit recording techniques, which is dominated by unisensory somatosensory and unisensory auditory neurons (Wallace et al., 2006) However, that same study (Wallace et al., 2006) showed that when an area became multisensory, neurons demonstrating multisensory properties were also identified at that time. Therefore it seems likely that multisensory areal convergence and multisensory neuronal convergence coincide, and the present data indicate that areal convergence is present in neonates.

Another consideration is the development of the multisensory neuron itself. Evidence from human perceptual development indicates that multisensory processing changes during infancy through childhood. In fact, the “perceptual narrowing’ theory of multisensory development is based on the observations that early forms of multisensory processing are more generally tuned, while the same stimulus combinations elicit different, more restricted sensitivities in older infants (Lewkowicz and A. A. Ghazanfar, 2009) . Furthermore, this perceptual data is consistent with that observed at the level of the multisensory neuron, where the signature feature of multisensory integration appears only after a protracted period of sensory experience that is likely to involve receptive field refinement (Wallace et al., 2006) and maturation of inhibitory interneuron function (Gogolla et al., 2014) .

Technical Considerations

While the sample sizes of each group in the present study are relatively small, the results show strong similarities in the patterns of connectivity within two unique populations. However, there is some variability in the imaging sequences used to image each population and in the age of the evaluation with the UNC cohort being slightly older than the UMD cohort which may contribute to the greater overall magnitude of connectivity within the UNC cohort. In addition, since these infants were not imaged immediately at birth, but at approximately 2-4 weeks later, the sensory exposure that each infant experienced in the first few weeks of life may have contributed to the results. Furthermore, some of the subtle changes in functional connectivity patterns that we see between the two cohorts may be the

result of the process of connectivity patterns emerging between 2 weeks in the UMB cohort and 3.5 weeks in the UNC cohort. Last, these findings are from resting state conditions while the infant was asleep in which the parametric assessment of sensory responses could not be examined. While this represents a limitation in comparing data obtained during sleeping conditions directly to those obtained during eyes closed conditions, previous work suggests that functional connectivity difference between sleeping and eye closed conditions are not significant in the sensory and visual resting state networks (Larson-Prior et al., 2009). Therefore, our results do not provide direct support for the ability of neonates to perform multisensory integration, but only that the functional architecture may already be present at this stage. Future studies should investigate the developmental features of multisensory integration, by evaluating response patterns to controlled unisensory and multisensory stimuli, to empirically establish a time-course for the phenomenon.

CONCLUSION

These results demonstrate that multisensory convergence, which is a prerequisite for multisensory processing, is already present near birth and, although not directly comparable, is consistent with the connectivity patterns for adult multisensory cortices. These results are consistent with features of cortical maturation as well as current theories of multisensory perceptual development.

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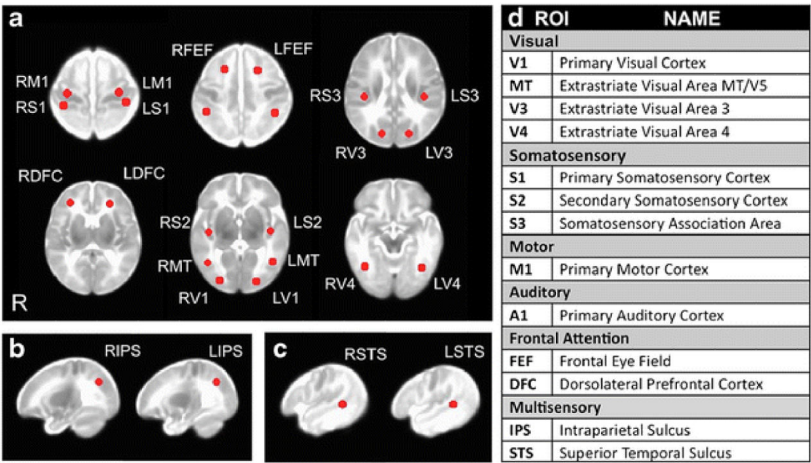
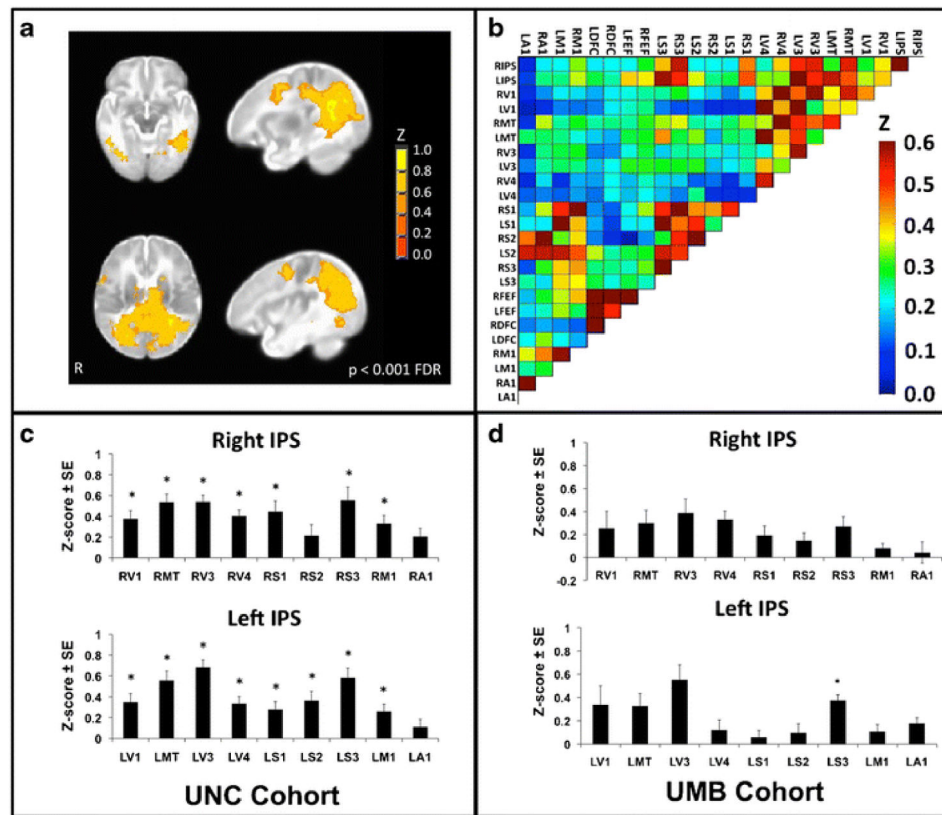
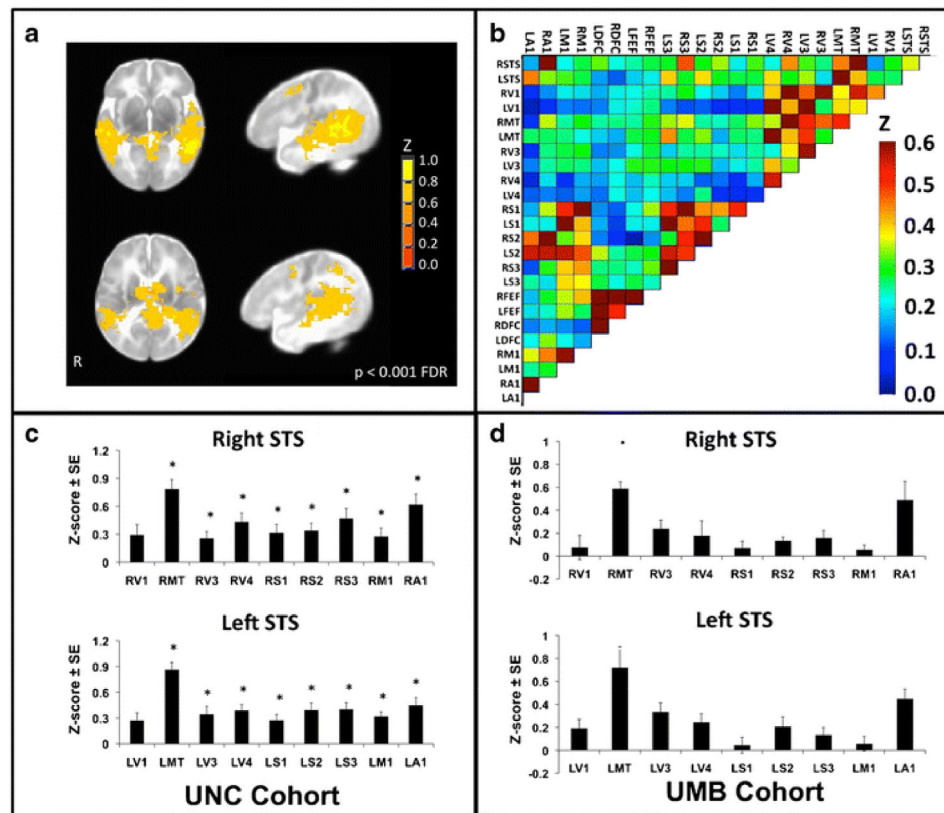


Fig 1.
a. Location of cortical unisensory and frontal ROIs b. Location of intraparietalsulcus (IPS) ROIs.c. Location of superior temporal sulcus (STS) ROIs. ROIs are overlaid on the UNC infant atlas for neonates (Shi et al., 2011). Definitions shown in Table 2.

**Fig 2.**

Functional connectivity of the intraparietalsulcus (IPS) from the UNC cohort (n=10) and UMB cohort (n=6).a. Seed based average group functional connectivity map from the bilateral IPS seed in the UNC cohort.b. Average pairwise functional connectivity matrices between cortical ROIs from the UNC cohort. Intensity represents average z-score. c. Bar graph of average connectivity between each IPS ROI and its ipsilateral cortical regions from the UNC cohort. d. Bar graph of average connectivity between the each IPS ROI and its ipsilateral cortical regions from the UMB cohort. * $p < 0.05$ (corrected) based on one sample t-test.

**Fig 3.**

Functional connectivity of the superior temporal sulcus (STS) from the UNC cohort (n=10) and UMB cohort (n=6).a. Seed based average group functional connectivity map from the bilateral IPS seed in the UNC cohort.b. Average pairwise functional connectivity matrices between cortical ROIs from the UNC cohort. Intensity represents average z-score. c. Bar graph of average connectivity between the each IPS ROI and its ipsilateral cortical regions from the UNC cohort. d. Bar graph of average connectivity between each IPS ROI and its ipsilateral cortical regions from the UMB cohort. * $p < 0.05$ (corrected) based on one sample t-test.

Table 1

Demographics of the UNC cohort and the UMD cohort

	UNC Cohort	UMD Cohort
n	10	6
Gender	5M/5F	3M/3F
Age at Birth (weeks)	38.6 +/- 1.3	39.0 +/- 1.8
Time since birth at Scan (weeks)	3.5 +/- 1.4	2.0 +/- 1.1

Table 2

Regions interrogated for the functional connectivity of IPS and STS

ROI	NAME
Visual	
V1	Primary Visual Cortex
MT	Extrastriate Visual Area MT/V5
V3	Extrastriate Visual Area 3
V4	Extrastriate Visual Area 4
Somatosensory	
S1	Primary Somatosensory Cortex
S2	Secondary Somatosensory Cortex
S3	Somatosensory Association Area
Motor	
M1	Primary Motor Cortex
Auditory	
A1	Primary Auditory Cortex
Frontal Attention	
FEF	Frontal Eye Field
DFC	Dorsolateral Prefrontal Cortex
Multisensory	
IPS	Intraparietal Sulcus
STS	Superior Temporal Sulcus