Brain & Language 126 (2013) 109–122

Contents lists available at SciVerse ScienceDirect

Brain & Language

journal homepage: www.elsevier.com/locate/b&l

Structural asymmetry of anterior insula: Behavioral correlates and individual differences

Christine Chiarello [a,*], David Vazquez [a], Adam Felton [a], Christiana M. Leonard [b]

[a] Department of Psychology, University of California, Riverside, Riverside CA, USA
[b] McKnight Brain Institute, University of Florida, Gainesville FL, USA

ARTICLE INFO

Article history:
Accepted 28 March 2013
Available online 13 May 2013

Keywords:
Insula
Cortical lateralization
Language lateralization
Handedness
Reading skill
Visual word recognition
Cortical surface area

ABSTRACT

The current study investigated behavioral correlates of structural asymmetry of the insula, and traditional perisylvian language regions, in a large sample of young adults ($N = 200$). The findings indicated (1) reliable leftward surface area asymmetry of the anterior insula, (2) association of this asymmetry with divided visual field lateralization of visual word recognition, and (3) modulation of the correlation of structural and linguistic asymmetry by consistency of hand preference. Although leftward asymmetry of cortical surface area was observed for the anterior insula, pars opercularis and triangularis, and planum temporale, only the anterior insula asymmetry was associated with lateralized word recognition. We interpret these findings within the context of recent structural and functional findings about the human insula. We suggest that leftward structural lateralization of earlier developing insular cortex may bootstrap asymmetrical functional lateralization even if the insula is only a minor component of the adult language network.

1. Introduction

Ideas about cortical regions recruited for language processing have evolved considerably in recent decades. In addition to classical language areas in left perisylvian cortex, a much more widespread network spanning both hemispheres has been shown to participate in language functions (Hickok & Poeppel, 2007; Price, 2010). Hence, one goal of contemporary research is to identify the functional significance of various components of this network, and to examine individual differences in brain organization for language. In most individuals during language tasks, regions within the left hemisphere respond with greater activation (Price, 2010) and synchronization (Saur et al., 2010) than comparable right hemisphere regions. Left hemisphere language specialization is also observable using behavioral techniques that lateralize initial receipt of verbal information to a single hemisphere (Bryden, 1982; Chiarello, 1988).

Numerous structural asymmetries have been identified in language relevant cortex (Foundas, Eure, Luevano, & Weinberger, 1998; Watkins et al., 2001), although the association between structural and functional lateralization is tenuous (Eckert, Leonard, Possing, & Binder, 2006). The left inferior frontal gyrus (pars triangularis and opercularis) and superior temporal plane (planum temporale and surrounding temporal–parietal areas) represent quintessential language cortex, and are structurally and/or functionally asymmetric (Chiarello, Welcome, Halderman, & Leonard, 2009; Price, 2012). Wernicke initially suggested that the insula might also be important for language function (Wernicke (1874) as cited by Weiller, Bormann, Saur, Musso, and Rijntjes (2011)), and in 1908, Augusta Dejerine-Klumpke described anatomical evidence that lesions to an area deep to the left pars opercularis including the anterior insula was associated with nonfluent aphasia (Roch Lecours & Caplan, 1984). Recent research implicates the insula in a wide variety of cognitive, sensory, and emotional functions (Menon & Uddin, 2010; Mutschler et al., 2009). Nieuwenhuys (2012), for example, lists over 15 different putative insula specializations. Functional neuroimaging and lesion studies also suggest participation of the insula in some language tasks (Dronkers, 1996; Mutschler et al., 2009), and one recent study claimed that insular volume asymmetry could predict functional language lateralization (Keller et al., 2011). However, the interpretation of some findings has been challenged (Hillis et al., 2004; Richardson, Fillmore, Rorden, LaPointe, & Fridriksson, 2012), and the very diversity of suggested insula functions raises questions about whether this region may subserve any language-specific processes.

The extent to which the human insula is asymmetrical in either structure or function is not well understood and requires further examination. In the current investigation, we examine structural asymmetry of the insula, and potential behavioral correlates, along with asymmetry in more traditional language regions. This

* Corresponding author. Address: Department of Psychology, University of California, Riverside, CA 92521, United States. Fax: +1 951 827 3985.
E-mail address: christine.chiarello@ucr.edu (C. Chiarello).

0093-934X/$ - see front matter © 2013 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.bandl.2013.03.005

research had several objectives. First, to document the extent of structural asymmetry, we measured asymmetries of cortical surface area in classical frontal and temporal language regions and in the insula in a large sample of healthy young adults. Second, we assessed the degree of association between these structural asymmetries and lateralized language processing using a composite measure of visual word recognition. If the insula participates in the language network, then we would expect a structure/function association that is at least as strong for the insula as for more traditional language areas. We additionally investigated the association between structural asymmetry and reading skill. Third, we considered whether consistency of hand preference affects structural asymmetries and structure/behavior relationships. Although behavioral differences have been documented between individuals with consistent and mixed hand preferences (see Prichard, Propper, & Christman, 2013 for recent review), the neural correlates of these differences have been largely unexplored. To preview our findings, we document herein (1) reliable leftward surface area asymmetry of the anterior insula, (2) the association of this asymmetry with lateralization of visual word recognition, and (3) modulation of the correlation of structural and linguistic asymmetry by consistency of hand preference. Before presenting these results, we present a brief review of relevant structural and behavioral investigations.

1.1. Regional structural and functional organization of human insula

The human insula has an approximately trapezoidal shape and in most individuals consists of 5 gyri, 3 anterior (short insular) and 2 posterior (long insular) gyri, separated by the deep central sulcus of the insula (Afif & Mertens, 2010). Although early cytoarchitectural research reported that the central sulcus of the insula approximated the boundary between agranular (anterior) and granular (posterior) cortex, a recent review and reanalysis supported a more concentric ventral to dorsocaudal organization (Nieuwenhuys, 2012). Comparative studies suggest an expansion of the anterior insula that may be associated with increased complexity of cognitive functions across mammalian species (Nieuwenhuys, 2012). The white matter organization of the insular region includes the extreme capsule, a portion of a ventral language pathway, that courses beneath the insular cortex (Axer, Klingner, & Prescher, in press).

Probabilistic tractography studies have documented gradual shifts in connectivity patterns between anterior and posterior insular regions (Cerliani et al., 2012; Cloutman, Binney, Drakesmith, Parker, & Ralph, 2012; Nanetti, Cerliani, Gazzola, Renken, & Keysers, 2009). The most anterior insular areas project to orbitofrontal cortex, pars triangularis and opercularis, and anterior temporal cortex, while the most posterior regions have projections to posterior STG and MTG and to somatosensory and posterior parietal cortex (Cerliani et al., 2012; Cloutman et al., 2012; Jakab, Molnar, Bogner, Beres, & Berenyi, 2011). A transitional pattern of connectivity was observed for intermediate insular regions (middle and posterior short gyri, anterior long gyrus) with projections to inferior frontal gyrus, premotor cortex, rolandic operculum, and temporal and parietal cortex (Cerliani et al., 2012; Cloutman et al., 2012). With respect to classical language areas, major projections were found between the dorsal anterior insula and BA 45, and from dorsal middle insula (middle and posterior short gyri) to BA 44 and 6. Hence the anterior insula had the highest connection probability with key frontal language areas (Cerliani et al., 2012). Resting state functional connectivity research also documents anterior to posterior insular shifts in connectivity, with additional dorsal/ventral differentiation of anterior insula functional connections (Cauda et al., 2011; Chang, Yarkoni, Khaw, & Sanfrey, in press; Deen, Pitskel, & Pelphrey, 2011). In particular, activity in dorsal anterior insula was associated with activity in the anterior cingulate, orbitofrontal cortex, and dorsolateral frontal, temporal and parietal opercular cortex, while ventral anterior insula activity was associated with superior temporal sulcus, amygdala, and frontal and temporal opercula activation (Chang et al., in press; Deen et al., 2011).

Activation of the insula has been observed in a wide variety of functional neuroimaging tasks (Chang et al., in press; Kurth, Zilles, Fox, Laird, & Eickhoff, 2010), and a number of broadly defined functions have been attributed to this brain region. As with structural findings, distinctions emerge between anterior and posterior insular regions. Posterior portions of the insula respond to visceral and interoceptive sensations, regulate physiological reactivity and homeostasis, and are involved in some sensorimotor functions, while anterior regions are more involved in introspecting about feelings (Craig, 2009; Kurth et al., 2010; Menon & Uddin, 2010). In addition, the anterior insula is hypothesized to play an important role in experiencing and interpreting social emotions (Lamm & Singer, 2010) and in social interaction (Guionnet et al., 2012). The perception of pain has also been linked to the insula (Nieuwenhuys, 2012), with recent fMRI evidence suggesting that the mid-posterior insula mediates the experience of pain, while the anterior insula is involved in the anticipatory anxiety of pain (Lin, Hsieh, Yeh, Lee, & Niddam, 2013). The anterior insula, along with the anterior cingulate, may function to detect and respond to salient stimuli (Menon & Uddin, 2010), and participate in attention and cognitive control processes (Menon & Uddin, 2010; Nelson et al., 2010). One model of insular function posits a posterior to anterior progression of processing from the representation of interoceptive sensations (posterior), to the integration of these sensations with emotionally salient environmental stimuli (middle), to awareness of the self in the immediate moment (anterior) (Craig, 2009). A recent meta-analysis of active task functional connectivity likewise identified an anterior cluster with long-range connections to regions involved in attention, and a posterior cluster with more local connectivity to sensorimotor regions (Cauda et al., 2012).

Meta-analyses across a wide variety of tasks indicate that the left and right anterior insula are some of the most frequently activated areas, implying a role in processes that are shared across many behaviors (Nelson et al., 2010), perhaps involving multimodal functional integration (Cauda et al., 2012; Kurth et al., 2010). It is becoming increasingly clear that a network perspective is important for understanding the role of the insula in perceptual and cognitive functions. Menon and Uddin (2010) identify the anterior insula and anterior cingulate as key components in a salience network which functions to select the most relevant internal and external stimuli for behavioral guidance. Furthermore, they posit that the anterior insula is critical for coordinating and switching between central executive and default mode networks, that is, to engage attention, working memory, and control processes while disengaging systems that are not currently relevant. Cauda et al. (2012) also identify the anterior insula as a hub that bridges anterior and posterior insular circuits. Such data raise the possibility that any insular involvement in language may involve the coordination or overlap of functional networks recruited for a broad variety of activities.

1.2. Evidence for insula asymmetry

Few studies have examined structural asymmetries in the insula. Two large scale studies using similar voxel based morphometry (VBM) methods reported slightly different results. Watkins et al. (2001) observed leftward asymmetry for gray matter in a superior portion of the anterior insula and the medial middle insula, and rightward asymmetry for a very inferior portion of the anterior in-