Linking Neural Activity to Mental Processes

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Abstract Brain imaging research has developed for more than two decades and has enriched our knowledge about human brain functions. Researchers have developed sophisticated methods of experimental design and data analysis in order to link observed neural activity to mental processes. This paper illustrates several methods that have been employed in studies of both low-level cognitive processes (e.g., visual perception) and high-level cognitive processes (e.g., social cognition). Neuroimaging findings obtained using these novel methods enhance our understanding of the neural mechanisms underlying human cognitive processes.

Keywords Brain imaging · Visual perception · Social cognition

Introduction

The major goal of psychological research is to understand mental processes so as to interpret and predict human behaviors. To do this, psychologists have developed different methods to uncover the mental processes involved in perception, attention, memory, decision making and so on. For example, psychophysics, based on techniques and theories formulated by Fechner (1860/1966), examines how human sensation and perception vary as a function of physical features of stimuli, allowing scientists to make inferences about underlying mechanisms. In order to

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Department of Psychology, Peking University, 5 Yiheyuan Road, Beijing 100871, China e-mail: shan@pku.edu.cn e-mail: ffang@pku.edu.cn uncover psychological processes underlying social behavior, social psychologists investigate how social feelings and behaviors are modulated by socially-relevant stimuli and social context through the recording of self-reports via questionnaires and interviews, etc.

Cognitive neuroscience research aims to uncover neural substrates underlying various human cognitive functions by using different neuroimaging techniques such as functional magnetic resonance imaging (fMRI) and event related potentials (ERPs). The integration of psychological methods with neuroimaging techniques has been demonstrated to be useful in linking neural activity with known mental processes. This paper reviews recent brain imaging studies in order to illustrate the methodological integration of psychological and neuroimaging research. The first section introduces the usefulness of combining psychophysics and fMRI in studies of the neural substrates of visual perception, while the second section illustrates the integration of social psychology and neuroimaging in researching the neural correlates of social cognition.

Linking neural activity to perception

The integration of psychophysics and fMRI gave birth to a new approach, namely, "correlational research" (Ehrenstein & Ehrenstein 1999), which aims to correlate subjective feelings and neural activity through quantitative methods. This approach examines if the blood oxygen level dependent (BOLD) signal in a specific cortical area can precisely predict a behavioral change measured by psychophysics or vice versa. Correct neural prediction of behaviors suggests that a cortical area may play a pivotal role in specific cognitive functions that induce such related behavior changes. For instance, while psychophysical research

measures thresholds of detection or discrimination of visual features, the correlational research investigates whether the magnitudes of neural activity correlate with threshold changes when detecting or discriminating perceptual stimuli. The correlation of BOLD signals and threshold changes provides evidence for a quantitative relationship between neural activity and subjective feelings. One example of the correlational approach is to assess the relationship between the contrast increment threshold and neural activity in the human visual cortex. Boynton et al. (1999) measured BOLD signals in the visual cortex and associated them with the changes in visual stimulus contrast. They found that the contrast increment was detected by human subjects when the fMRI responses in the early visual areas increased by a criterion amount. Furthermore, while two different contrast levels evoke different magnitudes of fMRI responses, subjects are only able to discriminate these two contrast levels when the BOLD signal difference in the visual cortex is larger than a specific value. Such evidence attests to the ability of BOLD signal changes as reasonable predictors of variations in contrast threshold.

Recent research also demonstrates correlations between subjective sensitivity adjustments in response to repeatedly presented stimuli (i.e., adaptation) and BOLD signal changes in specific brain areas. For example, Fang et al. (2005) exposed subjects to Gabor patches with specific orientations. After the adaptation procedure, BOLD responses in V1 and other early visual areas were measured using a test stimulus with different orientations. Fang et al. found that the magnitudes of BOLD signal in the visual cortex varied in proportion to the angular difference between the adapting and test stimuli (Fig. 1a and b). They also measured contrast detection thresholds after adaptation and found that BOLD signals in V1 closely matched the psychophysically derived contrast detection thresholds (Fig. 1c). The findings demonstrate a close linkage between psychophysical data and fMRI data, further indicating that fMRI may be as powerful as traditional neurophysiological techniques (such as single-unit recording) in uncovering the neural mechanisms underlying visual perception.

The combination of psychophysics and fMRI has also been used in research of high-level visual processing such as face recognition. A key issue in the facial recognition literature is how face identity and view are represented in human visual system. Leopold et al. (2001) found that, in the context of a computationally-derived 'face space', adaptation to an individual face specifically shifted perception along a trajectory passing through the adapting and average faces. This shift then selectively facilitated recognition of a test face lying on this trajectory and impaired recognition of other faces. For example, adaptation to the face anti-Adam could improve subjects' recognition performance for the face Adam with an identity strength of 0.1, relative to the no adaptation condition (Fig. 2a and b). The results suggest that faces falling along an identity axis within this space are coded by the same neural population and those falling along a distinctive axis are coded by a different population. Indeed, this was demonstrated in a recent work (Loffler et al. 2005) which showed that the adaptation effect in the fusiform face area (FFA) to the faces falling along an axis was stronger than when directed towards the faces falling along a circumference (Fig. 2c and d). This result was consistent with the prediction from the psychophysical data because the faces falling along an axis stimulated the same neural population while those falling along the circumference stimulated different populations.

Fang & He (2005) and Fang et al. (2007) also examined correlations between FFA activity and a perceptual illusion of face, namely, the viewpoint aftereffect. The viewpoint aftereffect refers to a phenomena in which a subject adapts to an object/face viewed from one side (e.g., 30° to the left of center), and then subsequently views the same object/ face presented from a near frontal view but perceives the viewing direction with a bias in the direction opposite to that of the adapted viewpoint (e.g. 2° to the right). The psychophysical results suggest face representation is viewercentered and different face views are represented in several high-level visual cortical areas. Fang et al. (2007) localized face viewing representation combining the physical measurement and the adaptation of BOLD signals. They found a robust correlation between changes of perceived viewing direction and the activity in FFA and superior temporal sulcus (STS), suggesting representation of face views in these brain areas. Taken together, the correlation between psychophysical data and fMRI data in visual areas provides important results for understanding the neural mechanisms underlying human visual perception.

Linking neural activity to social cognition

While cognitive neuroscience research has focused on exploring the neural correlates of perception, attention, memory, language, emotion, etc., recent neuroimaging studies have extended into the field of social cognition, aiming to uncover the neural substrates of cognitive processes engaged in social interactions and social behaviors. The emergence of social cognitive neuroscience provides new challenges to neuroimaging research in attempting to uncover how neural activity is linked to the processing of social information.

The social contents of stimuli differ from the perceptual meanings of the same stimuli in that social meaning of a stimulus may depend on sociocultural contexts and the subject's sociocultural background while perceptual mean-



ings are less context dependent. Neuroimaging studies of face recognition may simply contrast the neural activity elicited by pictures of faces with that elicited by pictures of non-face stimuli in order to identify brain areas involved in face recognition. For example, it is commonly accepted that

◄ Fig. 1 Orientation-tuned fMRI and psychophysical adaptation in human early visual cortex. a Region of interest (*ROI*) depicted on a flattened brain. *Green lines* are borders of early visual areas obtained from retinotopic mapping. b Event-related BOLD signals in V1 evoked by test stimuli whose orientations were different from the adapting stimulus by 0°, 7.5°, 30° and 90°, respectively. The monotonic increase in signal from the 0° to 90° test stimuli demonstrated an orientation-tuned fMRI adaptation. c Contrast detection threshold for the 0°, 7.5°, 30°, and 90° test stimuli after adaptation plotted against peak values of event-related BOLD signals in V1 evoked by the four test stimuli. Linear functions were applied to fit four individual subject's data (*gray lines* and *symbols*) and average (*dark line* and *symbols*)

increased activity in the FFA while watching face stimuli indicates that this area is involved in face recognition. In contrast, social cognitive neuroscience research does not take it for granted that the social meaning of a stimulus can be determined simply by activation in response to stimulus itself. The same stimulus can be endowed with different social meanings that have to be identified through subjective evaluations. For instance, studies of empathy for pain employed visual displays of body parts in painful or nonpainful situations (Jackson et al. 2005; Gu & Han 2007; illustrated in Fig. 3). Before applying these stimuli to fMRI studies, researchers had to confirm the significance of the stimuli by asking an independent group of subjects to rate the pain intensity shown in the pictures. This procedure is necessary because it helps to confirm the social meaning of the stimuli while providing the basis for further fMRI data analysis.

After the social meanings of stimuli are confirmed by subjective assessment, researchers may then utilize traditional methods of imaging data analysis to define neural activities underpinning specific social cognitive processes. For example, contrasts between BOLD responses induced by painful and non-painful stimuli were used to assess the neural correlates of empathy for pain (Jackson et al. 2005; Gu & Han 2007) and suggest that parts of the neural circuit engaged in the first-person pain experience, such as bilateral insula and the anterior cingulate cortex (ACC), are also involved in understanding and sharing the pain experience of others (Fig. 3). However, researchers also noticed that subjective feelings or evaluations could be different dramatically across participants. This implies the variance of neural activity associated with processes of social information across subjects. Under certain circumstances, subjective evaluations, such as political attitudes linked to the same target, can be even opposite among subjects. Consequently, simple contrasts between two conditions classified according to stimulus type may not produce robust activation in some cases. This reflects the consequence of the interplay between ontogenesis and sociocultural contexts and manifests the effects of personal experience on the neural substrates underlying social cognition.



Fig. 2 Face identity representation in human visual system. **a** Face/ anti-face fairs used in Leopold et al. (2001). **b** Computational derived face space in which the stimuli were generated. The original faces (*green ellipses*) are connected to the average face (*blue ellipse*) by an 'identity trajectory'. *Numbers* refer to the 'identity strength' possessed by the given face. **c** A neural population may encode face identity along an axis indicated by the red ellipse or along a circumference

indicated by the green annulus. **d** fMRI signals elicited by three different types of face stimulus blocks. In a block, faces could be sampled along an axis (*red bar*) or a circumference (*green bar*), or from a location (*blue bar*). The identity adaptation effect in the fusiform face area (*FFA*) among the faces falling along an axis was stronger than that among the faces falling along a circumference—the *red bar* is significantly lower than the *green bar*

To solve this problem, correlation analysis has been frequently used in social cognitive neuroscience research. Such a strategy assesses variations of neural activity in specific brain regions associated with certain social cognitive processes across subjects. The correlation analysis is useful to link the neural activity of one brain region with subjective feelings. Moreover, the results of a correlation analysis may help to test whether neural activities in some brain areas can be utilized to predict subjective reports or behavioral responses in social interactions. For example, Jackson et al. (2005) calculated correlations between neural activity in brain areas that showed increased activation in the contrast between painful and non-painful stimuli. They found that subjective ratings of the intensity of perceived pain correlated with the signal changes in ACC (Fig. 3) and thus provided further evidence that subjective feelings are related to neural activity in specific brain regions. A recent ERP study (Fan & Han 2008) also found correlations between the magnitude of ERP components and the subjective ratings of intensity of others' pain (Fig. 3). Interestingly, such correlations were evident for the shortlatency ERP components. The amplitudes of long-latency

Fig. 3 a Painful and b nonpainful stimuli used in Gu and Han (2007); c increased ACC activation to painful relative to non-painful stimuli observed in Jackson et al. (2005): d correlation between ACC activity and subjective ratings of others' pain observed in Jackson et al. (2005); e correlation between ERP amplitudes and subjective ratings of others' pain in Fan and Han (2008); f correlation between ERP amplitudes and subjective ratings of self-unpleasantness induced by perception of others' pain in Fan and Han (2008)



ERP components did not correlate with subjective reports. In addition, the ERP amplitudes in the same time window also correlated with subjective ratings of self-unpleasantness induced by the perception of another's pain. The findings that the neural activity in the same time window correlated with subjective feelings of both others' pain and one's own emotions lend support to the proposition that emotional sharing occurs early in the process of empathy for pain.

Given that adaptation of neural activity is an efficient index of neuroanatomical localization of perceptual processes as mentioned in the first section of this paper, studies of human social cognition have also tried to make use of this method. In a recent fMRI study, Jenkins et al. (2008) investigated if self and similar others are both represented

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in the ventral medial prefrontal cortex (vMPFC) in a personal trait judgment task. The authors required participants to make two consecutive judgments regarding the self, similar others, or dissimilar others. The rationale is that, if both introspection about self and inference about the minds of similar others engage vMPFC, judgments regarding similar others and self in two successive trials should induce repetition suppression of vMPFC activity relative to judgments regarding dissimilar others and self in two successive trials. Indeed, the authors observed repetition suppression of vMPFC activity when self-judgment was preceded by judgments of similar others. The findings thus provide strong evidence that thinking about the mind of a similar person may rely on referencing on one's own mental characteristics. Measurement of repetition suppression has not been widely used in research of neural mechanisms of high-level social cognition. However, this method will demonstrate powerful results in future studies of social cognition.

Research on neural mechanisms of social cognition has to consider the influence of sociocultural contexts. Recent social psychological research showed ample evidence that both low-level perceptual/attentional processing and highlevel social cognition are profoundly affected by sociocultural contexts in which cognitive functions develop (Nisbett & Masuda 2003). Specifically, people from Western cultures (European American) think in more analytic ways whereas people from East Asian cultures think in more holistic manners to perceive and understand the world. Recent neuroimaging studies have also shown evidence that cultural differences in cognition coexist with differences in the underlying neural substrates by cultures. Our recent transcultural neuroimaging research demonstrated that, for Chinese, judgment of personal trait of both self and close other (mother) generated enhanced activity in vMPFC, whereas only self-judgment resulted in increased vMPFC activity in Westerners (Zhu et al. 2007). The findings indicated that Westerners used an independent view of the self, thus activating the vMPFC only during self-representation, while Chinese used an interdependent view of the self, thus making them likely to employ this brain region to represent both the self and intimate others. Apparently, the neural structure of representation of self and others greatly depends upon sociocultural contexts. The cultural differences in neural substrates observed in recent work may extend to other social cognitive functions and should be examined in future research.

Future research under Pacific Rim interactions

Recent studies have shown more and more evidence for sociocultural influence on neural substrates of human perception and cognition (Han & Northoff 2008). Pacific Rim collaborations may facilitate future studies of cultureinvariant and culture-specific neural mechanisms underlying perception, social cognition, etc. For example, neural representation of same-race and other-race faces is an interesting and important question that can be addressed via Pacific Rim collaborations. Although it is well known that people are better at recognizing faces of their own race than faces of other races, the underlying neural mechanisms remain unknown. One possible hypothesis is that the human visual system is more subtly tuned to faces of one's own race than to faces of other races and the neuronal tuning curve for the same-race face is narrower than that for the other-race face. The combination of psychophysical and fMRI adaptations and collaborations between labs from different cultures will be able to test this hypothesis. Pacific Rim collaborations should also promote transcultural neuroimaging studies of social cognition. For instance, while previous fMRI studies have identified neural substrates of empathy for pain, it is unclear how the empathic responses are modulated by social relationships. One issue that may be addressed is if empathic responses are different to faces of the same and different races. Transcultural brain imaging studies of such issues may help to understand the neural basis of behavioral differences between people with different cultural backgrounds during social interactions.

Conclusion

The purpose of functional neuroimaging studies is to link neural activities to specific cognitive processes in the human brain and to employ certain patterns of neural activity to predict human behavioral responses. Extensive fMRI studies of multiple-level human cognition help to develop different methods to identify neural substrates of cognitive processes in the human brain. fMRI data analysis can extend from simple contrasts of two tasks to examining correlations between subjective feelings and BOLD signals in specific brain areas. These methods are useful to test the relationships between particular cognitive processes and neural activities in specific brain areas or specific patterns of activities in several brain areas.

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