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ERP adaptation provides direct evidence for early mirror neuron activation in the inferior parietal lobule

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ABSTRACT

Mirror neuron systems are frequently investigated by assessing overlapping brain activity during observation and execution of actions; however, distinct neuronal subpopulations may be activated that fall below the spatial resolution of magnetic resonance techniques. This shortfall can be resolved using repetition suppression paradigms that identify physiological adaptation processes caused by repeated activation of identical neuronal circuits. Here, event-related potentials were used to investigate the time course of mirror neuron circuit activation using repetition suppression within and across action observation and action execution modalities. In a lip-reading and speech production paradigm, the N170 component indexed stimulus repetition by adapting to both cross-modal and intra-modal repetitions in the left hemisphere. Neuronal source localization revealed activation of the left inferior parietal lobule during cross-modal relative to intra-modal trials. These results provide support for the position that the same neuronal circuits are activated in perceiving and performing articulatory actions. Moreover, our data strongly suggest that inferior parietal lobule mirror neurons are activated relatively early in time, which indicates partly automatic processes of linguistic perception and mirroring. Repetition suppression paradigms therefore help to elucidate neuronal correlates of different cognitive processes and may serve as a starting point for advanced electrophysiological research on mirror neurons.

1. Introduction

The importance of mirror neurons in higher cognitive processing has become increasingly evident in recent years. First described in primate area F5 in the lateral prefrontal lobe (di Pellegrino et al., 1992) and later also in area PF of the inferior parietal lobe (Fogassi et al., 2005), mirror neurons selectively fire during observation of specific hand or mouth movements as well as during execution of the same movements by other individuals. While characteristics of mirror neurons in primates have been studied in single or multiple unit recordings (Umilta et al., 2001), this has not been possible in humans. However, a recent study on intracranial measurements in pre-surgical epilepsy patients describes neurons with mirror properties in different cortex areas (Mukamel et al., 2010).

Studies investigating mirror neuron activity in humans have mainly used functional magnetic resonance imaging (fMRI) to show topographically overlapping activations during observation and execution of actions. Using this approach, mirroring of finger and hand movements during action observation and action execution was found in the pars opercularis of the inferior frontal gyrus (IFG; Iacoboni et al., 1999), in the inferior parietal lobule (Buccino et al., 2004), and in the superior temporal cortex (Molenberghs et al., 2010). When employing emotionally or socially relevant stimulus material, especially watching the pain of others, activations of the insula (Anders et al., 2011) and somatosensory cortices (see Keysers et al., 2010, for a review) were observed. These regions were confirmed as important nodes in the cortical mirror neuron network both in an analysis of unsmoothed fMRI data (Gazzola and Keysers, 2009) and in a recent meta-analysis (Molenberghs et al., 2012). In the language domain, fMRI studies and neurophysiological studies employing magnetoencephalography (MEG), electroencephalography (EEG), or transcranial magnetic stimulation (TMS) provided evidence for mirror neuron activation during speech perception (Fadiga et al., 2002; Nishitani and Hari, 2002; Pulvermüller et al., 2003, 2006, 2012; Wilson et al., 2004). Furthermore, it could be demonstrated that motor systems activation plays a functionally specific role in a speech perception and classification task (D'Ausilio et al., 2009). However, while intriguing, demonstration of overlapping or vicarious activity during observation and execution of actions and even the demonstration that the motor areas are critical for perceptual processing do not justify the conclusion that the same neuron circuits are involved in performance and perception of the same action. As even a small brain area includes millions of neurons, partly overlapping or even fully distinct sub-populations of modality-

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specific sensory and motor neurons may still underlie the observed large scale activations.

An elegant avenue to investigate the activation of specific mirror neuron circuits in humans is by using repetition suppression (RS) effects. RS describes the adaptation or reduction of neuronal activity in response to repetition of a certain stimulus (Henson et al., 2000; Soon et al., 2003; Dinstein et al., 2007; see also Grill-Spector et al., 2006, for a review). The rationale for implementing an RS paradigm is that an adaptive neuronal process can only be attributed to the activation of the same neuronal population (Miller et al., 1991). The reduction of a neuronal response to the repetition of a specific stimulus (e.g., black circle) can be compared to the response reduction following a non-identical repeated stimulus that is systematically modified along a certain dimension (e.g., black triangle). The degree of neuronal suppression to the modified stimulus may be used as a sensitivity index of the underlying neuronal response to that specific dimension (e.g., shape). RS is thus highly valuable for elucidating the functional correlates of neuronal signals.

As the activation of mirror neurons can be elicited in response to action observation, action execution, and speech (phoneme) perception, a suitable RS paradigm offers the possibility to detect mirror neuron activity for different underlying neurophysiological processes. Here, intra-modal RS effects indicate sensory (observation vs. observation) or motor (execution vs. execution) properties and, most important within the scope of this study, cross-modal RS indicates sensori-motor properties (observation vs. execution; execution vs. observation) of underlying neuronal processes. These sensori-motor properties may reflect mirror neuron characteristics. In line with this view, cross-modal fMRI adaptation effects were found in the inferior frontal gyrus (Kilner et al., 2009) and the inferior parietal cortex (Chong et al., 2008), thus strongly suggesting mirror neurons within these cortical regions, although negative results have also been reported (Lingnau et al., 2009). Consistent with the mirror neuron topography, electrophysiological studies with EEG and TMS provided evidence for mirror neuron-like adaptation effects over posterior cortex areas (Summerfield et al., 2011), in the ventral premotor cortex (Cattaneo et al., 2011), and the superior temporal sulcus along with the inferior frontal lobe and intraparietal sulcus (Ortigue et al., 2009).

We here set out to investigate repetition suppression of mirror neuron circuits using event-related potentials (ERPs). The motivation for this is two-fold: first, the hemodynamic response is a sluggish and indirect measure, following the neurophysiological response after a delay of seconds. In contrast, neurophysiological techniques allow for direct monitoring of neuronal activity patterns. Closely linked to the sluggishness of hemodynamic responses is a cognitive argument: fMRI results do not tell the researcher whether any brain response measured did immediately follow a presented stimulus and thus may reflect aspects of the stimulus-induced instantaneous perceptual processes, or whether a secondary late cognitive process following upon stimulus perception (e.g., second thought or optional imagery) might be reflected (for discussion, see Pulvermüller, 2005). This provides a second argument for the use of real-time neurophysiological imaging with exact temporal resolution, such as the ERP method applied here.

The rationale of the present study was to elucidate the time course of mirror neuron activity by measuring ERPs in a repetition suppression paradigm. Participants had to passively observe faces silently articulating speech sounds (observation condition) or to pronounce phonemes indicated by single letters (execution condition). Adaptation of ERP components was assessed in an intra-modal (identical letter or identical face) and a cross-modal (face–letter or letter–face combination) condition in response to letters and to faces forming these letters. Stimulus timing was based on previous studies on face-selective adaptation. Given the fundamental sensori-motor properties of mirror neurons, we expected comparable responses to action observation and action execution. Regarding the time course, evidence from animal studies points towards an early activation of mirror neurons, reflecting an automatic rather than volitional process, as already suggested by initial reports of resonance phenomena in monkeys (di Pellegrino et al., 1992; Gallese et al., 1996). Interestingly, recent studies in humans have been able to demonstrate that imitation during hand action games (e.g., rock–paper–scissors game) occurs automatically rather than intentionally (Cook et al., 2012; Belot et al., 2013). We thus hypothesized to find evidence of mirror neuron activity already at early, primarily exogenously driven stages of information processing (100–200 ms). Given the left-hemispheric specialization for language, we specifically hypothesized to find the postulated responses in the left hemisphere only.

2. Material and methods

2.1. Participants

Twenty healthy volunteers (11 females, 9 males) with a mean age of 26.55 ± 4.4 years with normal or corrected-to-normal vision and without any history (including family history) of psychiatric or neurological disorders participated in this study. Participants were right-handed, as indicated by a mean laterality index of 73.23 (Edinburgh Handedness Inventory; Oldfield, 1971) and of average intelligence, as evidenced by a mean verbal IQ of 105.80 in a multiple choice vocabulary test (Lehrl et al., 1995). All participants were native speakers of German. Ethics approval was given by the ethics committee of the Charité University Medicine Berlin, and the study was conducted in accordance with the Declaration of Helsinki and its amendments. All volunteers gave written informed consent before participating in the study and received monetary reimbursement for their efforts.

2.2. Basic design

An RS paradigm was used where participants were asked to passively observe faces forming specific letters (observation condition) and to read aloud two different letters as soon as they were presented on a screen (execution condition). Stimulus presentation was either intra-modal (identical pairs) or cross-modal (face–letter or letter–face pairings showing the same letter). Event-related potentials were recorded in response to the presentation of stimulus pairs (S1 = adapter stimulus/S2 = test stimulus). Underlying neurophysiological activity in response to repetitions was measured by subtracting S2 from S1 activation, particularly focusing on source localization of N170 effects.

2.3. Stimuli

Four black and white high resolution photographs of an unfamiliar female and male face forming the vowels 'A' and 'U' served as stimuli for the passive observation condition. The letters 'A' and 'U' served as imperative stimuli requiring vocalization of the depicted vowel in the active execution condition. All stimuli were presented on a light gray background using *Presentation* software (Neurobehavioral Systems, Albany, CA). Each stimulus was presented for 2000 ms and was displayed on a 24″ TFT computer screen with a viewing distance of approximately 60 cm and a visual angle of approximately 15 × 10° for the outer stimulus contour.

All stimuli were organized in pairs (S1/S2) with an inter-stimulus interval of 500 ms that was identified as optimal for eliciting RS effects of the N170 component (Harris and Nakayama, 2007; Kühl et al., 2013). Stimulus pairs were organized in two main categories: 'Intra-modal', that is repetition within modalities, i.e. sensory (observe/observe) or motor (execute/execute) domain, or 'cross-modal', that is repetition across modalities (observe/execute or execute/observe). Inter-trial intervals pseudo-randomly varied between 3 s and 4 s. A black fixation cross was visible in the center of the screen when no stimulus was present (see Fig. 1).