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The role of gamma band oscillations and synchrony on rubber hand illusion and crossmodal integration

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A B S T R A C T

The rubber hand illusion represents an illusory experience during the mislocalization of own hand when correlated visuotactile stimuli are presented to the actual and fake hands. The visuotactile integration process appears to cause this illusion; the corresponding brain activity was revealed in many studies. In this study, we investigated the effect of the rubber hand illusion on the crossmodal integration process by measuring EEG. The participants who experienced less intensive illusion showed greater congruency effect on reaction time (RT), greater power increase at the parietal zero electrode (Pz) and smaller interelectrode synchrony of the gamma band activity. On the other hand, the participants who experienced more intense illusion showed greater interelectrode synchrony. The results suggested that the gamma band activity in the parietal area reflects the visuotactile integration process and that its synchrony causes the illusory intensity.

1. Introduction

Crossmodal integration between tactile and visual information is required for adequate spatial cognition and intended locomotion in the visuospatial field. First described by Pavani, Spence, and Driver (2000), the visuotactile congruency effect has been considered as a behavioral index of the integration process in the brain. In this task, participants achieved a speeded localization response to vibrotactile targets presented to the thumb (held in a lower position) or the index finger (upper position) of either hand while simultaneously attempting to ignore visual distracters independently presented to a rubber hand with the same posture as the participants' actual hands, from either the same or different level of elevation. Performance was faster and more accurate if the visual and tactile stimuli are presented at the same elevation. This difference between the performances when distracters are presented at the same and different elevation has been considered as the visuotactile congruency effect. Although typically, the visuospatial congruency effect was less when the visuotactile stimuli were spatially apart (Spence, Pavani, & Driver, 2004; Spence & Walton, 2005), an experiment conducted by Pavani et al. (2000) revealed that this congruency effect could be observed also in the condition in which the visual distracter was presented to the rubber hand with the same posture as the participant's actual hand. The rubber hand setting could induce a phenomenon in which the subject observes a rubber hand being stroked with one's own hand, which is hidden and being synchronously stroked, causing an illusory attribution as if the rubber hand belongs to the subject's body (Botvinik & Cohen, 1998). According to these results, the effect of the rubber hand illusion could compensate for the spatial distance and enhance the congruency effect more as compared to the no-rubber-hand condition.

The brain areas involved in crossmodal integration have been revealed by functional imaging studies (for review, see Calvert & Thesen, 2004), and the time course of such activity has been revealed through EEG studies with high time resolution (Eimer & Driver, 2000; Eimer & Van Velzen, 2002). Moreover, it was demonstrated that the N140 component, which was modulated by crossmodal spatial attention, was greater after the training with the synchronous visuotactile stimuli to the rubber hand and the subject's own unobserved hand as compared to that with the uncorrelated stimuli (Press, Heyes, Haggard, & Eimer, 2008). In the peripersonal space, visual stimuli could activate neurons that also respond to tactile stimuli, named bimodal neuron, in parietal brain areas (Breveglieri, Galletti, Monaco, & Fattori, 2007; di Pellegrino, Làdavas, & Farnè, 1997; Duhamel, Colby, & Goldberg, 1998; Graziano, Cooke, & Taylor, 2000); considering this, the rubber hand illusion could integrate visuotactile stimuli with spatial distance by expanding the receptive field for the visuotactile stimuli of the real hand to the rubber hand and generate the effect of a crossmodal link at each sensory area. Generally, previous

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studies that investigated the time course of brain activity at the crossmodal link (Eimer & Driver, 2000; Eimer & Van Velzen, 2002; Press et al., 2008) focused on the modulation of the ERP component at the contralateral somatosensory area rather than the effect of the integration process at the parietal association area. Recently, our group conducted an EEG experiment (Kanayama, Sato, & Ohira, 2007) to investigate brain activity related to the integration process of visuotactile information while replicating the experimental settings employed in Pavani et al. (2000). In our study, exclusive power increases were observed in the gamma band (40–50 Hz) at electrode Pz and at 200–250 ms poststimulus in congruent visuotactile stimulation rather than in the ERP component that was observed during the earlier time course (N140) in the previous crossmodal studies (Eimer & Driver, 2000; Eimer & Van Velzen, 2002). The same gamma band component has been reported in semantic integration (Yuval-Greenberg & Deouell, 2007), while the audiovisual integration component was also observed as an early (around 100 ms) phase-locked (evoked) gamma band response (Sakowitz, Quiroga, Schurmann, & Basar, 2001; Senkowski, Talsma, Grigutsch, Herrmann, & Woldorff, 2007; Senkowski, Talsma, Herrmann, & Woldorff, 2005). Widmann, Gruber, Kujala, Tervaniemi, and Schröger (2007) have demonstrated early evoked gamma band response (before 100 ms) and later induced gamma band response (between 100 and 200 ms) for an audiovisual integration task, and suggested the early evoked component is sensitive to qualitative stimulus aspects while the later induced component involves matching process between expectation and stimulation. These results suggested that the induced gamma band activity in our previous study is robust for integration task and not limited to visuotactile stimuli. Further, the interelectrode synchrony of the above-mentioned gamma band activity was significantly correlated with the self-reported scores for rubber hand illusion experiences (Kanayama et al., 2007). The local synchrony and the interelectrode synchrony of gamma band activity have been known to be caused by the visual binding process (Rodriguez et al., 1999; Tallon-Baudry, Bertrand, Delpuech, & Permier, 1997). This could suggest that the synchronized activity modulates depth perception. These results suggest two steps in the process of crossmodal integration with the rubber hand illusion: first, the gamma band power increases in parietal areas occurs due to the integration of the congruent bimodal stimuli; thereafter, its synchronization with the activity of the other brain areas due to the illusory experiences modulates depth perception via the interplay between the visual and tactile sensations. However, a previous study could not clearly identify the effect of the rubber hand illusion on the crossmodal process because of the absence of the no-rubber-hand condition (Kanayama et al., 2007).

Although the rubber hand illusion has been identified and considered as a robust phenomenon in humans (Botvinik & Cohen, 1998; Constantini & Haggard, 2007), this illusion is known to be vulnerable to the experimental settings and can be abolished by orienting the rubber hand at 180° or 90° to the subject's own hand (Ehrsson, Spence, & Passingham, 2004; Tsakiris & Haggard, 2005) or by using a wooden rod as a substitute for the rubber hand (Tsakiris & Haggard, 2005). Indeed, the self-reported scores regarding the rubber hand illusion in studies on the visuotactile congruency effect were not higher than the midpoint for all items (Kanayama et al., 2007; Pavani et al., 2000), which suggests that most of the participants reported that they did not experience the illusory phenomenon. A recent study, involving 220 participants, revealed that 66% of the participants experienced the rubber hand illusion (Durgin, Evans, Dunphy, Klostermann, & Simmons, 2007). These results suggest individual differences in experiencing this illusory phenomenon; therefore, our study aimed to reveal not only the effect of the existence of the rubber hand but also the effect of the individual differences in the rubber hand illusion on the visuotactile congruency effect.

In order to estimate the ease of experiencing the rubber hand illusion, we adopted the Cambridge Depersonalization Scale (CDS: Sierra & Berrios, 2000), a questionnaire assessing the frequency and duration of the depersonalized experience. A depersonalized experience is a symptom of depersonalization disorder and has been considered as "an alteration in the perception or experience of the self so that one feels detached from, and as if one is an outside observer of, one's mental processes or body, feeling as if one is in a dream" (DSM-IV: American Psychiatric Association, 2000). Sierra and Berrios (2000) indicated that this definition was insufficient to explain its nature and that many patients with depersonalization disorder also complain of various symptoms including an altered body experience. Indeed, a questionnaire study regarding depersonalization showed "Anomalous Body Experience" as the main factor in the depersonalization disorder (Sierra, Baker, Medford, & David, 2005), while a case study revealed that a patient with a parietotemporal lesion reported the "Body Alienation" symptom (Sierra, Lopera, Lambert, Phillips, & David, 2002). These results indicated the relationship between depersonalized experiences and anomalies in body sensation. Moreover, some studies revealed the possible relationships between rubber hand illusion and schizophrenia (Peled, Pressman, Geva, & Modai, 2003; Peled, Ritsner, Hirschmann, Geva, & Modai, 2000) or eating disorders (Mussap & Salton, 2006). Schizophrenia and eating disorders include the symptoms related body perception or body image similar to depersonalization, which suggests possible relationship between depersonalization and rubber hand illusion. However, so far, no study has directly investigated this relationship. In order to investigate the effect of the individual differences in the rubber hand illusion, we designed the present experiment to confirm whether participants with high-CDS scores easily experience the rubber hand illusion. Our hypothesis was that the scores in the subjective reports on the rubber hand illusion of the high-CDS group would be higher than those of the low-CDS group.

In the present experiment, we aim to investigate the differences in the visuotactile congruency effect on the behavioral performances and EEG activities by dividing the participants into the following two groups by using CDS: those experiencing an intensive rubber hand illusion and those experiencing a weak illusion. If the rubber hand illusion promotes the crossmodal integration process, the high-CDS group would demonstrate a larger congruency effect and higher gamma band activity in the time course previously demonstrated (Kanayama et al., 2007). Additionally, the interelectrode synchrony in this activity to the congruent visuotactile stimulation, which was significantly correlated to the RT and the illusory experience in the previous study (Kanayama et al., 2007), would be higher in the high-CDS group. Furthermore, the effects of the rubber hand existence on the congruency effect and the gamma band activity were investigated because we wished to confirm that the group difference in the CDS scores stems from the effect of the rubber hand illusion. Our hypothesis was that in the absence of the rubber hand, the group differences should not be observed on the congruency effect, gamma band activity, or interelectrode phase synchrony.

2. Materials and methods

2.1. Screening

We administered the questionnaire to 362 undergraduate and graduate students in Nagoya University. Prior to this distribution, we carefully explained that the questionnaire was for those who volunteered to participate in this study, and it was not being enforced; therefore, they could opt out of the study whenever they