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Research report

Cross-modal repetition effects in the mu rhythm indicate tactile mirroring during action observation

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ABSTRACT

Similar cortical activations during the experience and observation of touch suggest the presence of a tactile mirroring system. However, the specificity of observation-related activity – i.e., whether observation excites the same representations as experience of that specific tactile stimulation – is still to be established. Furthermore, central mu rhythms are attenuated during the experience and observation of touch, and also during action observation and execution, making it unclear whether they index processing of predominantly tactile or motor features of observed actions. The present study used an electroencephalography (EEG) cross-modal repetition paradigm to assess the relative tactile and motor specificity of mu attenuation during action observation. Two experiments were carried out during which participants executed and observed actions in alternation, and the repetition of either tactile or motor features of the actions were manipulated. The mu signal over central electrodes varied as a function of tactile repetition, consistent with the claim of a tactile mirroring system and its reflection in the mu signal. Of note was the fact that mu attenuation was sensitive only to manipulation of tactile – not motor – properties of actions, suggesting that caution should be employed when interpreting mu effects during action observation as reflective of motor mirroring.

1. Introduction

When we observe others being touched, somatosensory cortical areas are active (e.g., Blakemore, Bristow, Bird, Frith, & Ward, 2005; Bufalari, Aprile, Avenanti, Di Russo, & Aglioti, 2007; Ebisch et al., 2008; Keysers et al., 2004; Martinez-Jauand et al., 2012; Schaefer, Heinze, & Rotte, 2012). In line with these findings, the alpha (7–14 Hz) oscillatory component of the central 'mu' rhythm (comprising both alpha and

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beta – 15–30 Hz – components; Hari & Salmelin, 1997; although the term will be used hereafter to refer solely to the alpha component) is attenuated both when receiving (Cheyne et al., 2003; Gaetz & Cheyne, 2006) and observing tactile stimulation (Cheyne et al., 2003; Höfle, Pomper, Hauck, Engel, & Senkowski, 2013; Perry, Bentin, Bartal, Lamm, & Decety, 2010). These findings suggest the presence of a tactile mirroring system, whereby observation of touch activates representations involved in processing the direct receipt of touch (note that our use of the word 'system' simply refers to similar distributed cortical representations activated in observation and receipt conditions; Banissy & Ward, 2007; Keysers, Kaas, & Gazzola, 2010).

Attenuation of the central mu rhythm is also associated with both action observation and execution (e.g., Cochin, Barthelemy, Roux, & Martineau, 1999; Muthukumaraswamy & Johnson, 2004a, 2004b; Muthukumaraswamy, Johnson, & McNair, 2004). It is distinguishable from the classical occipital alpha signal by its more anterior scalp distribution and the events which modulate it – namely, motor and tactile events as well as certain visual events (like action and touch observation), rather than only visual events. This central mu attenuation when observing and executing action has been assumed by many to reflect activity of the human motor mirror system which processes observed actions in terms of corresponding motor programmes required for execution (Cheng et al., 2008; Cochin et al., 1999; Ferrari et al., 2012; Lepage & Théoret, 2006; Muthukumaraswamy & Johnson, 2004a, 2004b; Muthukumaraswamy et al., 2004; Oberman et al., 2005; Oberman, Pineda, & Ramachandran, 2006; Oberman, Ramachandran, & Pineda, 2008; Pineda, 2005; Rizzolati, Fabbri-Destro, & Cattaneo, 2009; Ulloa & Pineda, 2007). However, if we indeed mirror observed touch, and mu oscillations can reflect tactile processing, this assumption may be invalid. Specifically, central mu oscillatory responses during action observation may instead reflect mirroring of the tactile components of an action (e.g., what it feels like to grasp an object), rather than the motor activity necessary to execute the action. This possibility is especially plausible given that source localization of mu effects (Cheyne et al., 2003; Hari et al., 1998; Rossi et al., 2002; although see van Wijk, Willemse, & Vandertop, 2012), and correlations between mu and blood-oxygen-level dependent (BOLD) responses (Arnstein, Cui, Keysers, Maurits, & Gazzola, 2011; Ritter, Moosmann, & Villringer, 2009), indicate that mu effects may be generated in the somatosensory cortex.

However, to provide evidence that these oscillatory responses reflect mirroring (either tactile or motor), specificity must be demonstrated. In the case of tactile mirroring, observation of tactile stimulation must excite the same representations as experience of that specific tactile stimulation, rather than increase somatosensory activity in a general, non-specific manner (see Cook, Bird, Catmur, Press, & Heyes, 2014; Oosterhof, Tipper, & Downing, 2013). To demonstrate motor mirroring, observation of action must excite the same motor representations involved in performing that specific action.

Recently, cross-modal repetition functional magnetic resonance imaging (fMRI) designs have been used to support claims of motor mirroring processes. Repetition suppression is the term used to describe the reduction observed in the neural response when events activating the same representation occur in succession. Cross-modal repetition suppression occurs when observation of Action A causes a smaller response when preceded by execution of Action A, than when preceded by execution of Action B. This pattern of results is taken to indicate that both the observation and execution of Action A share overlapping neural representation and therefore provides evidence of action mirroring (Chong, Cunnington, Williams, Kanwisher, & Mattingley, 2008; Grill-Spector, Henson, & Martin, 2006; Kilner, Neal, Weiskopf, Friston, & Frith, 2009; Lingnau, Gesierich, & Caramazza, 2009; Press, Weiskopf, & Kilner, 2012). To our knowledge, no studies have previously demonstrated cross-modal repetition effects on mu oscillatory responses. However, of relevance to mirror system investigations, Perry and Bentin (2009) used a unimodal electroencephalography (EEG) repetition design to show that repeated observation of the same grasp type resulted in reduced mu attenuation when compared to observation of different grasp types (see also Ortigue, Thompson, Parasuraman & Grafton, 2009).

At present, evidence for specific tactile mirroring beyond somatotopic matching (e.g., Blakemore et al., 2005; Kuehn, Muller, Turner, & Schütz-Bosbach, 2014) has not been obtained with any neuroimaging measure. Additionally, as noted above, specificity has not been investigated in mu attenuation, meaning that conclusions concerning its capability to index mirror processes – either tactile or motor – are premature. The specificity of responses during the observation of tactile stimulation, as well as relative contributions of tactile and motor mirroring to mu attenuation during action observation, was assessed in two experiments using an EEG cross-modal repetition design. Power in the alpha frequency range was measured over sensorimotor areas in response to repeated or non-repeated actions where repetition was defined according either to the tactile properties of an object (Experiment 1) or the motor, tactile, or both motor and tactile, features of the action (Experiment 2).

2. Materials and methods

2.1. Participants

Seventeen healthy participants took part in Experiment 1 (9 females, mean age = 25.82, range 19–43). Fifteen new participants (3 females, mean age = 27.70 years, range 18–41) took part in Experiment 2. Two participants in Experiment 1, and three participants in Experiment 2 were replacements for participants where more than 40% of trials were excluded (see below). All participants gave informed consent to participate in exchange for course credit or monetary compensation, had normal or corrected to normal vision and were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). Both studies were approved by the Research Ethics Committee within the Department of Psychological Sciences, Birkbeck, University of London.

2.2. Aims and study design

Experiments 1 and 2 used a cross-modal repetition design to test for tactile and motor specificity in mu attenuation during