



## 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.

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## 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; Rizzolatti, 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, Willemsse, & 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

action observation. Specifically, mini-blocks were presented in which action observation and execution alternated. In Repeat mini-blocks, actions with the same tactile or motor properties were observed and executed, while in Non-Repeat mini-blocks, different tactile or motor properties were present in observation and execution. According to repetition logic (e.g., Grill-Spector et al., 2006), if mu attenuation shows selectivity for specific tactile sensation or actions, it should differ in Repeat and Non-Repeat blocks. Mini-blocks, rather than single actions, were used as the unit of repetition because single cell data suggest that repetition effects in motor mirror representations may be cumulative (Kilner, Kraskov, & Lemon, 2014).

Experiment 1 was designed to manipulate the tactile components of observed and executed actions while holding the motor component constant across conditions. This was done by asking participants to carry out the same action (squeezing a ball) on balls with different textures. Two identical rubber balls were used, but one had a smooth texture and the other was covered in a black plastic mesh to alter its tactile properties. Oscillatory activity in the alpha frequency range at central electrodes was therefore examined in response to observation or execution of an action on a ball of a certain texture (e.g., Smooth) as a function of whether it had been preceded by observation or execution of an action on a ball with the same (Smooth) or a different (Mesh) texture (see Table 1). Therefore, by contrasting Repeat versus Non-Repeat mini-blocks, we examined whether mu power in response to observing or executing an action with certain tactile properties (e.g., squeeze a smooth ball) varied as a function of whether it had been preceded by observation or execution of an action with the same tactile properties (squeeze a smooth ball) or different tactile properties (squeeze a mesh ball). In all mini-blocks, participants alternated between observing and executing actions, and within a mini-block, observed and executed tactile properties were held constant to equate within-modality repetition

(i.e., if in a mini-block participants executed actions on a Smooth ball and observed actions on a Mesh ball, they would do so for the whole mini-block). If repetition effects (change in oscillatory attenuation when a texture is repeated vs not repeated) are observed in this experiment, they must reflect mirroring of the tactile rather than motor properties of the observed stimulus, because the motor properties of the two observed squeezes are the same. To investigate whether an action needs to be observed on the object in order to mirror its tactile properties, the Tactile-Action condition was contrasted with a Tactile-Arrows condition in which attention was drawn towards the object, including its tactile properties, by moving arrows rather than by a hand grasping the object.

Experiment 2 was designed to extend Experiment 1 by assessing the relative contribution of tactile and motor mirroring to the mu attenuation during action observation. This experiment used two action types: the same squeeze on a smooth ball as in Experiment 1 (Squeeze) and making writing movements with a pen (Write). In order to assess whether any observed specificity for an action reflects mirroring of the motor or tactile components, three conditions presented variants on the design outlined above. In the Motor + Tactile condition, participants observed and executed Squeeze and Write actions directed towards objects in which both the motor and the tactile components of the action were present. Squeeze actions consisted of all fingers moving inwards and outwards to squeeze the ball (motor component) and touch to proximal parts of all fingertips and the palm of the hand (tactile component). Write actions consisted of fingers making repetitive downward strokes (motor component) and touch to more distal aspects of the fingertips (tactile component). Therefore, any repetition effects (change in oscillatory attenuation when an action is repeated vs not repeated) should be present regardless of whether mu attenuation reflects mirroring of motor or tactile properties.

**Table 1 – Description of the different mini-block types according to the two experimental factors Condition and Repetition for Experiments 1 and 2.**

Experiment	Condition	Repetition	Action observed	Action executed	
Experiment 1	Tactile-Action	Repeat	Smooth ball squeeze Mesh ball squeeze	Smooth ball squeeze Mesh ball squeeze	
		Non-Repeat	Smooth ball squeeze Mesh ball squeeze	Mesh ball squeeze Smooth ball squeeze	
		Tactile-Arrows	Repeat	Arrows towards smooth ball Arrows towards mesh ball	Smooth ball squeeze Mesh ball squeeze
			Non-Repeat	Arrows towards smooth ball Arrows towards mesh ball	Mesh ball squeeze Smooth ball squeeze
	Experiment 2	Motor + Tactile	Repeat	Ball squeeze Pen stroke	Ball squeeze Pen stroke
			Non-Repeat	Ball squeeze Pen stroke	Pen stroke Ball squeeze
Motor-Only			Repeat	Mimed ball squeeze Mimed pen stroke	Mimed ball squeeze Mimed pen stroke
			Non-Repeat	Mimed ball squeeze Mimed pen stroke	Mimed pen stroke Mimed ball squeeze
Tactile-Only		Repeat	Ball moving into hand Pen moving into hand	Ball squeeze Pen stroke	
			Ball moving into hand Pen moving into hand	Pen stroke Ball squeeze	
		Non-Repeat	Ball moving into hand Pen moving into hand	Pen stroke Ball squeeze	
			Pen moving into hand Ball moving into hand	Ball squeeze Pen stroke	

In the Motor-Only condition, participants observed and executed the actions without the presence of the objects. This condition therefore included the motor components of the actions, but there was an absence of cutaneous stimulation. Finally, we included a condition where any repetition effects would reflect mirroring of the tactile properties of the actions. In this Tactile-Only condition, participants executed actions towards objects but observed videos where the hand did not move; instead, the ball or pen was seen moving into the hand and making contact at the same location as in the Motor + Tactile condition. Therefore, if oscillatory attenuation reflects mirroring of motor properties, repetition effects will be seen in the Motor + Tactile and Motor-Only conditions but not the Tactile-Only condition. If oscillatory attenuation reflects mirroring of cutaneous touch, repetition effects will be seen in the Motor + Tactile and Tactile-Only conditions but not the Motor-Only condition.

### 2.3. Visual stimuli

All video clips were presented with E-Prime 2.0 Professional software (Psychology Software Tools Inc., Sharpsburg PA, USA) on a 19 inch monitor (716 × 537 pixels) located approximately 40 cm from the participant.

The Tactile-Action visual stimuli in Experiment 1 consisted of video clips of 1500 msec duration during which a right hand squeezed either a yellow smooth ball or the same ball covered in a black plastic mesh. In the Tactile-Arrows condition two arrows were seen moving towards the same balls. The speed, location and distance traversed by the arrows in the Tactile-Arrows condition were matched approximately to the kinematics of the index finger and thumb movements in the Tactile-Action condition (each Tactile-Arrows video was matched to one of the Tactile-Action videos). Four different actors (two females) performed the two actions, for a total of 16 different stimuli.

The visual stimuli in Experiment 2 consisted of video clips as described above, of 1500 msec duration, during which a right hand executed actions on a black background. Tactile-Only clips were developed using a string to move the objects into the actor's hand. The string was subsequently edited out of each video clip using Adobe Photoshop 5.0 software (Adobe Systems Inc, San Jose, CA, USA). Four different actors (two females) generated the six video clips, resulting in a total of 24 different stimuli. Stills from the different video clips for both experiments are shown in Fig. 1.

### 2.4. Procedure

Participants sat comfortably in an electrically shielded, soundproofed and dimly lit room. They were instructed to avoid any movements other than those prescribed in the study, to keep eye blinks to a minimum and try to blink only in the inter-stimulus intervals. During both experiments, the participant's right hand was occluded from view with a box and movements were recorded with a webcam placed at the end of the box. The video recording of the participant's hand was live monitored by an experimenter and mini-blocks with execution mistakes were marked and later removed from the analyses.

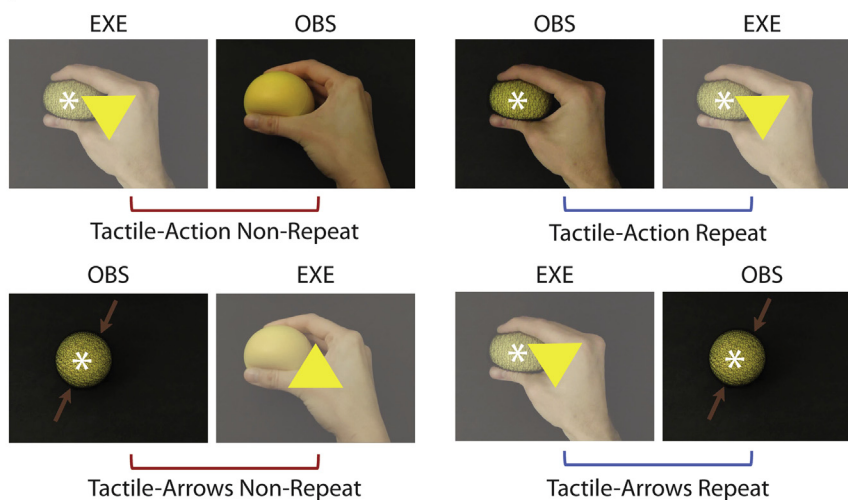
At the beginning of Experiment 1, participants were asked to manipulate the two balls (Smooth and Mesh) and describe each of them with five different words in order to familiarize themselves with the different textures and appearances. The two balls were then fixed within the occlusion box to allow for relatively error-free action execution. Participants were instructed to execute the actions in response to the presentation of a triangular cue presented on a black background for 1500 msec. Participants were to move their hand away from their body to perform a squeeze on one ball (signalled by an upward pointing triangle) and towards their body to perform the squeeze on the other ball (downward pointing triangle). The object locations in the box were counterbalanced across participants. Participants were asked to initiate the correct action only when they saw the triangle and to return to the resting position by the time that the triangle disappeared. Reaction times were not measured, but participants were asked to pace their action with the execution cues. They were also warned after practice and between each session if monitoring of their movements revealed that they executed actions excessively fast or slow. There were four types of mini-block in Experiment 1 according to the two main experimental factors: Repetition of texture (Repeat, Non-Repeat) and Condition (Tactile-Action, Tactile-Arrows), and 12 mini-blocks of each type.

The procedure in Experiment 2 was identical to that in Experiment 1 except for the following: at the beginning of the mini-block, participants received the instruction to execute the actions with or without objects. The same objects as those used in the video clips (ball and pen) were fixed within the occlusion box and participants were to execute the appropriate action in response to the triangle cue. In the Motor + Tactile and Tactile-Only conditions, contact with the appropriate object was made in these locations. In the Motor-Only condition, the participant's hand was positioned away from the objects such that no contact was made. There were six types of mini-block according to the two main experimental factors: Repetition (Repeat, Non-Repeat) and Condition (Motor + Tactile, Motor-Only and Tactile-Only), and 12 mini-blocks of each type.

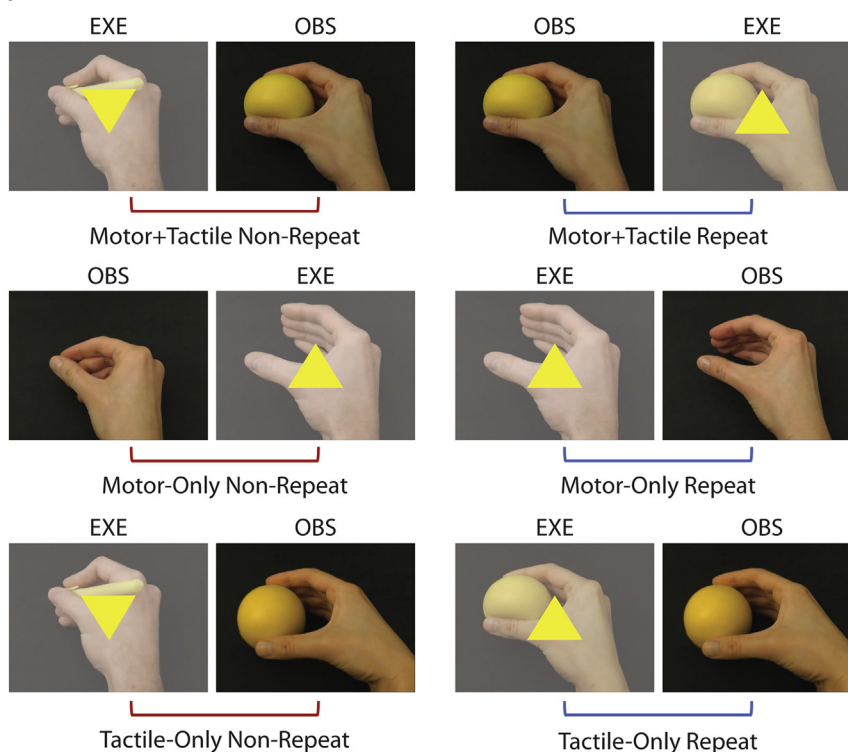
At the beginning of each mini-block, participants first saw the instruction "Block begin" (Experiment 1) for 5000 msec or the instruction indicating that they should execute the actions with or without the objects in the following mini-block (Experiment 2). These instructions were followed by 11 experimental trials (one mini-block). For each experimental trial, the participants first saw a fixation cross with a mean duration of 750 msec (500–1000 msec) followed by the presentation of a 1500 msec video clip or execution cue, and then a black screen for an ISI of a mean duration of 1750 msec (750–2750 msec). The first action presented/executed and the first trial type (observation or execution) were equally distributed in the mini-blocks and the hand models were pseudo-randomized so that all models were presented at least once in each mini-block. There was a 10 sec interval between each mini-block, and the experimental procedure was divided into two (Experiment 1) or three (Experiment 2) 25 min sessions. The mini-block presentation order was fully randomized within each session.



## Experiment 1



## Experiment 2



**Fig. 1 – Schematic representation of Repeat and Non-Repeat pairs of stimuli from all conditions of Experiments 1 and 2. The stimuli were presented for 1500 msec and participants always alternated between observation and execution. Ten repeated or non-repeated stimuli were presented in each experimental block, with repetition defined cross-modally (within-modality repetition was equated in Repeat and Non-Repeat blocks). Greyed out pictures in the execution trials are present for illustrative purposes only. Asterisks in Experiment 1 indicate the ball covered with a black mesh, for representational purposes only.**

### 3. EEG recordings and analyses

#### 3.1. Recording and preprocessing

EEG data was recorded at 500 Hz using Brain Vision Recorder (Brain Products GmbH, Munich, Germany) from 28 active Ag/

AgCl electrodes (Fp1, Fp2, F3, F4, F7, F8, Fz, FC1, FC2, FC5, FC6, FCz, Cz, C3, C4, CP1, CP2, CP5, CP6, P3, P4, P7, P8, Pz, T7, T8, O1, O2) mounted on an elastic cap (EasyCap, Brain Products GmbH, Munich, Germany) according to the 10/20 international placement system (Jasper, 1958). Three additional electro-oculogram (EOG) channels were used to monitor vertical and horizontal eye movements. Two were placed at 1 cm from the

outer canthi of the left and right eyes and the other one below the left eye. The signal was online filtered between .1 and 80 Hz with acquisition reference at the left and right mastoids. Electrode impedances were maintained at 10 k $\Omega$  or below.

All offline EEG analyses were performed with SPM8 (Wellcome Trust Centre for Neuroimaging, London, UK, [www.fil.ion.ucl.ac.uk/spm](http://www.fil.ion.ucl.ac.uk/spm)). The data were first bandpass filtered at 1 and 45 Hz and epoched at  $-200$  msec to  $1700$  msec relative to the beginning of the video clip or execution cue of trials 2–11 in each mini-block (trial 1 was discarded given that we were interested in investigating repetition effects). The same epoch duration was also extracted during a blank screen at the beginning of each mini-block to serve as a baseline period during which no actions were executed or observed. Trials were rejected if either the peak to peak amplitude of the trial exceeded  $135 \mu\text{V}$  at any of the EEG or EOG channels (Experiment 1: 16%, Experiment 2: 10%) or an incorrect movement was performed by the participant during the mini-block (Experiment 1:  $<1\%$ , Experiment 2: 2%). More specifically, in Experiment 1, 11 execution mistakes were noted (error rate of .0013%) leading to the removal of five experimental blocks from analyses (.006% of the data). In Experiment 2, 38 execution mistakes were noted (error rate .0035%) leading to the removal of 23 experimental blocks from analyses (2.12% of the data). Error rate separated by Repetition condition shows a similar rate in Repeat trials (.0012%) and Non-Repeat trials (.0014%) in Experiment 1 as well as in Experiment 2 (.003% and .004%, for Repeat and Non-Repeat trials respectively). Rejection rate was similar in all types of epoch. After artifact detection, the data were downsampled to 100 Hz prior to analysis.

### 3.2. Time-frequency analyses

Spectral changes in oscillatory activity were analysed using a Morlet wavelet decomposition transform with a width of seven cycles per wavelet, across a 5–45 Hz frequency range and  $-200$  to  $1700$  msec relative to event onset in experimental trials (the beginning of the video clip or the execution cue), or  $-2200$  to  $-300$  msec relative to the start of the block (baseline). The decomposition was performed for each trial, electrode and participant. Time-frequency maps were averaged within each experimental condition (or baseline period) using the SPM8 robust averaging procedure (c.f. Garrido et al., 2009), and log<sub>10</sub> transformed to normalize. All experimental conditions were subsequently baseline corrected by subtracting the average inter mini-block epoch, which was averaged across all such epochs in the experiment independent of condition.

### 3.3. Selection of sites and bands of interest

All analyses were carried out on the centrally located electrodes C3, C4, CP1 and CP2. The location of these sites has been consistently associated with mu attenuation during movement execution and observation in previous studies (e.g., Muthukumaraswamy & Johnson, 2004a, 2004b; Oberman et al., 2005; Proverbio, 2012). Furthermore, t-tests also confirmed that these locations showed significant mu attenuation relative to baseline during execution trials in the present experiments [Experiment 1:  $t(14) = 2.82$ ,  $p = .01$ ,  $d = .73$ ; Experiment 2:

$t(16) = 3.49$ ,  $p = .003$ ,  $d = .85$ ]. To investigate potential interactions between the effects of interest and laterality (although none were found), attenuation relative to baseline was averaged separately at the two left (C3, CP1) and the two right electrodes (C4, CP2) in order to create a two level Hemisphere factor (Left/Right) that was included in all statistical analyses.

To take into account inter-individual differences in the range of the mu attenuation, 3 Hz bands were chosen for each participant in the 7–14 Hz band. The selection was made by averaging all execution trials 0–1500 msec post stimulus (for consistency with main analysis, see below) in each experiment in all 3 Hz bands and choosing the band where the attenuation was strongest at electrodes C3, C4, CP1 and CP2 (see Babiloni et al., 2009; Klimesch, 1999; Muthukumaraswamy & Johnson, 2004a, 2004b). This procedure led to an average mu band of 9–12 Hz for Experiment 1 and 8–11 Hz for Experiment 2 (range 7–10 to 11–14 Hz in both experiments<sup>1</sup>). This selection criterion was orthogonal to any analyses of interest, which investigated differences in such attenuation as a function of different factors.

### 3.4. Effects of action type and repetition

Two three-way repeated measures analyses of variance (ANOVA) were then performed on the mu attenuation relative to baseline in each experiment, for the stimulus period (0–1500 msec post stimulus). Experiment 1 ANOVA included factors of Hemisphere (Left, Right), Repetition (Repeat, Non-Repeat) and Condition (Tactile-Action and Tactile-Arrows). Experiment 2 included the same factors, but Condition now had three levels (Motor + Tactile, Motor-Only, Tactile-Only) and Repetition referred to repetition of the action type rather than texture. The significance threshold was set at  $p < .05$  and a Greenhouse-Geisser correction was used when the sphericity assumption was not met.

## 4. Results

Results from all statistical analyses are presented in Table 2. Only results relevant to the cross-modal repetition effects that this study aimed to measure are presented in the following section.

### 4.1. Experiment 1

There was a significant main effect of Condition [ $F(1, 16) = 9.03$ ,  $p = .01$ , partial  $\eta^2 = .36$ ], indicating significantly stronger mu attenuation in the Tactile-Action condition relative to the Tactile-Arrows condition. Of critical interest, there was also a significant main effect of Repetition of texture [ $F(1,$

<sup>1</sup> It is worth noting that the average band is 1 Hz lower in Experiment 1 than Experiment 2, despite equivalent selected ranges. Frequency bands in both experiments are unambiguously alpha rather than beta range, given selection criteria, and therefore akin to ranges associated with somatosensory rather than motor cortex activation. Such small discrepancies between experiments most likely reflect individual differences, especially given that this difference was not significant [ $t(30) = 1.37$ ,  $p = .18$ ,  $d = .49$ ], but may in principle result from changes to the task.

**Table 2 – Results from the ANOVAs for both experiments.**

	DF	F	p	eta <sup>2</sup> <sub>partial</sub>
<i>Experiment 1</i>				
Hemisphere	1, 16	<1	.96	–
Condition	1, 16	9.04	<.05	.36
Repetition	1, 16	5.47	<.05	.26
<i>Experiment 2</i>				
Hemisphere	1, 14	3.66	.08	.21
Condition	2, 28	<1	.99	–
Repetition	1, 14	3.18	.10	.19
Condition*Repetition	2, 28	3.50	<.05	.20

Bold numbers indicate significant effects at  $p < .05$ .

16) = 5.47,  $p = .03$ , partial  $\eta^2 = .26$ ; see Fig. 2]. This effect is one of repetition suppression, whereby there was less mu attenuation when the tactile properties had been repeated between observation and execution. This repetition effect therefore indicates mirroring of tactile properties reflected in the mu response. Attenuation relative to baseline as a function of Repetition and Condition and Time-frequency plots (7–14 Hz) for Experiment 1 are shown in Fig. 2.

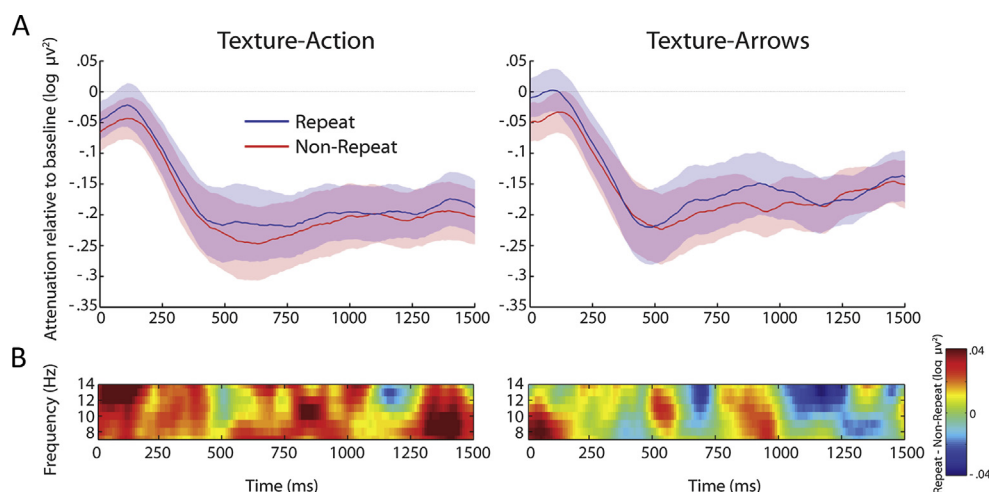
#### 4.2. Experiment 2

A marginally significant effect of Hemisphere [ $F(1, 14) = 3.66$ ,  $p = .08$ , partial  $\eta^2 = .21$ ] indicated stronger mu attenuation on the left than the right. This trend is potentially similar in nature to a marginally significant Hemisphere  $\times$  Condition interaction in Experiment 1 [ $F(1, 16) = 2.60$ ,  $p = .13$ , partial  $\eta^2 = .14$ ], which reflected stronger attenuation on the left for the Texture-Action condition only. These marginal effects may reflect stronger left attenuation when observing and executing actions with the right hand, but given that the effects (1) were only marginal and (2) did not interact with repetition effects, they will not be discussed further.

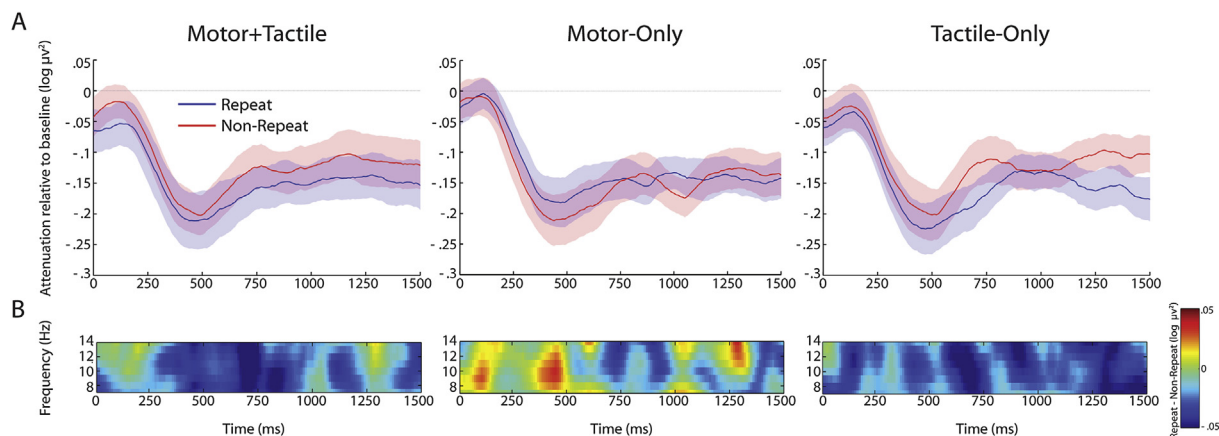
The main effect of Repetition was not significant [ $F(1, 14) = 3.18$ ,  $p = .10$ , partial  $\eta^2 = .19$ ]. However, there was a significant Condition  $\times$  Repetition interaction [ $F(2, 28) = 3.5$ ,  $p = .04$ , partial  $\eta^2 = .20$  see Fig. 3]. This interaction was decomposed with three planned two-tailed t-tests, assessing repetition effects in each of the conditions. These tests revealed significantly greater mu attenuation during Repeat than Non-Repeat mini-blocks in the Motor + Tactile [ $t(14) = -2.28$ ,  $p = .04$ ,  $d = .20$ ] and Tactile-Only [ $t(14) = -2.94$ ,  $p = .01$ ,  $d = .22$ ] conditions, but not in the Motor-Only condition [ $t(15) = .61$ ,  $p = .55$ ,  $d = .09$ ]. Therefore, there was a repetition effect in conditions where the tactile component was repeated (Motor + Tactile and Tactile-Only) but not the condition where only the motor component was repeated (Motor-Only). Interestingly, in this experiment the effect is one of repetition enhancement rather than suppression. Attenuation relative to baseline as a function of Repetition and Condition and time-frequency plots (7–14 Hz) for Experiment 2 are shown in Fig. 3.

## 5. Discussion

The present study first aimed to assess critically the existence of a tactile mirroring system; whether the perception of tactile stimulation in others activates specific representation(s) activated by the direct receipt of touch. To this end, an EEG cross-modal repetition design was used (Kilner et al., 2009; Press, Catmur, et al., 2012; Press, Weiskopf, et al., 2012; Segaert, Weber, de Lange, Petersson, & Hagoort, 2013) and mu attenuation was measured at central electrodes. If the product of a tactile mirroring system, mu attenuation should show specificity – activation of the same tactile representation in the observer as that which is observed – and therefore cross-modal repetition effects should be demonstrated when observation of tactile stimulation is alternated with the same tactile stimulation in the participant. Experiment 1 revealed



**Fig. 2 – (A) Time course of the attenuation relative to baseline as a function of time, Condition and Repetition, averaged over participant-specific mu bands for Experiment 1. (B) Average difference in power between Non-Repeat and Repeat conditions for the 7–14 Hz spectrum, across time, as a function of Condition for Experiment 1. Values above zero indicate stronger attenuation in the Repeat condition. Data were smoothed across time and frequency for display purposes using a 30 msec and a 3 Hz wide moving average.**



**Fig. 3 – (A) Time course of the attenuation relative to baseline as a function of time, Condition and Repetition, averaged over participant-specific mu bands for Experiment 2. (B) Average difference in power between Non-Repeat and Repeat conditions for the 7–14 Hz spectrum, across time, as a function of Condition for Experiment 2. Values above zero indicate stronger attenuation in the Repeat condition. Data were smoothed across time and frequency for display purposes using a 30 msec and a 3 Hz wide moving average.**

cross-modal repetition effects in the mu signal in a design where the motor components of observed and executed actions were held constant but the tactile components were either repeated or not.

These results provide evidence for the presence of a tactile mirroring system and add to other studies showing that similar patterns of somatosensory activation are observed when an individual is touched and when that individual observes another being touched (e.g., Blakemore et al., 2005; Keysers et al., 2004; Kuehn et al., 2014). They are consistent with findings of mu attenuation when receiving and observing touch (e.g., Cheyne et al., 2003; Gaetz & Cheyne, 2006; Höfle et al., 2013; Perry et al., 2010), and with evidence from studies of action execution suggesting that the mu signal may largely originate from primary somatosensory cortex (Arnstein et al., 2011; Cheyne et al., 2003; Hari, 2006; Hari et al., 1998; Ritter et al., 2009; Rossi et al., 2002). Mirroring of tactile components of observed actions indicated in the present study has also previously been suggested by findings showing activation of somatosensory cortices during the observation of hand actions (Avikainen, Forss, & Hari, 2002; Bufalari et al., 2007; Cheyne et al., 2003; Pihko, Nangini, Veikko, & Hari, 2010; Rossi et al., 2002). The fact that repetition effects were also observed in the Tactile-Arrows condition of Experiment 1, even when no tactile stimulation was observed, concurs with findings of somatosensory activation during the perception of graspable objects (Proverbio, Adorni, & D'Aniello, 2011) and is consistent with the findings of stronger mu attenuation during observation of graspable tools than non-tool objects (Proverbio, 2012).

A second objective of this study was to investigate if mu attenuation observed during action observation and execution (e.g., Cheng et al., 2008; Cochin et al., 1999; Muthukumaraswamy & Johnson, 2004a, 2004b; Oberman et al., 2005; Ulloa & Pineda, 2007) is due solely to mirroring of tactile features, or whether it also reflects mirror processing of the motor features as assumed in the previous literature. If mu attenuation reflects motor mirroring, then repetition

effects should be sensitive to repetition of the motor, rather than tactile, components of action. Mirroring of tactile features of action would be indicated if repetition effects are observed when tactile, rather than motor, components are the object of repetition. Experiment 2 showed that repetition effects are limited to the tactile components of actions, by comparing action conditions in which the motor components, tactile components or both were the focus of the repetition. Cross-modal repetition effects were again found in the mu signal, but only in conditions where the tactile components were repeated.

The finding that these repetition effects appear sensitive to tactile rather than motor components of action suggests that they are due to activity of the human tactile, rather than motor, mirror system. It is commonly assumed that mu attenuation observed over sensorimotor areas during action execution and observation is associated with activity that allows the understanding of observed actions by activation of one's own motor codes (e.g., 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, 2008; Pineda, 2005; Ulloa & Pineda, 2007). However, the present findings provide no evidence to support the hypothesis that mu attenuation during action observation is due to motor mirror processes, and caution should therefore be exercised when making such claims.

It should be noted that if repetition effects were observed in the 'Motor-Only' condition of Experiment 2 then they could have been driven by motor processing within pre-motor or primary motor cortical areas, and/or by somatosensory activity relating to the encoding of proprioceptive information (e.g., Prud'homme & Kalaska, 1994). However, no repetition effects were observed in this condition, suggesting that neither motor nor proprioceptive mirroring was reflected in mu attenuation. It could instead be argued that repetition effects were not observed in the Motor-Only condition because mimed actions were used as stimuli, and



early papers suggested that single cell responses within premotor cortex to observed actions decrease when observing mimed actions (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). However, there is now considerable evidence that mimed actions are mirrored in premotor cortex (e.g., Kraskov, Dancause, Quallo, Shepherd, & Lemon, 2009; Press, Catmur, et al., 2012), and the magnitude of the observed repetition effect was equivalent in the Motor + Tactile and Tactile-Only blocks, providing no evidence for a motor contribution to the mu effects. Nevertheless, one should not use such evidence to draw strong conclusions about the absence of motor mirroring.

There are likely attentional consequences of presenting chains of predictable events, given that attention is more likely to be directed towards surprising events (Itti & Baldi, 2009). However, care was taken to reduce the possibility that these could contribute towards repetition effects in the present study. First, participants with large numbers of exclusions and blocks with execution mistakes were removed from analysis (also note that execution mistakes were equivalent in Repeat and Non-Repeat blocks). Second, unimodal repetition was equated in the two block types. Therefore, although a cue to squeeze a ball for the sixth time may be processed to a lesser extent than a similar cue presented for the first time, this repetition was equated across our Repeat versus Non-Repeat comparison. Third, within the context of the experiment, Repeat and Non-Repeat events are equally likely. Nevertheless, future systematic examination of effects of stimulus predictability on locus of attention and repetition phenomena (see Segaert et al., 2013) will shed further light on this potentially complex interaction.

Experiments 1 and 2 observed different effects of repetition; in Experiment 1 repetition was associated with a decrease in mu attenuation while repetition led to greater attenuation in Experiment 2. Therefore, the results of Experiment 1 are more in line with classical findings that demonstrate repetition suppression when events activating the same representation are presented in close succession. However, repetition enhancement effects, like those observed in Experiment 2, have also been observed widely in the neuroimaging literature (see Segaert et al., 2013 for a discussion). The physiological mechanisms underlying repetition effects are currently a matter of debate, for both fMRI and EEG (Caggiano et al., 2013; Grill-Spector et al., 2006; Oosterhof et al., 2013; Segaert et al., 2013). Further unknown are the factors which determine whether repetition enhancement or repetition suppression is seen, although it is known that the direction of repetition effects is influenced by cognitive factors (such as explicit memory retrieval and attention-related factors), that repetition effects can change from enhancement to suppression and vice versa, and that both suppression and enhancement can be seen in the same area (see Segaert et al., 2013 for a summary).

We speculate that the fact participants needed to select between different action types in Experiment 2, but not Experiment 1, may have generated the different effects (see Press, Weiskopf, et al., 2012). Selection between two action types (Experiment 2) – rather than consistent performance of the same action (Experiment 1) – is likely to have resulted in different timing of action relative to stimulus in the two experiments, and timing is known to be crucial in determining

the direction of repetition effects (Segaert et al., 2013). For example, action preparation may have been faster in Experiment 1 than 2 given that participants were required to perform the same action rather than select between different actions. Under this account, suppression effects may be seen when executed events follow observed events in close temporal succession, with enhancement seen when there is a greater delay between events (Segaert et al., 2013; note also that in principle the timing implemented may have been more optimal for detecting tactile than motor effects in the current studies). Of course this account is speculative and future research should explicitly manipulate the temporal profile of events in order to test this hypothesis.

The relationship between EEG and BOLD repetition effects and those seen at the single neuron level are also presently unclear. Specifically in the case of motor mirroring mechanisms, there has recently been much debate concerning whether the firing rate of mirror neurons does (Kilner et al., 2014), or does not (Caggiano et al., 2013), change with repetition (although note that repetition effects at the level of local field potentials – which generate the EEG signal – are found in both of these studies). Regardless of these debates, the presence of repetition effects in neuroimaging modalities is thought to evidence selectivity (Grill-Spector et al., 2006; Oosterhof et al., 2013; Perry & Bentin, 2009), and therefore a cross-modal repetition design is appropriate for the purposes of the current experiment.

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## 6. Conclusions

In conclusion, the present study is the first, to our knowledge, to show cross-modal mirror repetition effects in EEG, and evidence for specific tactile mirroring with any neuroimaging measure. Results indicate that attenuation of the central mu rhythm is indeed an index of mirror processes, but suggest the mirror processes they index may be tactile rather than motor. These findings call for caution to be employed when interpreting the results from previous (or future) studies using mu attenuation as an index of motor mirroring.

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## Conflict of interest

The authors declare no conflict of interest.

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