

MEG adaptation reveals action representations in
posterior occipitotemporal regions

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Abstract

When we observe other people's actions, a number of parietal and precentral regions known to be involved in the planning and execution of actions are recruited for example seen as power decreases in alpha and beta frequencies indicative of increased activation. It has been argued that this recruitment reflects the process of simulating the observed action, thereby providing access to the meaning of the action. Alternatively, it has been suggested that rather than providing access to the meaning of an action, parietal and precentral regions might be recruited as a consequence of action understanding. A way to distinguish between these alternatives is to examine where in the brain and at which time point it is possible to discriminate between different types of actions (e.g. pointing or grasping) irrespective of the way these are performed. To this aim, we presented participants with videos of simple hand actions performed with the left or right hand towards a target on the left or the right side while recording magnetoencephalography (MEG) data. In each trial, participants were presented with two subsequent videos (S1, S2) depicting either the same (repeat trials) or different (non-repeat trials) actions. We predicted that areas that are sensitive to the type of action should show stronger adaptation (i.e. a smaller decrease in alpha and beta power) in repeat in comparison to non-repeat trials. Indeed, we observed less alpha and beta power decreases during the presentation of S2 when the action was repeated compared to when two different actions were presented indicating adaptation of neuronal populations that are selective for the type of action. Sources were obtained exclusively in posterior occipitotemporal regions, supporting the notion that an early differentiation of actions occurs outside the motor system.

Keywords: action observation, adaptation, magnetoencephalography, occipitotemporal regions, action-selective representations

1. Introduction

Numerous studies have shown that precentral and parietal regions are recruited during the observation of other people's actions (e.g. Grezes & Costes, 1998; Hari et al., 1998; Nummenmaa et al., 2014; Willems & Hagoort, 2009). It has been argued that this recruitment reflects a causal role of the observer's motor system in action understanding (Avenanti, Bolognini, Maravita, & Aglioti, 2007; Gallese & Goldman, 1998; Gallese & Sinigaglia, 2011; Rizzolatti & Sinigaglia, 2016). More specifically, action observation has been demonstrated to lead to the recruitment of visuomotor neurons that are also recruited during the planning and execution of similar actions (Rizzolatti et al., 2014). This 'simulation' has been suggested to provide access to the understanding of the observed action (e.g. Gallese & Sinigaglia, 2011; Grafton, 2009). Alternatively, it has been suggested that the observer's motor system is recruited in parallel to or as a consequence of action understanding (e.g. Caramazza, Anzellotti, Strnad, & Lingnau, 2014; Csibra, 2007; Hickok, 2009; Kilner, 2011; Mahon & Caramazza, 2008). According to this alternative view, the critical processes leading to action understanding might take place outside the motor system.

A brain region that plays a crucial role in action understanding should be (1) able to distinguish between (i.e., be selective for) different types of actions (e.g. pointing vs grasping). At the same time, such an area should show (2) invariance to the way in which the action is performed (e.g. using the left or right hand, hand or mouth; Caramazza et al., 2014; Dinstein, Thomas, Behrmann, & Heeger, 2008; Oosterhof, Tipper, & Downing, 2013; Rizzolatti & Sinigaglia, 2016). Importantly, the general recruitment of regions involved in the planning and execution of actions during action observation is not sufficient to assume action-selective representations in these areas (see also Dinstein et al., 2008).

A number of studies used fMRI adaptation to examine the first criterion, i.e. selectivity for observed actions (Chong, Cunnington, Williams, Kanwisher, & Mattingley, 2008; Dinstein, Hasson, Rubin, & Heeger, 2007; Hamilton & Grafton, 2008; Kilner, Neal, Weiskopf, Friston, & Frith, 2009; Lingnau, Gesierich, & Caramazza, 2009). The basic logic of adaptation paradigms is that the repetition of a given stimulus property (e.g. observed pointing followed by observed pointing) leads to an attenuation of the underlying neuronal signal in comparison to trials in which the stimulus property was not repeated (e.g. observed pointing followed by observed grasping; e.g. Grill-Spector, Henson, & Martin, 2006; Krekelberg, Boynton, & van Wezel, 2006; Larsson, Solomon, & Kohn, 2016; Sapountzis, Schluppeck, Bowtell, & Peirce, 2010). Crucially, this difference between repeated and non-repeated trials should only be obtained in areas containing neuronal populations that are selective for the repeated stimulus property. However, this approach has been criticized on the basis of the notion that mirror neurons might not adapt. Indeed, Caggiano et al. (2013) obtained no adaptation in the firing rate of F5 neurons to the observation of repeated actions and thus argued that fMRI adaptation studies on action selectivity should be interpreted with caution. Note that Caggiano et al. (2013) examined general adaptation to repeated actions, rather than action-selective adaptation. Moreover, it is worth mentioning that local field potentials, which are more closely related to the fMRI BOLD signal than the firing rate, did show adaptation. More recently, Kilner, Kraskov, & Lemon (2014) followed up this lack of adaptation in F5 neurons and found that the firing rate of mirror neurons does adapt, however, only if the action was repeated over 7-10 trials.

Mukamel et al. (2010) recorded single-cell responses in patients suffering from epilepsy for different observed and executed actions. They obtained matching responses of single neurons regarding the execution and the observation of the same

action in 8% of all recorded neurons. Interestingly, while 14% of recorded neurons in the supplementary motor area showed such a matching which is significantly higher than expected by chance, also neurons in the hippocampus, parahippocampal gyrus and entorhinal cortex yielded a matching that is significantly higher than expected by chance. As electrode location in the study by Mukamel et al. (2010) was determined by diagnostic reasons, nothing can be concluded for neurons in regions outside the diagnostic scope.

Regarding the second criterion, i.e. action invariance, it is debated which brain areas contain invariant action representations (in the following, we will refer to such representations as "abstract"). Whereas some studies reported that frontal and parietal regions contain abstract action representations (Cattaneo, Sandrini, & Schwarzbach, 2010; Hamilton & Grafton, 2008), more recent human fMRI studies found such abstract action representations in the inferior parietal lobule and the lateral occipitotemporal cortex (LOTTC), outside the classical motor system (Oosterhof, Tipper, & Downing, 2012; Oosterhof, Wiggett, Diedrichsen, Tipper, & Downing, 2010; Wurm, Ariani, Greenlee, & Lingnau, 2015; Wurm & Lingnau, 2015). Using multivariate pattern analysis (MVPA) of MEG data, Tucciarelli et al. (2015) found evidence for action-selective representations in the LOTTC that distinguish between pointing and grasping actions while generalizing across reach direction (left, right) and effector (left, right hand). Importantly, these abstract action representations were obtained in LOTTC earlier than in precentral regions. Taken together, these studies suggest that the LOTTC plays a crucial role in action understanding.

In light of the debate regarding the use of fMRI adaptation to examine neuronal populations with visuomotor properties, and challenges in using single cell recordings in epileptic patients, we chose an electrophysiological whole-brain approach in healthy

participants, namely MEG adaptation, to identify when, where, and in which frequency bands neuronal populations distinguish between observed pointing and grasping actions. Whereas few attempts have been made so far to combine adaptation paradigms with MEG (for exceptions, see Huberle & Lutzenberger, 2013; Simpson et al., 2015), this approach seems promising since it combines the advantages of MEG (i.e., high temporal resolution) with a paradigm that is likely to target specific neuronal populations thereby gaining spatial resolution. In each trial, participants were presented with two actions, S1 and S2. In repeat trials, the action presented in S1 and S2 was the same, whereas it was different for non-repeat trials (see Fig. 1A). We focused on modulations in the alpha and beta range, as decreases of oscillations in these frequency bands in motor and somatosensory regions (e.g. Caetano, Jousmäki, & Hari, 2007) or recorded over central electrodes or sensors (mu-rhythm) during action observation resemble those that occur during the actual execution of that action and therefore often have been interpreted as reflecting simulation or ‘mirroring’ (Hari et al., 1998; Muthukumaraswamy & Johnson, 2004; Muthukumaraswamy, Johnson, & McNair, 2004; Oberman, McCleery, Ramachandran, & Pineda, 2007; Pineda, 2005). We will use the terminology of alpha and beta independent of the spatial occurrence of the oscillations. The feasibility to investigate alpha and beta modulations within repetition suppression paradigms has been shown in previous electroencephalography (EEG) studies (Coll, Bird, Catmur, & Press, 2015; Engell & McCarthy, 2014).

We predicted that in areas that show action selectivity, the observation of S2 should elicit less alpha/beta decreases in repeat in comparison to non-repeat trials, regardless of variations in reach direction (left, right) or effector (left hand, right hand). We will refer to this effect as *action-selective adaptation*. If fronto-central alpha/beta

oscillations reflect action selective human mirror neuron system activity, we would expect to find action-selective adaptation in these frequency bands in fronto-central regions.

2. Methods

2.1 Participants

18 participants (12 female, 6 male) took part in this study. The mean age was 24.22 years (SD: 2.364) and all but one were right-handed. All participants had normal or corrected-to-normal vision. Participants provided written informed consent. The study was approved by the local ethics board from the University of Trento.

2.2 Stimuli

Stimuli were identical to those used by Tucciarelli et al. (2015). They consisted of video clips (833 ms) displaying simple center-out hand movements (see Fig. 1A). The clips depicted pointing or grasping movements (‘action’) towards the left or right side (‘reach direction’), performed with the left or right hand (‘effector’). Each video started with the index finger of an actor touching a central object (a polystyrene half-sphere). Next, a centre-out movement directed towards the leftmost or the rightmost of five half-spheres arranged on a semi-circle was presented. When the hand arrived at the outer half-sphere, the video stopped. To increase perceptual variability, the actions were recorded using four different actors (1 male) using a digital video camera. Only the hands (and part of the forearm) of the actors were visible in the field of view. We instructed the actors to keep the velocity and kinematics of the movements as similar as possible across the two different movements (pointing, grasping). We discarded videos, based on our perceptual judgment, in which the velocity or kinematics were

too dissimilar from each other. We obtained the movements performed with the left hand creating a specular copy of the recorded video via custom-written software (Matlab, Mathworks, Natick, NA). This resulted in 32 unique videos as a combination of action (2) x reach direction (2) x effector (2) x actor (4). To enable fixation and thus to avoid possible noise in the MEG signal due to eye movements, we superimposed a small white cross ($0.88 \times 0.88^\circ$) above the central half-sphere on each video.

2.3 Procedure

In each trial, participants were presented with two consecutive video clips (S1 and S2). The action in S1 and S2 was either the same (repeat condition) or different (non-repeat condition). In addition, we varied the effector (left, right hand) and reach direction (left, right) such that in half of the trials, S1 and S2 showed the same effector, whereas in the other half of the trials, S1 and S2 showed actions performed with two different effectors. Likewise, half of the trials consisted of repetitions of the same reach direction, whereas the other half consisted of two different reach directions for S1 and S2. For each participant, each of the 32 unique videos was repeated 12 times across the whole experiment for a total of 384 experimental trials. We presented the 384 trials in eight blocks of approx. 6 min. Since our main interest was to investigate the effects concerning action-selective adaptation, we fully balanced transition probabilities from one trial to the next for trials of repeated and non-repeated actions. To achieve this, we added three trials per run, for a total of 408 experimental trials ($384+8 \times 3$), leading to 204 trials of repeated and 204 trials of non-repeated actions. The three additional trials appeared intermixed with the other trials, thereby enabling balancing. Doing so, we were limited in balancing transition probabilities for the other two factors (effector, reach direction), leaving us with slight imbalances for reach direction and effector.

More specifically, 'repeat effector' trials were preceded more often by trials with 'repeat action' ($p < .05$) compared to 'non-repeat effector' trials, while 'non-repeat effector' trials were more often preceded by 'non-repeat action' trials ($p < .05$) compared to 'repeat effector' trials. Repeat direction trials were preceded by repeat direction trials more often than by non-repeat direction trials ($p < .05$), while non-repeat direction trials were more often preceded by non-repeat direction trials than by repeat direction trials ($p < .05$). Since these imbalances would make it hard to interpret any obtained differences between conditions, we did not analyse direction-specific or effector-specific adaptation effects. However, transition probabilities from S2 in trial N-1 to S1 in trial N were fully balanced.

Each trial started with a green fixation cross (800 ms) which served as a signal for participants to blink if needed (see Fig. 1B). Next, a white fixation cross (variable duration between 2000 and 2500 ms) appeared, followed by S1 (833 ms), another white fixation cross (800 ms), S2 (833 ms) and another white fixation cross (1000 ms). Thus, the interval between the offset of S2 and the onset of S1 of the next trial varied due to the variable duration of the first white fixation cross and was on average 4.05 s (see Fig. 1B).

To ensure that participants would pay attention to the movements depicted in the videos, in 10% of the trials S1 or S2 was followed by a catch trial (see also Tucciarelli et al., 2015, for a similar procedure). During a catch trial, participants were asked a question about the action, the reach direction or the effector presented in the previous video clip (e.g. *'Was the action pointing?'*). Since participants did not know when a catch trial would occur (i.e. in which trial, and whether it would occur after S1 or S2), and what the question would be, this ensured that participants paid attention to all three dimensions (action, effector, reach direction). Participants had to indicate their

answer via button press with the index or middle finger of the left hand. To prevent anticipatory responses, the mapping between response button (left, right) and response (yes, no) was assigned randomly in each catch trial. On average, 1.4 (standard deviation: 0.3) errors were made per run. Feedback was provided after each catch trial using a smiling or sad cartoon face. Catch trials were excluded from the analysis.

Stimuli were projected on a screen (screen resolution: 1280 x 1024 pixels; refresh rate: 60 Hz) that was placed about 130 cm in front of the participant. The screen was visible as a rectangular aperture of about 21.7 x 13.16°. Stimulus presentation and response collection was controlled using ASF (Schwarzbach, 2011), a toolbox for Matlab (Mathworks, Natick, MA) based on the Psychtoolbox (Brainard, 1997).

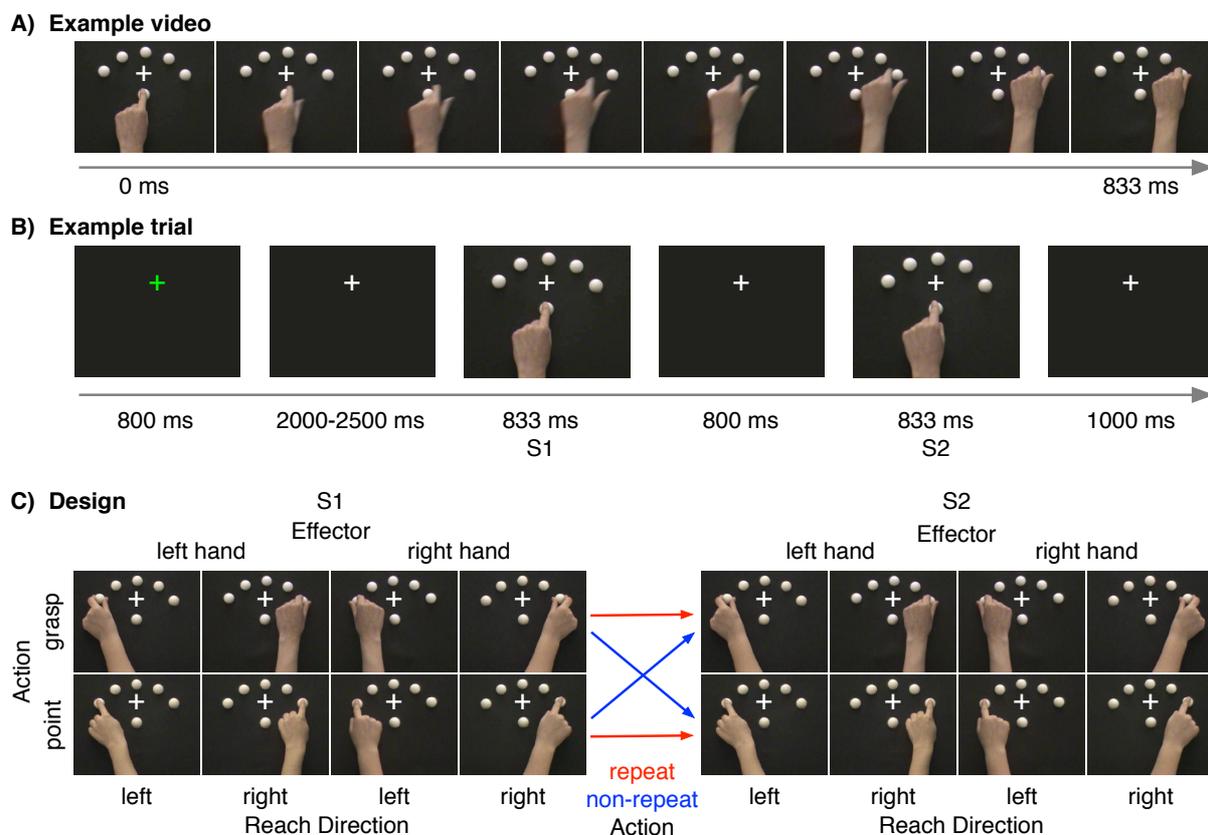


Figure 1: Schematic display of an example video, an example trial, and the adaptation design. A) Stimuli consisted of video clips (833 ms) showing simple reach-to-point or reach-to-grasp actions. B) A trial began with a green fixation cross (800 ms) indicating

a blink period followed by a white fixation cross (2000-2500 ms). Next, two action videos (S1, S2) were presented subsequently for 833 ms each, separated by a white fixation cross presented for 800 ms. Each trial finished with another white fixation cross (1000 ms). C) In repeat trials (red arrows), the action was the same in S1 and S2. In non-repeat trials (blue arrows), two different actions were shown in S1 and S2. Both in repeat and non-repeat trials, the effector and the reach direction were either the same (half of the trials) or different (half of the trials) in S1 and S2.

2.4 Data acquisition

MEG data were acquired using a 306-channels whole head MEG system (Neuromag, Elekta, Helsinki, Finland) with a sampling rate of 1000 Hz. The system consists of 204 planar gradiometers and 102 magnetometers. Five coils were attached to the participant's head, allowing to track the head position inside the MEG helmet. Digitalization of the headshape was carried out for later source reconstruction (Polhemus, Colchester, VT). The OEM system (OEM eye tracker, SensoMotoric Instruments; 60 Hz sampling rate) was used to record eye movements. Triggers were sent to the recording computer at the onset of each video. To control for possible delays between trigger arrival and actual stimulus presentation, a photodiode was used on the stimulation screen inside the shielded room. This information was later used to correct data for any delays in stimulus arrival.

2.5 Data analysis

Data were analysed using the Matlab-based FieldTrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011). Continuous data were filtered with a 1 Hz high-pass filter and then segmented into epochs around S1 with 1.6 s pre-stimulus and 4 s post-stimulus (i.e. containing the whole trial with S1 and S2 of 3.466 s, see Fig. 1 and 2A). Data were resampled to 300 Hz. We visually inspected all epochs for artefacts and

rejected trials containing muscular artefacts or channel jumps from the analysis. In a subsequent step, we transferred data into source space. To this aim, we used a template structural magnetic resonance image (MRI) and warped it to the subject's head shape (Polhemus points). This procedure is part of the standard SPM (<http://www.fil.ion.ucl.ac.uk/spm/>) procedure of canonical brain localization (Mattout, Henson, & Friston, 2007). LCMV beamformer filters were calculated separately for 1 to 100 Hz to transfer all data into source space using a single shell volume conductor model (Nolte, 2003) and individual dipole grids that were warped on a MNI grid template (372 voxels with a resolution of 2 x 2 x 2 cm).

Next, time-frequency analyses were computed on the basis of single trials between 4 and 30 Hz (Hanning window, 2 Hz steps) and -0.4 s and 3.2 s (50 ms steps) with moving windows of 500 ms length.

To calculate source level evoked responses, single trial data from the source space transition were filtered with a 1 Hz high-pass and a 30 Hz low-pass filter prior to averaging across conditions (repeat actions, non-repeat actions). A relative change baseline was calculated with 0.4- 0.1 s prior to S1 onset.

2.5.1 Action observation

To visualize general changes in brain activity obtained during action observation compared to baseline, we contrasted the whole time-frequency series and the evoked response against baseline (-.4 to -.1 s) for the whole trial (including S1 and S2).

2.5.2 Action-selective adaptation

Our main interest was to investigate whether the activity elicited by the action depicted in S2 would differ depending on the preceding action, i.e. whether S2 showed a

repeated or non-repeated action compared to S1. To measure adaptation, namely less neuronal excitability in repeat in comparison to non-repeat trials, we contrasted S2 for repeat and non-repeat trials. Importantly, we reasoned that this contrast would only be meaningful if a contrast of S1 for repeat and non-repeat trials would not show any differences. Therefore, we also calculated the differences in S1 between repeat and non-repeat trials. Note that S1 and S2 were extracted from the same trials.

To correct for multiple comparisons, all statistical contrasts were carried out using cluster-based permutation (1000 randomizations, $\alpha=0.05$, two-sided) with normalized change $[(\text{non-repeat} - \text{repeat})/(\text{non-repeat} + \text{repeat})]$ as test statistic. Both non-repeat and repeat conditions contained approximately 200 trials. The test statistic was repeated 1000 times on data shuffled across conditions and the largest value of a cluster coherent in time and frequency was kept in memory. The observed clusters were compared against the distribution obtained from the randomization procedure and were considered significant when their probability was below 5%. Statistics were calculated for all 372 voxels, with an average of 14 neighbouring voxels (neighbour calculation based on 3 cm distance as implemented in FieldTrip). Evoked response statistics were computed between 0 and 833 ms after S1 and S2 onset, respectively. For the time-frequency representation, 100 – 833 ms were analysed (sparing the abrupt and strong increase in power due to the onset of the evoked response), and statistics were calculated for 4 - 30 Hz. Note that all effects obtained for repeated vs non-repeated actions are computed on the basis of both repeated (half of the trials) and non-repeated (half of the trials) reach direction (left, right) and effector (left, right hand).

For visualization, source localizations of significant results and grand averages were interpolated onto a standard MNI brain as implemented in Fieldtrip using the linear projection method and then mapped onto inflated cortices using Caret (Van Essen et al., 2001). The grand averages of the source voxel data were calculated by averaging the source orientation component of each subject that captured most of the amplitude variance. Anatomical regions were labelled using the AFNI-atlas (Lancaster et al., 1997). For visualization of the average evoked response compared to baseline, we used source estimations for a 200 ms time window centered around the peak activity (0.21 s for S1 and 1.84 s for S2) in order to get a more stable activity pattern instead of using one single time point corresponding to the peak.

3. Results

3.1 General action observation

3.1.1 Evoked response: Figure 2A shows the evoked response during the observation of S1 and S2. Sources of the peak activity (0.21 ± 0.1 s after stimulus onset for S1 and 1.84 ± 0.1 s for S2, averaged over all trials) were localized in occipitotemporal areas (middle temporal and occipital gyrus, MOTG, Fig. 2B) for both S1 and S2 and also the Culmen for S1 (not shown in Fig. 2). As can be seen in Figure 2A, there is an increase of relative power around 3 s. We assume that this increase reflects the anticipation of the green fixation cross (i.e. the period during which participants are invited to blink), as well as early blinks.

3.1.2 Time-frequency representation: Grand averages of the time-frequency analysis averaged across subjects in time-frequency space show alpha and beta decreases during S1 and S2 relative to baseline (Fig. 2C). Sources related to S1 alpha band activity (8-10 Hz, 0.35-0.85 s; Fig. 2D, 1a) were located bilaterally in the inferior

occipital gyrus, middle temporal and occipital gyrus, precuneus, superior parietal lobe (BA7), pre- (BA4) and postcentral gyrus (BA3), and fusiform gyrus (BA19). The sources related to beta band activity were in similar areas as sources for alpha activity (Fig. 2D, Ib, 16-20 Hz, 0.35-0.55 s): bilateral precuneus, superior parietal lobe (BA7), pre- (BA4) and postcentral gyrus (BA3), middle temporal and occipital gyrus, as well as sources in left middle frontal gyrus (BA6). The main difference between alpha and beta of S1 was the distribution of the amount of power of these sources. For S2, sources of alpha band activity (Fig. 2D, IIa 8-10 Hz, 1.983-2.483 s) were mainly located in bilateral inferior and middle occipital gyrus, whereas sources for beta band activity (Fig.2D, IIb, 16-20 Hz, 1.983-2.183 s) were obtained in bilateral middle temporal gyrus (MTG) and middle occipital gyrus (MOG), precuneus, and superior parietal lobe (BA 5).

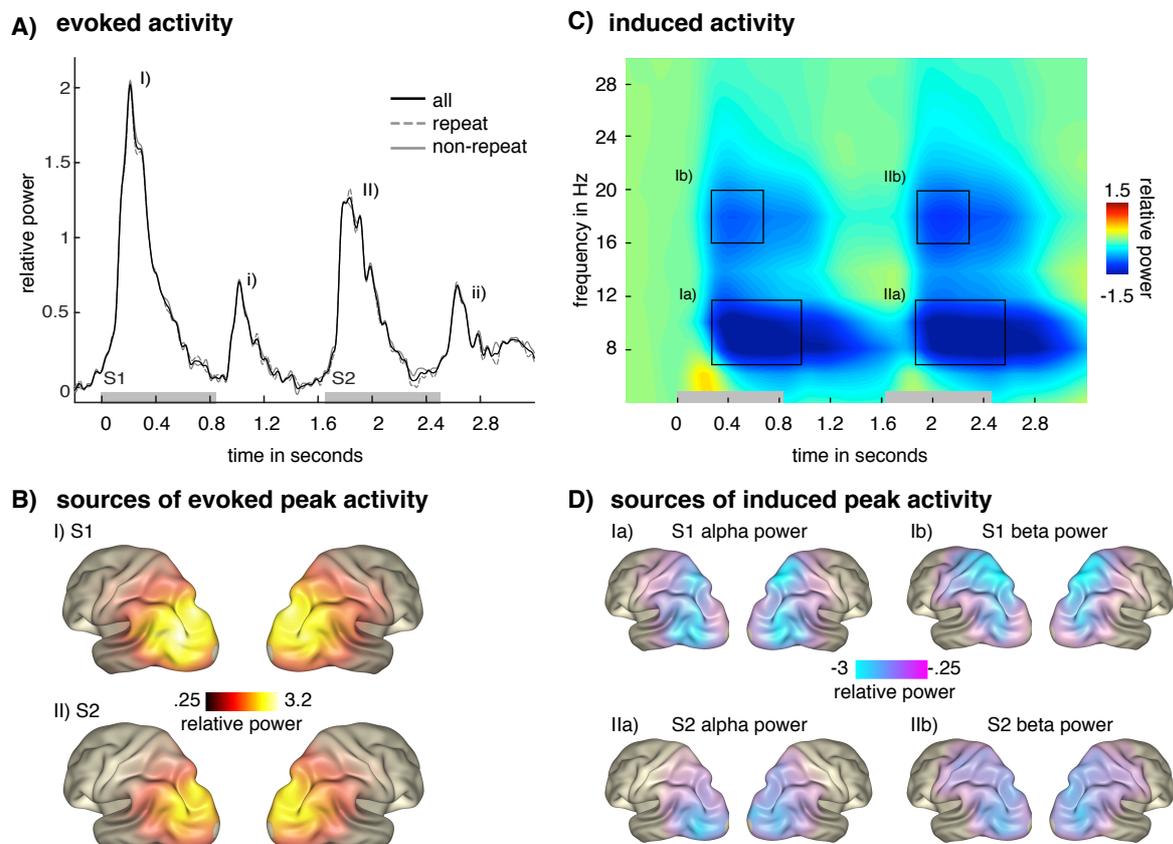


Figure 2: A) Evoked responses compared to baseline (collapsed across all source voxels), collapsed across all repeat and non-repeat trials (black solid), for repeat trials

(grey dashed), and non-repeat trials (grey solid). The horizontal grey bars indicate the time periods of the presentation of the two videos (S1: 0 to 833 ms, S2: 1633 to 2433 ms). (I) and (II) indicate the peaks following the presentation of S1 and S2, respectively. i) and ii) represent the peaks following the onset of the fixation cross. B) Source estimations for the evoked peak activities at 0.21 s (\pm 0.1 s, corresponding to S1, I) and 1.84 s (\pm 0.1s, corresponding to S2, II), collapsed over all repeat and non-repeat trials. For both S1 and S2, sources were mainly located in the MOTG. C) Time-frequency representation of the relative power changes induced by S1 and S2 averaged collapsed across all repeat and non-repeat trials compared to baseline in the alpha and beta band (collapsed across all source voxels). D) Source estimations of the power decreases in the alpha (a, 8-12 Hz) and beta (b, 16-20 Hz) band following S1 (I) and S2 (II). For S1, sources for modulations in the alpha band (Ia, 0.35-0.85 s) were found mainly in bilateral inferior occipital gyrus, middle temporal and occipital gyrus, precuneus, superior parietal lobe (BA7), pre- (BA4) and postcentral gyrus (BA3), and fusiform gyrus (BA19). S1 sources for modulations in the beta band (Ib, 0.35-0.55 s) were found mainly in the bilateral precuneus, superior parietal lobe (BA7), pre- (BA4) and postcentral gyrus (BA3), middle temporal and occipital gyrus, and in left middle frontal gyrus (BA6). For S2, sources of alpha band activity (IIa, 1.983-2.483 s) were found mainly in bilateral inferior and middle occipital gyrus, whereas sources for beta band activity (IIb, 1.983-2.183 s) were obtained in bilateral middle temporal and occipital gyrus, precuneus, and superior parietal lobe (BA 5).

3.2 Action-selective adaptation

3.2.1 Evoked response: We obtained no significant differences between non-repeat and repeat trials for the evoked response between 0 and 833 ms after S1 and S2 onset (see Fig. 2A for the similarity of the conditions).

3.2.2 Time-frequency representation: Correcting for multiple comparisons, the cluster-based permutation contrast between non-repeat and repeat trials between 100 and 833 ms post-stimulus (onset of S2 here time point zero) revealed a difference between non-repeat and repeat trials ($p < .05$) during S2. This effect occurred in the alpha band

between 10-14 Hz and 0.4-0.85 s after S2 onset (maximum of the difference: 0.5-0.75 s) and in the beta band between 16-20 Hz and 0.65-0.75 s (Fig. 3A and B). The effect was driven by relatively more positive alpha power during S2 of the repeat trials compared to the non-repeat trials, i.e. a smaller decrease, indicating adaptation in repeat trials. Source localization revealed sources of adaptation in the alpha band in the bilateral Cuneus (Fig. 3C I) and with a slightly later onset (ca. 0.65 s after S2 onset) involvement of the left middle temporal gyrus (MTG) and MOG in the beta band (Fig. 3C II). For S1, the cluster-based permutation contrast between non-repeat and repeat trials revealed no significant effects. As mentioned above, this finding served as a sanity check as a Null effect was expected due to the fact that transition probabilities between S2 in trial N-1 and S1 in trial N were balanced with respect to action, effector and direction.

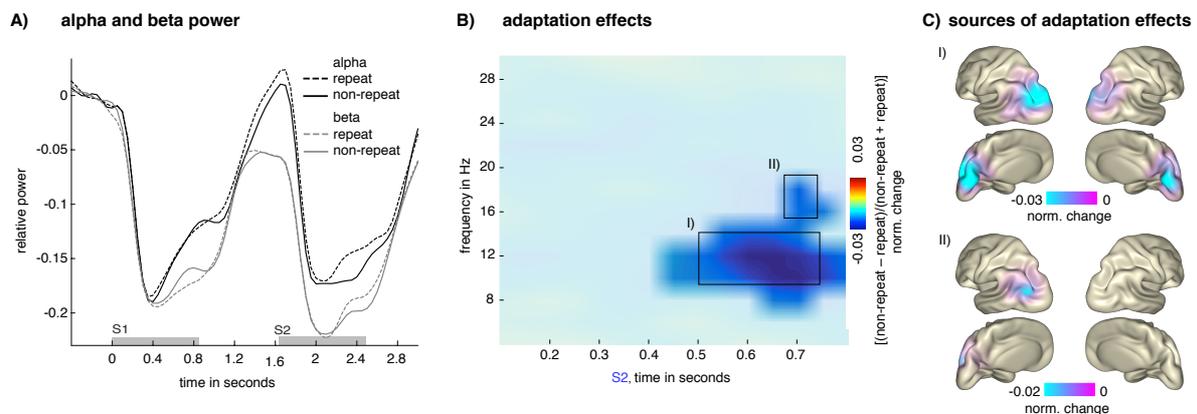


Figure 3 A) Alpha (12 Hz) and beta (18 Hz) power for repeat and non-repeat trials (averaged across all source voxels). B) Smaller alpha (I) and beta (II) decrease during repeat compared to non-repeat trials during S2 (time point zero refers to S2 onset) as revealed by the cluster-permutation test (averaged across all source voxels). C) Estimations locate sources of the alpha band effect (I, 10-14 Hz, 0.5-0.75 s) in the Cuneus, and sources of the beta band effect (II, 16-20 Hz, 0.65-0.75 s) in MTG and MOG. To determine the strength of adaptation, we computed the normalized change $[(\text{non-repeat} - \text{repeat})/(\text{non-repeat} + \text{repeat})]$.

4. Discussion

On a general level, we obtained strong alpha and beta band decreases during action observation in comparison to baseline. Main sources of alpha and also beta were found in occipitotemporal areas such as the middle occipital gyrus as well as the middle temporal gyrus. Decreased activity in the beta band extended into premotor areas (e.g. BA 6). These general changes in brain activity during action observation are consistent with a number of previous EEG and MEG (Gastaut & Bert, 1954; Grezes & Costes, 1998; Hari et al., 1998; Muthukumaraswamy & Johnson, 2004; Muthukumaraswamy et al., 2004) as well as fMRI studies (Grosbras & Paus, 2006; Iacoboni, Molnar-Szakacs, & Gallese, 2005). Importantly, as described above, a general recruitment of motor-related regions during action observation does not necessarily imply that these areas contain action-selective representations. Similarly, a study examining the influences of the baseline (static stimulus, blank trial) on action observation related mu-rhythm, reported that depending on the baseline the mu-suppression is neither specific for biological motion nor for central electrodes (Hobson & Bishop, 2016).

4.1 Action-selective adaptation in occipitotemporal regions

To identify areas containing action selective neuronal populations, we contrasted trials of repeated actions (which should lead to adaptation in action-selective neuronal populations) with trials of non-repeated actions (which should not lead to adaptation in these neuronal populations). We found a significant difference between these trials during the processing of S2 in the alpha and beta band in posterior occipitotemporal regions, with smaller alpha and beta decreases in repeat in comparison to non-repeat trials. By contrast, we obtained no signs of action-selective adaptation in premotor regions despite the fact that these areas showed the typical decreases of alpha and

beta power during action observation. The centrally recorded mu-rhythm has been suggested to reflect human mirror neuron system activity. We reasoned that if this was indeed the case, we should observe action-selective adaptation in these oscillations from frontal areas.

Crucially, we obtained no difference between repeat and non-repeat actions during the processing of S1, ruling out that any differences obtained during S2 are due to differential activity induced during the processing of S1. As action observation commonly produces alpha and beta decreases (see above), the finding of a smaller decrease during S2 in repeat compared to non-repeat trials qualifies as adaptation of sources relevant for action observation. This S2 difference started 400 ms following the onset of S2. Sources were located mainly in bilateral cuneus for alpha, and the left middle occipital gyrus and the middle temporal gyrus for beta. The MOG and MTG lie within the lateral occipitotemporal cortex (LOTC), which is known to be recruited during the processing of a wide range of action-relevant aspects such as body parts, tools, and basic and biological motion (for a recent review, see Lingnau & Downing, 2015). Using MVPA of fMRI data, it has been demonstrated that it is possible to decode upcoming movements on the basis of activity in the LOTC obtained during movement planning (e.g. Ariani, Wurm, & Lingnau, 2015; Gallivan, Chapman, Mclean, Flanagan, & Culham, 2013). Using MVPA of MEG data, representations of planned movements in the LOTC have been shown to generalize across the effector (Turella et al., 2016), in line with the view that this area contains abstract action representations that might contribute to the formulation of a motor plan (see also Verhagen, Dijkerman, Grol, & Toni, 2008), while other studies reported that frontal and parietal regions contain abstract action representations (Cattaneo et al., 2010; Hamilton & Grafton, 2008).

Using fMRI adaptation, Kable and Chatterjee (2006) demonstrated action-specific adaptation across exemplars in several subportions of the LOTC. Using MVPA of fMRI data, the LOTC and IPL have been shown to contain action-specific representations that generalize across the modality (observation, execution) and the viewpoint (first vs third person; Oosterhof et al., 2012). Moreover, the LOTC has been shown to contain representations of observed actions that generalize across the object involved (Wurm et al., 2015; Wurm & Lingnau, 2015), the task and the kinematics (Wurm et al., 2015). Likewise, Hafri, Trueswell, & Epstein (2017) were able to decode action categories irrespective of the visual format (photographs vs videos) in bilateral occipitotemporal and inferior parietal cortex, but also in left premotor and left middle frontal cortex. Using MVPA of MEG data, Tucciarelli et al. (2015) demonstrated that action representations that generalize across the effector (left vs right hand) and reach direction (left, right) can be found in the LOTC earlier than in frontal regions.

A meta-analysis of 11 studies reported the critical involvement the middle/superior temporal cortex for action understanding, in line with the results reported above, but also of inferior frontal cortex and the inferior parietal cortex (Urgesi, Candidi, & Avenanti, 2014). Using voxel-based lesion-symptom mapping study of 131 left-hemisphere stroke patients, Tarhan et al. (2015) showed that lesions in posterior regions of the LOTC were associated with deficits in action recognition, whereas lesions in primary motor, somatosensory cortex or inferior parietal lobe were associated with deficits in action production. Finally, patients that were born without upper limbs and thus are unlikely to have developed motor representations of their own arm movements show no deficits in recognizing or predicting actions performed with the upper limbs (Vannuscorps & Caramazza, 2015).

In summary, whereas a large number of studies are compatible with the idea that the simulation of observed actions in the observer's motor system provides the key to action understanding, a growing number of recent studies cast doubts on this view. Importantly, comparable to other studies that did report frontal adaptation, our study used short stimuli (individual movements lasting around 1 second or less (Kilner et al., 2014, 2009; Perry & Bentin, 2009) and egocentric perspective (Kilner et al., 2009; Perry & Bentin, 2009).

4.2 Action-selective adaptation: adaptation vs MVPA of MEG data

We used the same stimulus material as in the MVPA MEG study by Tucciarelli et al. (2015). Tucciarelli et al. (2015) obtained action selectivity in occipitotemporal regions earlier (200 ms) and in lower frequencies (theta band) than those we obtained in the current study (400 ms, alpha- and beta-band). These differences might be due to methodological differences in generalizing across effector and direction in the study by Tucciarelli et al. (2015) as well as the temporal smoothing of the MEG signal using the whole-brain searchlight-based MVPA approach, which limits the precision of the absolute onset of an effect (which was less relevant for Tucciarelli et al, 2015, since they were interested in the relative timing between the various sources). Importantly, despite these differences, both studies revealed action selectivity in posterior occipitotemporal regions.

4.3 Action-selective adaptation: induced vs evoked responses

Investigating the evoked field by applying a temporally and spatially unrestricted analysis on the whole brain (all voxels) and the entire time period of stimulus presentation, we did not find any signs of action-selective adaptation (repeat vs. non-

repeat trials). This is in contrast to a previous EEG evoked responses (ERP) study (Möhring, Shen, & Neuhaus, 2014) which investigated gesture-specific adaptation for pre-defined temporal components and electrodes. Using static pictures of different hand gestures, Möhring et al. (2014) examined ERPs (P1, N190, P2) in repeat and non-repeat gesture trials with varying interstimulus intervals (ISI, 200 ms, 500 ms, 800 ms or 1200 ms). They reported gesture-selective adaptation for the N190 localized in the extrastriate body area, whereas we failed to find such an effect. This might be due to differences in the stimulus material (static vs. dynamic; gestures vs. simple pointing/grasping movements). Furthermore, we used a fixed ISI of 800 ms, whereas Möhring et al. (2014) varied the ISI and reported strongest gesture-unselective P2 adaptation (note that here adaptation was calculated as S2/S1 ratio) for the shortest and smaller adaptation for longer ISIs, suggesting that the ISI is likely to influence adaptation. Moreover, Möhring et al. (2014) focused on pre-defined temporal components and associated electrodes, while our analyses of the evoked responses were temporally and spatially unrestricted (whole brain, whole time window), thereby not relying on prior assumptions.

In another study on EEG adaptation of the intention of hand movements, Ortigue and colleagues (2009) presented hand movements towards an object and different hand-object interactions representing different intentions (to grab a gun/ hair dryer to use vs. to move it). They reported adaptation as lower EEG global field power during observation of a repeated intention compared to a non-repeated intention. These differences were linked to brain state stability effects between 62 and 130 ms and 330 and 400 ms after the start of the hand-object interaction both in the superior temporal sulcus (STS) and the anterior intraparietal sulcus, suggesting that these sources might be involved in processing the corresponding hand-object interactions or intentions.

Regarding the latency at which this difference was obtained, it should be noted that the start of the hand-object interaction served as time point zero and not the start of the hand movement itself.

As mentioned earlier, we did not find action-selective adaptation at the level of the evoked response, which would be the closest to the measures of these other studies, most likely due to our whole brain/ whole time period analysis. Alternatively, as Kilner et al. (2014) showed that adaptation in firing rate occurs only after 7-10 repetitions, the absence of an effect in the evoked response in the current study might be due to the use of only two repetitions. The action-selective adaptation effect we obtained occurred in the time-frequency domain, reflecting the induced response. This effect of reduced alpha/beta decrease during the second stimulus in repeat trials compared to non-repeat trials expanded from MOG to the extrastriate body area, the area also found by Möhring et al. (2014) to show gesture-selective adaptation.

Another EEG study investigated action-selective adaptation, taking the frequency domain into consideration (Perry & Bentin, 2009), however only spectrally without temporal information. They found stronger alpha band decreases over central electrodes during observation of different sequential grasping movements of different objects compared to repetitive movements (Perry & Bentin, 2009). It should be noted that analyses were only carried out for four pre-selected electrodes, thus not taking full advantage of the spatial representation in the data provided by the 64-channel EEG.

Our study advances those previous investigations by analysing both the evoked response and the induced oscillatory activity with time-frequency representations on source level without any a priori assumptions about the spatial or temporal location of the effects.

5. Conclusion

We found action-selective adaptation in the alpha and beta band of the MEG signal, starting 400 ms after the onset of S2, with sources in posterior occipito-temporal regions, in line with previous results using MVPA of MEG data. By contrast, we obtained no signs of action selectivity in precentral regions, despite the fact that these showed the typical decrease of the alpha and beta band during action observation.

The present data are in line with a growing number of studies (i) that did not obtain support for the suitability of the mu-rhythm as a proxy of mirror neuron system activity suggesting that further studies are required to test this hypothesis and (ii) demonstrating selectivity for observed actions in occipitotemporal regions at varying levels of abstraction, supporting the view that these regions contribute to action understanding.

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References

- Ariani, G., Wurm, M. F., & Lingnau, A. (2015). Decoding Internally and Externally Driven Movement Plans. *Journal of Neuroscience*, *35*(42), 14160–14171. <http://doi.org/10.1523/JNEUROSCI.0596-15.2015>
- Avenanti, A., Bolognini, N., Maravita, A., & Aglioti, S. M. (2007). Somatic and Motor Components of Action Simulation. *Current Biology*, *17*(24), 2129–2135. <http://doi.org/10.1016/j.cub.2007.11.045>
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433–436. <http://doi.org/10.1163/156856897X00357>
- Caetano, G., Jousmäki, V., & Hari, R. (2007). Actor's and observer's primary motor cortices stabilize similarly after seen or heard motor actions. *Proceedings of the National Academy of Sciences*, *104*(21), 9058–62. <http://doi.org/10.1073/pnas.0702453104>
- Caggiano, V., Pomper, J. K., Fleischer, F., Fogassi, L., Giese, M., & Thier, P. (2013). Mirror neurons in monkey area F5 do not adapt to the observation of repeated actions. *Nature Communications*, *4*(May 2012), 1433. <http://doi.org/10.1038/ncomms2419>
- Caramazza, A., Anzellotti, S., Strnad, L., & Lingnau, A. (2014). Embodied Cognition and Mirror Neurons: A Critical Assessment. *Annual Review of Neuroscience*, *37*, 1–15. <http://doi.org/10.1146/annurev-neuro-071013-013950>
- Cattaneo, L., Sandrini, M., & Schwarzbach, J. (2010). State-dependent TMS reveals a hierarchical representation of observed acts in the temporal, parietal, and premotor cortices. *Cerebral Cortex*, *20*(9), 2252–2258. <http://doi.org/10.1093/cercor/bhp291>
- Chong, T. T. J., Cunnington, R., Williams, M. A., Kanwisher, N., & Mattingley, J. B. (2008). fMRI Adaptation Reveals Mirror Neurons in Human Inferior Parietal Cortex. *Current Biology*, *18*(20), 1576–1580. <http://doi.org/10.1016/j.cub.2008.08.068>
- Coll, M. P., Bird, G., Catmur, C., & Press, C. (2015). Cross-modal repetition effects in the mu rhythm indicate tactile mirroring during action observation. *Cortex*, *63*, 121–131. <http://doi.org/10.1016/j.cortex.2014.08.024>
- Csibra, G. (2007). Action mirroring and action understanding: An alternative account. In P. Haggard, Y. Rosetti, & M. Kawato (Eds.), *Attention and Performance XXII: Sensorimotor Foundations of Higher Cognition*. (pp. 435–459). Oxford: Oxford Press. Retrieved from http://books.google.it/books?hl=it&lr=&id=FfKlf_VZw_EC&oi=fnd&pg=PA435&dq=what+type+of+action+understanding&ots=0PouLH2fFs&sig=yXZfxVikK3q1w5Lu6SpZxd0wyG8
- Dinstein, I., Hasson, U., Rubin, N., & Heeger, D. J. (2007). Brain Areas Selective for Both Observed and Executed Movements. *J Neurophysiol*, *98*(3), 1415–1427. <http://doi.org/10.1152/jn.00238.2007>
- Dinstein, I., Thomas, C., Behrmann, M., & Heeger, D. J. (2008). A mirror up to nature. *Current Biology*. <http://doi.org/10.1016/j.cub.2008.01.044>
- Engell, A. D., & McCarthy, G. (2014). Repetition suppression of face-selective

- evoked and induced EEG recorded from human cortex. *Human Brain Mapping*, 35(8), 4155–4162. <http://doi.org/10.1002/hbm.22467>
- Gallese, V., & Goldman, A. (1998). Mirror neurons and the mind-reading. *Trends in Cognitive Sciences*, 2(12), 493–501. [http://doi.org/10.1016/S1364-6613\(98\)01262-5](http://doi.org/10.1016/S1364-6613(98)01262-5)
- Gallese, V., & Sinigaglia, C. (2011). What is so special about embodied simulation? *Trends in Cognitive Sciences*. <http://doi.org/10.1016/j.tics.2011.09.003>
- Gallivan, J. P., Chapman, C. S., Mclean, D. A., Flanagan, J. R., & Culham, J. C. (2013). Activity patterns in the category-selective occipitotemporal cortex predict upcoming motor actions. *European Journal of Neuroscience*, 38(3), 2408–2424. <http://doi.org/10.1111/ejn.12215>
- Gastaut, H. J., & Bert, J. (1954). EEG changes during cinematographic presentation. *EEG Clinical Neurophysiology*, 6, 433–444. [http://doi.org/10.1016/0013-4694\(54\)90058-9](http://doi.org/10.1016/0013-4694(54)90058-9)
- Grafton, S. T. (2009). Embodied cognition and the simulation of action to understand others. *Annals of the New York Academy of Sciences*, 1156, 97–117. <http://doi.org/10.1111/j.1749-6632.2009.04425.x>
- Grezes, J., & Costes, N. (1998). Top Down Effect of Strategy on the Perception of Human Biological Motion: a PET Investigation. *Cognitive Neuropsychology*, 15, 553–582. <http://doi.org/10.1080/026432998381023>
- Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Sciences*. <http://doi.org/10.1016/j.tics.2005.11.006>
- Grosbras, M. H., & Paus, T. (2006). Brain networks involved in viewing angry hands or faces. *Cerebral Cortex*, 16(8), 1087–1096. <http://doi.org/10.1093/cercor/bhj050>
- Hafri, A., Trueswell, J. C., & Epstein, R. A. (2017). Neural Representations of Observed Actions Generalize across Static and Dynamic Visual Input. *The Journal of Neuroscience*, 37(11), 3056–3071. <http://doi.org/10.1523/JNEUROSCI.2496-16.2017>
- Hamilton, A. F. de C., & Grafton, S. T. (2008). Action outcomes are represented in human inferior frontoparietal cortex. *Cerebral Cortex*, 18(5), 1160–1168. <http://doi.org/10.1093/cercor/bhm150>
- Hari, R., Forss, N., Avikainen, S., Kirveskari, E., Salenius, S., & Rizzolatti, G. (1998). Activation of human precentral motor cortex during action observation: A neuromagnetic study. *Proc Natl Acad Sci U S A*, 95(25), 15061–5. Retrieved from <http://www.ncbi.nlm.nih.gov/htbin-post/Entrez/query?db=m&form=6&dopt=r&uid=9844015%5Cnhttp://www.pnas.org/cgi/content/full/95/25/15061>
- Hickok, G. (2009). Eight Problems for the Mirror Neuron Theory of Action Understanding in Monkeys and Humans. *Journal of Cognitive Neuroscience*, 21(7), 1229–1243. <http://doi.org/10.1162/jocn.2009.21189>
- Hobson, H. M., & Bishop, D. V. M. (2016). Mu suppression – A good measure of the human mirror neuron system? *Cortex*, 82, 290–310.

<http://doi.org/10.1016/j.cortex.2016.03.019>

- Huberle, E., & Lutzenberger, W. (2013). Temporal properties of shape processing by event-related MEG adaptation. *Neuroimage*, *15*(67), 119–126.
- Iacoboni, M., Molnar-Szakacs, I., & Gallese, V. (2005). Grasping the intentions of others with one's own mirror neuron system. *PLoS Biology*. Retrieved from <http://dx.plos.org/10.1371/journal.pbio.0030079>
- Kable, J. W., & Chatterjee, A. (2006). Specificity of action representations in the lateral occipitotemporal cortex. *Journal of Cognitive Neuroscience*, *18*(9), 1498–1517. <http://doi.org/10.1162/jocn.2006.18.9.1498>
- Kilner, J. M. (2011). More than one pathway to action understanding. *Trends in Cognitive Sciences*, *15*(8), 352–357. <http://doi.org/10.1016/j.tics.2011.06.005>
- Kilner, J. M., Kraskov, A., & Lemon, R. N. (2014). Do monkey F5 mirror neurons show changes in firing rate during repeated observation of natural actions? *Journal of Neurophysiology*, *111*(6), 1214–26. <http://doi.org/10.1152/jn.01102.2012>
- Kilner, J. M., Neal, A., Weiskopf, N., Friston, K. J., & Frith, C. D. (2009). Evidence of mirror neurons in human inferior frontal gyrus. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *29*(32), 10153–10159. <http://doi.org/10.1523/JNEUROSCI.2668-09.2009>
- Krekelberg, B., Boynton, G. M., & van Wezel, R. J. A. (2006). Adaptation: from single cells to BOLD signals. *Trends in Neurosciences*. <http://doi.org/10.1016/j.tins.2006.02.008>
- Lancaster, J., Rainey, L., Summerlin, J., Freitas, C., Fox, P. T., Evans, A. C., ... Mazziotta, J. C. (1997). Automated labeling of the human brain: a preliminary report on the development and evaluation of a forward-transform method. *Human Brain Mapping*, *5*(4), 238–242. [http://doi.org/10.1002/\(SICI\)1097-0193\(1997\)5:4<238::AID-HBM6>3.0.CO;2-4](http://doi.org/10.1002/(SICI)1097-0193(1997)5:4<238::AID-HBM6>3.0.CO;2-4)
- Larsson, J., Solomon, S. G., & Kohn, A. (2016). fMRI adaptation revisited. *Cortex*. <http://doi.org/10.1016/j.cortex.2015.10.026>
- Lingnau, A., & Downing, P. E. (2015). The lateral occipitotemporal cortex in action. *Trends in Cognitive Sciences*. <http://doi.org/10.1016/j.tics.2015.03.006>
- Lingnau, A., Gesierich, B., & Caramazza, A. (2009). Asymmetric fMRI adaptation reveals no evidence for mirror neurons in humans. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(24), 9925–9930. <http://doi.org/10.1073/pnas.0902262106>
- Mahon, B. Z., & Caramazza, A. (2008). A critical look at the embodied cognition hypothesis and a new proposal for grounding conceptual content. *Journal of Physiology Paris*, *102*(1–3), 59–70. <http://doi.org/10.1016/j.jphysparis.2008.03.004>
- Mattout, J., Henson, R. N., & Friston, K. J. (2007). Canonical source reconstruction for MEG. *Computational Intelligence and Neuroscience*, *2007*. <http://doi.org/10.1155/2007/67613>
- Möhring, N., Shen, C., & Neuhaus, A. H. (2014). Spatiotemporal dynamics of early cortical gesture processing. *NeuroImage*, *99*, 42–49.

<http://doi.org/10.1016/j.neuroimage.2014.05.061>

- Mukamel, R., Ekstrom, A. D., Kaplan, J., Iacoboni, M., & Fried, I. (2010). Single-Neuron Responses in Humans during Execution and Observation of Actions. *Current Biology*, *20*(8), 750–756. <http://doi.org/10.1016/j.cub.2010.02.045>
- Muthukumaraswamy, S. D., & Johnson, B. W. (2004). Changes in rolandic mu rhythm during observation of a precision grip. *Psychophysiology*, *41*(1), 152–156. <http://doi.org/10.1046/j.1469-8986.2003.00129.x>
- Muthukumaraswamy, S. D., Johnson, B. W., & McNair, N. A. (2004). Mu rhythm modulation during observation of an object-directed grasp. *Cognitive Brain Research*, *19*(2), 195–201. <http://doi.org/10.1016/j.cogbrainres.2003.12.001>
- Nolte, G. (2003). The magnetic lead field theorem in the quasi-static approximation and its use for magnetoencephalography forward calculation in realistic volume conductors. *Physics in Medicine and Biology*, *48*(22), 3637–3652. <http://doi.org/10.1088/0031-9155/48/22/002>
- Nummenmaa, L., Smirnov, D., Lahnakoski, J. M., Glerean, E., Jääskeläinen, I. P., Sams, M., & Hari, R. (2014). Mental action simulation synchronizes action-observation circuits across individuals. *The Journal of Neuroscience*, *34*(3), 748–757. <http://doi.org/10.1523/JNEUROSCI.0352-13.2014>
- Oberman, L. M., McCleery, J. P., Ramachandran, V. S., & Pineda, J. A. (2007). EEG evidence for mirror neuron activity during the observation of human and robot actions: Toward an analysis of the human qualities of interactive robots. *Neurocomputing*, *70*(13–15), 2194–2203. <http://doi.org/10.1016/j.neucom.2006.02.024>
- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, *2011*. <http://doi.org/10.1155/2011/156869>
- Oosterhof, N. N., Tipper, S. P., & Downing, P. E. (2012). Viewpoint (in)dependence of action representations: an MVPA study. *Journal of Cognitive Neuroscience*, *24*(4), 975–989. http://doi.org/10.1162/jocn_a_00195
- Oosterhof, N. N., Tipper, S. P., & Downing, P. E. (2013). Crossmodal and action-specific: Neuroimaging the human mirror neuron system. *Trends in Cognitive Sciences*, *17*(7), 311–318. <http://doi.org/10.1016/j.tics.2013.04.012>
- Oosterhof, N. N., Wiggett, A. J., Diedrichsen, J., Tipper, S. P., & Downing, P. E. (2010). Surface-based information mapping reveals crossmodal vision-action representations in human parietal and occipitotemporal cortex. *Journal of Neurophysiology*, *104*(2), 1077–1089. <http://doi.org/10.1152/jn.00326.2010>
- Ortigue, S., Thompson, J. C., Parasuraman, R., & Grafton, S. T. (2009). Spatio-temporal dynamics of human intention understanding in temporo-parietal cortex: A combined EEG/fMRI repetition suppression paradigm. *PLoS ONE*, *4*(9). <http://doi.org/10.1371/journal.pone.0006962>
- Perry, A., & Bentin, S. (2009). Mirror activity in the human brain while observing hand movements: A comparison between EEG desynchronization in the ??-range and previous fMRI results. *Brain Research*, *1282*, 126–132. <http://doi.org/10.1016/j.brainres.2009.05.059>

- Pineda, J. A. (2005). The functional significance of mu rhythms: Translating “seeing” and “hearing” into “doing.” *Brain Research Reviews*.
<http://doi.org/10.1016/j.brainresrev.2005.04.005>
- Rizzolatti, G., Fogassi, L., Pellegrino, G. Di, Fadiga, L., Fogassi, L., Gallese, V., ... Fried, I. (2014). The mirror mechanism: recent findings and perspectives. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 369(1644), 20130420. <http://doi.org/10.1098/rstb.2013.0420>
- Rizzolatti, G., & Sinigaglia, C. (2016). The mirror mechanism: a basic principle of brain function. *Nature Reviews Neuroscience*, 17(12), 757–765.
<http://doi.org/10.1038/nrn.2016.135>
- Sapountzis, P., Schluppeck, D., Bowtell, R., & Peirce, J. W. (2010). A comparison of fMRI adaptation and multivariate pattern classification analysis in visual cortex. *NeuroImage*, 49(2), 1632–1640.
<http://doi.org/10.1016/j.neuroimage.2009.09.066>
- Schwarzbach, J. (2011). A simple framework (ASF) for behavioral and neuroimaging experiments based on the psychophysics toolbox for MATLAB. *Behavior Research Methods*, 43(4), 1194–201. <http://doi.org/10.3758/s13428-011-0106-8>
- Simpson, M. I. G., Johnson, S. R., Prendergast, G., Kokkinakis, A. V., Johnson, E., Green, G. G. R., & Johnston, P. J. (2015). MEG adaptation resolves the spatiotemporal characteristics of face-sensitive brain responses. *Journal of Neuroscience*, 35(45), 15088–15096.
- Tarhan, L. Y., Watson, C. E., & Buxbaum, L. J. (2015). Shared and Distinct Neuroanatomic Regions Critical for Tool-related Action Production and Recognition: Evidence from 131 Left-hemisphere Stroke Patients. *Journal of Cognitive Neuroscience*, 27(12), 2491–511. http://doi.org/10.1162/jocn_a_00876
- Tucciarelli, R., Turella, L., Oosterhof, N. N., Weisz, N., & Lingnau, A. (2015). MEG Multivariate Analysis Reveals Early Abstract Action Representations in the Lateral Occipitotemporal Cortex. *Journal of Neuroscience*, 35(49), 16034–16045. <http://doi.org/10.1523/JNEUROSCI.1422-15.2015>
- Turella, L., Tucciarelli, R., Oosterhof, N. N., Weisz, N., Rumiati, R., & Lingnau, A. (2016). Beta band modulations underlie action representations for movement planning. *NeuroImage*. <http://doi.org/10.1016/j.neuroimage.2016.05.027>
- Urgesi, C., Candidi, M., & Avenanti, A. (2014). Neuroanatomical substrates of action perception and understanding: an anatomic likelihood estimation meta-analysis of lesion-symptom mapping studies in brain injured patients. *Frontiers in Human Neuroscience*, 8. <http://doi.org/10.3389/fnhum.2014.00344>
- Van Essen, D. C., Drury, H. a., Dickson, J., Harwell, J., Hanlon, D., & Anderson, C. H. (2001). An Integrated Software Suite for Surface-based Analyses of Cerebral Cortex. *Journal of the American Medical Informatics Association*, 8(5), 443–459.
<http://doi.org/10.1136/jamia.2001.0080443>
- Vannuscorps, G., & Caramazza, A. (2015). Typical action perception and interpretation without motor simulation. *Proceedings of the National Academy of Sciences*, 113(1), 86–91. <http://doi.org/10.1073/pnas.1516978112>
- Verhagen, L., Dijkerman, H. C., Grol, M. J., & Toni, I. (2008). Perceptuo-motor interactions during prehension movements. *The Journal of Neuroscience : The*

Official Journal of the Society for Neuroscience, 28(18), 4726–4735.
<http://doi.org/10.1523/JNEUROSCI.0057-08.2008>

Willems, R. M., & Hagoort, P. (2009). Hand preference influences neural correlates of action observation. *Brain Research*, 1269, 90–104.
<http://doi.org/10.1016/j.brainres.2009.02.057>

Wurm, M. F., Ariani, G., Greenlee, M. W., & Lingnau, A. (2015). Decoding Concrete and Abstract Action Representations During Explicit and Implicit Conceptual Processing. *Cerebral Cortex*, bhv169. <http://doi.org/10.1093/cercor/bhv169>

Wurm, M. F., & Lingnau, A. (2015). Decoding Actions at Different Levels of Abstraction. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, 35(20), 7727–7735. <http://doi.org/10.1523/JNEUROSCI.0188-15>.