Responsivity of a human mirror neuron system to the transitivity of an action when the end result of a movement is visible but not when it is obscured

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Abstract

The human mirror neuron system (MNS) has been hypothesised to have a functional role in action understanding. Previous research has shown that, in the macaque, mirror neurons only respond to observed actions that are directed towards an object (transitive actions). In humans, a broadly distributed MNS does respond to observed actions, even when they are not directed towards an object (intransitive actions). However, some evidence has shown that the degree to which the MNS is activated in humans is modulated by transitivity. Given that the presence of an object provides more explicit information about the purpose of the action, it is suggested that a modulation of the MNS in response to transitivity is indicative of the functional role the system plays in action understanding. In the current study, 17 participants observed transitive and intransitive movements under two conditions while we recorded BOLD response using fMRI. In the first condition, the action and object were completely visible. In the second, the end of the action and what the action was directed towards (an object or nothing) was hidden from view. We show that areas within the MNS, in the left hemisphere, are responsive to transitivity only when the action and object are fully visible. We suggest that this demonstrates a limited role of an MNS in action understanding. When the goal is obvious and visible the MNS contributes to action understanding. However, when an inference is required for the goal to be achieved, the MNS does not contribute to action understanding.

Rationale

The functional role of a system in the brain that is active for action observation and action execution, a so-called mirror neuron system (MNS), is still under debate (see, Bonini 2018, for a recent review). Some argue that the cortical mirroring of observed actions in the MNS underpins intention understanding (Fogassi et al., 2005). A key study that contributes to this interpretation of the functional role of an MNS is that by Umiltà et al. (2001). In this study Umiltà et al. (2001) record single cell activation in macaque MNS regions. A functional property of MNs in the macaque is that they respond to transitive (object directed) but not intransitive movements. Umiltà et al. (2001) replicate this finding and also show that preferential activation to transitive movements is maintained even when the end part of the hand object interaction is hidden from view. Given the perceptual properties of a transitive and intransitive action are identical when hidden from view arguably, it is the understanding of the intention of the movement that is being coded by the MNs. Preferential activation to

transitive grasps in an MNS has also been shown in humans (Muthukumaraswamy et al., 2004). However, it remains an open question as to whether the human MNS is differentially active for transitive, compared to intransitive, movements when the actual interaction between object and effector is hidden from view.

Methods

Participants

Seventeen participants with normal or corrected-to-normal vision (5 males, 12 females), aged 18 – 46 (M = 22.5, SD = 6.61) took part in the experiment. All participants were right handed according to self-report.

Localiser

The current experiment involved a functional localiser. Four functional runs, each of 27 blocks and each block consisted of stimuli of one condition. The conditions were either observation or execution of a left hand or right hand, either making a whole hand grasp or a precision grasp. Each block lasted 15 seconds and was separated by a 6 second period of fixation followed by an instruction slide lasting 3 seconds. Block order was pseudo-randomized such that blocks were randomly presented once for each functional run, and all participants were presented with the blocks in the same order.

Main experiment

Data were collected for one functional run consisting of 24 trials. Each functional trial lasted 18 seconds and was preceded by a fixation cross for 6 seconds. The videos (see fig.1 for an example) were all of a hand making a reaching movement. The videos were one of four conditions: movement made was either transitive (actions directed towards an object) or intransitive (a pantomimed grasp not directed towards an object) AND were either in full view of the participant or the end of the movement was hidden from view.

Analysis

Group constrained subject specific (GcSS)

GcSS involves a combination of group level and individual level functional localisation. It constrains each individual's ROIs to areas that are also commonly activated across a proportion of other participants (Nieto-Castañón & Fedorenko, 2012). Individual participants' ROIs for a localiser task are overlaid in standard space. A probability map is created in which each voxel has a value of how many individual ROIs it appears in. The probability map is than overlaid with each individual ROI separately. Only voxels that exist in an individual ROI and in the probability map are entered into subsequent analyses for each participant.

In the current experiment, a 'mirror conjunction' was carried out at the individual level after transformation of each brain into Talairach space (Talairach & Tournoux, 1988). Specifically, a mass univariate conjunction analysis was performed within every voxel. All execution

conditions (collapsed across grasp and hand conditions) were contrasted with baseline and all observation conditions (collapsed across grasp and hand conditions) were contrasted with baseline. All individual participant ROIs were then overlaid such that, for each voxel, there was a value describing how many individual participant ROIs overlapped within that voxel. The resulting probability map was thresholded to exclude any voxels that were not in at least 20% of participants' individual ROIs. The probability map was then overlaid with each individual participant's ROI and any voxels active in both the individual participant and 20% of other participants were selected for the participants' GcSS ROI.

Main analysis

Mass univariate analyses were performed across the whole brain in Talairach space. In all cortical and sub-cortical voxels, visible transitive actions were contrasted with visible intransitive actions; hidden transitive actions were contrasted with hidden intransitive actions; visible transitive actions were contrasted with hidden transitive actions and visible intransitive actions were contrasted with hidden intransitive actions. Any voxels that did not reach an alpha threshold of $p < .005$ were excluded from further analysis. Any contrast that resulted in activation that overlapped with regions identified in the GcSS (see fig. 2) were included in subsequent analysis.
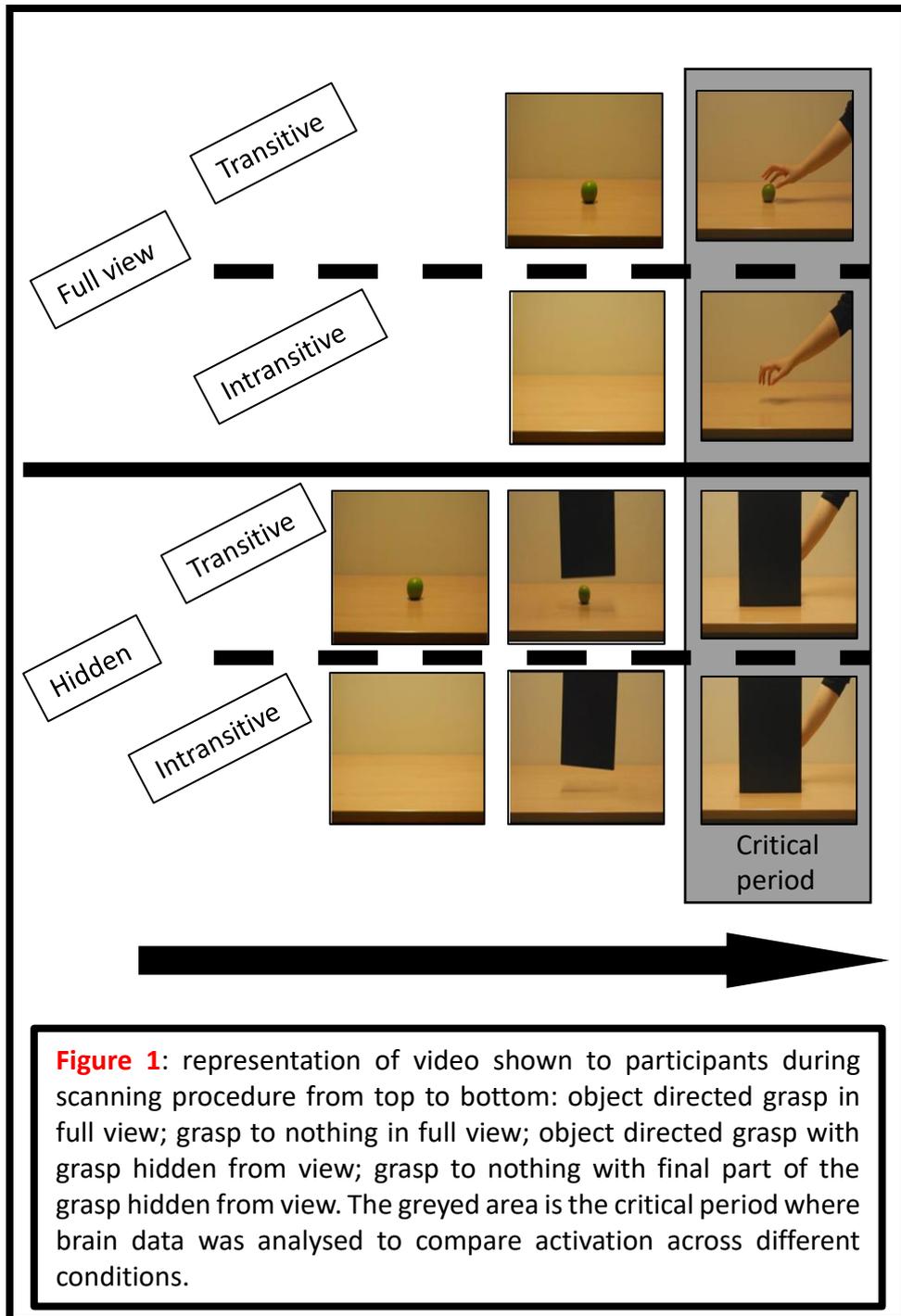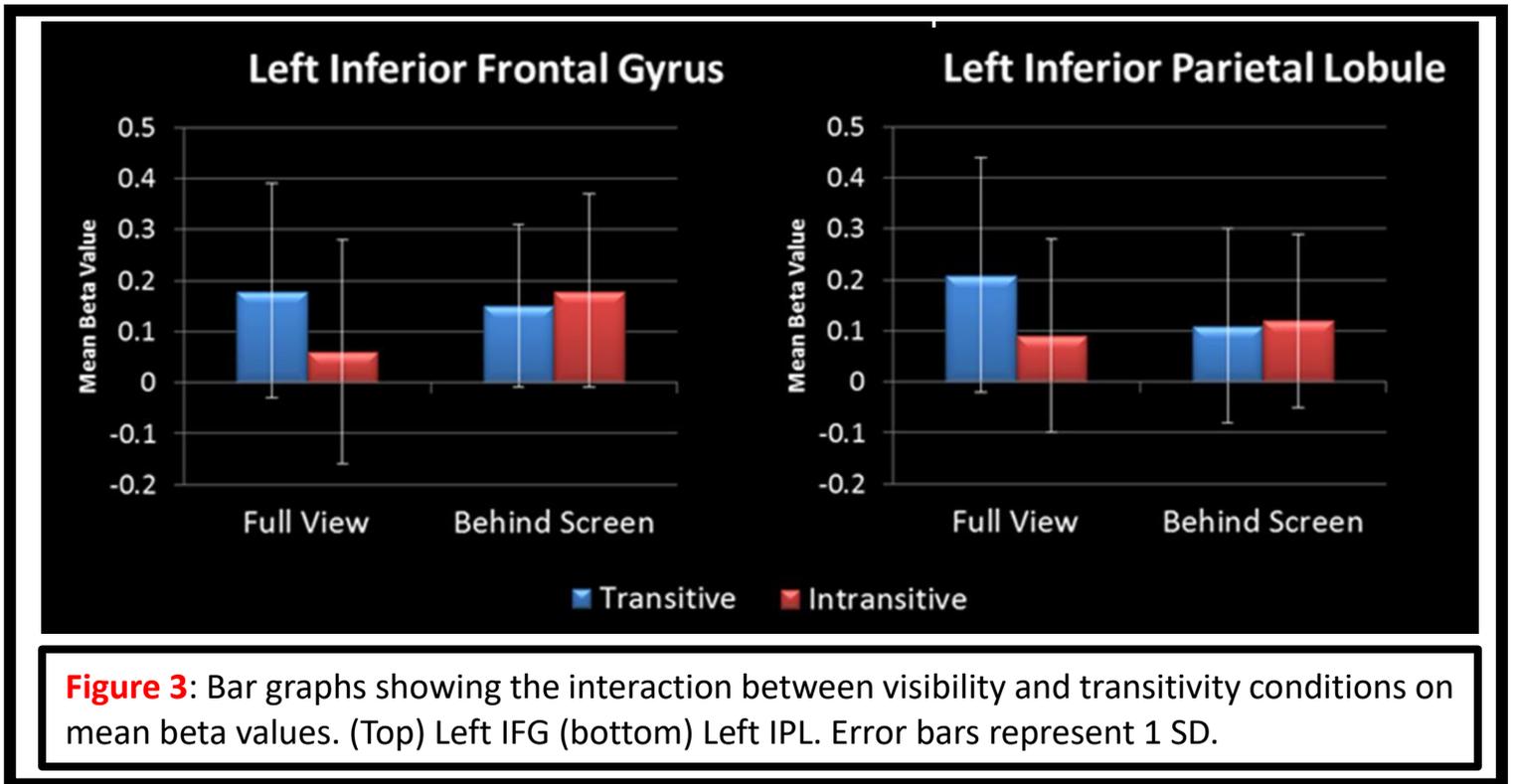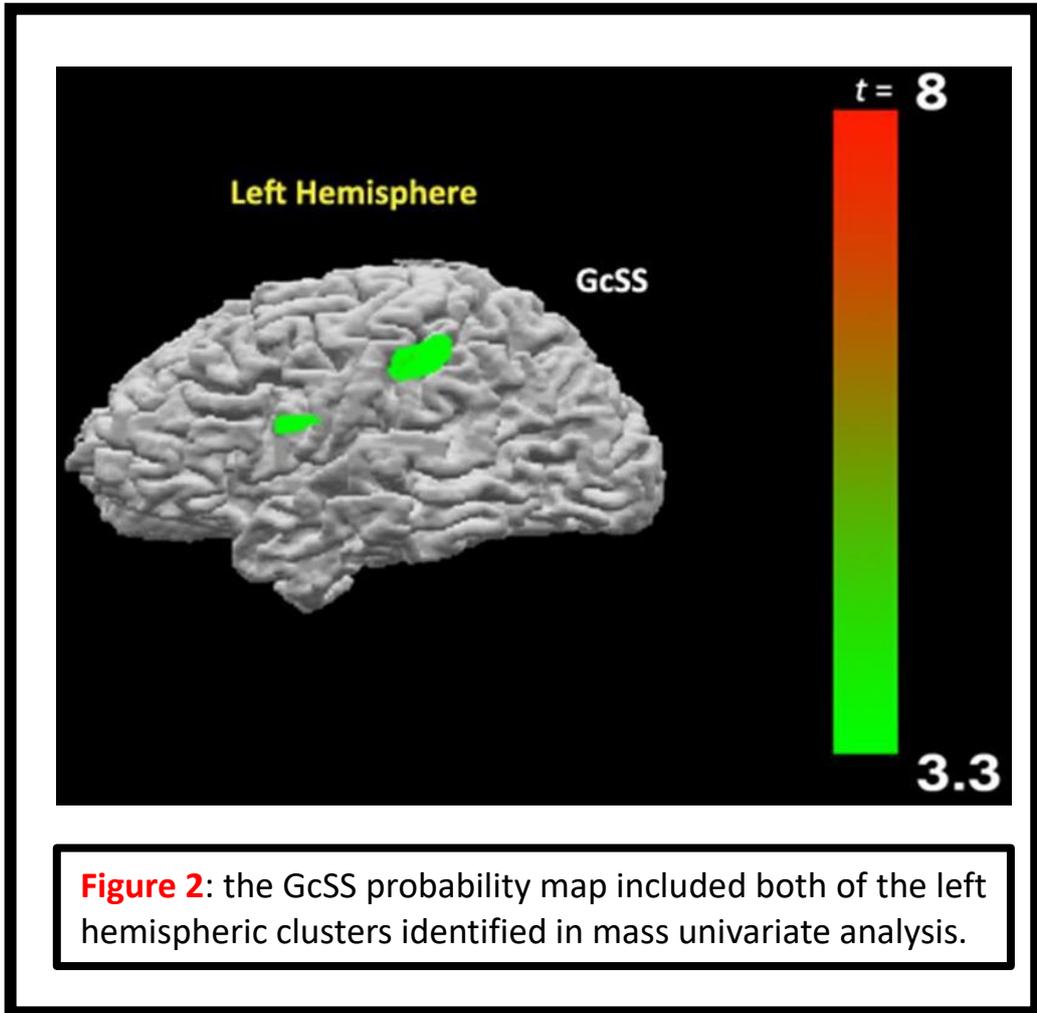
Results

Activation identified in the clusters in Figure 2 were analysed with a 2 (transitivity) x 2 (visibility) ANOVA. There was a significant interaction between transitivity and visibility conditions in the IPL and the IFG clusters, (IPL; $F(1, 14) = 12.12$, $p = .004$, IFG; $F(1, 14) = 6.84$, $p = .020$; see figure 3). To further analyse the observed interactions, paired t-tests were performed between each of the conditions for both ROIs. In the IPL ROI there was a significantly higher mean beta value for visible transitive actions (M = 0.21, SD = 0.23) than there was for visible intransitive actions (M = 0.09, SD = 0.19), $t(14) = 3.86$, $p = .002$. In the IFG there was also a significantly higher mean beta value for visible transitive actions (M = 0.18, SD = 0.21) than for visible intransitive actions (M = 0.058, SD = 0.22), $t(14) = 3.25$, $p = .006$.

Conclusion

These results suggest that a human MNS does not necessarily differentiate between transitive and intransitive actions when the interaction is hidden from view. However, a difference in the left hemisphere MNS network (the IPL and IFG) do show differences between transitive and intransitive actions when they are in full view. This suggests that an MNS is unlikely to be involved in intention understanding but is perhaps involved in the attribution of a goal when all perceptual information is available.

Figures

Figure 1: representation of video shown to participants during scanning procedure from top to bottom: object directed grasp in full view; grasp to nothing in full view; object directed grasp with grasp hidden from view; grasp to nothing with final part of the grasp hidden from view. The greyed area is the critical period where brain data was analysed to compare activation across different conditions.

Figure 2: the GcSS probability map included both of the left hemispheric clusters identified in mass univariate analysis.

Figure 3: Bar graphs showing the interaction between visibility and transitivity conditions on mean beta values. (Top) Left IFG (bottom) Left IPL. Error bars represent 1 SD.

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