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RESEARCH REPORT

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Distinct representation of ipsilateral hand movements in sensorimotor areas

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Abstract

There is ample evidence that the contralateral sensorimotor areas play an important role in movement generation, with the primary motor cortex and the primary somatosensory cortex showing a detailed spatial organization of the representation of contralateral body parts. Interestingly, there are also indications for a role of the motor cortex in controlling the ipsilateral side of the body. However, the precise function of ipsilateral sensorimotor cortex in unilateral movement control is still unclear. Here, we show hand movement representation in the ipsilateral sensorimotor hand area, in which hand gestures can be distinguished from each other and from contralateral hand gestures. High-field functional magnetic resonance imaging (fMRI) data acquired during the execution of six left- and six right-hand gestures by healthy volunteers showed ipsilateral activation mainly in the anterior section of precentral gyrus and the posterior section of the postcentral gyrus. Despite the lower activation in ipsilateral areas closer to the central sulcus, activity patterns for the 12 hand gestures could be mutually distinguished in these areas. The existence of a unique representation of ipsilateral hand movements in the human sensorimotor cortex favours the notion of transcallosal integrative processes that support optimal coordination of hand movements.

KEYWORDS

brain-computer interface, functional MRI, motor cortex, somatotopy

1 | INTRODUCTION

In the last decades, the role of the contralateral hemisphere in the generation of limb movement has been vastly studied (Vulliemoz et al., 2005). It has been shown that the majority of the sensorimotor pathways cross the midline towards the contralateral side of the body, and the strongest sensorimotor cortex activation is associated

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List of abbreviations: ANOVA, analysis of variance; BOLD, blood-oxygen-level-dependent signal; C1–C9, subjects 1–9; FA, flip angle; fMRI, functional magnetic resonance imaging; L1, L2, left-hand tasks 1 and 2; M1, primary motor cortex; PD, proton density; R1, R2, right-hand tasks 1 and 2; ROI, region of interest; S1, primary sensory cortex; SMA, supplementary motor area; SVM, support vector machine; TE, echo time; TR, repetition time.

with contralateral movements (Kim et al., 1993). However, there are strong indications that not all human motor fibres decussate in the brainstem (Alawieh et al., 2017) and that both hemispheres are connected by callosal pathways (Aboitiz et al., 1992), suggesting a role of the ipsilateral sensorimotor cortex in movement control, both in non-human (Donchin et al., 1998; Kermadi et al., 1998, 2000; Soteropoulos et al., 2011) and in humans primates (Debaere et al., 2001; Diedrichsen et al., 2013). Indeed, the corpus callosum and several cortical areas, including the premotor cortex, primary motor cortex (M1) and supplementary motor area (SMA), are thought to be involved in coordinating *bimanual* hand movements (Debaere et al., 2001; Diedrichsen et al., 2013; Eliassen et al., 2000). Additionally, the ipsilateral sensorimotor areas seem to play a role in *unimanual* movement control. Evidence for such function comes, among others, from transcranial magnetic stimulation studies (Kobayashi et al., 2003) and from studies showing task-related modulation of sensorimotor activity during movements of the ipsilateral hand (Buetefisch et al., 2014; Seidler et al., 2004; Verstynen, 2004). Another recent study found that in ipsilateral M1, blood-oxygen-level-dependent (BOLD) activity increases when the task required more precise motor movements (Barany et al., 2020). Furthermore, similar to the contralateral homunculus representation, the sensorimotor cortex contains a detailed and organized spatial representation of movements of different *ipsilateral* body parts (Downey et al., 2020; Fujiwara et al., 2017; Hotson et al., 2014; Scherer et al., 2009). However, although ipsilateral representation has been found even for individual fingers (Diedrichsen et al., 2013), it is also known that, in general, activation patterns elicited from complex hand movements, consisting of simultaneous flexion and extension of multiple fingers, are not simple a linear combination of these single-digit patterns (Hamed et al., 2007). We therefore studied ipsilateral activation patterns for complex, multidigit hand movements, and the role of the sensorimotor areas in ipsilateral hand movement control, by directly investigating whether complex unilateral movements of the left and right hand could be distinguished from each other within one hemisphere.

We investigated the representation of complex hand gestures with high-field (7 tesla) functional magnetic resonance imaging (fMRI). Nine healthy, able-bodied volunteers performed six unimanual hand gestures associated with the characters ‘8’, ‘F’, ‘L’, ‘S’, ‘W’ and ‘Y’ of the American Manual Alphabet, with their right and left hand (in separate runs). As in our previous work (Bruurmijn et al., 2017), we divided the sensorimotor cortex into four regions of interest (ROIs: M1, S1, pre-M1 and post-S1) to study the hand gesture representations in detail, where M1 represented the posterior part of the precentral gyrus (primary motor cortex), pre-M1 the anterior part of the precentral gyrus, S1 the anterior part of the postcentral gyrus (primary somatosensory cortex) and post-S1 the posterior part of the postcentral gyrus.

2 | METHODS

2.1 | Subjects

For the current study, we re-analysed data recorded for an earlier study (Bruurmijn et al., 2017). Nine healthy, able-bodied control subjects (mean age 44 ± 21 years, four females, all right handed as confirmed by the Edinburgh Handedness Inventory; Oldfield, 1971) performed a hand gesture task, although functional brain images were acquired using 7-Tesla MRI. All subjects gave written informed consent to participate in this study, which was approved by the Medical Research Ethics committee Utrecht, according to the Declaration of Helsinki (World Medical Association, 2013).

2.2 | Gesture task

In a single 7-T fMRI scan session, subjects performed a unimanual hand gesture task. Prior to scanning, subjects were familiarized with the hand gestures, which were associated with the characters ‘8’, ‘F’, ‘L’, ‘S’, ‘W’ and ‘Y’ of the American Manual Alphabet. In the week before scanning, subjects practiced at home for 15 min/day in making the gestures with each hand.

One task run consisted of 10 trials per gesture. During the task, one of the six characters was presented pseudorandomly on the screen every 15.6 s for subjects C1 and C2, and every 16 s for the other subjects. Subjects made the gesture corresponding to the character shown and held the gesture for 6 s before relaxing. Each subject performed four task runs: two runs with the right hand (R1 and R2) and two runs with the left hand (L1 and L2). Before each run, the subject was instructed which hand to use. This yielded a total of 20 trials per gesture for each hand.

2.3 | Data acquisition

MRI data were recorded using a Philips Achieva 7-T MRI system with a 32-channel head coil. Anatomical T1- and PD-weighted images were acquired first (TR/TE = 6/1.4 ms, FA = 8°, voxel size = 1 × 1 × 1 mm^3). For scans during the Hand Gesture Task, an EPI sequence was used (TR/TE = 1,300/27 ms for subjects C1 and C2, TR/TE = 1,600/27 ms for all other subjects, FA = 70°, acquisition matrix size = 104 × 129, 26 slices, no gap, voxel size = 1.6 × 1.6 × 1.6 mm^3).

2.4 | Task preprocessing

Functional scans from the hand gesture task were preprocessed using SPM12 (http://www.fil.ion.ucl.ac.uk/spm/). Scans were aligned and coregistered with the anatomical T1. For each subject, a beta-map and a t-map were calculated per run (L1, L2, R1 and R2) by fitting a general linear model (GLM), using the contrast 'movement versus rest', without making a distinction between the different gestures. All statistical maps were calculated in subject space.

2.5 | Regions of interest

M1 and S1 are the primary ROI, obtained in subject space using the Destrieux Atlas (Destrieux et al., 2010) and Desikan–Killiany Atlases (Desikan et al., 2006). However, to also assess higher level motor cortex as well, the areas anterior to M1 (pre-M1, part of the premotor area) and posterior to S1 (post-S1, roughly corresponding with Brodmann area 2) were also included as ROIs. These four ROIs are therefore defined as follows, in which we have used the names of the regions in DKA and DA, and where '+' denotes the voxel-wise union and '^' denotes the intersection of two regions. M1 consists of the primary motor cortex and the posterior part of the precentral gyrus ($PrecentralGyrus_{DA} + [CentralSulcus_{DA} \wedge PrecentralGyrus_{DKA}]$). S1 consists of the primary sensory cortex, the anterior part of the postcentral gyrus ($PostcentralGyrus_{DA} + [CentralSulcus_{DA} \wedge PostcentralGyrus_{DKA}]$). Pre-M1 covers the anterior part of the precentral gyrus ($PrecentralSulcus_{DA}$) and post-S1 the posterior part of the postcentral gyrus ($PostcentralSulcus_{DA}$).

2.6 | Decoding 12 gestures from one hemisphere

To assess the discriminability of hand gestures in the sensorimotor cortex of both the contralateral and ipsilateral hemisphere, a decoding approach was used similar to that of previous work from our group (Bleichner et al., 2013; Bruurmijn et al., 2017). This analysis consists of several steps: voxel selection, classifier training and classifier testing, applied on volumetric data in subject space and on the right and left hemisphere separately.

Data were split in training and test sets. Per subject, two left and two right hand task data sets were acquired in four separate fMRI runs (L1, L2, R1 and R2), whereas the classifier was trained on contralateral and ipsilateral movements simultaneously. This may have an effect on the overall activation patterns for both hands. This effect was minimized by varying the order of the tasks across subjects. Moreover, the training and test sets were strictly separated. This was done by selecting one run per hand as training set, resulting in four training sets consisting of one left and one right hand run (L1&R1, L1&R2, L2&R1 and L2&R2). In each case, the remaining runs constituted the test set for validation. For each choice of the training set, the voxel selection was done separately, to prevent any bias that would be introduced by the test set.

Per training set, a combined t-map was compiled by taking, from the L and R 'movement versus rest' t-maps described above, for each voxel the highest t value from either the left- or right-hand t-map. Subsequently, from each of the four principal ROIs, the 250 voxels with the highest absolute t values were selected from the training set. The BOLD signal in these voxels was detrended and transformed into z-scores for each separate run. For each trial, the BOLD amplitude was averaged around its peak, which occurs roughly between 6 and 8 s, by taking the mean of Scans 5, 6 and 7 for subjects C1 and C2 and Scans 4, 5 and 6 for other subjects (due to their difference in fMRI repetition time). This resulted in a 'feature vector' of 250 features per trial.

For the classifier, a support vector machine (SVM) was used, using a linear kernel and parameter C set to a fixed value of 1. Because an SVM is a binary classifier, multiple SVMs needed to be combined. For each pair of gestures, a separate SVM was trained to distinguish between those two gestures (e.g., to distinguish a 'right hand 8' from a 'left hand F'). This results in 66 binary classifiers. For classifying a single trial, each of the binary SVMs then casts a vote for the 'winning' gesture. The gesture with the most votes from all binary classifiers was chosen as the classifier result ('prediction'). All 66 binary SVMs had an equal weight in the voting process.

Training a classifier on the training set and applying it on the test set result in a 'predicted' gesture for each trial in the test set. The classification accuracy was calculated as the percentage of correctly classified gestures. Because four training sets were created per subject (together with four associated test sets), the classification procedure was repeated for each training/test set combination, resulting in four independent classification scores. These four classification scores were averaged resulting in one classification score per ROI per subject.

To obtain the chance level (and associated confidence interval) for the classification, the classifier was also trained on data with random permutations (Combrisson & Jerbi, 2015) of the gesture label for each subject, hemisphere and ROI. This procedure was repeated 500 times to obtain a distribution of the chance level. Averaging over these iterations yielded a chance level of 8.3% ± 0.06% (which is in agreement with the theoretical chance level for 12 classes). If the confidence interval of the classification scores does not contain the chance level of 8.3%, the classification is considered to be better than chance.

As a post hoc test, the effects of hemisphere and ROI were evaluated using a two-way repeated measure analysis of variance (ANOVA) with ROI and hemisphere as within-subject factors, at a significance level of .05.

Confusion matrices give insight not only in the accuracy of classification but also in the nature of errors. The confusion matrices were constructed as a cross-table, in which each cell indicates in percentages how many trials from a particular gesture ('actual gesture') were classified as another gesture ('predicted as …'). Separate confusion matrices were assembled per subject, hemisphere and ROI. Per hemisphere and ROI, one confusion matrix was calculated by averaging across subjects.

Each confusion matrix can be viewed as composed of four quadrants (submatrices). The upper left and bottom right quadrant reflect the 'within-hand' confusion: Values on the diagonal denote correct classifications, and off-diagonal values reflect confusions with a different gesture from the same hand (e.g., between W_L and F_L). The top right and bottom left quadrant reflect the 'between-hands' confusion: The values on the diagonal of these submatrices indicate trials that were classified as the correct gesture type, but with the wrong hand (e.g., between W_L and W_R).

For each subject, confusion matrices for all ROIs were averaged. A mean within-hand confusion score was calculated by averaging all the off-diagonal values in the top left and bottom right quadrant. A mean between-hands confusion score was calculated by averaging all the diagonal values of the top right and bottom left quadrant. A paired-samples t test was then conducted to compare the mean scores between within-hand and between-hand errors.

3 | RESULTS

For both the left and the right hemisphere, activation maps associated with *contralateral* hand gestures showed a hotspot in both the pre- and the post-central areas, mainly inside the central sulcus (Figure 1). During *ipsilateral* hand movements, however, activation was generally lower in regions around the central sulcus (right M1 and left and right S1), but not in regions further away from the central sulcus, both in anterior and posterior direction. This difference in mean activation was tested by paired-samples t tests on average beta value per ROI for ipsilateral minus contralateral activity with Bonferroni-corrected alpha of $.05/8 = .006$, as there were 4 ROIs in each hemisphere: left pre-M1: $t_8 = -2.40$, $P = .04$; left M1: $t_8 = -3.38$, $P = .01$; left S1: $t_8 = -6.15$, $P < .001$; left post-S1: $t_8 = -2.11$, $P = .07$; right pre-M1:

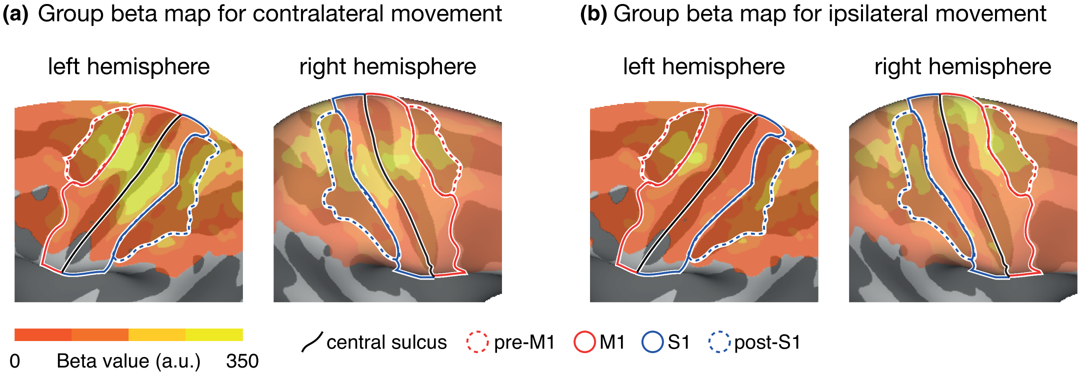
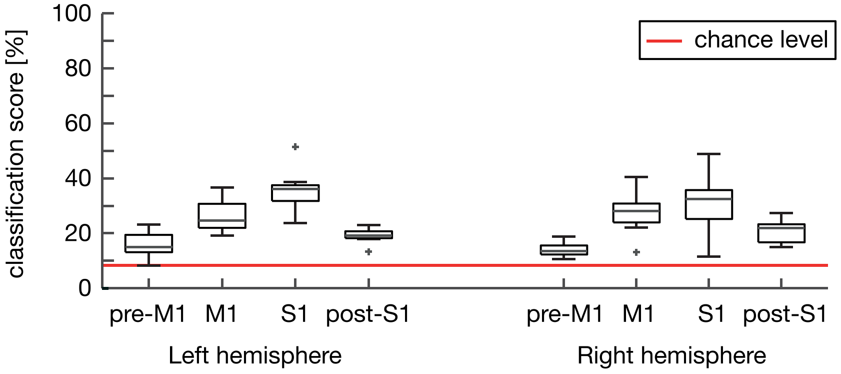


FIGURE 1 Group activation patterns for contralateral and ipsilateral hand gestures. Colours indicate beta values averaged over subjects and are displayed on the average FreeSurfer brain, in which light and dark grey reflect gyri and sulci, respectively. The central sulcus and regions of interest (ROIs) for classification are delineated. (a) Beta maps for contralateral movement (right hand activity plotted on the left hemisphere and left hand activity plotted on the right hemisphere). (b) Beta maps for movement of the ipsilateral hand. Ipsilateral activity is mostly located anterior and posterior to the central sulcus, whereas activity inside the sulcus is low

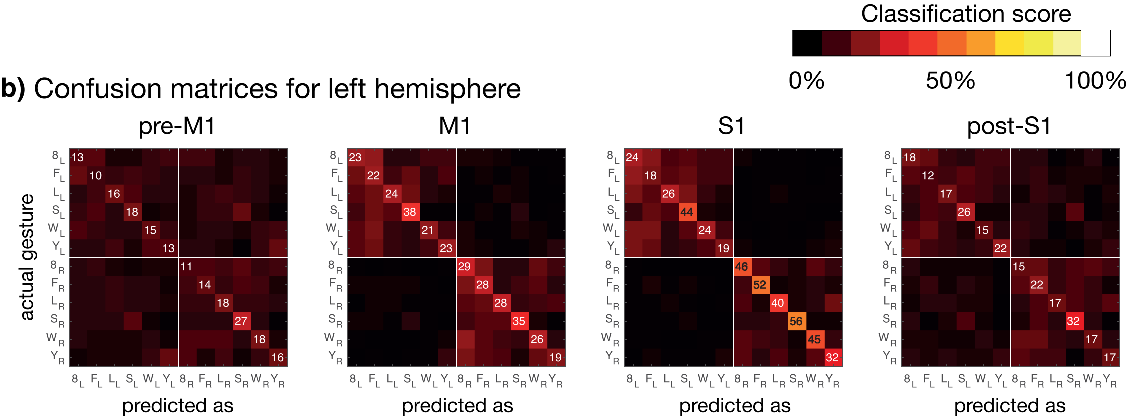
$t_8 = -2.41$, $P = .04$; right M1: $t_8 = -4.02$, $P = .004$; right S1: $t_8 = -4.77$, $P = .001$; right post-S1: $t_8 = -4.24$, $P = .003$.

For ROIs M1, S1 and post-S1 of both the left and the right hemisphere, the classification scores for decoding 12 gestures were significantly higher than chance level (Figure 2a, group-mean scores ranging from 14.0% to 35.4%, chance level 8.33%), indicating that it is possible to discriminate between the representation of hand gestures for the left and right hand from the *same* subareas of the sensorimotor cortex. Two-way repeated measures ANOVA revealed that there was a significant main effect of ROI ($F_{3,6} = 10.8$, $P = .008$), with M1 and S1 demonstrating the highest classification scores. There was no significant main effect of hemisphere ($F_{3,6} = 1.06$, $P = .43$) and no significant interaction effect of ROI and hemisphere on the classification score ($F_{3,6} = 3.77$, $P = .08$). This indicates that, although sample sizes are

(a) Classification scores



(b) Confusion matrices for left hemisphere



(c) Confusion matrices for right hemisphere

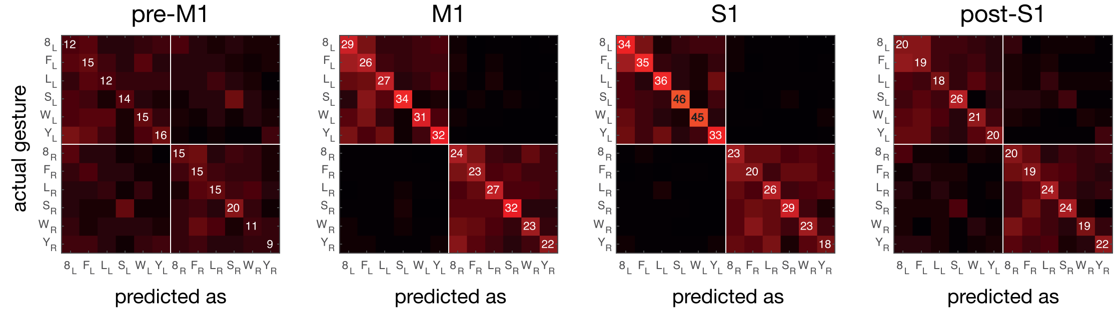


FIGURE 2 (a) Classification scores for all 12 classes (contralateral and ipsilateral hand movements), per region of interest (ROI). The red line indicates chance level for 12 classes (8.3%, as simulated by the random permutation test). (b and c) confusion matrices for decoding ipsilateral and contralateral gestures from four ROIs in the left (b) and right (c) hemisphere, averaged across subjects. The rows of the matrix reflect how the trials for each gesture were classified (in percentage). The diagonal thus shows the percentage of correctly classified trials for each gesture. Subscripts indicate gestures of the left ('L') and the right ('R') hand small, there is currently no evidence that there is a difference between hemispheres.

Confusion matrices (Figure 2b,c) reveal that gestures from the contralateral hand generally demonstrated higher classification scores than gestures from the ipsilateral hand. A paired-samples *t* test showed a significant difference between within-hand and between-hands confusion scores ($t_8 = 2.63$, $P = .03$), indicating that confusion is more likely to happen between different gestures of the same hand (e.g., W_L with F_L) than between the same gestures of the left and right hand (e.g., W_L with W_R). This result may be explained by the difference in amplitude between ipsilateral and contralateral activations mentioned above. Because the tasks involved only moving one hand at a time, it is possible that the activity that was found for the ipsilateral hand is just a 'mirrored' version of the representation on the contralateral hemisphere, with only a lower amplitude, which in itself would drive classification (Scherer et al., 2009). However, if this were true, the BOLD patterns for a gesture made with the ipsilateral and contralateral hand would be highly similar. To investigate this, we plotted the average beta patterns per gesture (see Figure 3 for the left hemisphere of one representative subject C4). These patterns show that the same gesture generates different spatial patterns for the contralateral and ipsilateral hand, supporting the notion of a distinct and independent representation of the ipsilateral hand gestures within the sensorimotor cortex.

A potential bias for the presence of ipsilateral activity could be uninstructed movement of the contralateral hand during ipsilateral trials. However, finger flexion measurements using a data glove worn during the tasks confirmed that gestures were executed unimanually (Figure 4).

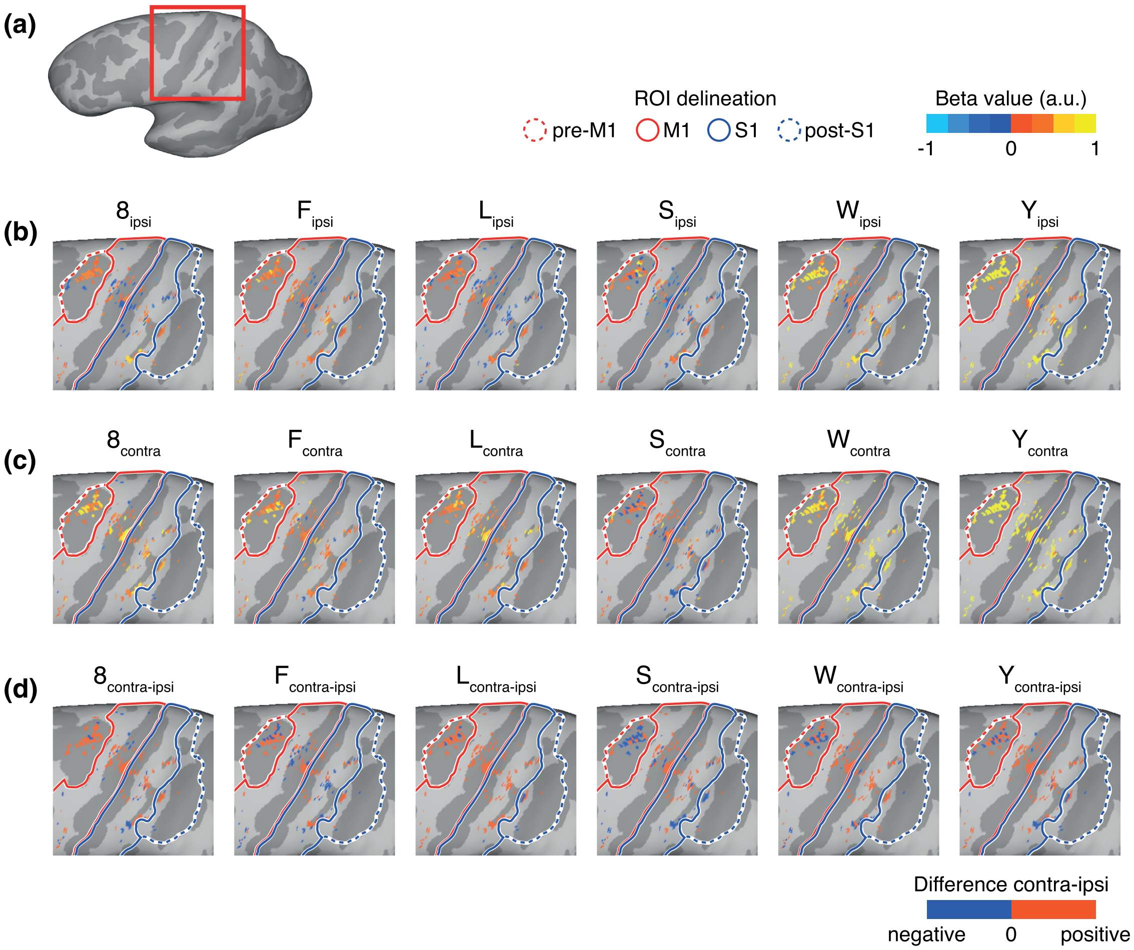


FIGURE 3 Activity in voxels selected for classification, for ipsilateral and contralateral gestures on the left hemisphere for one subject (C4). (a) Inflated brain surface from FreeSurfer, where light grey indicates gyri, and dark indicates sulci. The red box indicates the zoom window in the lower panels. (b) Beta pattern for each ipsilateral gesture (left hand movement). The regions of interest (ROIs) used for classification are delineated. (c) Beta values for each contralateral gesture (right hand movement). (d) Differential beta pattern per gesture (contra–ipsi)

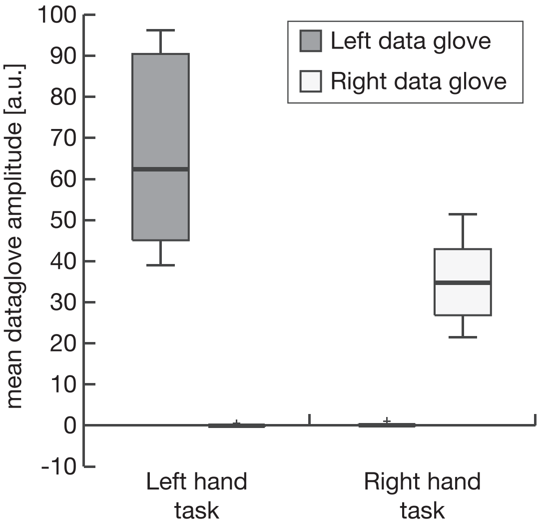


FIGURE 4 Data glove amplitudes (averaged over all trials and subjects in arbitrary units) for both hands during the left hand task and the right hand task. The amplitudes of the hand that needs to be kept still are small with respect to the amplitudes of the hands with which the tasks were executed

4 | DISCUSSION

Our present results reveal the existence of a detailed representation of ipsilateral hand gestures in the human sensorimotor cortex that can be distinguished from the representation of contralateral hand movements in this area, indicating that (subpopulations of) neurons within the human sensorimotor cortex are distinctly associated with ipsilateral hand movement. Importantly, the difference in representation is not merely the result of different levels of activation between ipsilateral and contralateral hand gestures but is associated with spatially distinct activation patterns, especially in primary somatosensory and motor cortex.

Observations about the activity of ipsilateral hand movement activity are in line with earlier reports (Buetefisch et al., 2014; Diedrichsen et al., 2013; Hanakawa et al., 2005; Verstynen, 2004), as well as with single-cell studies in non-human primates that demonstrated that the sensorimotor cortex contains subsets of neurons that activate specifically during ipsilateral movement (Donchin et al., 1998; Kermadi et al., 1998; Tanji et al., 1988). The current study extends these findings to humans and shows ipsilateral hand movement representation at the level of mm-sized neuronal ensembles, which may indicate higher concentrations of ipsilateral neurons responding in specific foci. The ROIs M1 and S1 demonstrated the highest classification scores, despite relatively low activity levels. This finding shows that to the ability to decode detailed movements from the cortex does not require high activity in the target regions and agrees with previous findings from Diedrichsen et al. (2013).

We propose that the observation that both hands activate differentiable patterns in the same hemisphere reflects the presence of at least a subset of cross-callosal projections that conveys information about movements of one hand from the contralateral to the ipsilateral sensorimotor area and that exhibits a convergence on specific foci within the ipsilateral hand area that are distinct from foci in the same region activated during contralateral hand movements. These findings indicate that at least part of the cross-callosal projections is concentrated in foci that are at a spatial scale that is detectable with fMRI (1.5–2 mm). If ipsi- and contra-lateral hand movement representations are in reality more detailed than this range (smaller ensemble sizes than 1.5–2 mm), the current resolution may have led to averaging across adjacent ensembles, and classification may improve with increasing fMRI resolution.

Transcallosal projections have been attributed both inhibitory and excitatory roles (Van der Knaap & Van der Ham, 2011). The specificity of ipsilateral patterns for different gestures shown in the current study, only visible with a classification algorithm, cannot be explained by the concept of cross-callosal inhibition of the hand region. Given the reports on inhibitory function (Beaulé et al., 2012); however, we argue that both excitatory and inhibitory projections exist, but that the former bears functional relevance in terms of informing one hemisphere of the movements of the ipsilateral hand, thereby integrating information from both hemispheres and contributing to optimal coordination of hand movements with respect to the rest of the body. This mechanism may also explain why unilateral stroke often affects contralateral and ipsilateral movements (Colebatch & Gandevia, 1989; Sainburg & Duff, 2006).

According to recent work, examining active finger presses and passive finger stimulation of one hand in both hemispheres, ipsilateral representations are mostly associated with planning and initiation of motor acts and less with feedback control, because ipsilateral finger-specific representation was most clear in premotor and parietal regions (Berlot et al., 2019). However, despite the lower activity in the M1 and S1 ROIs, we found the highest decoding accuracy in these areas, indicating that ipsilateral and contralateral representations are especially distinct in these primary sensorimotor areas, which would be in line with a role for ipsilateral areas during the actual execution phase of the hand gestures. Different levels of complexity of the movements performed in this study and the work of Berlot et al. (2019) may be associated with this discrepancy. Indeed, increasing movement complexity is known to be associated with increased activation of ipsilateral M1 (Buetefisch et al., 2014; Seidler et al., 2004; Verstynen, 2004), and transcallosal integration and ipsilateral movement control have been suggested to be especially relevant or pronounced for more complex movements (Van der Knaap & Van der Ham, 2011).

However, there are several shortcomings to the current study. First, performance of the SVM could have been made worse by requesting subjects to only move a single hand during each task run. For recording all hands, the task run was repeated to obtain two runs for the right hand and two runs for the left hand. When decoding both hands from the same hemisphere, runs for different hands needed to be combined. The recalibration at the start of each run of fMRI scans may have made the BOLD estimates within runs slightly more similar, which could bias the classifier towards correct identification of at least the hand. Therefore, the training set did not include trials from within the same run as the test set. Acquisition of all data in a single run would have allowed a leave one out training scheme, thereby increasing the size of the training set. A single run is however impractical due to excessive challenging of the subject and scanner hardware.

A second limitation lies in the possibility of ipsilateral decoding to be driven by variations in difficulty between the movements. Whereas the gestures 8 and F, and W and Y are similar in terms of complexity of movement execution (8 and F are each other's mirrored version in terms of flexion and extension of the fingers, and so are W and Y), the gesture S amounts to making a fist and can be regarded as less demanding. However, the confusion matrices of the classification scores for each gesture, demonstrated that the classification results were not exclusively driven by this difference in complexity, because the diagonal pattern (indicating correct classification) was also present for the other gestures.

Lastly, the choice of parameters for training the SVM may have been suboptimal. In this study, classifiers were trained and tested on each subject individually. This was done because activity distributions vary between subjects, and it is crucial to capture minute variations for discriminating between complex gestures. The training of the classifier is affected by a priori choices of hyperparameters or a training kernels, and ideally, these choices are optimized for every subject. This however requires substantial amounts of data for independently tuning and testing the classifier, which were not available due to the limitations of an fMRI design. This process would become more accessible with using other recording techniques, such as intracranial recordings, which have a superior temporal resolution.

Taken together, we here provide support for the existence of patches of sensorimotor cortex that are uniquely associated with the execution of complex ipsilateral hand gestures and propose transcallosal interhemispheric information transfer as a mechanism for the generation of such activity. Our findings shed light on the importance of ipsilateral activity beyond the coordination of bimanual movements.

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CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHOR CONTRIBUTIONS

LCMB, NFR and MJV conceived and planned the experiments. LCMB carried out the experiments, collected and analysed the data and presented the results, under supervision of NFR and MJV. LCMB, MR, MPB, NFR and MJV wrote the manuscript and provided critical feedback.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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