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Grasp-specific high-frequency broadband mirror neuron activity during reach-and-grasp movements in humans

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Broadly congruent mirror neurons, responding to any grasp movement, and strictly congruent mirror neurons, responding only to specific grasp movements, have been reported in single-cell studies with primates. Delineating grasp properties in humans is essential to understand the human mirror neuron system with implications for behavior and social cognition. We analyzed electrocorticography data from a natural reach-and-grasp movement observation and delayed imitation task with 3 different natural grasp types of everyday objects. We focused on the classification of grasp types from high-frequency broadband mirror activation patterns found in classic mirror system areas, including sensorimotor, supplementary motor, inferior frontal, and parietal cortices. Classification of grasp types was successful during movement observation and execution intervals but not during movement retention. Our grasp type classification from combined and single mirror electrodes provides evidence for grasp-congruent activity in the human mirror neuron system potentially arising from strictly congruent mirror neurons.

Key words: ECoG; mirror neurons; decoding; motor.

Introduction

Mirror neurons in monkeys exhibit a variety of specific firing properties, especially regarding action goals (Fogassi et al. 2005) and movement parameters (Caggiano et al. 2015). For example, early studies reported that some mirror neurons preferably respond to object grasping movements and that others respond to object placing or object manipulation movements (Gallese et al. 1996). Gallese et al. (1996) also classified mirror neurons according to the visuo-motor congruency between observed and executed actions: Mirror neurons that respond to a broader action class (e.g. object grasping) have been denoted as broadly congruent, whereas mirror neurons whose firing patterns additionally depend on how an action is effectively executed (e.g. a specific grip type) have been denoted as strictly congruent. Different groups of broadly congruent mirror neurons could still be specific in terms of the executed action, while they would respond to the observation of various grip or hand action types (Gallese et al. 1996). It is unclear whether such mirror neurons with high specificity exist in humans. Human mirror system research largely focuses on neuronal population-level responses, as single-cell studies are invasive, and therefore, only possible as a rare byproduct of therapeutic treatment (Engel et al. 2005). We are aware of 1 study investigating single-neuron responses during mirrored hand grasping who reported mirror neurons in medial frontal and medial temporal cortices (Mukamel et al. 2010). However, specific single-neuron activity could influence the population-level activity which is accessible with direct cortical recordings in humans.

Repetition suppression using fMRI has been suggested as a method to uncover stimulus-specific neuronal responses

(Grill-Spector and Malach 2001; Dinstein et al. 2007; Barron et al. 2016), though single-cell monkey data do not support the notion of mirror neuron adaptation (Caggiano et al. 2013). Multivariate pattern analysis (MVPA) is an alternative approach that is widely applied in fMRI (Haynes and Rees 2006; Dinstein et al. 2008; Hollmann et al. 2011; Reichert et al. 2014) and electrophysiological measures (Holdgraf et al. 2017), which has been used to investigate the common neural coding of motor actions (Oosterhof et al. 2010; Quandt et al. 2012; Wissel et al. 2013), although the interpretation of MVPA results can be challenging (Oosterhof et al. 2013; Holdgraf et al. 2017).

Alternatively, decoding algorithms can uncover the presence of movement-specific information in neuronal population signals. ECoG studies have shown a strong relationship between the localized cortical activity and decoding movement parameters (Crone et al. 1998; Dürschmid et al. 2014), including movement trajectory (Schalk et al. 2007; Pistohl et al. 2008) and movement kinematics (Flint et al. 2017), decoding the digit used to execute a finger movement (Shenoy et al. 2007; Wissel et al. 2013), and decoding natural grasp types (Pistohl et al. 2012). Together, these studies indicate that decoding movement parameters from high-frequency broadband activity (HFA) is a viable approach to demonstrate the presence of information about these parameters in the recorded brain activity. Note that these studies used HFA during movement execution only and did not target mirror activity.

Perry et al. (2018) investigated the neuronal activation changes with ECoG recordings using a reach-and-grasp observation and delayed imitation task, where patients were asked to first watch a video of someone grasping an object with a specific grasp type,

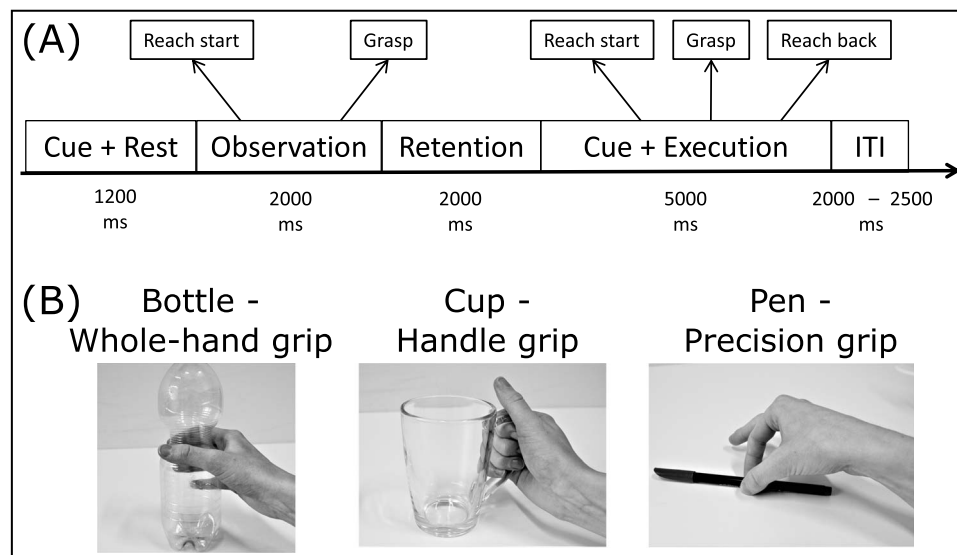


Fig. 1. A) Trial overview: Each trial starts with an auditory cue, followed by a video showing a reach-and-grasp movement during which subjects have to remember an object and grasp types which they imitate after a retention period. B) Object-specific grasp types.

to remember the object and grasp type, and then imitate the grasp with an object in front of them. Based on data combined over grasp types, Perry et al. (2018) reported mirror activity in classic mirror system areas, including somatomotor cortices, parietal areas, and inferior frontal gyrus. In addition, they defined mnemonic mirror activity, a previously unreported phenomenon that describes significant modulations of activity during movement observation and for delayed imitation. The phenomenon of mnemonic mirror HFA was recently confirmed by Dreyer and Rieger (2021) in MEG recordings. The current study is a reanalysis of 4 subjects from Perry et al. (2018) for whom movement tracking data with high temporal resolution were available, with a focus on the different grasp types (see Fig. 1B for grasp types) performed in the study. Our goal is to assess for evidence of strictly grasp congruent human mirror activity by decoding the grasp types using ECoG HFA from combinations of multiple mirror electrodes. Additionally, we analyzed single electrodes to gain insight into probable cortical areas where grasp congruent mirror activity is present. Our results support the notion of strictly grasp congruent (Gallese et al. 1996) mirror activity in several cortical areas, among others in supplementary motor area around the central sulcus, and in the vicinity of the intraparietal sulcus.

Methods

Subjects

We recorded 4 patients with intractable epilepsy who underwent surgical treatment in 3 different clinical sites. All patients had subdural ECoG grids implanted for seizures' focus localization, including coverage of putative mirror neuron regions. Data from all subjects have been published in Perry et al. (2018) with a different analysis approach and research question. Table 1 depicts sex, age, handedness as well as task and electrode information for these patients.

The neurosurgical treatment sites were University of California Irvine Medical Center (S01 and S02), Stanford University Hospital (S03), and University of California San Francisco Medical Center (S04). Note that electrode placement decisions were solely made by the respective medical teams on medical considerations. All

patients gave written informed consent, and the study protocol was approved by the Institutional Reviews Boards and Committees on Human Research of the respective sites and by the University of California, Berkeley.

Experimental setup

The experiment was conducted as described in detail in Perry et al. (2018). Here, we provide a short summary: The participants were comfortably seated in their hospital beds with a laptop and 3 objects (a bottle, a cup, and a pen) placed on a table in front of them. The object locations remained the same throughout the experiment. An overview of the trials can be seen in Fig. 1A.

Each trial started with a short (0.2 s) auditory cue followed by a background image being shown for 1.2 s. Then, a video of a person reaching toward and grasping 1 of the 3 objects with the natural object-specific grip type (bottle—whole-hand grip, cup—handle grip, and pen—precision grip) was presented. The videos showed a frontal perspective with visible arm and upper body as if the actor in the videos would sit opposite of the participants. The participants were instructed to observe the movement and remember the object and grip type which they had to repeat later. The videos were followed by a 2-s retention period which ended with another auditory cue. This signaled the participants to perform a reach-to-grasp movement to grasp the remembered object with the respective grip type, hold the grasp for a short time, and then move their hand back to the rest position on their lap. The time until the next trial was randomly set between 7 s and 7.5 s, allowing the participants to perform the movements at their own pace, although the targeted movement time was <5 s. The hand shown in the video as well as that used for the movement was contra-lateral to the location of the main ECoG grid (see Table 1 for grid hemisphere). Each block consisted of 40 trials, and 2 blocks were recorded for each subject.

The paradigm was presented using E-Prime2 (Psychology Software Tools, Sharpsburg, PA, United States) and the experimental timing was verified via a photodiode attached to the laptop screen which was directly connected to the ECoG-amplifier.

Table 1. Subject overview, including age, handedness, electrode hemisphere with respective task response hand, and number of valid reach-to-grasp trials.

Subject (sex)	Age	Handedness	Task response hand	Grid hemisphere	Valid trials
S01 (f)	35	Right	Left	Right	52
S02 (f)	48	Right	Right	Left	61
S03 (f)	23	Right	Left	Right	69
S04 (m)	36	Right	Right	Left	76

Motion tracking

We employed motion tracking systems during the ECoG recordings since the reach-to-grasp task involved self-paced movements with variability in movement execution. Motion tracking capabilities differed between subjects and recordings sites. The movements of S01 and S04 were tracked via deidentified video recordings, and the movements of S02 and S03 were tracked via inertial measurement units placed along the participants' arm. These tracking approaches allowed us to identify correct task execution, via verifying the grasp type, and to extract the movement timing information. Incorrect trials with wrongly executed movements as well as trials with any tracked movement during the observation and retention intervals were discarded.

ECoG recording and electrode locations

For S01 and S02, ECoG signals were recorded using a Nihon Kohden recording system (Tokyo, Japan) with a 128-channel JE-120A amplifier and sampled 5,000 Hz. For S03 and S04, ECoG signals were recorded using a Tucker-Davis Technologies recording system (Alachua, FL, United States) with a 256-channel amplifier and Z-series digital signal processing card and were sampled at 1525.88 Hz (S03) and 3051.76 Hz (S04), respectively.

The hemisphere covered with electrodes for each subject is listed in Table 1. Neighboring electrodes were 1 cm apart for all grids and strips. To localize the single electrodes on the cortical surface, preoperative structural MRI and postimplantation computed tomography (CT) scans were used. Affine point-based registration with BioImage Suite was used to transform the CT coordinates to MRI space for electrode localization. Anatomical accuracy of the final coregistrations was verified on an individual subject basis. Transformations to the Montreal Neurological Institute (MNI) brain were calculated. In addition, FieldTrip (Oostenveld et al. 2011) was used for automatic anatomic labeling in MNI space (Stolk et al. 2018). MNI coordinates, functional labels, and anatomical labels according to the AAL atlas (Rolls et al. 2020) can be found in the supplementary materials. Only cortical surface electrodes, no depths electrodes, were used for further analysis.

ECoG preprocessing and HFA extraction

All ECoG electrode time series were visually inspected by a neurologist. Intervals with epileptic activity were marked and removed from the analysis. In addition, noisy channels (e.g. with loose contacts) were removed. ECoG signals were downsampled to 1,000 Hz and then band-pass-filtered between 0.1 Hz and 200 Hz. Powerline noise was removed using notch-filters at 60 Hz, 120 Hz, and 180 Hz. All filters were Butterworth filters applied with MATLABs "filtfilt" function. The filtered data was rereferenced to a common-average reference. The above preprocessing approach was applied to each experimental block individually before combining blocks. Further analysis was done using custom Python

scripts (Pedregosa et al. 2011; Ramachandran and Varoquaux 2011; Gramfort et al. 2013).

ECoG data were then cut into 2-s epochs according to the experimental triggers for observation and retention as well as into 3-s epochs starting from the movement start using triggers acquired via motion tracking.

To assess HFA power, epoched data were band-pass-filtered in 10-Hz wide bands from 65 Hz up to 195 Hz and were Hilbert-transformed to obtain the envelope of the band-limited high gamma signal. The absolute values were then averaged to constitute 1 high gamma envelope signal over time. The average high gamma envelope from a baseline period (−0.6 s to −0.2 s before video onset) was subtracted from each sample of the respective epoched high gamma envelope.

The epoched high gamma envelope was then averaged over trials for individual conditions (observation, retention, and execution) and subjects and tested for significant differences against baseline power. This was done using running t-tests for every sample over time on the full dataset, independent of grasp type. Channels were considered as significant when they held at least 100-ms consecutive samples below a false discovery rate-controlled significance threshold of 0.05 (Benjamini and Hochberg 1995), an approach similarly employed in prior HFA studies (Perry et al. 2018; Dreyer and Rieger 2021). Significant channels were then used for grasp type classification as described in the next section.

ECoG decoding

Grasp type classification was performed on an individual subject basis with a 1-versus-rest classification scheme. In this scheme, 1-versus-rest classifiers were trained for every grasp type, and the classification result is obtained by taking the maximum of the classifier scores which means the most confident models wins. We classified grasp types separately during the observation, memorization, and execution intervals. We used an L2-regularized logistic regression classifier for all grasp type classifications. Results were crossvalidated with 50 iterations of stratified shuffle splits, each randomly splitting the data in to 80% training and 20% test data.

First, we used electrode combinations for the classification by using all electrodes that showed significant HFA modulations during the respective conditions. That means the number of combined electrodes could be different for classification during movement observation compared to the number of electrodes used for movement execution. Note that this approach does not directly target the mirror neuron system but shows that grasp type classification is possible. For movement execution, successful grasp type classification would replicate prior ECoG decoding studies (e.g. Pistohl et al. (2012)) and would provide evidence that our HFA signals differentiate between grasp types providing a basis for grasp type decoding from mirror signals.

Table 2. Number of electrodes with significant HFA modulations during the respective conditions.

Subject	Tested electrodes	Observation	Retention	Execution
S01	98	13	1	22
S02	95	24	11	50
S03	107	29	13	40
S04	95	18	4	31

In a direct test of grasp-specific mirroring, we included all channels that showed significant HFA changes during both movement observation and execution (mirror electrodes). Note that the conditions were still classified independently, and only the selected input features depended on multiple conditions. Accurate classification from these distributed electrodes would provide evidence for a degree of grasp specificity of the human mirror neuron system.

As a final step, we assessed the classification performance on a single electrode basis using standardized HFA over time for the respective conditions as input features but only for electrodes that showed significant HFA modulations during the movement observation and execution phases.

As we used 3 different grasp types in the experiment, the theoretical chance level was 0.33 for all classification approaches. In addition, we calculated an empirical chance level (Rieger et al. 2008; Combrisson and Jerbi 2015) for each electrode and electrode combination using permutation tests (1,000 repetitions) with randomized class labels to verify significant classification performance. Classification performance was denoted significant when the balanced accuracy was higher than in 95% of the randomized classification runs from the permutation tests.

Results

Behavioral results

Across all subjects, around 19% (62 out of 320 trials) were discarded (see Table 1 for details) due to movement during the observation or retention phases, no movement during the execution phase, or grasping the wrong object during the execution phase. For the remaining valid trials, the average reaction time (time between auditory cue and movement start) was 0.43 s (SD: 0.55 s), and the average time between movement start and grasp closure around the object was 1.68 s (SD: 0.45 s). Reaction and grasp time distributions did not differ for the different grasp types.

Significant HFA band changes

We found significant overlapping HFA electrodes between the 3 conditions over several cortical areas for all subjects. An overview of the number of significant electrodes can be seen in Table 2.

Figure 2 shows a spatial overview of all electrodes of all subjects. Colors represent results of tests for significant HFA modulations during the 3 intervals. Overlapping electrodes in which HFA was significantly changed during both movement observation and execution (mirror electrodes) are colored yellow and electrodes in which HFA was significantly changed during all 3 conditions (mnemonic mirror electrodes) are colored white.

A list of all functional electrodes can be found in the supplementary materials together with their MNI coordinates and AAL locations. We found mirror electrodes in a variety of cortical areas, among others over pre-/postcentral gyrus (S02, S03, and S04), dorsal premotor cortex (S01), superior temporal gyrus (S01

and S04), inferior frontal cortex (S02 and S03), superior and middle parietal gyri in the vicinity of the intraparietal sulcus (S02 and S04), and in supplementary motor area (S02 and S03). These areas are consistent with reports from prior human mirror system research (Buccino et al. 2004; Caspers et al. 2010) and replicate the results of Perry et al. (2018). Although the total number of tested electrodes was similar between subjects, the number of overlapping electrodes differed between the subjects, which can be expected due to the different cortical electrode coverage. We found 2 mirror electrodes for S01 (none of them mnemonic), 21 mirror electrodes for S02 (9 of them mnemonic), 14 mirror electrodes for S03 (9 of them mnemonic), and 11 mirror electrodes for S04 (3 of them mnemonic). These electrodes (white and yellow electrodes in Fig. 2) were used for single-electrode classification to test them for grasp specificity.

Classification results

We applied logistic regression classification on different combinations of electrodes with significant HFA modulations to decode grasp types in the respective conditions. Table 3 provides an overview of classification accuracies for all subjects, conditions, and multielectrode combinations.

Overall, grasp type classification with combinations of electrodes provided significant results in the movement observation and movement execution conditions. We did not find grasp-specific classifications in the movement retention condition. Moreover, S01 showed significant classifications only during the execution condition. A possible reason is that this participant showed minimal mirror activity with only 2 mirror electrodes. Even though the grasp type has to be remembered, the mnemonic mirror HFA modulations do not seem to be strongly specific to the grasp type. For the other conditions, decoding performance was best when using all significantly modulated HFA electrodes per condition. This could be expected, as the combined electrodes were specific to each condition, meaning that they included mirror electrodes and additional electrodes that were only significantly modulated during the tested condition. Using combined mirror electrodes, decoding grasp type from movement observation or execution data was possible in 3 out of 4 subjects. Our results provide evidence for the notion that the distributed HFA mirror activity is grasp type specific carrying information about grasp type during the observation and the execution condition.

Finally, classification performance of single channels could provide even more spatially specific information about the cortical areas contributing to grasp-specific mirror activity. Overall, a small number of single mirror (or mnemonic mirror) electrodes (14 out of 48; 29%) gave significant classification results during movement observation or execution: no electrodes for S01, 7 electrodes (2 mnemonic) for S02, 1 electrode (1 mnemonic) for S03, and 6 electrodes (2 mnemonic) for S04. A subgroup of the significant classification electrodes can be seen in Fig. 3.

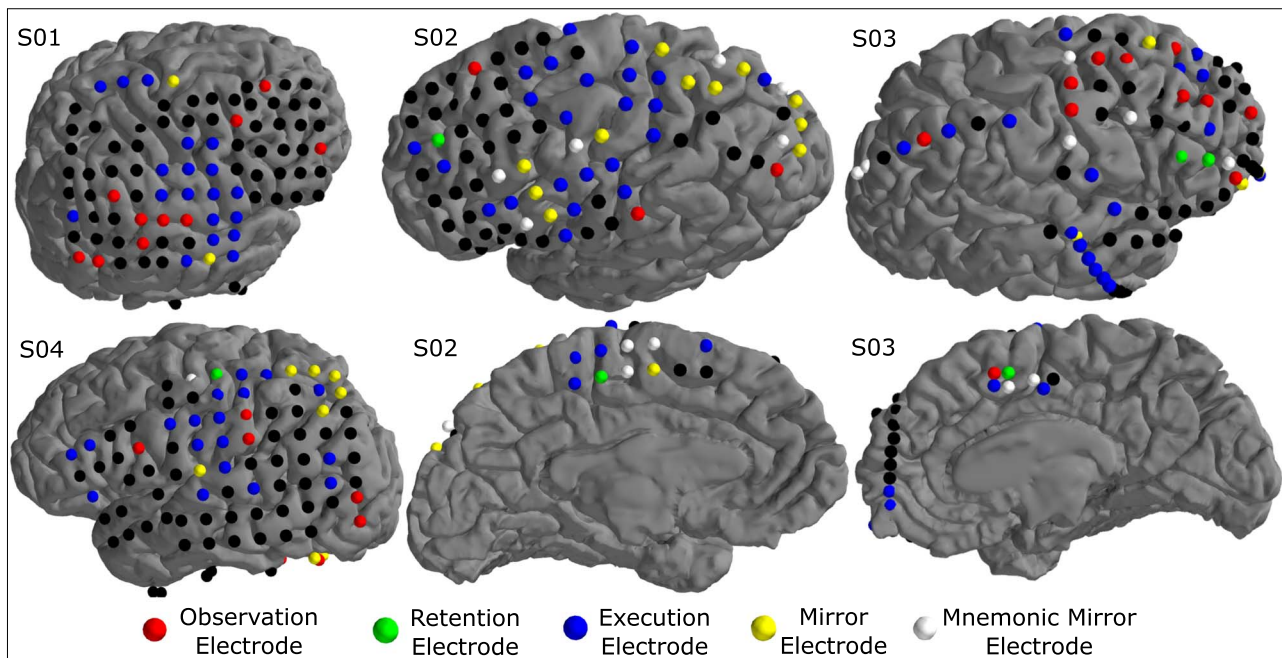


Fig. 2. Electrode locations for all subjects on individual anatomy. Electrode colors denote significant HFA modulations: black—not significant; red—significant during movement observation; green—significant during movement retention; blue—significant during movement execution; yellow—significant during movement observation and execution (mirror electrodes); and white—significant during movement observation, retention, and execution.

Table 3. Multielectrode classification accuracies for all subjects and conditions based on all significant HFA electrodes per condition or HFA mirror electrodes.

Electrode combination	Subject	Observation	Retention	Execution
All significantly modulated electrodes per condition	S01	0.36	0.36	0.61*
	S02	0.54*	0.35	0.74*
	S03	0.50*	0.31	0.53*
	S04	0.58*	0.41	0.62*
Mirror electrodes	S01	0.35	0.26	0.38
	S02	0.60*	0.42	0.63*
	S03	0.53*	0.39	0.54*
	S04	0.52*	0.38	0.60*

*P-value < 0.005; upper bound for estimated guessing level ($P = 0.05$) ≈ 0.42 – 0.44 .

The remaining electrodes were located either interhemispheric (1) or subtemporal (3). MNI coordinates as well as functional and anatomical labels can be found in the supplementary materials. Classification accuracies for single electrodes were in a similar range as the combined electrodes: 0.45–0.63 for S02, 0.49 for S03, and 0.49–0.56 for S04. Upper bounds for the estimated chances levels were similar as well: between 0.42 and 0.44 depending on the electrode.

We found significant classifications in mirror electrodes around central sulcus, in supplementary motor area, and along the intraparietal sulcus. These areas have been shown to be part of the human mirror neuron system (Caspers et al. 2010). To the best of our knowledge, this is the first study demonstrating grasp specificity that was postulated for strictly congruent mirror neurons by decoding grasp type from human HFA mirror activity.

Discussion

We tested whether 3 different grasp types can be discriminated from the population HFA during different phases of a mirror neuron paradigm. This could demonstrate grasp-congruent activity in

the human mirror neuron system. We first replicated HFA mirror and mnemonic mirror activity in classic mirror neuron sites (somatomotor, inferior frontal, and parietal cortices) as reported by Perry et al. (2018) and similarly by Dreyer and Rieger (2021) using MEG. Electrodes in these areas showed significant HFA modulations during the observation and execution of a natural reach-to-grasp movement for everyday objects, and some showed additional significant HFA modulations during the retention phase between observation and delayed execution (mnemonic activity). Three different grasp types and objects were performed during the experiment: bottle—whole-hand grip, pen—precision grip, and cup—handle grip. Using crossvalidated logistic regression classification tested against an empirical guessing level, we successfully classified the observed and executed grasp type from the HFA mirror activity from distributed mirror electrodes. In addition, we were able to classify the grasp type from HFA modulations in some single mirror electrodes located in supplementary motor area, around the central sulcus, and in the vicinity of the intraparietal sulcus. All these areas have been previously reported as parts of the human mirror neuron system (Caspers et al. 2010).

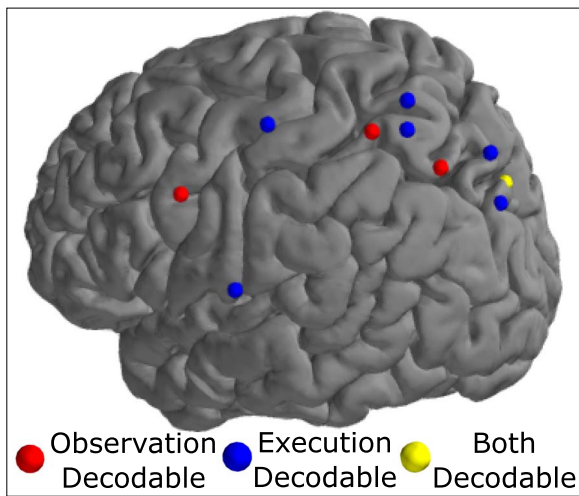


Fig. 3. Subset of electrodes from all subjects transformed to a standard brain that showed significant HFA modulations during movement observation and execution as well as significant grasp type classification performance in either condition.

Moreover, we were able to significantly classify grasp type using inferior temporal electrodes which might be related to the object type rather than the grasp movement, as they were located over fusiform gyrus (Sergent et al. 1992). Grasp specificity of mirror neuron activity so far has been reported in monkey single-cell recordings for a subtype of mirror neurons denoted as strictly congruent mirror neurons (Gallese et al. 1996). The successful classification of grasp types from human HFA mirror activity reported here provides evidence indicating the existence of grasp-specific mirror system activity in humans. As ECoG modulations have been shown to be correlated with single-cell activity (Manning et al. 2009; Ray and Maunsell 2011; Leszczyński et al. 2020), the congruent HFA we report could potentially arise from single, strictly congruent mirror neurons. We based our analyses on the definition of Perry et al. (2018) and classified grasp types in the different conditions separately. However, this cannot exclude that neuronal activity specific to the different conditions contributed to the successful classification in addition to the overlapping mirror neuron activity. This limitation could potentially be overcome by using crossmodal classification. However, training a classifier on 1 modality and classifying on the other modality introduces additional technical and interpretational problems. We used different feature spaces (interval lengths) for the natural movements with varying temporal dynamics in the execution condition but with nonvarying dynamics in the observation condition. For a crossmodal classifier to adapt to such a scenario, a different analysis approach using a different feature space would be needed, which is beyond the scope of this paper. Moreover, while successful crossmodal classification could be considered as a support for overlapping mirror neuron activity, a failure could be due to several effects in a complex multivariate classifier and would not be informative.

While decoding worked well when combining distributed mirror electrodes, our analysis revealed a relatively small number of single electrodes that could be used for significant grasp type decoding which can be explained by a variety of reasons. For example, ECoG electrodes capture population activity from thousands of neurons and strictly congruent mirror neurons only make up a subset of all mirror neurons in monkeys (31.5% in Gallese et al. 1996), which suggests that their signal-to-noise

ratio is limited in single electrodes but increases when combining distributed electrodes. A similar notion has been mentioned by Waldert et al. (2015) who were not able to consistently decode grasp types from local field potentials in monkeys. Also, we employed natural, self-paced grasping movements to increase ecological validity, which inherently creates variability during movement execution. Gallese et al. (1996) also reported mirror neurons in monkeys that stop firing as soon as a grasp is placed around an object and other mirror neurons that start firing while an object is held. Our ECoG electrodes likely captured activity from both types whenever the grasp was placed during our execution analysis window used for the classification. Even though we applied motion tracking to capture the actual movement start, variability throughout the movement likely influenced the classification performance. The question whether the observation of specific movements activates specific mirror neurons is also relevant for neurorehabilitation. Action observation treatment has been introduced for recovery from motor impairment (Ertelt et al. 2007; Buccino et al. 2012; Pelosin et al. 2013; Buccino 2014). If specific actions activate specific mirror neurons in humans, the use of a variety of movements in action observation treatment could benefit the recovery process.

Perry et al. (2018) introduced the term mnemonic mirror activity for electrodes that showed sustained modulations not only during movement observation and execution but also during the delay period between these 2 intervals when the movement to be executed is held in memory. We tested the grasp congruency of the mnemonic activity during the retention period with our decoding approach. However, we did not achieve a significant classification accuracy during the retention period. The grasp type memory might not be coded in the mirror system sites themselves but likely also recruit frontal and subcortical (basal ganglia for example) memory areas (Marvel et al. 2019). In addition, premovement planning activity can be expected during the late parts of the retention phase, which is not necessarily grasp type specific as the initial, ballistic phase of the reach movement is similar toward all objects. Also, the number of electrodes with significant HFA modulations during retention was much lower than during observation and execution, indicating that potentially fewer neurons are recruited to hold the specific grasp type in memory.

Our study has some limitations. Recording times for individual patients were constrained by the medical settings and the patients' ability to cooperate under such settings. Therefore, the overall trial numbers were limited. Grasp type decoding did not work in 1 out of the 4 subjects who was the subject with the least amount of valid trials. This subject also had the least amount of significantly modulated HFA electrodes during all conditions. While there might be several reasons for this, more trials would have potentially allowed us to draw clearer conclusions, especially about the unsuccessful classification sites, which for some electrodes might be due to a lack of training data. Further human intracranial research combined with single-cell studies may be needed to draw unambiguous conclusions about grasp-congruency.

In conclusion, our classification results show that the information about grasp types can be decoded from distributed HFA mirror activity as well as from single HFA mirror electrodes localized in classic mirror neuron areas by using human ECoG population signals. This provides evidence for the existence of grasp-congruent mirror neuron activity in humans, potentially arising from strictly congruent mirror neurons previously reported only in monkeys.

Supplementary material

Supplementary material is available at *Cerebral Cortex* online.

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Conflict of interest statement: None declared.

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