Crossmodal and action-specific: neuroimaging the human mirror neuron system

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The notion of a frontoparietal human mirror neuron system (HMNS) has been used to explain a range of social phenomena. However, most human neuroimaging studies of this system do not address critical ‘mirror’ properties: neural representations should be action specific and should generalise across visual and motor modalities. Studies using repetition suppression (RS) and, particularly, multivariate pattern analysis (MVPA) highlight the contribution to action perception of anterior parietal regions. Further, these studies add to mounting evidence that suggests the lateral occipitotemporal cortex plays a role in the HMNS, but they offer less support for the involvement of the premotor cortex. Neuroimaging, particularly through application of MVPA, has the potential to reveal the properties of the HMNS in further detail, which could challenge prevailing views about its neuroanatomical organisation.

Introduction

In the early 1990s a seminal paper [1] reported the existence of neurons in macaque frontal area F5 that showed remarkable tuning properties: these neurons not only fired when the monkey executed a specific action (such as grasping a pellet of food) but also when it observed an experimenter performing the same action. Soon, more reports of this type of visuomotor neurons, later termed ‘mirror neurons’, followed. Some of the key findings were that, first, neurons with similar properties were found in macaque parietal regions PF and PFG [2,3], which together with F5 [1,4] were termed the frontoparietal ‘mirror neuron system’ (Figure 1a) [5,6]. Second, mirror neurons also respond when an object is initially viewed but the subsequent reach-to-grasp is obscured by a screen [7], showing an influence of contextual knowledge on mirror neuron activity. Third, some mirror neurons respond differentially to the observation of the same motor act (e.g., grasping) in the context of different actions (e.g., grasping to eat or placing an object), suggesting a mechanism by which the final goal of a series of actions could be understood [2,3]. Fourth, the class of mirror neurons is heterogeneous with respect to tuning properties of individual neurons on various dimensions including hand and direction preference [4], distance to the observed actor [8], and viewpoint of the observed action [9].

If humans are endowed with such neurons as well, many have argued that this would provide an explanation for how people solve the ‘correspondence problem’ [4,10] of imitation and of learning and understanding actions performed by others. Given the anatomical location of F5 – in the premotor cortex – a popular interpretation was (and is) that this occurs through a simulation or direct matching mechanism, where observing someone else activates the same motor circuits as when executing that action ‘from within’, through a ‘motor resonance’ process [5,6,11]. According to this interpretation, people can understand the actions of others by mapping them directly onto their own motor repertoire. More generally, the idea that visual and motor representations of actions share a common neural ‘code’ may also help explain findings showing that task-irrelevant spatial [12], symbolic [13], body-related [14], and affordance [15] aspects of stimuli can affect subsequent action responses. Similar effects are also found in more-complex situations, as in the ‘chameleon’ effect – the tendency of humans to mimic the actions of social partners [16]. Furthermore, such a mirror mechanism [5,6] has also been proposed to underlie more general processes – beyond action representations – such as the automatic understanding of the feelings (i.e., empathy) [17] and thoughts (i.e., mentalising) [18] of others. It is also argued that mirror neurons play a role in language acquisition [19] given the close proximity of macaque F5 and its putative human homologue of Broca’s area. Finally, it has been suggested that a dysfunction of mirror neurons is the underlying mechanism of autism [20] (but see [21]).

The putative explanatory power of mirror neurons for this wide range of human social phenomena has led to the prediction that ‘mirror neurons will do for psychology what DNA did for biology’ [22]. Although not without critics...
[21–27], these thoughts— all resting on the concept of a ‘human mirror neuron system’ (HMNS) [5,28,29]— make the effort to identify and characterise this system all the more important [30].

A human ‘mirror neuron system’?
Macaque and human brains differ significantly, therefore the findings from macaques do not necessarily extend to humans in a straightforward manner. Indeed, the last-known common ancestor of macaques and humans is estimated to have lived 30 million years ago, resulting in partial but imperfect homology between the species [31]. For example, although early visual areas seem to map well, significant differences have been found between macaques and humans in higher-level associative areas of the intraparietal cortex [32] for tool use [33] and motion processing [34]—functions and regions that may be related to action understanding.

Moreover, the invasive character of neurophysiological recordings has led researchers to turn to other methods to seek evidence for a HMNS (but see [35]). A large body of such studies has employed blood oxygenation level dependent (BOLD) functional magnetic resonance imaging (fMRI). The use of fMRI and other systems-level methods, such as transcranial magnetic stimulation [36] and magneto- and electro-encephalography [37], introduces important challenges to the study of the HMNS. In varying ways, researchers have identified key properties of mirror neurons determined from single-cell studies and attempted to extrapolate and extend those properties to make systems-level predictions about the activity of large cortical regions. In the following sections of this opinion article, we show that although some of these attempts fall short (and are further limited by the constraints imposed by standard fMRI approaches), more recent studies have extended this logic (and fMRI methods) to paint a more precise picture of the HMNS.

Crossmodal responses: necessary but not sufficient
Many previous fMRI studies of the HMNS have followed the logic that the presence of mirror neurons in a region can be inferred when an increased response results from observing and executing actions compared with a baseline condition without a task. In other words: a crossmodal response across the visual and motor modalities. Ostensibly these studies provide overwhelming evidence in support of a HMNS by showing such a response for viewed and executed actions in frontal and parietal regions [6], putative homologues of macaque areas F5 and PF/PFG. Indeed, the idea of a frontoparietal HMNS has become so dominant in human neuroimaging literature that, through reverse inference [38], fMRI responses in these regions have occasionally been taken as evidence for mirror neuron activity [30].

As a recent meta-analysis [39] showed, however, such findings are not specific to canonical frontoparietal regions but extend to many other regions including the early visual cortex, superior temporal cortex, and the cerebellum (Box 1). Another study that used ‘unsmoothed’ data to reduce artefactual overlap between distinct but adjacent regions reported that 93% of crossmodally responsive voxels were outside the canonical HMNS [40]. It seems likely that general effects of task engagement, attention, or response selection processes—present during action observation or execution but not during baseline periods—are responsible for many of the apparent crossmodal effects found in these studies [30]. Apart from such a baseline explanation, the limited spatial resolution of fMRI—where a single voxel may contain thousands of neurons—means that distinct but spatially overlapping neural populations, with different visual or motor tuning properties, could lead to what has been termed the ‘alarming possibility’ [40] that many reported crossmodal BOLD responses are not necessarily the result of crossmodal neurons [41]. In other words, such crossmodal responses may be necessary but are not sufficient to make strong inferences on the HMNS (Box 2).

A crucial ingredient: action specificity
A further key property of mirror neurons is action specificity [30,42]. That is, according to a direct-matching account
Box 1. Are there mirror neurons everywhere?

Although a series of studies report evidence for mirror neurons in macaque areas F5 and PF/PFG [1,4], more recent studies have shown neurons with similar tuning properties elsewhere. For example, in a study [87] in which macaques were trained to manipulate a cursor on a screen, certain neurons in primary motor cortex M1 that modulated their firing rate during active cursor manipulation also encoded information during passive observation. Because the modulation of firing rate was similar during performance and observation, these neurons showed evidence for action-specific, crossmodal representations (see also [88]). Other studies have shown crossmodal responses for attended location in lateral intraparietal cortex (LIP) [89], mental rehearsal in dorsal premotor cortex [90], and visuotactile responses in the ventral intraparietal cortex [91]. Furthermore, in humans, recent work in epilepsy patients also revealed neurons with such action-specific, crossmodal neural tuning properties [35]. These neurons were found in the supplementary motor area and in and around the hippocampus and presupplementary motor area – outside the canonical frontoparietal network, perhaps reflecting memory- or emotion-related processes.

Whether or not crossmodal, action-specific neurons found outside the canonical frontoparietal network should be termed ‘mirror neurons’ is a matter of definition. Some have defined a ‘mirror mechanism’ based on the requirement that observation of an action is associated with the firing of a set of neurons in the cortical motor system [6], which implies that by definition mirror neurons cannot be found outside the cortical motor system (although neurons in the primary motor cortex presumably would qualify). Alternatively, many would argue that cells or regions that exhibit the key properties reviewed here – irrespectively of anatomical location – should be considered as candidate parts of the HMNS [24,92].

Setting definition issues aside, several studies have shown that different mirror neurons in canonical areas show a wide variety of tuning properties (Box 2). An intriguing possibility is that mirror neurons are not a special category of neurons but rather one example of neurons exhibiting crossmodal tuning properties as found elsewhere in the somatosensory and auditory systems. There is little evidence, however, that neurons with such properties are found everywhere in the brain, and it is likely that other factors, such as brain development constraints and connectivity between functional regions, limit where in the brain such neurons exist [93].

Whether the neurons found outside the canonical areas show similar properties, and/or are associated with different processes such as memory or mental imagery, is an empirical question. For example, one intriguing possibility is that the mirror neurons found in human hippocampus [35] are instances of concept cells that represent actions abstractly [81]. Such questions can ultimately only be resolved by neural recordings.

Box 2. Interpreting responses from neighbouring locations: a tale of heterogeneous populations

In many brain regions, spatially neighbouring neurons show remarkably different response profiles. A classic example is orientation columns in macaque primary visual cortex (V1), where different columns show different responses as a function of the orientation of gratings. Such different response profiles are also found in multimodal areas, where neighbouring neurons may respond more strongly to one of multiple modalities, such as vision and touch [94] or vision and hearing [95].

Further, single neurons can be found that respond to multiple modalities. Crucially, this does not imply, however, that such neurons process information across the different modalities. As an illustration, Lemus et al. [96] measured neural responses in the macaque somatosensory and auditory cortices while the monkeys performed tactile and auditory discrimination tasks. In both cortices neurons were found that responded to their principal modality as well as to their nonprincipal modality (i.e., to tactile stimuli in auditory cortex and to auditory stimuli in somatosensory cortex), which might, ostensibly, challenge the notion of modality-specific cortical areas. When considering discrimination of different stimuli in the same modality, however, in both cortices only stimuli in the principal modality could be distinguished. In other words, although responses were modulated for both modalities, stimulus specificity was limited to the principal modality. This example illustrates that even at a single-cell level – which is not affected by spatial resolution limitations, as in fMRI (Box 3) – an overall increased response for conditions of interest versus some baseline does not imply information processing at a stimulus-specific level. This principle is important for interpreting univariate fMRI studies that identify HMNS regions as those that respond above baseline to visual stimuli and motor behaviour [40].

Interpreting spatially neighbouring responses is complicated further by the heterogeneity of neural responses that can be found in certain areas. Macaque area F5, where the first mirror neurons were found, is a prime example. Most neurons in this area are only involved in executing movements, whereas other neurons are only responsive to observed actions but not executed actions [4]. Indeed, the classic mirror neuron responding strictly congruently to the same action when produced and seen only makes up around 5% of all neurons [4] (Figure 2). Within this class of mirror neurons there is further specialisation with respect to hand and direction preference [4], viewpoint [9], and distance to observed actions [8].

Direct measurement of such fine-grained levels of neural organisation is beyond the resolution of noninvasive imaging methods such as fMRI, which makes interpreting human neuroimaging data even more challenging. One possible avenue is the application of more sophisticated methods such as RS or multivoxel pattern analysis (Box 3) to provide indirect evidence for neural response properties at a population level.

[6], different actions must elicit distinguishable neural signatures, regardless of whether they are seen or executed. Considered at the level of a neural population, one might expect that the response associated with a particular action should be similar whether that action is performed or observed but should be dissimilar for different actions (Figure 2).

The first attempts to address this criterion with fMRI employed BOLD RS to infer neural response properties at a subvoxel level. In these RS studies, a specific action is first observed (or executed) and followed by execution (or observation) of either the same or a different action. According to a neural fatigue interpretation, a reduced response after repeating the same action compared to a different action is evidence for action-specific coding. Apart from interpretational challenges with RS (Box 3), evidence from initial investigations has been mixed. Considering the four recent studies that employed RS and tested visual and motor modalities: one study found action-specific coding within modalities that did not generalise between modalities [43]; two found asymmetric RS, where observed actions followed by executed actions (or vice versa) showed RS but the reverse order did not [44,45]; and one found crossmodal action-specific RS in both directions [46]. Unsurprisingly, this collection of results has not facilitated a consistent view on the HMNS. Interpretation of these findings is further complicated by a recent finding that, at a neural level, neurons in macaque F5 do not adapt to
repeated observed actions [47]. This implies that, if human mirror neurons show similar firing properties to those in macaques, RS is not a suitable technique to study their properties in humans.

Multivariate pattern analysis
An alternative approach to study action specificity of neural representations is multivariate pattern analysis (MVPA) [48–51]. This sensitive approach has been used successfully to decode subtle differences between stimulus-evoked activity patterns and even to reconstruct static and dynamic percepts from brain signals [52]. Such sensitivity is important if the proportion of mirror neurons in a region is small, as suggested by macaque (~5% to ~17% [4]) and human (~8% [35]) studies. Importantly for the study of the HMNS, MVPA has also been used to discriminate between spatially overlapping populations [53] (Figure 2c). Using this approach, the similarity of patterns evoked across groups of fMRI voxels by specific actions, when viewed and when performed, can be quantified. Areas where the same action (across the visual and motor domains) produces more similar patterns than different actions would be shown to have two key traits for a HMNS: crossmodality and action specificity. A trade off in this approach is that it necessarily considers neither single neurons nor single voxels, but identifies the properties of representations that span across a cortical region.

The first application of MVPA to investigate the HMNS was in the auditory–visual domain, demonstrating effector-specific (hand versus mouth) generalisation across heard and performed sounds in the parietal cortex [54], although these effects could potentially be explained by large-scale somatotopic organisation of the parietal cortex [55]. A subsequent MVPA study [56] used observed and executed manual actions, and showed action-specific coding within the visual and motor modalities in a set of a priori regions of interest. However, no evidence was revealed for the critical case of crossmodal representations. Evidence for such representations was subsequently found using a data-driven searchlight-based mapping approach [57], in which pattern similarity was computed in small disc-shaped regions covering the entire cortical surface (Figure 2c). Two experiments revealed that regions in the anterior intraparietal sulcus (aIPS) and lateral occipitotemporal (OT) cortex showed crossmodal, action-specific patterns of activity [58]. Transitive (object-directed) and intransitive (without object) manual actions implicated similar regions. Likewise, tests with live actions and with pre-recorded videos of actions produced highly similar results. No evidence was found for similar response profiles in the frontal cortex. Interestingly, this data-driven approach pointed to the engagement of OT, a region outside the canonical frontoparietal network, suggesting that areas typically considered part of the visual system can also show motor properties at the action-specific level (see also [35,59] and Box 1).

Aside from identifying candidate HMNS regions that show crossmodal, action-specific activity patterns, it is important to characterise the nature of the representations in these regions and their relationship to psychological variables. One organising principle for describing an action distinguishes between the goal of an action (such as lifting...
Box 3. Interpretation challenges for repetition suppression (RS) and MVPA

It has been claimed that fMRI RS supports inferences about neural populations at a subvoxel resolution [97,98]. In this approach, two trials are presented that share a characteristic of interest (e.g., action type) in rapid succession. Presumably, this results in a (non-time-invariant) response in the neural population that represents the characteristic of interest of the first stimulus. In a neural fatigue interpretation, this prior activation reduces response to a subsequent stimulus possessing this same property [99]. For example, an observed action can be followed by execution of either the same action or a different action. Neural populations that show crossmodal action-specific coding are expected to produce a lower response for executing the same action than a different action.

Interpretations of such results remain challenging, however, because studies suggest that such suppression effects are modulated by stimulus predictability, attention, neural tuning, and the time-scale of stimulus presentation. Other studies have shown that stimulus repetition may enhance (rather than suppress) the BOLD response [99]. Finally, recent findings indicate that effects of repetition on neural and BOLD activity can be distinct [100], which, in the context of the study of mirror neurons in macaque area F5 [47], raises questions about validity.

Multivoxel pattern analysis [48–51] considers data across a spatially extended group of voxels. This approach reflects the assumption that many processes involve neural populations with a spatial extent spanning many voxels and that clusters of voxels, rather than individual voxels, should be treated as the unit of interest in fMRI analysis [101].

Unlike RS, which enforces the use of counterbalanced trial condition sequences and seriously limits the number of trial conditions, the use of MVPA for ‘representational similarity’ analyses has shown the feasibility of using a large variety of conditions in a single experiment and across modalities (neurophysiology and fMRI) and species (macaques and humans) [76].

Despite these advantages, the neural mechanisms that underlie MVPA are poorly understood. An early proposal suggested that MVPA was based on biased sampling of different neural populations at a subvoxel resolution (hyper acuity) [50], but more recent work suggests a more complex mechanism that may involve a multiscale organisation and possibly an important role for neural vasculature [102]. Another limitation is that MVPA depends, by definition, on the combined signal of multiple voxels, and several studies have found that increasing the number of voxels increases sensitivity (up to a certain limit). This means that – in particular for data-driven approaches such as information mapping – MVPA entails a compromise between spatial specificity and sensitivity to discriminate between conditions of interest.

a cup) and the implementation of the action (such as using a precision or whole-hand grip). In an MVPA study in which goal and implementation were varied orthogonally, evidence for a posterior-to-anterior goal-to-implementation gradient was found in aIPS [58]. This finding is consistent with earlier suggestions of a more abstract representation of actions in posterior parietal regions, relative to more implementation-related representations in anterior parietal regions [60,61].

A further issue to which MVPA has been applied concerns whether crossmodal effects could be due to mental imagery. For example, earlier work on the visual cortex demonstrated that the lateral occipital complex showed stimulus-specific responses for ‘X’- and ‘O’-shaped stimuli, irrespectively of whether they were observed or covertly imagined [62]. According to such an interpretation, apparently crossmodal response patterns could be due to visual or conceptual representation of actions that are activated during action execution. To address this question, participants performed actions while receiving visual input of their own actions during some trials, and imagined covertly performing the same actions during other trials [63]. This study found evidence for action-specific coding that generalised across active performing and passive imagery in the anterior parietal cortex, but no such evidence in frontal or occipitotemporal regions. Although speculative, this may be interpreted as evidence for high-level action representations in aIPS that involve modality-independent rather than motor representations or visual representations of specific actions. This interpretation is consistent with its anatomical location between, and functional connections with, the visual and motor cortices.

Viewpoint invariance

Observing our own actions is typically associated with a particular ‘first-person’ visual perspective on those actions. By contrast, we typically see others’ actions from a variety of different ‘third-person’ perspectives. A key property of macaque mirror neurons is that they seem to relate the motor aspects of an action (which are inherently personal or ‘first person’) to the visual aspects of the same action even when that action is performed by others and, hence, seen from a different perspective [64]. This characteristic is considered to underlie the matching of one’s own actions to the observed actions of other individuals, which, in turn, ostensibly provides a neural underpinning for relating others’ behaviours to one’s own.

In another MVPA experiment [65], participants viewed videos showing actions either from a first-person viewpoint (as if they performed actions themselves) or from a third-person viewpoint (as if they observed someone else performing actions). In aIPS and OT regions robust, crossmodal, action-specific patterns of activity were observed for both viewpoints. In the ventral premotor cortex (PMv) – a core region of the canonical frontoparietal HMNS – first-person viewpoints generalised between the visual and motor modalities (Figure 2c), consistent with an earlier RS study [46], but generalisation to third-person viewpoints was not statistically distinguishable from chance. These results are consistent with recordings in macaque area F5 showing that the majority of recorded mirror neurons showed viewpoint-dependent coding [9], with a (nonsignificant) trend for more neurons coding for first-person views than for lateral- or opposite-side-person views. Heterogeneous responses in F5 were also shown at a larger spatial scale using fMRI, showing different response profiles to observed actions and objects across different subregions in area F5 [66]. Taken together, these findings from different scales and levels of analysis raise questions about how the premotor cortex may be involved in understanding the actions of others. At the finest level, many mirror cells appear not to generalise fully to all views of an action; by analogy to the representation of faces and objects, view-dependent local representations may act in concert to produce view-independent properties collectively. However, the MVPA results do not indicate such a
representation at the population level in this region in humans. The question of view (in)dependence is an absolutely central one to the mirror neuron system framework, and more studies are required on single neurons and with MVPA. Meanwhile, an alternative possibility that must be considered is that human premotor areas are engaged for observation of one’s own actions (for example in eye–hand coordination required for object manipulation), whereas the more posterior parietal and occipitotemporal regions are involved more in understanding the actions of others [58].

Concluding remarks and future directions

Recent advances in fMRI methods have been applied to examine the HMNS by extrapolating some of the key properties of mirror neurons to the population level. Already, these first steps paint a picture that differs in some ways from the canonical frontoparietal model of the HMNS (Figure 1) that emerged from the first wave of fMRI studies in this area.

First, with MVPA, PMv shows stronger first-person than third-person view representations of actions, which could mean it is less involved in representing the actions of other individuals [65] than the self. Because one of the purported roles of the HMNS is to understand other people’s actions (observed from a third-person viewpoint), further study is required to establish the critical conditions under which PMv generalizes between observed and executed actions. Second, the anterior parietal cortex showed the most consistent coding of actions, with engagement that generalises across the visual, motor, and imagery modalities [67–69]. The consistency of parietal activations across many studies suggests it may be a fundamental hub in the HMNS. These findings are consistent with an abstract representation of action goals in the anterior parietal cortex [60] with a possible extension to effector-related somatosensory properties in the somatosensory cortex [70]. Finally, a region in the lateral occipitotemporal cortex shows crossmodal, action-specific, view-independent action representations [58,59]. Although traditionally this has been considered as a visual region, with neighbouring representations of visual motion [71], body parts [72], and object form [73], numerous recent findings implicate the general region in haptics, motor behaviour, and tool use [59,74,75]. A case is therefore emerging that this OT region should be considered a candidate part of the HMNS.

Although MVPA on fMRI data is subject to limitations (Box 3), we argue that these methods offer tools to test key properties of action representations in ways not accessible to other techniques. They can elucidate not only the existence and location of regions that show crossmodal, action-specific representations but also begin to unpack the nature of their neural coding. Applying MVPA opens the way for similarity-based analysis [76] and investigating shared representations across individuals [77]. Both seem particularly useful to advance our knowledge on how humans represent their own actions and those performed by others. To clarify the population properties of macaque mirror neurons further, MVPA can also be applied to neurophysiology data [78]. More generally, application of representational similarity MVPA to fMRI and neurophysiological data in macaques and humans [79] would provide further insights to how information from these modalities can be meaningfully interpreted and integrated.

Mirror neurons were first found in the (pre)motor cortex, which undoubtedly influenced the hypothesis of a direct-matching mechanism in the canonical frontoparietal HMNS, where actions are “understood ‘from the inside’ as a motor possibility, rather than ‘from the outside’ as a mere visual description” [6]. More recent findings of crossmodal, action-specific representations far outside the human motor system—in occipitotemporal cortex [58,59,65] and hippocampus [35]—suggest that this hypothesis is incomplete [24]. In these non-motor regions (and possibly in the HMNS as well) actions may be encoded at an abstract level [24–26,61]. Further afield, recent findings point to crossmodal or abstract representations of emotions [80] and of person knowledge [81]. Collectively, these kinds of findings from diverse domains may each represent the result of general associative mechanisms [23,61]. Such an account would be consistent with the claim that crossmodal, action-specific representations are susceptible to effects of action-specific sensorimotor training [82–84]. Thus, a promising avenue for future research is to study how such sensorimotor training affects mirror responses at a single-neuron level in macaques [85] (Box 4).

A priority for future work in macaques would be to study putative homologous regions of the non-motor regions identified in humans, and to compare these to mirror neurons in the premotor and parietal cortices. Finally, to integrate and compare results across humans and macaques, a promising avenue is the application of MVPA—and in particular representational similarity analyses [86]—to fMRI, electrophysiological, and electrocorti graphical data, which will also bridge the gaps caused by imperfect brain homologies and different measurement modalities. More generally, as similar approaches are applied to other domains, we may begin to improve our understanding regarding general principles of how the brain integrates primary sensory and motor information to form abstract representations of knowledge [81].

Acknowledgements

We thank Marius Peelen, Emily Cross, and Nikolaus Kriegeskorte for helpful suggestions on an earlier version of this manuscript. We
acknowledge the Economic and Social Research Council, the Leverhulme Trust, and the Boehringer Ingelheim Fonds for funding support.

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