

The Neurocognitive Mechanisms of Imitation

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Imitation is a complex behaviour built on many different cognitive components. This review examines whether the mirror system provides a unitary brain system, dedicated to imitation. The data suggests we can distinguish a visuomotor stream which permits both imitation and other visual-to-motor transformations, and also a top-down control mechanism. Working together, these systems permit both social and object-learning imitation to allow flexible human social behaviour.

Introduction

Imitation behaviour is easy to recognise in daily life, but the underlying mechanisms are complex. The presence and significance of imitation in animals has been debated since Darwin's work, and even these early writers realised that imitation is not a single behaviour [1]. Researchers studying human imitation have parsed imitation into copying of goals (emulation) versus copying of action forms (mimicry) [2,3]; copying of familiar versus novel actions [4] and copying to learn about objects versus copying to be social [5]. The present paper reviews what we know about the neural and cognitive mechanisms underlying different types of imitation, and addresses two overall questions: (1) might the human mirror neuron system provide a single, dedicated imitation system? and (2) if not, what role do other brain systems play in imitation?

Mirror neurons in imitation

The core problem in imitation is a correspondence problem – how to convert the patterns of light on the retina into a pattern of muscle activation which generates a 'matching' action. The current textbook answer to this problem is that performed and observed actions are matched by 'mirror neurons'. These neurons, first discovered in inferior frontal and inferior parietal brain regions of the macaque monkey, are engaged during both observation and execution of hand actions [6]. In humans, there is evidence for an overlap of perceived and performed actions in similar brain regions [7,8].

Based on the original monkey studies, the human mirror system was defined as the inferior frontal and inferior parietal cortices [6]. Early neuroimaging studies which directly examined imitation behaviour also report activation of inferior frontal [9], premotor and parietal regions [10,11]. In a review of 20 studies, Molenburghs et al found that premotor and parietal cortex were consistently activated, while inferior frontal cortex was not [12]. Thus, in the present paper we consider the core imitation network to comprise the human

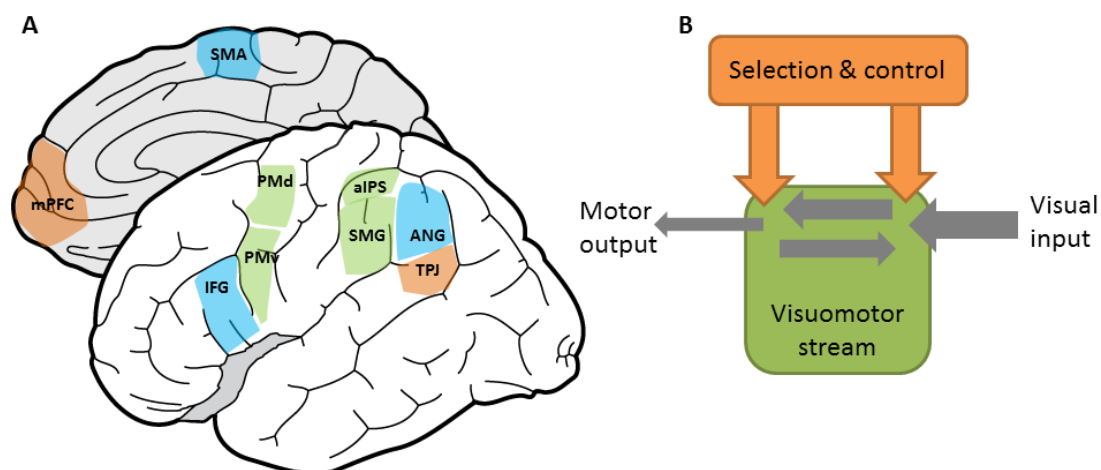


Figure 1 A. Brain systems for imitation. The dorsal premotor cortex (PMd) and ventral premotor cortex (PMv) together with anterior intraparietal sulcus (aIPS) and superior marginal gyrus (SMG) form a core circuit for visuomotor transformations (green). Other sensorimotor regions including inferior frontal gyrus (IFG), supplementary motor area (SMA) and angular gyrus (ANG) may also contribute (blue). Top-down control of imitation involves medial prefrontal cortex (mPFC), temporoparietal junction (TPJ) and other prefrontal regions (orange). B. Cognitive model. A simple cognitive model of imitation, comprising a visuomotor stream modulated by top-down selection and control processes. Colour matches between A and B indicate where links can be made between brain regions and cognitive processes.

inferior parietal lobe (SMG and aIPS) and the premotor cortex (PMv / PMd), with possible extension to IFG (see Fig 1A for localisation and abbreviations). We consider what role these regions play in imitation and other visuomotor transformations.

One valuable approach to the study of imitation is to define how neural activation correlates with imitation fidelity. For example, [13] recorded brain activity with fMRI while participants observed complex action sequences, and then asked participants to perform the sequences. While an extensive brain network was activated during observation, only activation of the right anterior intraparietal sulcus predicted imitation accuracy. Another study using both delayed and online imitation also found positive associations between right parietal cortex and imitative accuracy, with a negative relationship between left parietal / right ventral premotor cortex and imitative accuracy [14]. Together, these studies strongly implement the core parietal – premotor network in the imitation of novel actions.

However, these results do not mean that this network exists *exclusively* to allow imitation. Many non-imitative tasks engage the same brain systems. In a key study, Newman-Norlund showed that right IFG and bilateral IPL are active when participants imitate, but are even more active when they perform non-imitative actions [15]. Robust non-mirror activations can be seen following sensorimotor training. For example, Catmur et al trained participants to perform a foot movement when they saw a hand movement, and vice versa. Such participants then show engagement of ‘foot’ regions of premotor cortex when observing hand movements in fMRI [16]. Performance of object-directed actions robustly engages the IPL-premotor network [17,18]. Finally, viewing abstract cues which

have been linked by prior learning to motor responses can also activate premotor cortex [19–21].

These results are all compatible with a model in which the IPL-premotor cortex circuit functions as a network for visual to motor transformations. In social-psychology terms, this network provides a perception-behaviour expressway [22]. In cognitive terms, it links a visual stimulus such as an observed action or a graspable object or a learnt cue, to a motor output [23]. Such a network is likely to be strongly driven by associative learning [24] and thus would have a preference for imitation purely because there are many opportunities to associatively link a visual image of an action to motor performance of the same action. Under this model, there is no ‘a priori’ difference between mirror neurons and other visuomotor neurons within the same network (such as canonical neurons). All these neurons function to detect possible movements in the world and prepare to perform those movements [25,26]. The model implies that imitation is not necessarily special, but could be treated like any other sensorimotor behaviour. To return to the question posed above, there is little evidence that the mirror neuron system is *dedicated* to imitation alone, rather it seems to be part of a more flexible sensorimotor network. The next section considers whether understanding imitation needs more than this one brain network.

Is there more to imitation?

A key characteristic of human imitation is selectivity – every imitative action involves elements of selection – which bits should I copy and which should I ignore? There is increasing evidence that mPFC has a critical role in the selection and control of imitative actions. The first study of imitative control examined how people inhibit the tendency to imitate. Brass & colleagues compared a task where people must inhibit imitation of simple finger movements to a Stroop task where they must inhibit word-based prepotent responses. Performing the imitation-inhibition task engaged medial prefrontal cortex, a region previously associated with theory of mind [27]. Two other studies replicate the result [28,29] though others find different patterns [30].

A number of recent studies have examined how social cues affect the control of imitation. Medial prefrontal cortex (mPFC) has a role in controlling imitation based on eye gaze [31] and social priming [32]. Temporoparietal junction (TPJ) controls imitation based on animacy cues [33]. Neural activations during imitation also vary according to the race [34] and gender [35] of both the participant and the model who is imitated. Together, these studies show that imitative responding is not just the domain of the core premotor-parietal visuomotor circuit. Rather, the decision to imitate draws on a large number of social signals and a wide ranging brain network to produce a complex and nuanced social behaviour. Unravelling how and why imitation is controlled is an active area of research.

Putting these studies together, we have a neurocognitive model of imitation behaviour as illustrated in Fig 1B. In this model, a visuomotor stream provides the basic mapping from perceived actions to performed actions. However, a control mechanism is required to select which imitative (or non-imitative) actions to actually perform. The control mechanism most likely involves medial prefrontal cortex, but could draw on subcortical and other systems too. This model is called STORM (social top-down response modulation) [36], and provides an overall framework which can describe the basic systems underlying imitation and how they might fail (see below). Note that the structure of this imitation

model closely parallels the model of visuomotor control set out by Cisek & Kalaska [23]. The key difference between these two models is whether there are dedicated top-down control mechanism for social behaviours such as imitation, or whether all actions follow the same domain general rules. Distinguishing between these will be an important future direction.

Disorders affecting imitation

One way to test the validity of cognitive models is to examine how a behaviour changes in neuropsychological and psychiatric disorders. A large number of conditions affect imitation. If the core visuomotor circuit of premotor / parietal cortex is damaged, then patients often have apraxia which includes substantial imitation difficulties. Within this category, different neural pathways affecting different types of imitation can be distinguished [37]. In contrast, patients with damage to the frontal lobes can show utilisation behaviours and echopraxia [38], both behaviours where the patient performs or imitates an action afforded by the environment. This is concordant with the division proposed above, between imitation in the visuomotor stream and control of imitation in prefrontal cortex.

Turning to developmental disorders, autism has been strongly linked to difficulties in imitation, and hence in some papers to mirror neuron systems [39]. However, neuroimaging studies of imitation in autism suggest that this is not a straightforward case of dysfunction of the MNS. In one study, children with autism showed differences in IFG activation during emotional imitation [40], but another study found differences in mPFC [41]. Activation of mPFC in a theory of mind task also predicts automatic imitation performance in participants with autism [42]. These results point to differences in the control of imitation in autism (prefrontal mechanism) rather than imitation itself [43]. Behavioural studies of imitation in autism lead to a similar picture, as children with autism show normal performance on many instructed, goal-directed imitation tasks but reductions in performance in spontaneous or social imitation tasks (reviewed in [3][44]). Thus, studies of imitation in autism confirm the distinction between implementation of imitation and top-down control of imitation.

Box 1: Being imitated

An increasing number of studies in social psychology suggest that being imitated by someone else is an important social signal [45]. However, little is known about the neurocognitive systems underlying detection of imitation, or how they relate to performance of imitation. Two papers suggest substantial overlap between imitating and being imitated [46] [10]. Others suggest that being imitated engaged reward-related brain networks [47][48]. Defining the cognitive processes involved in the detection of imitation by others and how these relate to social evaluation will be important in the future.

Varieties of imitation

The model presented above implies that all types of imitation behaviour can be understood in terms of a single visuomotor stream, plus a top-down control mechanism. Can the enormous variety of imitation behaviours shown by humans [4] be understood in

terms of this simple system? It is hard to know at present, because few neuroimaging studies have directly compared different types of imitation in a theory-driven way (see [49] for an exception in the study of goal-directed imitation). Present work is also substantially limited by the types of actions studied – almost all papers reviewed here focus on the performance and imitation of simple hand/finger actions. This is largely because the fMRI scanner is a very restrictive environment for performing imitation research - participants are limited in the actions they perform, must keep their heads still and can rarely see their own hands. Thus, studies of imitation almost all use very simple hand actions as stimuli. It is possible that imitation in a social context, or imitation of goal sequences (cognitive imitation [50]) activate different brain networks.

One critical distinction from theory is between imitation for social interaction and imitation for object learning [5,51]. This maps onto the STORM framework, because the top-down control from mPFC seems to be primarily driven by social demands, while the basic visuomotor stream can perform object and goal-directed imitation. Studies show that both the visuomotor stream and mPFC are strongly engaged and interconnected in a context of reciprocal social imitation [52]. Imitation of social actions also engaged prefrontal regions [53]. However, imitation in naturalistic settings and the full range of imitative behaviours remain to be studied (see future directions). Understanding the relationship between different types of imitation behaviour, for example between imitation of goals and overimitation [54], will be very important.

Box 2: Future directions

This brief review has highlighted a number of important future directions for imitation research. These include:

- How does top-down control of imitation work, and does it differ from top-down control of non-social actions?
- Can the visuomotor stream be fractionated and if so, how?
- What cognitive systems are involved in the detection of mimicry?
- What brain mechanisms allow imitation in genuinely interactive contexts?
Methods like functional near-infrared spectroscopy may allow us to get out of the constrained tube of an fMRI scanner and see imitation in real life.
- How do different types of imitation map onto different brain systems?

Conclusions

This brief review presents a basic neurocognitive model of the processes involved in imitation. In this model, a core visuomotor stream in parietal-premotor cortex together with (social) control signals from prefrontal cortex allow humans to engage in detailed, selective imitation of actions. This model has the power to help us understanding a wide range of findings in the domains of typical and atypical imitation behaviour. Understanding the detailed computations involved in imitation, and moving from fMRI to more realistic contexts, will be important in future.

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*** This paper directly links imitative fidelity to activation of the parietal lobe.**

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**** this paper sets out clearly the case that imitation is not just for learning about objects but has an important social function – a claim that now recurs over 30 years later.**

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