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Imitation: is cognitive neuroscience solving the correspondence problem?

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Imitation poses a unique problem: how does the imitator know what pattern of motor activation will make their action look like that of the model? Specialist theories suggest that this correspondence problem has a unique solution; there are functional and neurological mechanisms dedicated to controlling imitation. Generalist theories propose that the problem is solved by general mechanisms of associative learning and action control. Recent research in cognitive neuroscience, stimulated by the discovery of mirror neurons, supports generalist solutions. Imitation is based on the automatic activation of motor representations by movement observation. These externally triggered motor representations are then used to reproduce the observed behaviour. This imitative capacity depends on learned perceptual-motor links. Finally, mechanisms distinguishing self from other are implicated in the inhibition of imitative behaviour.

Introduction

Could you learn to tango by telephone? Maybe, but it would be much easier to learn by watching the steps than by listening to instructions. When movements are visible, we can copy them; we can just do what we see. Imitation – copying body movement – appears to be simple. However, the ease with which humans imitate raises a question, sometimes known as the correspondence problem [1], that is proving difficult to answer: When we observe another person moving we do not see the muscle activation underlying their movement but rather the external consequences of that activation. So how does the observer's motor system 'know' which muscle activations will lead to the observed movement?

It is important to solve the correspondence problem because imitation provides a foundation for language acquisition, skill learning, socialisation, and enculturation. A review of current progress on this problem is timely because the discovery of mirror neurons has stimulated considerable interest in action observation and imitation among cognitive neuroscientists, and the function of these intriguing cells is itself a focus of controversy (Box 1). In this review, we outline recent accounts of the correspondence problem, considering whether imitation can be understood within a general learning and motor control framework (generalist theories) or whether it depends on a special purpose mechanism (specialist theories). We then review research on the role of learning in imitation and observation of biological motion. Finally, we discuss a problem for generalist theories: If imitation depends on

Box 1. Mirror neurons: What do they do? What are they for?

Mirror neurons in the premotor area F5 of monkeys are active both when the animal observes and when it executes a specific action (for a review see [52,53]. The discovery of these cells has had a revolutionary impact, turning perception–action interaction into a focus of intensive, interdisciplinary research worldwide. Naturally there has been a great deal of speculation about the function of mirror neurons, including proposals that they mediate, not only imitation, but also action understanding, empathy, language development [54,55], and action simulation [56]. However, at present, direct experimental evidence for the involvement of mirror neurons in one or all these functions is relatively weak.

Progress in research on the function of mirror neurons might have been hampered by a failure to distinguish clearly between two questions: What do they do?, What are they for? Imitation might well be one of the things that mirror neurons do; under some conditions, in some species, mirror neurons could be involved in the generation of imitative behaviour. However, mirror neurons could *do* imitation without being *for* imitation; they could be involved in generating imitative behaviour without imitation being the function that favoured their evolution by natural selection. In other words, imitation and other functions of mirror neurons could be exaptations rather than adaptations [57].

Generalist theories of imitation (see text) imply that mirror neurons – and other neural systems that are active during both action observation and action execution – can do imitation but are not for imitation. They suggest that mirror neurons acquire their properties in the course of ontogeny as a side-effect of the operation of general associative learning and action control processes (see [58] for a similar view). Once established, mirror neurons might be involved in the generation of imitative behaviour (and in several other functions), but, according to generalist theories, the properties of mirror neurons are not innate, and the learning and action-control processes that lead to their formation evolved in response to much more general adaptive problems. Empirically, the question of whether there are neurons with mirror properties present at birth remains unresolved. However, the finding that mirror neurons for tool use can develop during ontogeny [59] suggests that learning plays a crucial role.

Monkeys have mirror neurons but, according to some authors, they do not imitate. If this is true, it is evidence against the hypothesis that mirror neurons are for imitation [53], but it is consistent with the generalist perspective. The environments in which humans develop might be such that they yield mirror neurons with greater imitation-relevant specificity, and/or human imitation might represent the interplay between mirror neurons and more complex cognitive abilities [26,51].

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shared representations of perception and action, how can we distinguish between internally generated and externally triggered motor representations.

Generalist and specialist theories of imitation

Current theories of imitation offer *specialist* or *generalist* solutions to the correspondence problem (see Figure 1). Specialist theories suggest that imitation is mediated by a special purpose mechanism. The most prominent specialist theory is the active intermodal matching (AIM) model [2,3] (Figure 1a). AIM proposes that, when a body movement is observed with the intention to imitate, the initial, visual representation of the movement is converted into a 'supramodal' representation which contains information about 'organ relations'. AIM does not specify exactly how this information is encoded, but it implies that the code is the *lingua franca* of the perceptual-motor world. Supramodal coding allows a visual representation of an observed action to be matched up with a pattern of motor activation that can produce the same action. Historically, discussion of the AIM model has centred on the controversial question of whether newborn infants can imitate facial gestures (for critical discussion of this issue see [1,4]). We do not believe that further discussion of this issue here will facilitate understanding of the correspondence problem. It is preferable, in our view, to evaluate theories of imitation in terms of their capacity to account for a broad range of empirical findings.

Generalist theories assume that imitation is mediated by general learning and motor control mechanisms. There are two, complementary generalist theories under active development: ideomotor theory (IM) (Figure 1b), which subsumes imitation within a general account of motor control [5–7], and the associative sequence learning model (ASL) (Figure 1c), which claims that the capacity to imitate is a product of general processes of associative learning [1,8]. IM assumes that all actions are represented in the form of 'images' of the sensory feedback they produce, and that such representations are used to initiate and control body movements. From the perspective of IM observing somebody else executing an action leads to an activation of an internal motor representation in the observer because the observed action is similar to the content of the equivalent motor representation. This preactivated motor representation is then used to imitate the observed behaviour. Hence, the ease with which humans imitate is due to the general organization of motor control rather than a special purpose mechanism dedicated to imitation. In the goal directed theory of imitation (GOADI) Bekkering and colleagues have extended this approach by claiming that goals play a crucial role in the representation and imitation of actions [9,10].

ASL complements IM by explaining imitation, not only of 'transparent' actions such as finger movements, but also 'opaque' actions such as facial expressions, where the observer's image of the model is not normally similar to

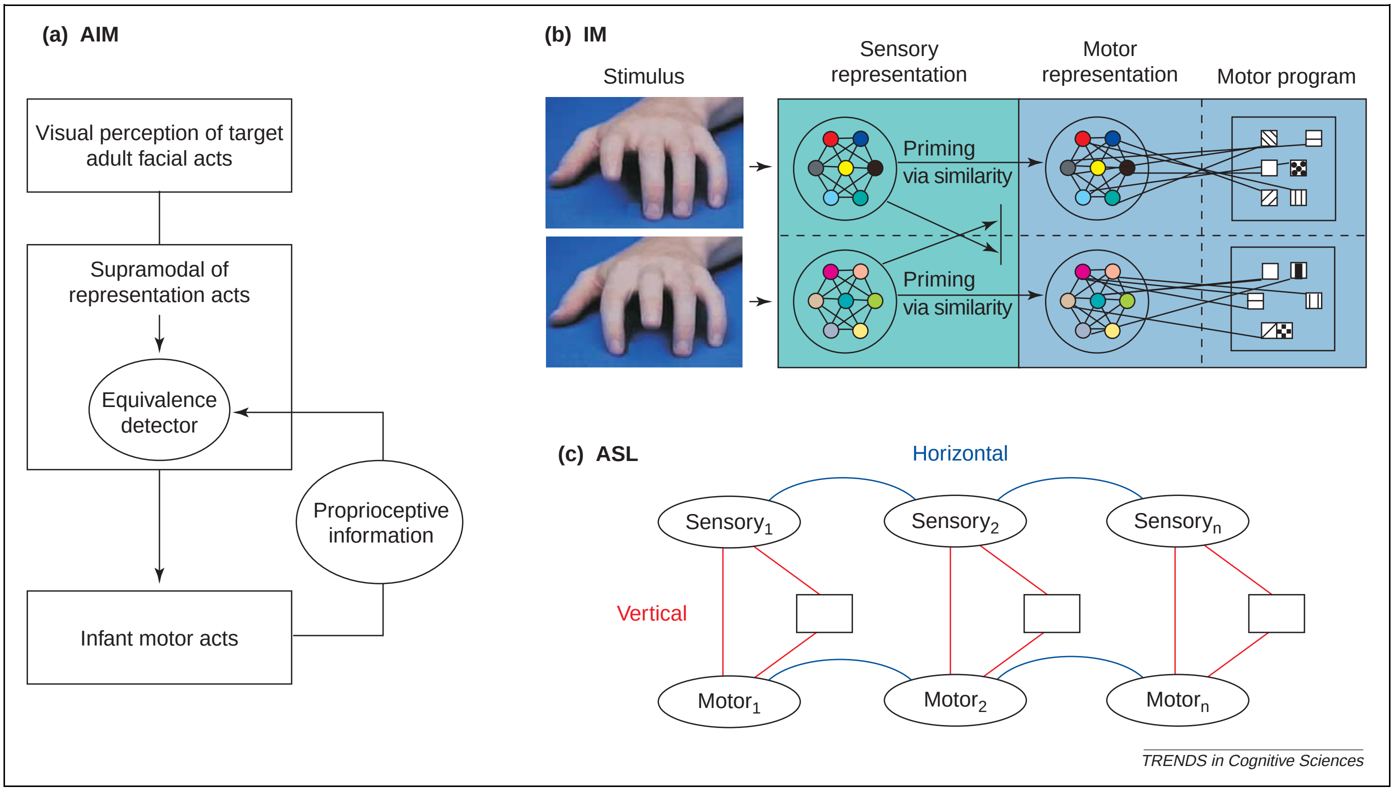

Figure 1. Three models addressing the correspondence problem of imitation. **(a)** Active Intermodal Mapping (AIM) theory assumes that visually perceived acts are actively mapped onto motor output via a supramodal representation system. **(b)** Ideomotor theory (IM) assumes that actions are represented in the form of the sensory feedback they produce. A perceived action leads to priming of the corresponding motor representation because of the representational overlap of the sensory and motor representation. IM assumes that the visuo-motor translation required for imitation results from the general organization of motor control. **(c)** The Associative Sequence Learning (ASL) model assumes that visual (sensory) representations of action become linked to motor representations (encoding somatosensory information and motor commands) through Hebbian learning. In environments where the same action is simultaneously seen and executed, links are formed between visual and motor representations of the same action. These contiguity-based 'matching vertical associations' mediate priming of motor representations by action observation.

the sensory feedback received during performance of the same action. ASL does this by postulating that each action-guiding image is a compound of two action representations – one encoding visual information (what the action looks like), and the other containing somatosensory information and motor commands (what the action feels like and how it is initiated). The visual and motor components become linked through Hebbian learning. Like IM, ASL assumes that learning of this kind can occur whenever we look down and watch our own actions. However, it points out that self-observation of an opaque movement will normally give rise to a 'nonmatching vertical association', i.e. to a visuo-motor link that cannot support imitation because the visual component is not similar to the visual input received during observation of another person performing the same action. Performance of an opaque movement leads to the establishment of a 'matching vertical association', a visuo-motor link that can support imitation, only in the kinds of environment created by optical mirrors, imitative social partners and explicit training regimes.

Motor activation by movement observation

As outlined above, generalist theories assume that imitation is based on general purpose learning and motor control mechanisms. They also assume that imitation is achieved by activation of motor representations through observation of action. One would not expect the operation of such a mechanism to be restricted to situations where imitation is intended. By contrast, one would expect an efficient specialist imitation mechanism to be 'switched on' only when needed.

Behavioural evidence of motor activation by movement observation (see [7,11,12] for reviews) has been provided by Prinz and colleagues in a series of reaction time experiments using interference paradigms [13–15]. The logic behind their approach is very simple. If observation of an action, A, leads to activation of an internal motor representation of A, then observation of A while preparing to execute an alternative action, B, should interfere with performance of B. In accordance with this hypothesis it has been shown, where A and B are lifting and tapping a finger, respectively, or opening and closing a hand, that movement execution is faster when accompanied by observation of a congruent movement than when it is accompanied by observation of an incongruent movement [13–16]. Interference effects of this kind occur both when kinematic aspects of the movement are observed [17–19], and when the terminal posture is presented alone [15,20].

In neuroimaging studies, participants need not be required to perform any action at all. Therefore, these studies provide yet clearer evidence that passive observation of action is sufficient to generate motor activation (see [21,22] for reviews). A large number of studies have now demonstrated that passive observation of action leads to activation of a set of brain regions known to be involved in movement execution [23–27] (see Box 2). Interestingly, although motor activation also occurs during observation of abstract stimuli, it seems to be strongest for the observation of human biological motion (Box 2).

Imitation is typically effector-specific; we imitate hand movements with our hands rather than our feet, and foot movements with our feet rather than our hands. Therefore if, as generalist theories suggest, imitation is mediated by the same mechanisms that underlie motor activation during action observation, one would expect those mechanisms to distinguish between effectors. Several transcranial magnetic stimulation studies (for a review see [28]) and neuroimaging studies [29–31] have pointed in this direction. The imaging studies suggest somatotopic organization for observed movements in motor-related areas [29–31], particularly in premotor cortex.

Box 2. The power of human biological motion

Observation of biological motion (feasible movements of biological agents) is especially powerful in generating motor activation. Observation of an action, A, interferes more with execution of an incongruent action, B, when A is performed by a person, a biological agent, than when A is performed by a robot [17,18,60] (see Figure I for an example of experimental stimuli). Similarly, neuroimaging has indicated stronger activation of cortical areas involved in movement execution while observing movements of a human hand than while observing movements of a robotic hand [61], stronger activation when the observed hand was real than when it was 'virtual' [62], and more motor activation when the observed movements of a biological agent were biomechanically possible than when they were biomechanically impossible [63,64].

Buccino and colleagues [65] compared motor activation during observation of human and non-human biological motion. In their study people observed actions performed by humans and by members of other species. For actions in the human response repertoire (biting) activation in inferior frontal gyrus and the inferior parietal cortex was very similar regardless whether the action was performed by a human, a monkey or a dog. However, for actions that are not normally part of the human response repertoire (barking) no frontal activation was found.

Taken together, these studies suggest that observation of human biological agents is an especially effective in generating motor activation. However, areas like the inferior parietal cortex seem to be strongly 'tuned' (innately or through learning) to biological motion, whereas frontal regions like Broca's area seem to be concerned with more abstract aspects of the action like the goal [25,66,67]. This latter point is further supported by a recent demonstration that premotor areas involved in the processing of biological motion are also activated by sequences of abstract stimuli [68].

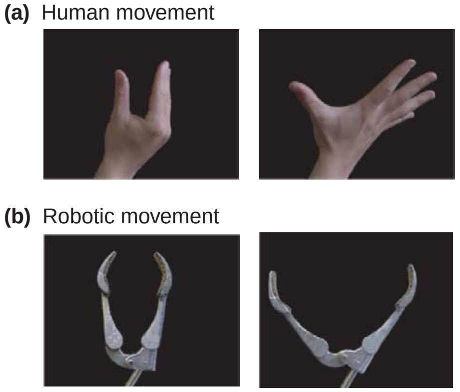

Figure I. Stimuli used by Press and colleagues [60] in an interference paradigm to compare the extent to which observation of **(a)** human, and **(b)** robotic hand movements elicit automatic imitation.

Are there special imitation mechanisms?

The previous section summarized evidence that movement observation leads to specific activation of motor-related

Box 3. Is the inferior frontal gyrus necessary for imitation?

It is now widely acknowledged that the inferior parietal cortex is involved in imitation, but the role of the posterior part of the inferior frontal gyrus (BA 44/45) remains controversial. The posterior inferior frontal gyrus (pIFG) is thought to be the human homologue of premotor area F5 in monkeys; the region containing mirror neurons (see Box 1). Several studies have found activation in pIFG during imitation tasks [23,25,33,69], but it has been argued that this activation was due to experimental confounds [22,70]. Functional brain imaging cannot provide a definitive answer to the question of whether a brain region is necessary for a specific cognitive function because the evidence that it provides is always correlational. Recently, Heiser and colleagues [71] investigated this question using repetitive transcranial magnetic stimulation (TMS) which temporarily disturbs the function of a specific brain area. They reported that imitation was selectively impaired when TMS was applied above the left pIFG (Broca's area). However, TMS is not precise enough to ensure that the functional lesion did not involve both pIFG and the adjacent ventral premotor cortex.

An old, and usually neglected, literature on neurological patients with ideomotor apraxia is not fully consistent with the hypothesis that pIFG is necessary for imitation [33]. It has been known for a century that these patients have difficulty in imitating complex movements. However, their lesions do not always include frontal areas, and, even when they do, the inferior frontal gyrus has not been implicated specifically [72].

Further work is needed to establish whether pIFG is necessary for imitation. A productive approach would be to examine whether other cognitive functions attributed to this area, like language production, interfere with imitation.

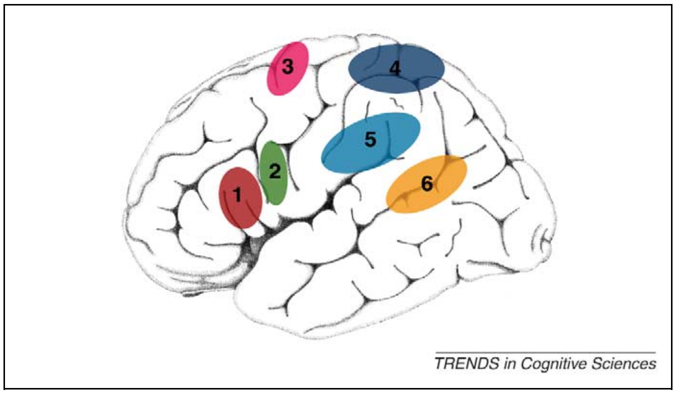

Figure 2. Areas of shared activation during movement observation and imitation. A schematic, lateral view of the human cortex showing areas that have consistently been found to be active during imitation tasks and during passive observation of biological motion. (1) the pars triangularis and the pars opercularis of the inferior frontal gyrus, (2) the ventral premotor cortex, (3) the dorsal premotor cortex, (4) the superior parietal lobule, (5) the inferior parietal cortex, and (6) the posterior superior temporal sulcus. Figure adapted from Duvernoy [73].

neuronal and functional representations. Activation of this kind might provide a sufficient basis for imitation or, as the specialist view would suggest, there might be neural circuits specific to imitation.

Many neuroimaging studies have now investigated the brain regions involved in imitation. They have identified a limited number of areas – including the inferior frontal gyrus (pars opercularis and pars triangularis), the dorsal and ventral premotor cortex, the inferior parietal cortex, the superior parietal lobule and the posterior superior temporal sulcus – that are consistently active during imitation [23–27,32–34]. Although the role of some of these areas in imitation is still controversial (Box 3), most studies have failed to find areas that are reliably active during imitation but not during passive observation of action [23–27] (Figure 2).

If we assume that special purpose mechanisms tend to be implemented in distinctive cortical areas, the failure to find 'hot spots' that are active during imitation but not during passive movement observation is supportive of generalist solutions to the correspondence problem.

The role of learning in imitation

Generalist theories, particularly the ASL model, predict that whether and how well a person imitates will depend on their past experience. I will be able to imitate an observed action, A, only if I have had the opportunity to form a link between visual and motoric representations of A. Specialist theories do not necessarily deny the importance of learning, but the most prominent contemporary example, the AIM model, suggests that the capacity to imitate is innate.

Relatively few behavioural studies have investigated the role of learning in imitation, but they have been broadly supportive of the generalist position. Heyes and colleagues [16] showed that automatic imitation (e.g. the spontaneous tendency to open ones hand when observing hand opening) can be abolished by a brief period of training, suggesting that the influence of movement observation on movement execution can be relatively easily modified by experience. Similarly, Tessari and Rumiati [35] found that imitation of overlearned (meaningful) gestures is easier than imitation of novel (meaningless) gestures, and proposed a dual-route hypothesis which, like the generalist ASL model, suggests that imitative performance can be either direct or linguistically mediated. Another study relevant to learning found stronger automatic imitation effects when body movements were viewed from an 'own person' perspective (at the angle from which one views ones own movements) than from an 'other person' perspective [36]. This finding was recently confirmed with transcranial magnetic stimulation [37]. This is what one would expect if, as generalist theories suggest, imitation depends on experience of ones own actions. By contrast, specialist theories would predict either that perspective is irrelevant (supramodal representations might be view-independent) or that the 'other person' perspective is privileged because the function of the special purpose mechanism is to imitate other people.

The results of two neuroimaging studies indicate that activation of cortical areas involved in imitation and movement observation depends on learned expertise in performing the observed movements. Using an elegant experimental design, Calvo-Merino and colleagues [38] presented capoeira dancers, expert classical ballet dancers and non-dancer control participants with video-clips of closely matched capoeira and ballet movements (Figure 3). The capoeira experts showed stronger activation in the premotor, parietal and posterior STS regions when observing capoeira movements than when observing ballet movements, and the ballet experts showed stronger activation in the same areas when observing ballet movements than when observing capoeira movements.

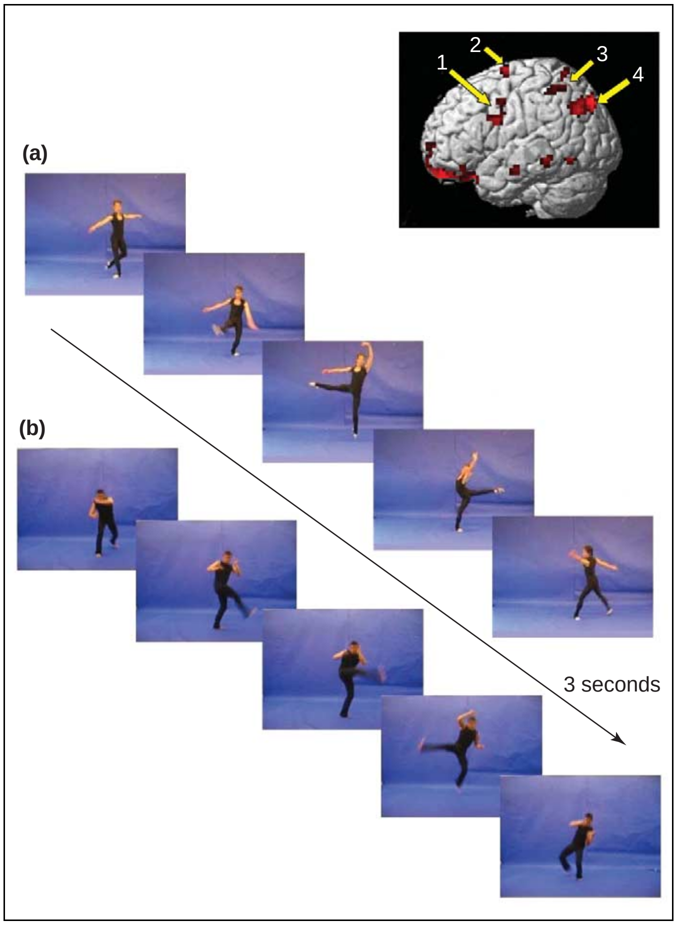

Figure 3. Neural activation during movement observation depends on expertise. Examples of **(a)** classical ballet movement, and **(b)** capoeira movement shown by Calvo-Merino and colleagues [38] to capoeira dancers, classical ballet dancers, and non-dancer controls in their study of the effects of expertise on motor activation by movement observation. The capoeira experts showed stronger activation in the premotor, parietal and posterior STS regions when observing capoeira movements than when observing ballet movements, and the ballet experts showed stronger activation in the same areas when observing ballet movements than when observing capoeira movements. The activation map on the right side of the graph shows this interaction in the ventral premotor cortex (1), dorsal premotor cortex (2), the intraparietal sulcus (3) and the posterior superior temporal sulcus (4) of the left hemisphere.

Similarly, Haslinger and colleagues [39] found that observation of piano playing was associated with stronger motor activation in pianists than in musically naïve controls, and that the two groups did not differ when observing control stimuli consisting of serial finger-thumb opposition movements.

In another learning-relevant study, Buccino and colleagues [26] scanned musically naïve participants while they were observing and reproducing guitar chords. They found activation in the lateral prefrontal cortex just before these novel actions were reproduced, and proposed a model of imitation learning in which the basic motor elements are activated via movement observation and are then selected and recombined, in prefrontal cortex, to match the models action. This hypothesis is highly compatible with the imitation learning mechanism assumed by the generalist ASL model [1]. Here matching vertical associations are automatically activated by movement observation and then combined via horizontal associations. The number and identity of the vertical associations which are activated depends on the motor repertoire of the imitator, whereas the ability to recombine such elements relies on another set of cognitive mechanisms concerned with serial order processing.

Why don't we imitate all the time?

We have argued that there is strong evidence for the assumption that the observation of an action leads to activation of an internal motor representation. However, if, as the ideomotor theory suggests, the action representations that prompt imitation are of the same kind, and have the same origins, as those that guide internally-generated action, why don't we confuse observed actions with our own intentions and copy every movement that we see [7,40]?

Research involving neurological patients indicates that this problem is not purely theoretical. Some patients with prefrontal lesions are echopractic; they tend to imitate observed behaviour, rather than to follow verbal or symbolic instructions [41]. Sometimes this even leads to compulsive 'imitation behaviour' [42,43].

In two imaging studies, Brass and colleagues [44,45] investigated the functional and neuronal mechanisms involved in inhibition of imitative response tendencies. These studies showed that the inhibition of imitative behaviour involves cortical areas which are known to be involved in distinguishing self from other, rather than response inhibition *per se*. The anterior fronto-median cortex and the right temporo-parietal junction were activated when an instructed movement had to be executed during observation of an incongruent movement. Decety and colleagues [46] found that a similar area in the right inferior parietal cortex was important in distinguishing imitation (self copies other) from being imitated (other copies self). The right inferior parietal cortex was especially active when participants were being imitated, and the left inferior parietal cortex was particularly active when participants were imitating. The right temporo-parietal junction has repeatedly been show to play a crucial role in determining self agency [47–49] and perspective taking [50], possibly by representing movements in allocentric coordinates [47].

These findings provide support for the view that action observation activates motor representations of the same kind that guide internally-generated action. If they did not, it would be unnecessary for inhibition of imitation to call on mechanisms that distinguish self and other [45].

Conclusion

More than a century of research on imitation has left us with a crucial functional problem: how are we able to transform a visual representation of an action into motor output. In the present review we have considered whether recent work in cognitive neuroscience has helped us to solve this correspondence problem. Even though research in cognitive neuroscience has rarely been designed to address the problem, it seems to be accumulating evidence that the key to solution is automatic activation of existing motor representations. The strength of this activation appears to be modulated by learning. So far there is no compelling evidence of a special purpose mechanism

Box 4. Questions for future research

- What kind of experience is important in development of the capacity to imitate?
- What is the inferior frontal gyrus doing during imitation?
- How can the results of patient studies be reconciled with those of neuroimaging?
- How is imitative potential brought under intentional control?
- Are IM and ASL entirely complementary theories of imitation, or do they make some differential predictions?

dedicated to imitation. Instead, the existing data support the generalist view that imitation operates on general learning and motor control mechanisms.

Within the broader perspective of research on the evolution of cognition, evidence that imitation depends on general rather than special purpose mechanisms is consistent with other work – for example, on face processing, spatial memory, and theory of mind – indicating that ontogenetic processes transform human cognition mechanisms (see [51] for review). Within the field of research on imitation, a priority for future research is to examine how the imitative capacity, which seems to be an emergent property of the motor system, is brought under intentional control (see also Box 4). This ability to facilitate, reorganize, coordinate and inhibit externally triggered motor representations may be what distinguishes human imitative capacity from that of other species.

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