

From visuo-motor interactions to imitation learning: Behavioural and brain imaging studies

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Abstract

We review three areas of research and theory relating to the involvement of motor processing in action observation: behavioural studies on imitation learning, behavioural work on short-term visuomotor interactions, and related neurophysiological and neuroimaging work. A large number of behavioural studies now indicate bi-directional links between perception and action: visual processing can automatically induce related motor processes, and motor actions can direct future visual processing. The related concept of direct matching (Rizzolatti *et al.*, 2001) does not, however, imply that observed actions are transduced into a corresponding motor representation that would guarantee an instant and accurate imitation. Rather, studies on the mirror neuron system indicate that action observation engages the observer's own motor prototype of the observed action. This allows for enhanced action recognition, imitation recognition, and, predominantly in humans, imitation and observational learning. Despite the clear impact of action observation on motor representations, recent neuroimaging work also indicates the overlap of imitation learning with processes of non-imitative skill acquisition.

Keywords: *Direct matching, visuomotor priming, imitation, observational learning, mirror neuron system*

Introduction

Over the past 15 years, researchers in cognitive psychology and neuroscience have made considerable efforts to study the interactions between action perception and motor processes. Action observation has been shown to exert long-range as well as instant effects on motor behaviour, and vice versa. Specific regions of premotor and posterior parietal cortex become activated during both action observation and execution, and the well-known discovery of mirror neurons (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996) indicates that even at the level of individual neurons, the neural coding of perceived and performed actions exhibits a remarkable degree of overlap. In this review, we pursue two aims. First, we provide a structured overview of recent advances in fundamental behavioural and neurophysiological research. Our selection of studies has been driven, at least in part, by their relevance for the understanding of imitation learning of complex motor actions such as those used in sports. The second, more specific aim is to assess, for each of the reviewed areas of research, the concept of *direct matching*, briefly defined as the involvement of motor processing in

action observation (Brass & Heyes, 2005; Rizzolatti, Fogassi, & Gallese, 2001; Wilson & Knoblich, 2005).

A phenomenon that has sometimes been associated with direct matching is precise behavioural copying, as illustrated in an anecdote by the ethologist Konrad Lorenz:

Social psychologists know that children imitate the movements of adults with the highest precision of form and for plain fun, long before they have understood the meaning of the behavioural pattern . . . My oldest grandson, at nearly two years of age, had been deeply impressed by the gracious reverence of a Japanese friend, and he imitated it in a way which one could well describe as “non-imitable”, since no adult would have been able to instantly achieve an equally accurate copy.

(Lorenz, 1977, p. 196, our translation)

Lorenz restricts the capacity for precise copying largely to humans and, as a special case, bird song. Whereas he readily suggests that primates such as chimpanzees are capable of understanding the meaning of an observed action (and might try to imitate an inferred goal via trial and error), he

emphasizes that non-human primates show only a rudimentary capacity for precise behavioural copying, and that the term “aping” is thus actually misleading (see Visalberghi & Fragaszy, 2002). Koffka (1925/1980) also distinguished between imitation of a movement and imitation of a purposeful action to meet the same result. He further believed that there is a gradual rather than categorical difference between movement and action imitation, and that a pure case of movement imitation would not exist: “A photographic reproduction of the separate movements involved is never found” (p. 309). This accords with everyday experience that expertise cannot be propagated between individuals within the blink of an eye. Mirror neurons are not plain mirrors, and direct matching is normally neither as direct nor as well-matched as the name might suggest. Accordingly, at the end of each main section we summarize the contributions of current research on the neurocognitive mechanisms of direct matching, and make suggestions for further research.

We focus on three broad areas of research: behavioural studies of observational learning (Section 1), behavioural research on short-term visuomotor interactions (Section 2), and neurophysiological and neuroimaging work (Section 3). In the first section, we review basic research on observational learning for five major task domains: sequence learning, timing, task dynamics, configural actions, and inter-limb coordination. Each task domain has been intensely studied in recent years (except for configural actions), and research specifically directed at observational learning has then built on the respective research traditions and paradigms. Given that observational learning of complex sport skills is reviewed elsewhere in this special issue of the journal, we focus here on laboratory studies that trade-off such a more applied perspective against the better isolation of a task dimension and opportunities for fine-grained experimental manipulations. For similar reasons, basic research has typically used practice periods consisting of pure observational exposure (here called *observational practice*), whereas the more general term *observational learning* (or *imitation learning*), which can also involve periods of physical practice, has been of greater interest for more applied research, including the optimal scheduling of both kinds of practice (Schmidt & Lee, 2005, ch. 11).

In Section 2, we turn to moment-to-moment interactions between perception and action, typically studied in visuomotor priming paradigms, and to the related theoretical frameworks. Psychological research has made substantial progress towards uncovering the involved cognitive mechanisms by studying concurrent perception–action coupling (Prinz & Hommel, 2002), and some of the experi-

mental paradigms developed here have later been successfully employed in neuroimaging work. Although the step from research on moment-to-moment visual guidance of action towards understanding longer-term motor skill acquisition is certainly not a trivial one (Whiting, Vogt, & Vereijken, 1992), it is reasonable to assume that skill learning emerges, at least in part, from the modulation and restructuring of multiple basic mechanisms of perception–action coupling. In our view, uncovering the microstructure of imitation learning along these lines is one of the major challenges for future research.

In Section 3, we review neurophysiological studies on the mirror neuron system in monkeys and humans, including those on imitation learning and expertise. In line with the second aim of this review, the main issue pursued throughout Section 3 is what aspects of observed actions are typically represented in the mirror neuron system, and which conclusions can be drawn from this for imitative perception–action matching in general and in the context of imitation learning in particular. Both visuomotor priming research and neurophysiological work on perception–action matching have their own methodological constraints (e.g. on actions that can be performed in a whole-body fMRI scanner). For such reasons, Sections 2 and 3 are not structured along task domains but rather reflect each field’s inherent foci and developments.

Our review has its limitations. We have not included work with neuropsychological patients (Buxbaum, Johnson-Frey, & Bartlett-Williams, 2005; Goldenberg, 2006), computational approaches (Billard & Dillmann, 2006; Schaal, Ijspeert, & Billard, 2003), social-psychological studies on unconscious imitation (Chartrand & Bargh, 1999; Ferguson & Bargh, 2004), and work on imitation in newborns and infants (Meltzoff & Moore, 1997). A good part of this work has been reviewed in Meltzoff and Prinz (2002) and, more recently, in Hurley and Chater (2005).

1. Behavioural approaches to imitation learning

Sequence learning

Learning a sequential motor skill consists of acquiring fluency in the execution of already familiar basic movements in a certain “novel” sequence. Sequential learning has mostly been studied with the serial reaction time task (SRT). This task was originally introduced by Nissen and Bullemer (1987) to demonstrate implicit sequence learning. In the standard SRT task, participants see a sequence of asterisks appearing on a screen and respond by pressing a button corresponding to the respective

screen position. A typical sequence would consist of ten such elements and would be constantly repeated in the practice phase. In their original study, which was not specifically related to observational learning, Nissen and Bullemer (1987) found that when the sequence was switched to random after prolonged training, participants' reaction times increased significantly, indicating the acquisition of sequential knowledge during training. Yet at the end of practice, participants were still unable to generate the sequence deliberately without cues. Therefore, Nissen and Bullemer regarded the learned sequential knowledge as *implicit* (for a review, see Keele, Ivry, Mayr, Hazeltine, & Heuer, 2003).

Howard, Mutter, and Howard (1992) used the SRT task to study observational practice. They found that pure observation of the stimuli during the practice phase resulted in transfer of sequential knowledge to a motor test. In a further observational SRT study, Heyes and Foster's (2002) participants observed another individual executing the respective key presses during the practice phase. Like Howard *et al.* (1992), Heyes and Foster were able to demonstrate a practice effect of pure observation. Yet, Kelly and Burton (2001) found no practice effect in their study with an observational SRT. Based on further SRT experiments with secondary task designs, Kelly, Burton, Riedel, and Lynch (2003) concluded that observational practice in the SRT task was different from the learning processes in the classical SRT, in that the former relied on the acquisition of *explicit* sequence knowledge.

A further issue regarding the now generally well-established effects of observational practice in the SRT is when the matching between perception and action takes place. One could argue that observational learning consists of the learning of perceptual regularities. In the motor test phase, the visual processing (or anticipation) is facilitated by the previous practice and then leads to an improved performance for learned sequences. According to this hypothesis, perception–action mediation takes place only in the motor test phase where improved visual predictions enable faster motor responses. The motor system would not be involved during observational practice, a view that we call *late mediation* (Vogt, 2002). In contrast, *early mediation* accounts (Vogt, 2002) assume that perception–action mediation takes place directly during action observation.

Both early and late mediation hypotheses have been proposed regarding observational sequence learning with the SRT. Howard *et al.* (1992) assumed that their observational SRT learning effect was due to the learning of the visual stimulus sequence, thus adopting a late mediation account. In contrast, Heyes and Foster (2002) explained their observational learning effect as being due to early

mediation. They proposed that observational practice directly activated the motor representations of the related responses and that this enabled the learning of a response sequence. Bird and Heyes (2005) recently supported this hypothesis by demonstrating effector dependency of observational practice. Effector-dependent learning is regarded as indicative of genuine motor learning (Hikosaka, Nakamura, Sakai, & Nakahara, 2002). Bird and Heyes (2005) found that the observational practice effect for a sequence of finger movements only occurred when the observers used the same effectors as seen during training and did not transfer to responding at the same locations using different digits. This counterintuitive finding is a clear indication of early mediation.

Timing

There is little doubt that various temporal aspects of performance can be learned through observation (Schmidt & Lee, 2005), and accurate imitation, even of unfamiliar temporal patterns, is often achieved instantly. For example, pianists have little difficulty in reproducing complex timing patterns played to them, particularly when these are embedded in musical phrases (Clarke & Baker-Short, 1987). Also, researchers of motor control have successfully used auditory information related to the model's performance for skill acquisition (e.g. Doody, Bird, & Ross, 1985). The prevalent interpretation of these findings was that a sensory template was created during auditory or visual exposure to the model, and that this later guided motor performance. Alternatively, Vogt (1995) provided evidence for the idea that motor representations are formed already during exposure to the model. Participants' consistency in motor performance was markedly enhanced, to the same extent as via physical practice, through repeated observation of a rhythmical movement of a marker representing the required arm movement. Rather than assuming that perception–action mediation occurred only after the training, the effect of observation on a rather low-level aspect of performance (consistency of relative timing) supported an early mediation account, as did the study by Bird and Heyes (2005). Using a short-term timing imitation task, Vogt (1996a) provided further evidence for early mediation, followed by a large number of studies indicating visuomotor interactions on even shorter time scales (see Section 2). An early and elaborate analysis of common sensory and motor components in the imitation of time ratios by skilled musicians was provided by Sternberg and Knoll (1984). In their data-driven model, judging time ratios and producing them (performed as separate tasks) shared no cognitive process, whereas imitation

of time ratios overlapped with processes of both judgement and production.

Timing tasks also provide clear evidence that modelled events are not mechanically copied, but that, for example, metrically structured patterns are more accurately reproduced than non-metrically structured patterns (Summers, Hawkins, & Mayers, 1986). Furthermore, imitative performances can exhibit persistent temporal deviations from a displayed spatiotemporal pattern when this violates biological optimization principles (Vogt, Stadler, & Kruse, 1988). Thus, observed actions are structured and reproduced using the observer's existing motor repertoire and generative "signatures". This confirms Koffka's (1925/1980) claim that imitative actions are not "photographic" copies.

A timing task was also used to explore action-perception transfer (APT; Hecht, Vogt, & Prinz, 2001). Whereas the study of observational learning, or transfer from perception to action (PAT), has a long history, virtually no research was available to indicate if motor practice would transfer to perceptual skills. In addition to perception-action transfer, we were also able to demonstrate action-perception transfer: participants who received motor practice in a rhythmical timing task without any visual information showed improved performance, relative to a control condition, in a subsequent visual timing discrimination task. However, a passive kinaesthetic practice condition produced performance gains similar to the APT condition. These results can thus also be explained by inter-modal transfer from proprioception to vision.

Finally, it is no coincidence that the auditory modality has often been used in the modelling of timing aspects of motor performance, given its particular sensitivity to temporal patterns. For example, Shea, Wulf, Park, and Gaunt (2001) demonstrated that an auditory model presented in addition to a visual template while practising a keypress-controlled timing task improved retention performance. Also, observational practice that included the auditory model enhanced relative but not absolute timing. Even purely visual model displays that contain timing information are often spontaneously recoded by participants into a subvocal, song-like format (Franks & Stanley, 1991; Vogt *et al.*, 1988). This nicely illustrates motor encoding (here, the generation of song-like patterns) of visually presented models and renders explanations in terms of purely sensory "templates" unlikely.

Task dynamics

A further aspect of motor skill learning is the adaptation to specific task dynamics (e.g. familiarization with a tool, or the exploration of a new

movement environment). One might expect that this skill dimension, due to its exploratory character, is less accessible to observational practice than other task domains, and that physical practice should be clearly superior. Vogt (1996b) studied this issue in a pendulum positioning task where participants had to move a slider along a horizontal track to a stop position. A pendulum was attached to the slider, and the participants' task was to perform the movement in such a way that the swing of the pendulum was at a minimum when arriving at the target position. Optimal performance in this task requires a biphasic movement, with a brief stop half way through the trajectory to let the pendulum "catch up", and crucially depends on exploring (and coupling to) the task dynamics. Contrary to expectation, pure observational practice resulted in learning effects approaching those of unguided physical practice (or "discovery learning"). One explanation for this result was that the availability of a model served to short-cut the participants' exploration of the task dynamics, possibly by synchronizing their own, covert motor planning to the overt performance of the video model and in this way experiencing process-outcome relationships.

Mattar and Gribble (2005) ran an elegant series of studies on the observational learning of task dynamics using Shadmehr and Mussa-Ivaldi's (1994) force field paradigm. Participants were asked to move a robotic arm to certain locations while the trajectory of the movement was systematically perturbed, such that a novel mechanical environment was simulated. Mattar and Gribble (2005) found that participants observing another person learning a clockwise force field performed significantly better when subsequently performing in the same environment than participants in control conditions of rest, observation of a person learning a counter-clockwise force field, or observation of a person trying to learn a randomly varying force field. In addition, participants who performed a cognitive distractor task during observational practice showed the same benefit as the participants in the undistracted group, but performing rhythmic arm movements during observation compromised learning. The authors conclude that the effect is unlikely to be dependent on cognitive strategies and that participants implicitly engaged neural systems for movement planning and control during observational practice (in our terminology: *early mediation*). Mattar and Gribble's (2005) study is particularly convincing because it was not particular movements, but rather representations of the force field and predictions about its effect on the movement that were learned, which is difficult to explain without assuming that the observer's own motor system was involved. Finally, Mattar and Gribble suggested that observing

the model's errors was crucial for the observational practice effect, which is in line with previous findings on expert versus non-expert models (Schmidt & Lee, 2005).

Configural actions

Memory for movements that involve specific configurations of body parts, such as finger postures, can be dissociated from memory for spatially oriented actions with a single effector (Smyth & Pendleton, 1989). Configural actions can be intransitive (as in sign language) or object-related (as in chords on a piano or guitar). Although configural actions appear to be very promising candidates for observational practice procedures, related psychological research on this topic, and on the learning of configural actions more generally, is limited.

The most elaborate study on the learning of configural actions to date is that of Hazeltime, Aparicio, Weinstein, and Ivry (in press), using a task that required simultaneous keypresses with two or three fingers as on a piano. Regarding chord learning, which involved the immediate copying of the chord pattern displayed in each trial, the authors confirmed that, primarily, individual chords are learned and not a generalized visuo-motor matching system. Two further experiments addressed the issue of whether the learned chords were represented predominantly in a motor or visuospatial format. One of these studies included chord observation blocks, in which participants were asked to make spatial judgements about the displayed chords, alternating with blocks that involved overt responses. The chords could either be identical or different for both tasks. Clear improvements in reaction times during the practice phase were found for both tasks, but, surprisingly, chord identity across tasks did not enhance performance further in either task during practice. In the subsequent motor test, responses were quicker for chords that were familiar from the practice phase than for novel chords. Over both test blocks, this effect was stronger for the chords overtly performed during practice than for chords shown in the observation/judgement task, although performance for the latter chords approached that for the executed chords in the second test block. The authors interpreted the results in favour of configural learning being predominantly response-based (i.e. relying on physical practice). However, it is also possible that a more straightforward observational learning condition, including the display of fingers producing the chord (rather than the key positions alone) and without the requirement for spatial judgements, might exert effects more similar to those of overt execution. Thus, it would certainly be premature to dismiss the possibility of observational

practice effects in configural tasks based on these results.

Inter-limb coordination

An apparatus used to study observational learning effects on whole-body coordination is the ski-simulator (Whiting, Bijlard, & DenBrinker, 1987). In the study of Whiting and colleagues, participants performed slalom-type ski movements over a 5-day training period. The apparatus consisted of a platform mounted on a set of rails, held in mid-position by strong rubber bands. Participants who watched the video-recording of a skilled performer while executing the ski movements themselves exhibited more fluent movements and greater consistency of fluency and frequency than participants left entirely to discovery learning (physical practice). During observational practice, participants did not copy the model exactly (as indexed by amplitude, frequency, and fluency). Accordingly, Whiting *et al.* interpreted the effects as indicating a mediating or regulating effect of observational practice.

In a subsequent study, however, Vereijken and Whiting (1990) could not replicate the beneficial effect of a model on learning the ski-task. Both the on-line imitation (or "synkinetic") task and a deferred (or "echokinetic") task produced equivalent or poorer results on the dependent measures at the end of practice than physical practice alone. The authors interpreted these results "in defence of discovery learning". However, another possible explanation is that an expert performer was used as the model, whereas using a learner (as in Mattar & Gribble, 2005) might convey a wider spectrum of the task space and thus be more efficient. Unfortunately, no data are available using a non-expert model or pure observational practice in the ski-task.

Whereas the ski-task involves both whole-body coordination and an exploration of the dynamical characteristics of the body-platform system (Vereijken, Van Emmerik, Bongaardt, Beek, & Newell, 1997; Vereijken, Van Emmerik, Whiting, & Newell, 1992), bimanual coordination tasks represent inter-limb coordination in a more pure form and have become the subject of intensive investigation in recent years (Swinnen & Wenderoth, 2004). The effects of pure observational practice, however, have not yet been studied in such tasks. One might expect that increased stability of a newly acquired coordination pattern, such as a particular phase relationship between two effectors in rhythmical actions, would be indicative of genuine motor involvement during observation, similar to effector dependence, consistency of timing, and force field adaptation as reviewed above. However, the studies by Mechsner and colleagues (Mechsner, Kerzel, Knoblich, &

Prinz, 2001; Mechsner & Knoblich, 2004) on immediate visuomotor interactions during performance of bimanual tasks would caution against such an interpretation. These authors proposed a largely perceptual basis for bimanual coordination and suggested that not motor coordinative states but perceptual goals are the dominant organizing principle in inter-limb coordination. Therefore, possible effects of observational practice of coordination tasks do not necessarily indicate early mediation. In addition, the available empirical evidence on various forms of modelling inter-limb coordination, mostly studied in combination with physical practice, appears to be more mixed than in other task domains (for reviews, see Hodges & Franks, 2002, 2004; Hodges *et al.*, this issue). Interestingly, providing the learner with reduced or condensed task-relevant information such as, for example, the toe trajectory in the study of Hodges, Hayes, Breslin, and Williams (2005), can be equally or more effective than displaying the motion of all joints. This result is in line with the beneficial effects of verbal and visual attentional cueing during observational learning (Janelle, Champenoy, Coombes, & Mousseau, 2003).

Casile and Giese (2006) employed an inter-limb coordination task to study action–perception transfer, using a similar design to that of Hecht *et al.* (2001). Casile and Giese showed that the discrimination of point-light displays of gait patterns was selectively enhanced after purely motor training of a corresponding, novel phase relationship of the upper limbs, thus providing further evidence for direct matching. However, the authors did not study whether the kinaesthetic information available during motor training might have been sufficient for the transfer effect; thus the same caveat applies to this study as to the original work by Hecht *et al.* (2001).

Summary

In behavioural studies of imitation learning, the neurocognitive processes that occur during observational practice are inferred from the observable effects on the subsequent performance in the practised task or a related one, and via manipulating the conditions of observational practice. Several of the reviewed studies have gone beyond the plain assertion of improvements in task performance after observational practice, namely the demonstration of effector specificity (Bird & Heyes, 2005), effects on consistency of timing (Vogt, 1995), and force field-specific practice effects (Mattar & Gribble, 2005). These studies provide evidence for the “penetrability” of genuine motor processes by observational practice procedures. We interpret this as *early mediation* of sensory and motor processing, a

specification of “direct matching” in the context of imitation learning.

Penetrability, however, is not complete determination. Reports of instant and accurate reproductions, as in Lorenz’s (1977) anecdote, are scarce. For example, participants in Vogt and colleagues’ (1988) study showed persistent deviations from an artificially constructed, isochronous model display even after over 150 demonstration–imitation cycles. This was likely due to generative principles of trajectory formation (Rosenbaum, 1991, ch. 7), which are largely shared between human models and imitators. Moreover, even where an exact reproduction might be encountered, this could well be due to this shared general architecture of human motor control, rather than being a clear indication of a putative capacity for “photographic” copying. In addition, observational practice might reflect certain aspects of an observed action better than others, as indicated by the better reproduction of relative than of absolute timing found by Shea *et al.* (2001; see also Badets, Blandin, & Shea, 2006). With these possible limitations in mind, the studies reviewed indicate that observational practice can exert effects on a variety of dependent measures and that these effects do not seem to be restricted to a single task domain, though more research is required, particularly for configural actions and bimanual coordination. In fact, one of the most elaborate demonstrations of observational practice effects to date comes from a domain in which one might least expect these effects: the learning of task dynamics (Mattar & Gribble, 2005). The distractor task condition in Mattar and Gribble’s study also provides evidence that observational practice goes beyond the choice of cognitive strategies, which has often been seen as its primary mechanism (Kohl & Shea, 1992). Nevertheless, more research is needed regarding the possible implicit versus explicit nature of observational learning.

Finally, two studies are now available that indicate transfer from pure motor practice to visual discrimination (Casile & Giese, 2006; Hecht *et al.*, 2001), providing a methodology complementary to observational practice studies regarding the demonstration of direct matching. In addition to its theoretical relevance, the phenomenon of action–perception transfer indicates a possible formative role of physical practice in preparing periods of observational practice, which can explain the beneficial effects of combining both forms of practice in applied training schemes (Schmidt & Lee, 2005).

2. Concurrent visuomotor interactions: Findings and theories

A complementary route to studying direct matching is the investigation of short-term interactions

between perception and action. Typically, studies in this area do not involve learning, and the effects occur without or even against instruction. Many of the related empirical studies have been motivated by the common coding approach (Prinz, 1990, 1992, 1997), which essentially assumes that, on a certain level of cognitive analysis, an observed action is represented in the same format as the corresponding executed action. Common coding should manifest itself not only in voluntary imitation, but also in concurrent, non-intentional visuomotor interactions. Prinz (1990) refers to an early report of a related phenomenon by Eidelberg (1929), namely that of spontaneous imitation. Eidelberg instructed his participants to perform pointing actions to verbal command (e.g. to point to their nose, or to a lamp in the room), while he simultaneously performed a pointing action to one of these objects. When the experimenter's verbal command and gesture were incongruent, participants were unable to avoid mistakes. That is, they tended to imitate the observed gesture and ignore the verbal command, which they were always instructed to follow. This can be classified as a visuomotor priming effect, in that execution was affected by the visual display. As instructed, the latter was irrelevant for performing the task. Before we turn to the different theoretical frameworks, we give a brief overview of the related empirical findings on visuomotor priming.

Priming by observed actions is only one, albeit important, class of effects of stimulus–response compatibility (Hommel & Prinz, 1997), in which, generally, the overlap between certain features of a display with certain features of a response affects execution. For example, responding with the right hand is normally facilitated when the stimulus is located on the same side (Hommel & Prinz, 1997). Also, object properties such as orientation and size can prime corresponding motor parameters (e.g. Craighero, Fadiga, Umiltà, & Rizzolatti, 1996; Tucker & Ellis, 1998; but see Cant, Westwood, Valyear, & Goodale, 2005).

One of the earliest formal studies on stimulus–response compatibility with biological stimuli was conducted by Kornblum and Lee (1995), who demonstrated a compatibility effect between key responses using the index or middle finger of the right or left hand, and a corresponding display showing an outline drawing of the two hands. The imperative stimuli were letters cueing which key should be pressed. On which fingertip the letter would appear in a given trial was irrelevant to performing the task, but responses were indeed facilitated when cue and response location were compatible (e.g. the right index finger) rather than conflicting. Brass, Bekkering, Wohlschläger, and Prinz (2000) extended this set-up to an imitation-

like task with movie displays of finger movements. Their stimuli showed the same movements that the participants performed as responses. Reaction times were faster when participants observed a movement of the same finger that they used for their response. This stimulus–response compatibility effect was stronger for displays of moving fingers than for spatial cues as used by Kornblum and Lee (1995). By comparing lifting with tapping, Brass, Bekkering, and Prinz (2001) further demonstrated that the compatibility effect was partly related to movement direction and partly due to movement type. Showing these effects in a simple response task (i.e. not requiring a choice of response) provided further evidence for the automaticity of the priming effect.

Stürmer, Aschersleben, and Prinz (2000) studied stimulus–response compatibility with more complex hand movements. Participants were exposed to a movie display of a coloured hand that was either spreading or closing, and had to respond to the colour by performing the same actions in a pre-defined colour-to-action mapping. Robust stimulus–response compatibility effects were found for movie displays as well as for pictures of end-postures of the movements, which was interpreted to indicate two distinct (movement-based and posture-based) mechanisms. Using kinematic measures, Castiello, Lusher, Mari, Edwards, and Humphreys (2002) and Edwards, Humphreys, and Castiello (2003) demonstrated priming effects from observing object-oriented prehensile actions. The effects were found to be specific to a naturally moving hand, as opposed to an observed robot or constrained human hand.

These stimulus–response compatibility studies all show similar effects: Action displays facilitate the execution of resembling actions. A particularly convincing study regarding the involvement of action plans in action observation was conducted by Flanagan and Johansson (2003), who showed that the coordination of an observer's eye gaze and an observed hand action was predictive in the same way as gaze–hand coordination during action execution. The task-specific pattern of eye movements is difficult to explain without assuming that the observers engaged neural systems normally involved in the coordinated control of eye and hand movements, and is thus a clear-cut behavioural demonstration of direct matching.

The studies reviewed so far indicate short-term effects of perception on action, or *visuo-motor* priming. In contrast, *motor-visual* priming refers to situations where execution affects visual processing, likely related to the predictions of the sensory consequences that are made during action planning. Craighero, Bello, Fadiga, and Rizzolatti (2002) instructed participants to prepare a grasping

movement towards a bar in one of two orientations and to execute the prepared movement in response to a visual prime stimulus. They found that responses were faster when the primes showed a grasping hand compatible with the prepared action, relative to an incompatible prime, and interpreted this as an indication of action planning to affect visual processing (i.e. a motor-visual effect). Building on this work, Vogt, Taylor, and Hopkins (2003) presented pictures of a grasping hand in a horizontal or vertical orientation, either as seen in first-person perspective or as another individual's hand (as in a mirror). We interpreted the priming effects found for the first-person perspective as motor-visual priming and the effects for the mirror-like perspective as visuo-motor priming (Figure 1). Further evidence for motor-visual priming was provided in a recent series of studies by Miall *et al.* (2006), again by manipulating the congruency between a performed hand action (fist vs. flip) and a displayed sequence of hand pictures. In line with the results of Vogt *et al.* (2003), these effects were specific to displays in the first-person perspective and showed rapid decay when a 500-ms delay was introduced between successive stimulus presentations.

Finally, interference effects between perception and production have also been reported. Kilner, Paulignan, and Blakemore (2003) showed that the execution of a horizontal or vertical rhythmical arm movement was affected by the observation of another human's simultaneously executed arm movement when this was performed in an incompatible plane.

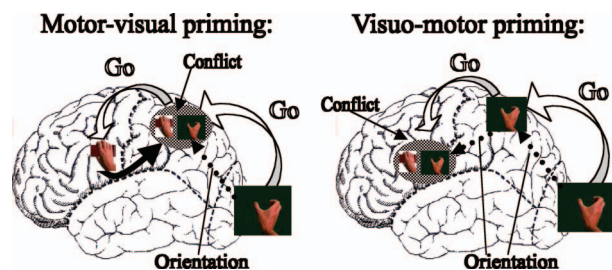


Figure 1. Flow of information in two forms of priming, as proposed by Vogt *et al.* (2003). (Left) Motor-visual priming originates from motor preparation in premotor areas (here: “grasp horizontally oriented bar”). The related expected sensory consequences (black arrow to posterior parietal areas) then modulate the processing of visual input. In the case of a response-incongruent go-signal (here: picture of vertically oriented hand; white arrows), a conflict to the sensory prediction would arise. (Right) In visuo-motor priming, the visual display can carry two conflicting pieces of information. For example, the background colour of the display instructs execution of a horizontal grasp (white arrows), and the vertically oriented hand shown automatically primes execution of a vertical grasp (dotted line). This is likely to create a conflict in motor processing, although a conflict might also arise at earlier processing stages (as in visuo-motor priming). Note that for illustration purposes, both panels show hand postures in first-person perspective.

Also, interference effects have been found in motor-visual priming (Hamilton, Wolpert, & Frith, 2004; Kunde & Wühr, 2004; Müsseler, 1999; Schubö, Prinz, & Aschersleben, 2004). Yet, except for Hamilton *et al.* (2004), these studies did not use displays of human actions.

In summary, visuomotor priming research provides good support for the idea that action perception automatically involves corresponding motor representations (*visuo-motor* priming) and that, conversely, visual processing can be modulated by motor planning (*motor-visual* priming). We have already referred to one theoretical framework that predicted both directions of priming, as well as action-perception transfer and perception-action transfer reviewed in Section 1 – namely, the common coding approach (Prinz, 1990, 1992, 1997). This framework has been developed further into the “theory of event coding” (Hommel, 2004; Hommel, Müsseler, Aschersleben, & Prinz, 2001) and is also referred to as “ideomotor theory” (Prinz, 2002, 2005), according to its roots in James’s (1890) proposal that voluntary actions are initiated via anticipatory “ideas”, or representations, of the environmental effects they habitually produce. According to ideomotor theory, observing somebody else’s action is an alternative, perceptually driven case of action initiation and based on the same principle of effect-guided action selection. Furthermore, Prinz (2005) maintains that the similarity between the external stimulus event and the action-related representation predicts the strength of this perceptual induction. In addition to facilitation, the theory of event coding also explains interference effects. According to Hommel *et al.* (2001), lower-level processes of action planning and perception cannot access the same high-level action code at exactly the same time. Two concurrent tasks relying on the processing of one code should thus lead to mutual impairment. Priming of the subsequent event occurs only when the resembling perception and action follow each other.

In the theory of event coding, visuomotor priming effects are explained by a shared cognitive architecture for representing perceived and motor events, whereas Heyes’s (2001, 2005) associative account of imitative phenomena explains visuomotor priming effects on the basis of learned associations. In contrast to the theory of event coding, Heyes’s account assumes distinct representations for action plans and perceived events and that links between the two are formed by experience. Non-matching sensory and motor representations (e.g. watching someone kicking a ball and performing a catching action) can be associated in the same way as matching representations (as in imitation), simply governed by the frequency of exposure. Heyes (2001, 2005) explains visuomotor priming effects

by assuming that individuals have typically acquired stronger associations between matching than between non-matching representations, as a result of environmental contingencies that favour the formation of matching associations:

Co-activation of sensory and motor representations of the same perceptually transparent movement occurs whenever the individual observes, unaided, their own motor output, and, in the case of perceptually opaque movements, through experience with mirrors, of being imitated, and of socially synchronous movement in response to a common stimulus.

(Heyes, 2001, p. 258)

While both the theory of event coding and Heyes's associative account can explain the reviewed visuomotor priming effects, differential studies concerning the two accounts are rare. One related approach is to investigate the sensitivity of perception–action couplings to learning. Heyes, Bird, Johnson, and Haggard (2005) replicated a typical stimulus–response compatibility effect with hand gestures, and in a second experiment they demonstrated that the effect disappeared after a short training on incompatible stimulus–response assignments. They concluded that the original stimulus–response compatibility effect was acquired by learning (in everyday life), since an architectural explanation would have predicted it to be robust against contrasting practice.

Direct perception–action coupling has been claimed to have an important functional role in observational learning. The associative account of visuomotor mediation is indeed grounded in a theory of associative sequence learning (Heyes, 2005), which can explain the related effects reviewed in Section 1. Associative sequence learning assumes that, when an individual repeatedly observes a certain novel sequence of actions, each of the constituting familiar action elements activates its corresponding motor representation via existing associations, not necessarily involving overt execution. This repetitive activation of a sequence of motor representations forms links between elementary motor representations. This “linkage of motor representations constitutes motor learning, produces a new motor primitive, and improves the potential fluidity of imitative movement” (Heyes, 2005, p. 162).

Whereas both Prinz's and Heyes's accounts of imitative actions can be classified as direct matching accounts, the theory of goal-directed imitation (Bekkering, Wohlschläger, & Gattis, 2000; Wohlschläger, Gattis, & Bekkering, 2003) assumes that imitation is guided by cognitively specified goals. According to Wohlschläger *et al.* (2003), an observed

action is cognitively reconstructed as a hierarchy of goals and subgoals, and only the main goal is transferred to the imitator's motor system, not necessarily resulting in a similar motor pattern. The perceived main goal triggers those motor routines that are most strongly associated with achievement of this goal in the observer's own motor repertoire. Consequently, “these motor programmes do not necessarily lead to matching movements, although they might do so in many everyday cases” (Wohlschläger *et al.*, 2003, p. 503). This theory is supported by findings that children usually make systematic mistakes in imitation. For instance, when children are asked to imitate certain contralateral hand movements (e.g. touching the left ear with the right hand), they often imitate the goal, touching the ear, but do so with the ipsilateral effector (Bekkering *et al.*, 2000; Gattis, Bekkering, & Wohlschläger, 2002). Similar effects have been found in adults undertaking more difficult or speeded tasks (Wohlschläger *et al.*, 2003).

Summary

The findings reported in this section all provide evidence for direct matching. They indicate rapid, automatic, and bi-directional visuomotor couplings and thus ground and extend the work on imitation learning reported in Section 1. Also in the studies on concurrent interactions, we have not encountered reports of “photographic copying”, which is in line with Koffka's (1925/1980) claim. Thus, the emphasis of the theory of goal-directed imitation on imitative performance as emerging from the observer's own motor repertoire, although perhaps trivial, is important. Nevertheless, the possible existence of visuomotor couplings “below” the level of cognitively represented goals, perhaps one of the most fascinating topics in imitation research, seems to be programmatically excluded from the theory of goal-directed imitation – unless one wants to conceptualize *any* aspect of an observed action as a potential goal, in which case the theory becomes undifferentiated and difficult to falsify. Regarding future behavioural research on concurrent interactions, more research is needed to probe for the effects of subtle manipulations of the model's movement kinematics on performance. Such effects are not captured in priming studies that, to date, have mostly used categorically distinct displays (e.g. fist vs. flip). However, subtle manipulations are not always successful. In a pilot study reported in Vogt (2002), modulations in the model's reaching movements were simply not copied.

The similarities and differences between the current theories are too complex to capture in the present context, but a few notes are worth making.

The theory of event coding has been criticized for ignoring the complexity of visual and motor processing (see commentaries in Hommel *et al.*, 2001) and for singling out a particular level of “late perceptual” and “early motor” processing as privileged for code commonality, given that sensori-motor interactions can be found on practically all levels of the sensori-motor system. Among the theories reviewed, Heyes’s (2005) associative account best encompasses imitation learning. In addition, it is a challenge to any theory that assumes structural similarity between sensory and motor representations, rather than their contiguity to govern the strength of visuomotor interactions (see also Keyser & Perrett, 2004), just as behaviourism was a challenge for Koffka. Brass and Heyes (2005) classify both Prinz’s (2005) ideomotor and Heyes’s (2005) associative sequence learning accounts as “generalist theories” of imitation, given that they rely on general mechanisms of learning and motor control, including the ideomotor principle. In associative sequence learning, this generality is programmatically wide, with the risk of losing sight of human-specific imitation capabilities. Byrne (2003, 2005) has made a strong case for imitation as a special faculty. He suggests that the capacity for imitation learning, requiring powerful cognitive processes of de- and re-composing complex behaviour, might have co-evolved with the perceptual decomposition power of the mirror neuron system that had originally evolved in response to social needs, namely action understanding (Byrne, 2005; see also Arbib, 2005; Lyons, Santos, & Keil, 2006). With this pointer to ethology and evolution – yet another area of imitation research not covered in the present review – we now turn to neurophysiological mechanisms.

3. Neurophysiological and neuroimaging studies

In object-oriented actions, individual visual properties such as object size and orientation are directly coupled to parameters of execution such as grip aperture and hand orientation (Jeannerod, 1996). Building on this well-studied and neurophysiologically grounded concept of *visuomotor channels*, Vogt (2002) proposed a strict analogy between object-oriented and imitative actions. The main idea was that a similar “piecemeal” specification of action as in object-oriented actions might also be operational in imitative actions. This would imply (1) that the parameters of motor control are at least overlapping between object-oriented and imitative actions, and (2) that the visual processing of observed actions is capable of structuring the visual input in terms of the same parameters. For example, an observed hand opening could then be directly matched to the

observer’s corresponding parameter of motor control. The second assumption is the more speculative of the two, but Wilson and Knoblich (2005) have recently put forward a similar argument in support of their motor-visual account of action perception. As will become clear in the following, the available neurophysiological studies with monkeys do not seem to provide support for Vogt’s (2002) proposal of parameter-wise visuo-motor matching and are indeed more compatible with a high-level specification of direct matching. Nevertheless, for the human case more research is needed for a final verdict.

3.1. Mirror neurons in the macaque monkey

The study of neural correlates of action representation has a long history. Allers and Scheminzy (1926) recorded electromyographic (EMG) activity of human participants while they imagined performing certain actions, and the experimenters were able to “guess” the imagined action from the amplified, audible signal (see also Jacobson, 1932; Wehner, Vogt, & Stadler, 1984). Berger and Hadley (1975) studied EMG correlates of action observation and found that arm EMG activity was stronger when participants watched wrestling actions, and that lip EMG activity was stronger for stuttering. Although the phenomenon of motor involvement during representing actions, either via imagery or during observation, was thus known for a long time, its cortical mechanisms were left unspecified by these early studies.

The discovery of “mirror neurons” (DiPellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese *et al.*, 1996) has provided an important insight into the possible neural implementation of links between action observation and execution. Mirror neurons discharge both when individuals perform a specific goal-directed action and when they observe another individual executing the same, or a related, action. The synchrony between temporal landmarks of the observed action (e.g. finger closure during grasping) and the neuronal firing is strict and impressive. Neurons with mirror properties have first been found in premotor area F5c in the macaque monkey. Area F5c forms a circuit with posterior parietal area PF, which also contains neurons with mirror properties (Fogassi *et al.*, 2005; Gallese, Fadiga, Fogassi, & Rizzolatti, 2002). Both areas together form the mirror neuron system [the possible human homologues of these areas are shown in Figure 2: PMv and dPO/vPO are likely homologues of F5, and the inferior parietal lobule (IPL) is the likely homologue of PF; see Section 3.2]. Area PF receives input from the superior temporal sulcus (STS), which is devoted to the visual processing of posture and movement of conspecifics (Allison, Puce, & McCarthy, 2000;

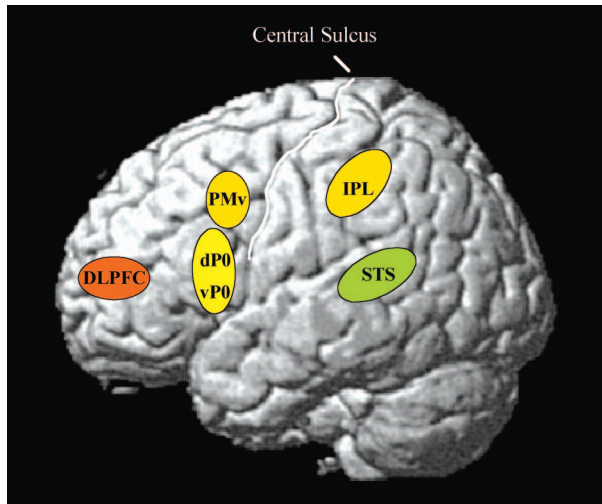


Figure 2. Some of the human cortical areas involved in action observation, imitation, and/or imitation learning, superimposed on a single subject anatomical template (Holmes *et al.*, 1998). DLPFC = dorsolateral prefrontal cortex; PMv = ventral premotor cortex; dPO and vPO = dorsal and ventral sectors of pars opercularis of inferior frontal gyrus respectively (together with the rostrally adjacent pars triangularis of inferior frontal gyrus, not shown, these regions form Broca's area); IPL = inferior parietal lobule; STS = superior temporal sulcus.

Jellema, Baker, Oram, & Perrett, 2002; Keysers & Perrett, 2004). Thus, F5c is not only dedicated to motor planning and execution (Rizzolatti *et al.*, 1988), but it also engages in matching observed actions that are initially processed in higher-order visual areas to its "motor vocabulary". Schubotz and von Cramon (2004) even state that the classical "motor planning" concept of the premotor cortex is now superseded by that of a "multipurpose action – perception matching interface" (p. 5472).

Although it might be tempting to conclude that F5c mirror neurons translate any observed action, familiar or novel, into a motor representation ready for execution, this conclusion would be ill grounded. Empirically, it is hampered by the fact that imitative behaviour has never been observed in the context of the above studies and, more generally, by the lack of evidence for imitative behaviour in macaques (Tommasello & Call, 1997; Visalberghi & Fragaszy, 2002). Macaques can, however, recognize if their actions are concurrently imitated by an experimenter, as recently demonstrated using a preferential looking paradigm (Paukner, Anderson, Borelli, Visalberghi, & Ferrari, 2005). Furthermore, viewing the mirror neuron system as a transducer of any biological motion input into corresponding motor commands would ignore two important characteristics of F5c neurons, *semantic coding* and *distal reference*, as well as the *postulate of motor origin*.

Semantic coding. A humanoid robot with near-perfect, low-level imitative tracking capabilities (e.g.

to accommodate anatomical differences between actor and imitator) might be computationally conceivable, but the architecture to support such imitative visuo-motor matching would almost certainly require modules with properties different to those of F5c mirror neurons. Area F5c codes primarily high-level, semantic properties of goal-oriented actions (e.g. "retrieving an object" or "cracking a peanut") and tends to abstract from motor details such as the effector used (right or left hand, or even hand or mouth) or the speed in which a movement is performed (Rizzolatti & Craighero, 2004). Thus, an attempt to reconstruct the kinematic details of an observed action from the collective activity of F5c mirror neurons would very likely fail. Rather, from the outset, the prevalent interpretation of the biological function of mirror neurons in monkeys has been that of *understanding* observed actions, by matching them to the observer's own motor repertoire (Rizzolatti & Craighero, 2004; Rizzolatti *et al.*, 2001); in other words, by placing the observed action into a motor semantic network (Rizzolatti, 2005a). This function includes extrapolating hand-object contact in partially occluded actions (Umiltà *et al.*, 2001) and context- or intention-dependent action coding (Fogassi *et al.*, 2005).

Distal reference. The latter interpretation is further supported by research indicating that proximal stimuli that engage a particular F5c mirror neuron do not need to exhibit surface similarity to its motor properties. A clear-cut demonstration of this is Kohler and colleagues' (2002) finding that F5c neurons also respond to action-related sounds, such as tearing paper. Mirror neurons thus seem to engage in uncovering the underlying distal motor event from various associated proximal stimuli (Wilson & Knoblich, 2005).

The postulate of motor origin. At present, the developmental origin of mirror neurons is unknown. Is the selective connectivity from posterior areas to F5c hard-wired, or is it largely shaped by experience? Rizzolatti and Luppino (2001, p. 897) speculated that initially a link between a certain motor prototype (area F5c) and the vision of the agent's own hand (areas STS and PF) is formed with experience and that this link is only subsequently generalized to the hands of other individuals (see also Arbib, 2005; Keysers & Perrett, 2004). We call this the *postulate of motor origin* of the action-related semantic network: meaning emerges from self-performed action and its consequences. Accordingly, only observed actions that are already in the observing monkey's motor repertoire should engage F5c mirror neurons. This view has recently been qualified by Ferrari, Rozzi,

and Fogassi (2005) with their demonstration of tool-responding mirror neurons. In previous studies (Gallese *et al.*, 1996, Rizzolatti, Fadiga, Gallese, & Fogassi, 1996), display of actions with tools had indeed not modulated the firing of mirror neurons. In Ferrari and colleagues' (2005) study, the monkeys had been visually exposed to tool actions (using a stick and a pair of pliers) over several months, and the most likely explanation for their positive finding is that an already established motor meaning, the "taking possession of an object", was eventually generalized from hand actions to the tool actions (p. 221). Thus, this finding is compatible with the postulate of motor origin. Although the tool actions were eventually represented in the mirror system, they were not translated into the monkeys' motor repertoire: no attempts to imitate tool use were observed, as one might predict if mirror neurons were visuo-motor transducers. Once more, Ferrari and colleagues' study underlines the abstract, high-level nature of coding in F5c mirror neurons, and it cautions against the ill-grounded view that observed actions represented in area F5c should be readily available for imitative execution.

Before we move on to the mirror neuron system in humans, it is important to locate the monkey's mirror system in a wider context. The PF–F5c circuit is only one of a number of segregated parieto-premotor circuits that are devoted to specific sensorimotor transformations and operate in parallel (Jeannerod, Arbib, Rizzolatti, & Sakata, 1995; Rizzolatti, Luppino, & Matelli, 1998). A good example is the AIP–F5ab circuit, which consists of the monkey's anterior intraparietal area and of F5ab "canonical neurons" – a different subpopulation of F5 than F5c mirror neurons (Rizzolatti & Craighero, 2004). The AIP–F5ab circuit is involved in the moment-to-moment transformation of intrinsic three-dimensional object properties, such as size and orientation, into motor parameters of grip formation. Whereas F5ab neurons also fire during object observation in the absence of overt movement (Murata *et al.*, 1997), they are more typically involved in guiding overt action. Thus, the on-line, low-level coupling of parametric aspects of the visual world to motor output is certainly not out of reach for monkey brains. Moreover, such couplings are critical for survival and have a long evolutionary history (Goodale, 1995).

Given the formal similarity of the AIP–F5ab and the PF–F5c circuits, one might find it puzzling that only one of these circuits, AIP–F5ab, engages in the on-line translation from vision to overt action, whereas F5c mirror neurons are, at a given point in time, either involved in execution or observation, but not in both simultaneously. There are at least three plausible explanations for this discrepancy: First, the

primary biological function of F5c mirror neurons, action understanding, does not require overt recapitulation of the observed action. Second, it is most likely computationally more demanding to couple one's own action to an ongoing action of another person than to a static or linearly moving object. Third, in stark contrast to object-oriented actions, the capacity for on-line behavioural copying is not immediately useful: "In everyday life, copying an action is typically useless and frequently dangerous. If an animal observing a conspecific eating some food imitates its movements, it will never get the food" (Rizzolatti, 2005b, p. 55). Humans are much more ready to engage in such immediately useless behaviour (see Section 3.2).

In contrast to the macaque, great apes exhibit imitative behaviour, even according to the strict criteria of ethologists that include the novelty of the action. Interestingly, Byrne and Russon (1998) proposed that the imitative capabilities of non-human primates might be best characterized by "program-level imitation", which they define as imitation of high-level, strategic aspects of an observed action, and contrast with "action-level imitation" of specific, low-level details. This proposal is consistent with the high-level, semantic properties of mirror neurons in the monkey. On an evolutionary scale, it would suggest an increasing access of overt action to the details or nuances of the observed behaviour, namely from mainly high-level aspects of the observed action in monkeys to optionally including low-level motor properties in humans (for recent comparative evidence, see Horner & Whiten, 2005; Lyons *et al.*, 2006; for the distinction between high-level and low-level resonance, see Rizzolatti, Fadiga, Fogassi, & Gallese, 2002). However, at present no neurophysiological studies regarding a mirror neuron system in great apes are available, and with the advent of brain imaging techniques such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI), researchers have moved on to study neural correlates of action observation and imitation directly in the human brain.

3.2. *The human mirror neuron system and imitation*

In the first phase of imaging studies on the human mirror neuron system (MNS), starting in the mid-1990s, researchers were primarily aiming to verify if action observation would also engage motor areas of the human brain. As a result, a large number of studies employing electroencephalography (EEG), magnetoencephalography (MEG), transcranial magnetic stimulation (TMS), PET, and fMRI indicated that this is indeed the case (for reviews, see Fadiga & Craighero, 2004; Iacoboni, 2005; Rizzolatti

& Craighero, 2004; Rizzolatti *et al.*, 2001; Wilson & Knoblich, 2005). As in the monkey, the human MNS consists of two key regions: (1) the caudal part of the inferior frontal gyrus (IFG, pars opercularis) plus the adjacent ventral premotor cortex (PMv), and (2) the rostral part of the inferior parietal lobule (IPL; see Figure 2). [For the likely anatomical correspondence of these areas with the monkey's F5c–PF circuit, see Rizzolatti and Arbib (1998) and Grèzes, Armony, Rowe, and Passingham (2003).] Also, the primary motor cortex (Hari *et al.*, 1998; Järveläinen, Schürmann, & Hari, 2004; Nishitani & Hari, 2000, 2002; Tremblay *et al.*, 2004) and dorsal premotor cortex (Buccino *et al.*, 2004c; Grèzes *et al.*, 2003; Leslie, Johnson-Frey, & Grafton, 2004) have been found to be activated during action observation. As in the monkey studies, the human superior temporal sulcus was found to be involved (see Saxe, 2006), and it is likely that it acts as a visual relay to IPL and frontal lobe structures (e.g. Nishitani & Hari, 2000, 2002). Based on the latter MEG studies, Nishitani, Schürmann, Amunts, and Hari (2005) described the activation sequence during the imitation of lip movements as originating in occipital visual cortex and followed in 20- to 60-ms steps by STS, IPL, IFG, and finally primary motor cortex.

The overlap between cortical structures involved in action observation and imitation has also been assessed, and more recently researchers have begun to study the observation and imitation of novel actions. In the following, we review selected studies on observation and imitation of familiar actions, and in Section 3.3 we turn to neural correlates of expertise and imitation learning.

Whereas most of the early studies on action observation used displays of hand actions, Buccino *et al.* (2001) showed that a wider repertoire of actions, including mouth and foot actions, are represented in the human MNS, and that, in contrast to the monkey's MNS, pantomimed movements can engage the human MNS (see also Grèzes *et al.*, 2003). Further studies indicated that the human MNS can be activated by the observation of intransitive actions (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Iacoboni *et al.*, 1999; Maeda, Kleiner-Fisman, & Pascual-Leone, 2002; Sakreida, Schubotz, Wolfensteller, & von Cramon, 2005; Wheaton, Thompson, Syngeniotis, Abbott, & Puce, 2004) and not only by object-oriented actions as in the monkey. In addition, the human MNS appears to code the time course of the observed action (Gangitano, Mottaghy, & Pascual-Leone, 2001). These studies confirm that the human MNS is better prepared for coding the low-level details of an observed action than that of the monkey (see Section 3.1), the capacity of which is potentially beneficial for socially motivated imitation as well as for imitation

learning. Nevertheless, like the monkey's MNS, the human MNS is highly capable of coding action goals (e.g. Johnson-Frey *et al.*, 2003), including inferring intentions from others' actions (Iacoboni *et al.*, 2005; but see Jacob & Jeannerod, 2005).

As is apparent from Section 3.1, the availability of a MNS does not grant imitation capabilities. Similarly, before Iacoboni and colleagues' (1999) study, it was unclear if human imitation would rely on the MNS or on other brain structures. Building on the paradigm by Brass *et al.* (2000), Iacoboni *et al.* (1999) used a minimalist display, the movement of a single finger, and directly compared cortical activations during action observation and on-line imitation. They found two areas were involved in both tasks: the pars opercularis of the left inferior frontal gyrus, and the right anterior parietal region. Iacoboni *et al.* (1999) interpreted the frontal activation to reflect the motor goal ("lift the finger") and the anterior parietal activation to reflect the precise kinaesthetic aspects of the movement (e.g. how much the finger should be lifted).

Based on a reanalysis of seven fMRI studies from Iacoboni's laboratory, Molnar-Szakacs, Iacoboni, Koski, and Mazziotta (2005) recently proposed a division of labour within the pars opercularis (PO) of the left inferior frontal gyrus. They found its dorsal-most sector (dPO) involved in both observation and imitation, whereas its ventral sector (vPO) was only activated during imitation. The authors conclude that the dorsal-most sector of the pars opercularis "shows mirror properties that may allow one to understand an observed action by matching it to one's own neural representation of that action, and its ventral most sector likely contains neurons with functional properties that allow forward modeling in a network with posterior, higher order visual neurons in STS" (p. 992). A related ventral-wards shift within the pars opercularis from observation to motor preparation and execution was found for more complex actions (Buccino *et al.*, 2004c; Vogt *et al.*, 2006). Iacoboni (2005) suggests three stages in which imitative actions might unfold: (1) an initial pictorial description of the observed action in the superior temporal sulcus is followed by (2) coding of the action goal and the means to achieve it in the frontoparietal MNS, and (3) efferent copies are sent from the MNS (in vPO) back to the superior temporal sulcus, "where there is a matching between the predicted sensory consequences of the planned imitative action and the visual description of the observed action" (p. 634).

Consistent with our discussion of the monkey's MNS, Iacoboni and colleagues (see also Miall, 2003) do not seem to imply a putative instant and perfect visuo-motor transduction in the human MNS. They essentially propose a feedback-based system

reminiscent of Meltzoff and Moore's (1997) iterative and comparison-based model of facial imitation in infants. In contrast to the latter, however, Iacoboni's conceptualization allows for internal feedback-based corrections in advance of overt execution. To summarize, what is initially transferred from vision to motor areas is not a detailed, low-level motor programme, but more likely an action prototype or action meaning (in dPO), which then guides motor planning and fine-tuning according to a more detailed representation of the observed action represented in superior temporal (STS) and posterior parietal (IPL) areas.

In the case of object-oriented actions, it is plausible that this fine-tuning further incorporates information about the object. In support of this, Buccino *et al.* (2001) found evidence for object-related processing in parietal areas already when participants were watching object-oriented actions, without the intention to imitate. Participants were most likely using their object-oriented processing circuit (analogous to the AIP–F5ab circuit in the monkey) and their mirror neuron circuit in parallel. The study by Grèzes *et al.* (2003) provides an in-depth analysis of both circuits in humans.

In more recent research, numerous further issues about the human MNS have been explored, for example its lateralization (Aziz-Zadeh, Koski, Zaidel, Mazziotta, & Iacoboni, 2006; Mühlau *et al.*, 2005), inhibitory mechanisms (Alegre, Lazaro, Valencia, Iriarte, & Artieda, 2006; Brass, Derrfuss, & von Cramon, 2005), perspective effects (Jackson, Meltzoff, & Decety, 2006; Koski, Iacoboni, Dubeau, Woods, & Mazziotta, 2003), motor versus visuo-spatial representations (Chaminade, Meltzoff, & Decety, 2005), and the extent to which robot-like (Tai, Scherfler, Brooks, Sawamoto, & Castiello, 2004; but see Press, Bird, Flach, & Heyes, 2005) or biomechanically impossible displays (Costantini *et al.*, 2005) elicit activations in the MNS. A further focus of current research is the conspicuous multi-functionality of the human inferior frontal gyrus beyond action recognition and imitation. In the left hemisphere, pars opercularis and pars triangularis of the inferior frontal gyrus (corresponding to Brodmann's areas 44 and 45, respectively) form Broca's area, an area known for its involvement in speech production and recognition (Bookheimer, 2002). Although this co-location of action and speech coding has a fascinating and plausible evolutionary origin (Arbib, 2005; Rizzolatti & Arbib, 1998) and likely reflects the matching of rapid sequential motor and sensory events as a common requirement in speech and action domains (Nishitani *et al.*, 2005), this co-location can nevertheless be seen as a possible confound for imitation research, in the sense that activations in Broca's area might reflect silent

naming of the observed actions. Hamzei *et al.* (2003) found an overlap of activations in Broca's area for action recognition and verb generation, supporting the hypothesis of a shared anatomical substrate for both functions, although activation peaks for both tasks were always different in individual participants. More recently, Higuchi, Imamizu, Chaminade, and Kawato (2004) identified a sector of Broca's area (dPO) shared between listening to speech and motor imagery of tool use, in addition to other, non-overlapping regions. Their tool use tasks were unlikely to involve naming. More likely, these results reflect shared computational requirements between language and tool use, such as the sequential application of learned rules. Furthermore, the transcranial magnetic stimulation (TMS) study by Heiser, Iacoboni, Maeda, Marcus, and Mazziotta (2003) indicated identical impairments of imitation performance induced by repetitive TMS applied to pars opercularis of either left or right inferior frontal gyrus, which is not compatible with a (lateralized) linguistic mediation hypothesis and thus seems to indicate the "essential role of Broca's area in imitation" (*ibid.*). This debate is ongoing, however (for a contrasting conclusion, see Makuuchi, 2005), and we thus refrain from a final judgement in the present context.

3.3. Neural correlates of expertise and imitation learning

Naturally, the focus of interest for the sport sciences regarding the MNS is on imitation learning (observational learning) – that is, the imitation of actions not yet in the behavioural repertoire of the observer. Whereas the studies discussed above used relatively simple and highly practised movements, only a handful of studies are available to date that directly address imitation learning or expertise effects in action observation. The basic idea that action observation might not only exert concurrent effects but also affects (within-session) motor memory was only recently confirmed in the elegant TMS study by Stefan *et al.* (2005). They demonstrated that an extended period of observing repetitive thumb movements biased subsequent TMS-evoked thumb movements to fall within the direction of the observed movement. Effects of expertise on the MNS were analysed in the MEG study by Järveläinen *et al.* (2004). As predicted, observation of either object-oriented use of chopsticks or of non-goal-oriented tool use both produced a suppression of the ~20 Hz motor-cortex rhythm in response to median nerve stimulation; however, "no significant correlations were found between rebounds and the self-evaluated chopstick proficiency" (p. 189). Nevertheless, the difference between object-oriented and meaningless tool use was positively correlated

with the participants' frequency of using chopsticks over the last 12 months (ranging from 2 to 20 times in their sample). That is, motor and/or visual experience enhanced the selective attunement to meaningful, object-oriented actions.

Calvo-Merino, Grèzes, Glaser, Passingham, and Haggard (2006) pursued this issue further using fMRI by contrasting cortical activations when dancers with expertise in either classical ballet or capoeira watched videos of either style of dance. Activations in the MNS were stronger when participants watched the dance in which they were experts, whereas the same areas were not differentially activated in non-expert control participants. The results of this study could be explained by visual or motor experience, but in a further study the authors singled out the effect of motor expertise by using gender-specific ballet displays (Glaser, Calvo-Merino, Grèzes, Passingham, & Haggard, 2004). They obtained essentially the same effects as in the first study, thus confirming Calvo-Merino and colleagues' (2005) conclusion that "action observation evokes individual, acquired motor representations in the human mirror system" (p. 1248), rather than a disembodied, neutral description. The results are thus nicely in line with the "postulate of motor origin" of action understanding as discussed above. However, the instruction to assess, during the scanning, "how tiring" participants thought each movement was, has likely contributed to their selective motor engagement. It is thus important to assess to what extent the results depended on the particular instructions used (see below).

In imitation learning, the objective is to incorporate an unfamiliar observed action into one's own motor repertoire. Buccino *et al.* (2004c) investigated the initial stage of this process in a study where non-guitarists were scanned while imitating unfamiliar guitar chords, each of which was presented only once. An event-related fMRI paradigm was employed, in which the three stages of each trial – action observation, motor preparation, and execution – could be analysed separately. Results indicated that: (1) the MNS was strongly activated in this condition throughout the three stages of a trial; (2) activations in the MNS were markedly stronger during observation in order to imitate than during observation without purpose; (3) the MNS could also be activated endogenously (in the preparation and execution of events) in a condition where participants saw an empty guitar neck and were asked to plan and execute a chord of their own choice (EXE); and (4), in addition to the MNS, the left dorsolateral prefrontal cortex (DLPFC) was found to be activated during motor preparation of imitative and internally guided execution (IMI and EXE).

To begin with the latter finding, the prefrontal cortex has been shown to be involved in a variety of motor and cognitive tasks particularly in the early stages of learning, when novel mappings between sensory inputs and motor output are created and the requirements for supervisory control, including the modulation of lower-level systems and monitoring the success of ongoing behaviour, are high (Kelly & Garavan, 2005; Miller & Cohen, 2001; Shallice, 2004). As the most likely interpretation of the role of the DLPFC in the chord task, we suggested that this area engages in the *selection* and *recombination* of motor elements as represented in the MNS (for a comparison of this account with a working memory account, see Passingham & Sakai, 2004; Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000).

In a second study (Vogt *et al.*, 2006), we directly contrasted the imitation of novel and practised chords, assuming that the practised chords would attract less supervisory control (in the sense of selection and recombination operations) than the novel chords. As expected, the DLPFC was found to be more strongly involved in observation and preparation of the novel chords. Nevertheless, one might be surprised to find a cortical area known for high-level supervisory control engaged in a task that just required the copying of a given hand posture from a spatially compatible display, and that it was activated to the same extent regardless if a chord model was visually available or if the instruction was to make up a chord in the absence of a visual model as indicated by result (3) above. These findings fit in with the general theme of this section, namely that imitation is not plainly a process of visuo-motor transduction, but that it is assisted by processes of aligning predicted and desired effects, and, in the case of imitation learning, of selecting and possibly restructuring existing motor representations. In conclusion, imitation learning seems to exhibit a remarkable overlap with other, apparently more creative, forms of motor learning.

Also, activation of the MNS during the observation of unfamiliar actions in Buccino *et al.* (2004c) might be viewed as unexpected, given Buccino and colleagues' (2004b) finding that the human MNS was more strongly involved when participants watched actions of non-conspecifics that could be mapped onto the observer's motor system than for actions without such a possible mapping, such as a dog barking. Our interpretation is that, in the chord task, participants were well capable of motorically representing individual finger movements, and that this was reflected by the premotor activations. Interestingly, observation and motor preparation of practised chords evoked significantly weaker activations in the MNS than that of novel chords (Vogt *et al.*, 2006), a finding apparently in direct contrast to that of Calvo-Merino

et al. (2005, 2006); see also the recent study by Cross, Hamilton & Grafton (2006). Several factors could have contributed to this result, including the more frequent “checking” of individual finger positions and the stronger top-down modulation of the MNS in the case of the non-practised chords. A clear-cut prediction from our findings is that activation intensities as reported in Calvo-Merino *et al.*, (2005, 2006) should reverse if participants are instructed to watch familiar and novel dance styles with the intention of imitating them later.

Zentgraf *et al.* (2005) recently found that observation of sequential gymnastics movements induced stronger activations in the MNS (left inferior parietal lobule and PO of left inferior frontal gyrus) when participants were instructed to watch with the intention to imitate, compared with observation to judge the quality of performance. The authors did not manipulate participants’ familiarity with the observed actions, thus no direct conclusions can be drawn regarding our prediction above, but Zentgraf and colleagues’ study demonstrates the sensitivity of activations to different instructions (see also Grèzes, Costes, & Decety, 1998). In addition, they found that the supplementary motor area (SMA) was differentially activated by the two instructions, with the pre-SMA found to be more strongly activated for the evaluative instruction, and the SMA proper more strongly activated for the imitation instruction. Zentgraf *et al.* (2005) explained the latter finding by the requirement to transform the observed movement sequences to body-centred coordinates.

4. Summary and conclusions

The direct matching hypothesis holds that we “understand actions when we map the visual representation of the observed action onto our motor representation of the same action” (Rizzolatti *et al.*, 2001, p. 661). It was originally formulated in the context of the neurophysiological mechanisms of understanding and imitating action, as reviewed in the previous section. We have examined the related research with an emphasis on the particular aspects of observed actions that are assumed to be represented in the MNS, specifically regarding its putative capacity for a “piecemeal”, low-level specification of a motor representation by an observed action (Vogt, 2002). For the MNS in macaque monkeys, the prominent characteristics of semantic coding and distal reference are not in line with this view of the MNS as a visuo-motor transducer. In addition, imitation behaviour is not typically found in macaque monkeys, but they are capable of recognizing when they are being imitated. Accordingly, direct matching in the monkey is likely to subservise two functions: action recognition and imitation recognition. Action

recognition (Buccino, Binkofski, & Riggio, 2004a; Rizzolatti & Craighero, 2004) is based on the observing animal’s capability to perform the observed action, and imitation recognition (Paukner *et al.*, 2005) is based on the observing animal’s current behaviour and its match to the observed behaviour. For action recognition, semantic coding and distal reference are useful functional properties, and presumably a motor representation of the low-level kinematics of the display is neither required nor useful. More research is needed to clarify if imitation recognition in the monkey is sensitive to correspondence in low-level kinematic properties, or if it relies on similar high-level coding as is assumed for action understanding.

The human MNS shows an enhanced capacity for representing and imitating observed actions in many respects. One prominent aspect is the enhanced hierarchical depth of parsing and planning (Byrne & Russon, 1998); another is the coding of low-level details such as the time-course (Gangitano *et al.*, 2001) and even task-irrelevant aspects of the observed action (Horner & Whiten, 2005). Nevertheless, recent modelling of subcomponents of the human MNS (Molnar-Szakacs *et al.*, 2005) does not seem to imply that a low-level motor programme is generated during action observation that is ready for accurate execution, and no neurophysiological or behavioural evidence for such a putative, instant visuo-motor transduction is available to date.

Direct matching is direct since it occurs almost instantly, as indicated by both the behavioural work reviewed in Section 2 and by neuroimaging work (Nishitani *et al.*, 2005). Furthermore, direct matching involves a matching and no transduction. Also, Rumiati and colleagues’ (2005) recent PET study, which builds on multiple route models from neuropsychology, is compatible with this view. According to the authors, the dissociation found between “direct” and “indirect” (semantic) routes for action imitation of meaningless and meaningful actions, respectively, does *not* imply that observers “simply map the action seen directly into a motor output” (p. 1429).

The effects of observational practice in a wide spectrum of motor tasks, as reviewed in Section 1, are likely to be due to a number of distinct neurocognitive mechanisms. Direct matching is one highly probable candidate, and more work would be desirable on the interaction between short-term visuomotor priming and observational learning. In addition, supervisory control processes are not only involved in non-imitative motor learning but also play a crucial role in observational learning. Both aspects, direct matching and supervisory control, have been combined in Buccino and colleagues’ (2004c) minimalist model of imitation learning. We proposed that the observed activations of the

MNS reflect the motor representation of familiar elements in the display. In addition, prefrontal structures engage in supervisory control of this process, resulting in a restructuring of the motor elements to form a novel motor action.

In conclusion, imitation learning is first and foremost *learning*. Although observing experts and learners can strongly impact on one's own performance in various ways, motor expertise cannot be propagated between individuals within the blink of an eye. In light of the available evidence for direct matching, future research can now be directed towards exploring the neurocognitive mechanisms of observational as well as physical practice in greater detail. Whiting *et al.* (1987) interpreted their results with reference to a statement by Ricoeur (1966), with which we wholeheartedly agree:

“Whatever explanation is adopted, it has to deny the reflex character of imitation forcefully: imitation never presents the stereotyped, isolable, irrepressible characteristics of a reflex. A similar action... is a power of regulation and not of mechanical production” (p. 248).

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