



Action Imitative and Prediction Error–Induced Contagions in Human Actions

Hiroki Nakamoto, Tsuyoshi Ikegami, Gowrishankar Ganesh

► To cite this version:

Hiroki Nakamoto, Tsuyoshi Ikegami, Gowrishankar Ganesh. Action Imitative and Prediction Error–Induced Contagions in Human Actions. *Handbook of Embodied Cognition and Sport Psychology*, The MIT Press, pp.381-412, 2019, 978-0262038508. lirmm-02159036

HAL Id: lirmm-02159036

<https://hal-lirmm.ccsd.cnrs.fr/lirmm-02159036>

Submitted on 18 Jun 2019

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Title: Action-driven and prediction-driven contagions in human actions

Authors: T. Ikegami¹, H. Nakamoto², G. Ganesh³

Affiliations: ¹Center for Information and Neural Networks, National Institute of Information and Communications Technology, 1-4 Yamadaoka, Suita city, Osaka, 565-0871, Japan.

²Faculty of Physical Education, National Institute of Fitness and Sports in Kanoya, Shiromizu 1, Kanoya, Kagoshima 891-2393, Japan.

³CNRS-AIST JRL (Joint Robotics Laboratory), UMI3218/RL, Intelligent Systems Research Institute, 1-1-1 Umezono, Tsukuba, Ibaraki 305-8568, Japan.

Acknowledgements:

This work was partially supported by JSPS KAKENHI Grant #16H05916 and #26120003 (to T.I.), #16K12999 and #26702025 (to H.N.), and #15616710 and #13380602 (to G.G.). The authors declare no competing financial interests.

Abstract

Human actions are affected by “motor contagions”; implicit effects on an observer’s actions caused by viewing other people’s actions. Though these contagions are ubiquitous, affecting speech, gestures, everyday movements and sports, the mechanisms underlying them are still not fully understood. In this chapter we will review the known forms of motor contagion and show that they can be characterized into two types. First, action driven contagions, which include most previous contagion reports and which manifest as similarities between specific features (like the kinematics, outcome or goal) of an individual’s action, and an action they observe. Second, prediction driven contagions, which we define here and which have only recently begun to be explored, are driven by differences between predictions of how another will act and observations of how they actually do act. These lead to implicit modifications of the motor representations in an individual but may not manifest as similarities between action features. We will explore the conceptual mechanisms that can explain these contagions and propose an extension to the previously suggested *Dual Route Model* of sensorimotor processing so as to explain the entire contagion spectrum. Finally, in the light of this characterization, we will discuss possible strategies to control, prevent and compensate for motor contagions, and optimize performance by athletes.

1. Introduction: Motor contagion

The next time you see a corner kick in a soccer match, make note of a strange and funny behavior;

when the ball flies into the goal area, you will notice that it is not just the strikers and defenders (around the strikers) who jump to try to *head* the ball, but in fact most of the players on the field, even those who are nowhere near the ball, execute a jump in synchrony. The jumps by the other players are smaller, unconscious (players asked later report not being aware they had done it), and obviously serve no purpose as they are far from the ball, sometimes even outside the penalty area. The behavior shows that our own actions are affected by environmental cues and behaviors observed in others, probably due to an overlap of action production and action perception processes in the brain Rizzolatti and Craighero (2004); (Blakemore and Frith 2005). This overlap leads to a blurring of differences in the sensorimotor system, between one's actions and perceptions of other's actions by oneself, and is a core feature of embodied cognition (Shapiro 2010).

Right from birth, action observation and subsequent imitation (Meltzoff and Moore 1977; Cook et al. 2014; Stahl and Feigenson 2015; Piaget and Cook 1954) play a key role in the development of our motor behaviors. *Imitation learning* is an explicit process where an individual consciously copies actions he/she observes in others, and it is believed to be crucial for optimizing behaviors in high dimensional systems, like our body (Schaal 1999; Schaal, Ijspeert, and Billard 2003). However, there exists a second category of observation-induced action modifications, like the soccer example, that are unconscious, affect behaviors without an individual willing it, sometimes serve no discernible purpose, and often occur even without an individual realizing it. These so called *motor contagions* include a wide range of effects on an individual's action intention, goal or kinematics, and are arguably still not completely understood. In this chapter we will review the different motor contagions reported in the literature. We will show that, while most contagions are driven by features like the kinematics, intentions or goals of observed actions, and lead to an increase in similarity between one's actions and those observed in others, other contagions do not manifest as an increase in similarity to observed actions. We will discuss the possible mechanisms underlying this second category of motor contagions and propose an extended conceptual model to explain the complete contagion spectrum. Based on these discussions, we will then analyze how athletes may control, prevent and compensate for these contagions during performance.

2. Previous characterization of Motor contagion

Over the past two decades, studies have identified a variety of motor contagions in adult human behavior (Kilner, Paulignan, and Blakemore 2003; Blakemore and Frith 2005; Chartrand and Bargh 1999; Heyes 2011). These have been characterized and given different names depending on the action feature that they affect and the context in which they are activated. We will start by reviewing these characterizations.

2-1 Automatic imitation

Automatic imitation is a covert form of imitation in which the observation of task-irrelevant body movements involuntarily facilitates one's own performance of similar movements in terms of

kinematics (Heyes 2011; Heyes 2013). Stürmer et al. (2000) examined hand opening and closing by participants while they viewed one of two hand actions on a computer screen. The color of the viewed hand changed abruptly from flesh color to either blue or red. Participants were asked to respond to the blue stimulus by opening their hand, and respond to the red stimulus by closing their hand. Although the observed action (open or close) was task-irrelevant, responses were faster when the action of the stimulus hand was compatible with the correct response than when the stimulus action was response incompatible. Observation of a compatible action clearly facilitated action execution. Brass et al. (2000) asked participants to rest their fingers on a table and observe a movie that showed the left hand of a human model on the screen and facing the participant. The participants were instructed to lift their right index finger when they observed the digit ‘1’ on a screen, and lift their right middle finger when they observed a ‘2’. The experiment included three observation conditions: in the congruent condition, the model lifted a finger corresponding to the presented number (i.e. index finger for 1 and middle finger for 2); in the incongruent condition, the model lifted a finger that did not correspond to the presented number (i.e. the middle finger for 1 and index finger for 2); and finally in the baseline condition, the model did not lift any finger. The participants showed a shorter reaction time to initiate their finger movements in the congruent condition compared to the baseline condition while they showed a longer reaction time in the incongruent condition compared to the baseline condition.

Automatic imitation is believed to be modulated by a similarity in topographical properties of body movements (Heyes 2011; Heyes 2013) such that observation of index finger movements by the model affects the participant’s index but not middle finger movements. However, the same result may also be explained by the phenomenon of spatial stimulus-response compatibility (Craighero et al. 1996; Fitts and Seeger 1953; Simon 1969) where a sensory stimulus facilitates the accuracy or speed of a response with similar spatial characteristics. To exclude this possibility, Brass et al. (2001) repeated their previous experiment (Brass et al. 2000) with a different set of movies of the human model, that were flipped upside down (Fig. 1). Even though the flipping made the observed movement incongruent in external space, the authors observed that the participants again showed a shorter reaction time when lifting or tapping a finger congruent with what they observed in the movie. This experiment indicates that automatic imitation cannot be explained only by spatial stimulus-response compatibility, and is rather a consequence of topographical movement features of observed body stimuli.

The above automatic imitation phenomena were caused by task-irrelevant stimuli that were presented over the task-relevant stimuli. On the other hand, Leighton & Heyes (2010) confirmed that automatic imitation takes place even when the task-irrelevant stimulus is presented on the left and right sides of the monitor, i.e. in the peripheral visual field, while the participant attended to a small task-relevant stimulus on the center of a computer monitor. This result shows that automatic imitation can occur when observers do not intend to pay direct spatial attention to the action stimuli and hence has the potential to affect team sports like soccer, basketball and hockey, without players

realizing it.

Automatic imitation leads not only to temporal (i.e. a change in reaction time), but also spatial interference. Kilner et al. (2003) reported an interference effect of observed biological movements on one's own movements. In their experiments, participants made rhythmic arm movements in a vertical or horizontal direction while observing an experimenter who made either similar (congruent) or orthogonal (incongruent) arm movements in front of them (facing the participants). The variability of the participant's own movements was observed to be larger in the incongruent condition, compared to the congruent condition and no observation (baseline) condition. Interestingly, this interference effect was not observed when participants observed incongruent but biologically implausible movements performed by a robot.

To examine whether automatic imitation is *really automatic*, Cook and colleagues (2012) developed a unique experimental paradigm using the rock-paper-scissors game. Their paradigm involved only two of the three rock, paper and scissors conditions. Participants were exposed to a strategic context where imitating the opponent's gesture (i.e a draw) led to a sub-optimal monetary reward. Either one or both players were blindfolded in their experiment. The frequency of a draw was at chance level (50%) when both players were blindfolded, but the researchers observed a significantly higher (than chance) level of draws when only one player was blindfolded. This result suggests that the observation of the blindfolded opponent made the player with vision unconsciously imitate the opponent's gesture even though it resulted in a loss in his/her monetary reward. Similar evidence for the automatic nature of automatic imitation is also presented by the work of Belot and colleagues (2013).

Automatic imitation can be theoretically explained by interactions between the two routes of the *Dual Route Model* of sensorimotor processing (Fig. 2) (Heyes 2011; Heyes 2013). This theoretical account originates from studies on stimulus-response compatibility (Zorzi and Umiltà 1995). The model proposes two sensory-motor processing routes. One process is via a conscious or conditional route (dashed line in Fig. 2). This conscious route is based on short-term associations between sensory representations and motor representations that can be formed immediately and flexibly through task instructions. This route accounts for task relevant actions. The other process is via an unconscious or unconditional route which is developed by long-term associations between sensory representations and motor representations developed through experience (Heyes et al. 2005; Catmur, Walsh, and Heyes 2007). This unconscious route cannot be altered directly by intentional processes and is thus automatically driven even by a task-irrelevant stimulus. During action observation, the unconscious route processes the observed action kinematics (such as movement trajectory, velocity or posture of body parts). The sensory (visual) representations of the actions then automatically activate corresponding motor representations, consequently resulting in an action with the same kinematics as the one observed. Therefore, when both task-irrelevant and task-relevant stimuli activate the same motor representation (i.e. in congruent conditions), the task performance is

facilitated. However, when the task-irrelevant and task-relevant stimuli result in the activation of different motor representations (i.e. in incongruent conditions), the task performance is hampered due to a competition between the two representations.

It is important to note here that the Dual Route Model is not the only model proposed in the literature to explain contagions (Heyes 2011; Heyes 2013). We will, however, limit our discussions to the Dual Route Model in this chapter due to its simple structure, and the fact that the issues relevant to the Dual Route Model are valid for multiple possible mechanisms.

2-2 Emulation (Intention/goal imitation)

Emulation (Byrne and Russon 1998; Whiten et al. 2009) can be considered the second category of motor contagion. Emulation leads to imitation of the intention or goal of an observed action. Emulation thus requires not just action observation, but also action understanding (Blakemore and Decety 2001; Rizzolatti and Craighero 2004; Brass et al. 2007) and has been suggested to play a role in various social functions.

In the experiments by Bekkering and his colleagues (2000; Gleissner, Meltzoff, and Bekkering 2000), pre-school children were instructed by an experimenter to “Try to imitate me as if you were my mirror. You do what I do”. The experimenter then touched either his/her left or right ear with either his ipsilateral or contralateral hand. The children consistently touched the correct ear but predominantly used their ipsilateral hand to do so, even when the experimenter used his/her contralateral hand. In other words, the subjects successfully imitated the goal of the observed action but did not imitate the action kinematics.

To confirm that the error in contralateral touch imitation was not due to difficulty in touching the ears across one’s body, the authors manipulated the saliency of the observed goal in their stimulus. They performed a control experiment in which the experimenter reached, not for their ear but, for a space in air near the ear with their contralateral hands. In this case, the same children successfully imitated the action kinematics, making significantly more contralateral touches than before. These results suggest that even pre-school children can hierarchically decompose observed actions into sub-components, at least the goal and kinematics, and when they are asked to imitate a goal-directed observed action, they tend to imitate the goal rather than the kinematics. On the other hand, they tend to imitate the kinematics for actions that are not perceived to have a goal.

Goal-imitation has also been observed in adults. Bird et al. (2007) examined imitation errors in adult participants using the pen-and-cup task, that was originally developed by Wohlschlager et al. (2003). The participants were asked to observe actions performed by a model in the video and imitate it in an anatomically compatible but egocentrically incompatible way. The observed actions were experimentally manipulated into three hierarchical action subcomponents: object (hierarchically high), effector (middle), movement path (low). In the video, the model moved a centrally located pen into one of two colored cups (objects) using either their right or left hand (effector). The action was performed with one of two different grasps (the thumb pointing up or

pointing down) leading to different arm movement trajectories. The participants showed fewer object errors than effector errors and fewer effector errors than grip errors, which is consistent with the idea that imitation of a hierarchically higher action component takes priority over the imitation of a lower one.

While the above studies explicitly instructed participants to imitate actions performed by others, a series of studies by Castiello and his colleague have shown that emulation can be implicit. Edwards et al. (2003) asked participants to observe an experimenter performing a goal-oriented action to reach and grasp either a *large* or *small* object, and then the participants performed the same grasping action for an object of similar size (congruent condition) or an object of different size (incongruent condition). The participants took a shorter time to reach peak velocity in grasps in the congruent compared to incongruent condition, implying that the observed congruent actions implicitly facilitated the participant's action performance. This observation effect appears to be similar to automatic imitation, but a clear distinction was observed in a second experiment where the participants did not observe the reaching action but observed only the reached object. Interestingly, even in the absence of an action, the time taken to reach peak velocity by participants was reduced during the congruent (object observation) condition compared to the incongruent condition. This result is therefore referred to as "automatic emulation" (Heyes 2011). Assuming that, similar to proposals for automatic imitation, a representation coding an object as an action goal may automatically activate a corresponding motor representation leading to an action required for the same goal achievement, automatic emulation may also be explained by the presence of unconscious sensory-motor processing route as in Fig. 2.

How does the understanding of intentions (hierarchically higher than the goal) behind observed actions affect one's own actions? To address this issue, Castiello (2003) developed an experiment paradigm involving motor interference due to a *distractor*. In the previous work (Castiello 1999), they had showed that a goal-directed action to a task-relevant target is implicitly affected by objects acting as distractors; when a target to be grasped by participants is presented alongside a distractor of a different size, the amplitude of peak grip aperture increased with increase in the size of the distractor. Based on this result, Castielo (2003) examined whether the interference effect was transferred between individuals through action observation or not. Participants were first asked to observe a human model who reached and grasped an object presented either in isolation or flanked by a smaller object (the distractor). They were subsequently asked to make the same action for the same target object presented in isolation. The results showed a significant transfer of interference effects from the model to the observer; the amplitude of the participant's peak grip aperture was modulated by the size of the distractor for observed actions performed by the model. Importantly, the interference effects were found even after the participants observed catch trials where the target and distractor were presented to the model, but he/she did not move (though the model was allowed to look at the objects).

Additional experiments confirmed that the interference effects occurred only when the observer

could monitor the gaze direction of the model. The effects were suppressed when the upper part of the model's body was visible but with the face invisible or when the model's gaze was constrained by asking the model to fixate on the target while performing the action. These results suggested that the motor intention of the model could be inferred by monitoring the model's gaze and, importantly, that the understanding of the model's intention could affect the observer's own actions.

Similar to goal emulation, intention emulation probably also results from the activation of motor representations corresponding to the representations coding the intention of the observed action. Therefore, this contagion may also be characterized as automatic emulation. To summarize, the observations reviewed in this section indicate that emulation is a motor contagion that results in individuals imitating the intention or goal of observed actions.

2-3 Outcome mimicry

The third type of motor contagion is one that has been reported to affect one's action outcomes (De Maeght and Prinz 2004). In a virtual reality experiment setup with baseball batters (Gray 2002), (Gray and Beilock 2011) asked batters of varied experience to hit a baseball towards the center field following observation of one of three stimuli: 1) *action*, in which a simulated ball was shown traveling from the home plate to the left, right, or center field, 2) *outcome*, in which a ball was shown resting in either the left, right or center field, and 3) *verbal*, in which the word "left", "right", or "center" was shown written on the screen. Note that the stimuli did not include any human action and only consisted of a ball traveling to a particular location, a stationary ball at a particular location in the baseball field, or merely a textual message indicating the location where the ball had landed. The researchers observed that the hits of the 'experienced' batters were affected by the action and outcome stimuli, while those of the 'less experienced' batters were affected only by the action stimuli. Specifically, if a batter observed a ball traveling to the left field, his/her subsequent hit was more to the left even though he was instructed to hit towards the center field, and if the batter observed a ball traveling right, then his/her subsequent hit was more to the right. These results can be interpreted as mimicry of the observed outcome, which we will refer to as outcome mimicry, and may partly explain the belief in baseball that "hitting is contagious" (Bock, Maewal, and Gough 2012).

Outcome mimicry has been shown of, not just observed outcomes, but also anticipated outcomes. Previous studies in sports psychology have demonstrated that expert athletes can anticipate domain-specific action outcomes rapidly and accurately by visually detecting and extracting kinematic cues inherent to an opponents' action (Abernethy and Zawi 2007; Jackson and Mogan 2007; Huys et al. 2009). Takeuchi and colleagues (2014) investigated the effect on outcome mimicry of the degree of difficulty in anticipating the outcome of a hammer throw. In their experiment, varsity hammer throwers watched videos of model hammer throwers who made throws to the left, right or center of the field. The actual flight of the hammer was occluded in the videos such that the participants could only observe the throwing action but not the hammer trajectory. Some of the throws in the video

were purposely made with exaggerated actions to facilitate the anticipation. Following the video, the participants were asked to make throws to the center of the field. There was no evidence of imitation of the model's kinematics by the participants. Outcome mimicry however, was observed. Participant throws were biased towards the direction they anticipated for the model's throw. Crucially, this bias was observed only after the videos in which the throws were easy to anticipate.

Again, like automatic imitation, goal imitation and intention imitation, the reported outcome mimicry is also implicit and unintentional. Although, both the aforementioned studies explicitly instructed participants to hit or throw a ball towards a specific direction, participants ended up being biased by the observed outcome even though it did not directly assist their own task.

Gray and Beilock (2011) reported that highly-experienced batters are more affected by the outcome of others' actions because experienced athletes are expected to have a stronger link between an observed outcome and the motor action required to achieve that outcome. These results can again be explained by the unconscious sensory-motor processing route; a representation which codes for an observed outcome may automatically activate a corresponding motor representation, consequently resulting in an action corresponding to the same outcome (Fig. 2).

2-4 Motor mimicry

It has been known for a long time that humans are prone to mimic an observed individual's body postures and mannerisms without intention (Charny 1966; Condon and Ogston 1967; Kendon 1970; LaFrance and Broadbent 1976) during social interactions. Such automatic imitation or mimicry in social situations is referred to as *motor mimicry* and also known as the *Chameleon effect* (Chartrand and Bargh 1999). In contrast to automatic imitation, emulation and outcome imitation, that manifest as changes in reaction time and/or accuracy of movements, motor mimicry manifests as changes in behaviors and behavioral choices. They are usually quantified by the frequency of occurrence of certain actions or behaviors (Heyes 2011).

Chartrand & Bargh (1999) provided the first valid demonstration of motor mimicry by showing a cause and effect relationship between observed behaviors and one's own behaviors in a social context. Their experiments manipulated the *cause*: the mannerisms and behaviors of partners (confederates of the experiment) and examined the *effect* on the occurrence (frequency) of the same mannerisms in interacting participants'. Participants in their experiment took turns with a confederate to describe a series of photographs in two sessions. In one session, the confederate rubbed his face but did not shake his foot while in the other session, the confederate shook his foot but did not rub his face. The experiment observed that participants rubbed their face more often in the session with the face-rubbing confederate than in the session with the foot-shaking confederate, while they shook their foot more often in the session with the foot-shaking confederate than in the session with the face-rubbing confederate. This result provided the first causal evidence to show that individuals unintentionally mimic behaviors or mannerisms of another individual with whom they interact.

Motor mimicry has been linked to increased liking, rapport, or prosocial attitude (van Baaren et al. 2004; Chartrand and Bargh 1999) during social interactions and has been proposed as an important unconscious communication tool used by humans. Chartrand & Bargh (Exp 2, 1999) conducted another experiment in which a confederate mimicked mannerisms of participants during the same social interaction as the above-mentioned main experiment. After the interaction with the confederate, the participants who were mimicked reported the confederate to be more likable and the interactions to be smoother, even though they had not been aware of being mimicked.

Van Baaren et al. (2004) performed experiments similar to the second experiment by Chartland & Bargh (1999) to examine whether mimicry makes an individual more prosocial. In their experiment, confederates mimicked mannerisms or body postures of a participant during a social interaction, following which that confederate, or a new confederate, “accidentally” dropped 6 pens in front of the participant. The participants who had been mimicked were observed to pick up more pens, in comparison to those who had not been mimicked. These results suggest that mimicry makes an individual show more favorable rapport, or prosocial attitude, towards not only the individual who performed the mimicry, but also toward other people. The finding that motor mimicry enhances prosocial behavior suggests that it serves to strengthen social bonds and may play an important role in the building of any close-knit community, like a sports team.

Finally, although there is still no direct evidence that motor mimicry is based on the same mechanism as automatic imitation, emulation, or outcome imitation, motor mimicry has been explained by a perception-behavior link assuming the existence of an automatic connection between representations coding observed behaviors and motor representations enabling the same behaviors (Chartrand and Bargh 1999).

3. A new type of contagion

The four types of motor contagions that have been studied predominantly in the past, and which we reviewed in the above section, have one common characteristic; they are all contagions induced by features of an observed action – either kinematics, outcome, goal or intention, or overall behavior. For this reason, we will characterize them here as *action-driven contagions* (or ADCs). We will now introduce a new type of contagion that is induced, not by features of observed actions, but by differences between features of an observed action and features that an observer has (often implicitly) *predicted* for that action. In other words, with these contagions a given action can cause vastly different motor effects in an observer depending on what the observer has predicted about the action. These contagions, which we will call *prediction-driven contagions* (or PDCs), are thus fundamentally different from action driven contagions.

In a study with darts experts, Ikegami and Ganesh (Ikegami and Ganesh 2014) asked darts experts to watch videos of a novice thrower. Part of the video was masked such that while a novice thrower was visible to the experts, his/her dart flight trajectory and dart-board were not. The experts were asked to predict the outcome of the novices’ throws (in terms of the location on the dartboard) by

viewing the novices' throw kinematics. In their first experiment the authors showed that the experts' own throws progressively deteriorated after repeated video observation-prediction sessions. Interestingly, they observed that the deterioration was correlated with the improvement in the action prediction by the experts.

To test these observations further, the authors modulated the improvement in the experts' prediction of the observed novices' throws in a second experiment, and examined its effect on their darts performance. They manipulated two prediction errors that helped the experts to improve their outcome prediction. The first is the *outcome prediction error* - the difference between the outcome predicted by the expert from the observed novice's action, and the actual outcome provided to the expert orally by the experimenter. The second is the *kinematics prediction error* - the difference between the novice kinematics the expert actually observed and the kinematics expected by the expert based on the goal he believed the novice was aiming for. The outcome prediction error was suppressed by not providing the experts with the actual outcome of the novices' throws. The kinematics prediction error was suppressed by altering the experts' beliefs about the novice's goals – the authors misinformed the expert at the start of the experiment that “the novice does not always aim for the board center but aims for unknown targets provided by us”, and that “only the trials in which the novice was successful are presented”. This misinformation was expected to remove any prior goal belief that the experts may have had.

In the absence of these two prediction errors, the experts' prediction ability did not change over the course of the experiment. Interestingly, the darts performance of the experts was also observed to remain unchanged in this experiment, even though the experts watched the same dart videos as in the first experiment. These results indicated that the experts' darts performance was affected by prediction rather than pure observation of the novices' dart throws.

Prediction driven contagions may also lie at the heart of several observational motor learning results. Gribble and his colleagues (Mattar and Gribble 2005; Brown, Wilson, and Gribble 2009; Brown et al. 2010; McGregor, Cashaback, and Gribble 2016) have reported that observation can help individuals learn the dynamics of a novel task, or the so called *internal model* of the task environment (Kawato 1999; Wolpert, Ghahramani, and Jordan 1995; Shadmehr and Wise 2005), faster. In their studies they observed that participants who observed another individual performing the same adaptation task showed faster adaptation to the so called viscous-curl force field (Shadmehr and Mussa-Ivaldi 1994), in comparison to control participants who did not observe anybody, or participants who observed an individual adapting to a different force field. Wanda et al. (2013) performed a similar experiment where participants were asked to watch individuals learning to make straight reaching movements toward a single target in the viscous-curl force field. A straight movement in this field requires one to learn a pattern of lateral hand forces corresponding to their reach velocity. Then the observing participants are subsequently asked to make reaching movements toward the same target. Utilizing the error clamp technique (Scheidt et al. 2000) that allows for the measurement of lateral hand forces during reaching movements, Wanda and colleagues showed that

the participants can reproduce the temporal pattern of force characterizing the movement that they observed without any physical experience of the force field. That is, they developed an internal model corresponding to an observed movement simply through action observation. Numerous studies on human motor learning have shown that learning of internal models is driven by prediction errors: differences between actions actually performed and those predicted by a participant. Similar prediction errors, but in this case differences between observed actions performed by another individual and actions the observer participant predicts that individual to produce, may contribute to the participant learning the internal model by observation. The observational motor learning results reported by these studies may therefore also be categorized as prediction-driven contagions.

To examine possible changes in internal models (though at a more trial by trial level) during their darts study, Ikegami and Ganesh analyzed the interactions between the expert's ability to predict the outcome of observed actions and their ability to *self-estimate* the outcome of their own actions (Ikegami and Ganesh 2016). The self-estimation was measured as the distance between where experts' dart landed, and where the experts self-estimated them to have landed (in a no-visual feedback conditions). First, the authors observed that the improvement in the experts' outcome-prediction ability caused a deterioration in self-estimation accuracy. The experts tended to always self-estimate their throws to be near the center of the darts board, even when their throws landed far from the center. However interestingly, this self-estimation was not random, and though wrong, showed a significant correlation with where their darts landed. Next, the authors showed that the trial by trial qualitative changes in the darts performance, self-estimation and the corresponding correlation by each expert, can be explained by a state-space model that assumes that the self-estimation is used by the experts as feedback (in the absence of vision) to regulate their dart throws. Critically, the quantification of their model revealed that the deterioration occurred due to a specific change in the expert's *outcome forward model*, a mapping between throw action kinematics and consequence (dart landing position on the dartboard). On the other hand, no consistent change was observed in the experts' ability to make action corrections corresponding to the (erroneous) self-estimation, usually attributed to the controller or darts *inverse model* (a mapping from a dart landing position to the throw action kinematics).

The above results support the claim that prediction-driven contagions are caused by modifications of sensorimotor mappings or internal models. Crucially, note that these modifications are aimed at reducing prediction errors, and depend not only on the observed action, but also on what the observer predicts. Thus PDCs may not lead to imitation of the observed action features. For example, in the study of Wanda et al. (2013), the force output profiles indicated that the observer's reaching movements were biased after observation, but not toward the same direction as the observed movements, but in the opposite direction to the observed movement (See Fig. 3). While in their simple two-dimensional movement experiment, the prediction driven contagion leads, in a sense, to an *anti-imitation*, or mirroring of an observed action feature (specifically hand forces), the effects can be difficult to predict in high-dimensional tasks involving multiple joints. Thus, prediction-

driven contagions may not manifest as similarities between observed and performed action kinematics or outcomes.

4. Comparing prediction driven contagion and action driven contagions

The core cause of ADC is believed to be associations between representations which encode features of an observed action, such as kinematics, outcome, goals, or intentions, and motor representations of actions with those same features. These associations are assumed to develop through long-term experience or learning, and possibly to be genetically pre-specified (Cook et al. 2014), enabling an automatic transformation of an observed action feature to the corresponding motor response (Heyes 2011). Observation of an action first activates a representation which encodes a feature of the action, this in turn automatically activates the corresponding motor representation that leads to a movement with the same feature. Which feature leads to contagion probably depends on the saliency of the task and attentional characteristics of the observer (see section 2-2). From the behavioral view point, ADCs lead to an increase in the similarity between one or more features of one's actions and of actions observed in others.

On the other hand, evidence suggests that PDCs are caused by prediction errors (differences between what one expects and what one sees). PDCs may not lead to direct imitation of any movement feature, and may in fact lead to effects mirroring the observed movement features (Wanda, Li, and Thoroughman 2013). Furthermore, they have been reported to persist for several action trials after action observations (Wanda, Li, and Thoroughman 2013; Ikegami and Ganesh 2014). These characteristics, combined with the fact that prediction errors are known to critically influence sensorimotor mappings or internal models (Wolpert and Kawato 1998; Tseng et al. 2007), suggest that in contrast to ADCs, PDCs lead to a change in the motor representations in the brain (Ikegami and Ganesh 2014; Ikegami and Ganesh 2016). To explain these two types of motor contagions, we therefore propose an extension of the Dual Route Model of Fig. 2.

We propose to extend the Dual Route Model by highlighting the role of predictions by the brain, about observed actions (Fig. 4).

According to the original Dual Route Model (Heyes 2011; Heyes 2013), the interaction between the unconscious route, triggered by the “action observation”, and the conscious route triggered by the “task instructions”, induce ADCs in the observer. The extended model hypothesizes that, in parallel, the prediction system utilizes the same “action observation” and “task instructions” to predict or estimate subsequent action features in the observed agent. Discrepancies between the predicted features and actual features seen in the observed agent generate *prediction errors* that lead to a modification of the prediction system. It has been suggested that the motor system is at least partially involved in prediction of observed actions (represented by dashed enclosing line) (Wolpert, Doya, and Kawato 2003; Aglioti et al. 2008; Ikegami and Ganesh 2014; Ganesh and Ikegami 2016; Ikegami and Ganesh 2016), which suggests that the changes in the prediction system (double line with arrow in Fig. 4) are equivalent to changes in the motor representations in the brain. Our

extended model thus suggests that PDCs are caused by the prediction-error driven modifications of the motor representations in the brain. An interesting implication of this conceptual model is that in the presence of prediction errors, both ADCs and PDCs can occur in parallel. However, this possibility remains to be tested in practice.

The Dual Route Model proposes that observed actions automatically activate corresponding motor representations in the brain. This suggestion is supported by the *common coding theory* introduced by Prinz (1997) and by recent neural recordings in studies investigating the so called mirror neurons (Rizzolatti and Craighero 2004; Rizzolatti and Sinigaglia 2010). Our proposed extended model (Fig. 4) goes a step further and suggests that action observations can in fact change motor representations in the brain (Ikegami and Ganesh 2014). Overall, these ideas agree well with the proposed theme of *Conceptualization* in embodied cognition (Shapiro 2010; Shapiro 2013). Details about this theme are available in the other chapters in this book.

5. Application to Sports

Athletes and coaches have often claimed to have experienced contagion during training and games. Some anecdotal experiences have been reported by researchers. In one of his interviews, Ichiro Suzuki, one of the most consistent batters in Major League Baseball in recent times, disclosed that he refrains from closely watching poor batters on his team before playing because it affects his own batting performance (2007, June 19, *Yukan Fuji*, reported in Ikegami and Ganesh 2014). Gray and Beilock (2011) reported similar comments from coaches in US major league baseball; “One guy starts hitting well, the other guys are gonna catch on” (Tommy Lasorda, Los Angeles Dodgers); “Absolutely, hitting is contagious. You get a bunch of these guys hitting, hopefully the guys that aren’t hitting right now will catch on fire” (Charlie Puleo, New York Mets).

In addition to factors like mood contagion (Totterdell 2000) and social contagion (Boss and Kleinert 2015), motor contagions, both action-driven and prediction-driven, are arguably the key causes of these empirical observations in sports. Therefore, an understanding of why motor contagion occurs will not only contribute to our theoretical understanding of sensory-motor representations and plasticity in the brain, but will also shed light on whether and how individuals can control motor contagions in order to improve their sports performance and alleviate unwanted performance decrements. In this section, we will discuss issues regarding the controllability of motor contagions and the applicability and relevance of motor contagion research to sports performance and motor learning.

5-1. Controlling motor contagions

Athletes in professional sports need to obtain maximum performance and they need to resist any adverse effects from motor contagions, while capitalizing on any favorable ones. As discussed in the previous sections, numerous studies have shown that motor contagions can affect one’s actions, goals and intentions very implicitly and unconsciously. It would seem as if motor contagions are

uncontrollable. However, it is common knowledge that while we imitate some actions, we don't imitate others. Several studies have thus proposed the presence of an inhibitory mechanism and/or an action-control mechanism that prevents us from imitating all the time (Brass and Heyes 2005; Schutz-Bosbach et al. 2009; Spengler et al. 2010; Cross et al. 2013).

Though the exact mechanism driving motor contagions is still unclear, as we have discussed, contagions arguably result when an observed action activates a corresponding motor representation. Brass, Ruby, & Spengler (2009) investigated the existence of functional mechanisms in the brain that control the activations of motor representations due to action observation. They reported that a reduced imitative response in an imitation-inhibition task (i.e., reduced contagion) was accompanied by increased activation (Brass et al. 2000) (see details section 2-1 in this chapter) in the medial prefrontal cortex (mPFC) (see also, Brass and Heyes 2005, Spengler, von Cramon, and Brass 2009). Furthermore, they reported an overlap between the brain activations during reduced contagions and the brain activations related to self-related processing and/or complex social-cognitive tasks. These overlaps were observed in the anterior fronto-median cortex (aFMC) and the temporo-parietal junction (TPJ). From these results they hypothesized that information processing about one's self may increase the ability to achieve one's own motor intentions and resist motor contagions. That is, self-related processing may play a fundamental role in the control of motor contagions (see also, Schutz-Bosbach et al. 2009).

Based on this hypothesis, they investigated whether self-focus enhances control of one's own actions and/or inhibits motor contagion during an imitation-inhibition task (Spengler et al. 2010). In their study, self-focus was elicited by engaging participants in a self-referential task, namely judging evaluative statements (e.g., "Leipzig is a pleasant town."). On the other hand, the non-self-focus tasks involved judgments of neutral statements that required retrieval of semantic memory ("Leipzig is the capital of Germany."). Participants performed alternating trials of the self-referential (or non-self-referential) task and an imitation-inhibition task. They observed that contagion (visible as interference in the inhibition-imitation task) was reduced after the self-focus tasks. Furthermore, Schütz-Bosbach and colleagues (2009) reported a decrease in motor evoked potential induced by Transcranial Magnetic Stimulation (TMS) of primary motor areas when observed actions are attributed to one self, compared to when the same actions are attributed to another agent. These findings suggest that self-related processing can enhance the resistance of actions to motor contagions.

As described in section 2-1, automatic imitation describes a special case of the stimulus-response compatibility effect. Traditional stimulus-response compatibility studies have suggested that automatic response activation can be suppressed in preparation for trials in which the automatic response to an observed action is likely to interfere with task-relevant behavior (e.g., Vu and Proctor 2004). To investigate whether such suppression in preparation also occurs for automatic imitation, Cross and Iacoboni (2014) measured muscle-specific cortico-spinal excitability during action observation, by using TMS when participants prepared to execute imitative or counter-imitative

responses to action stimuli. They found that cortico-spinal excitability was suppressed during the preparation of counter-imitation actions, compared to the preparation of imitative actions. Automatic imitation, therefore, can be suppressed when the automatic response is likely to interfere with a task goal.

Similar to the above ADC studies, there is evidence that PDCs can be controlled and suppressed as well. PDC in darts experts (see, section 2-5; Ikegami and Ganesh, 2014) was observed when an expert's prediction about the kinematics and outcome of an observed action differed from the kinematics and outcome the expert actually observed. In contrast, when specific goal beliefs or feedback about outcomes were removed during observation, PDC was attenuated. In their study, the authors removed the outcome feedback by withholding information about the outcome of the actions the darts experts observed, while they altered experts' beliefs about the model's goal by misinforming the darts experts about the intention of the observed model. Their results suggest that PDCs can be suppressed by not predicting observed actions. This suppression has important implications for sports that frequently include action predictions. This point will be discussed in a later section.

Motor contagions are not always detrimental, but can also facilitate performance. Eaves et al. (2012) showed that passive observation of a rhythmical action can bias the frequency of the observer's subsequently performed rhythmical actions. In their subsequent study, the authors investigated how action frequency was further modulated by simultaneous motor imagery of one's own action during observation of an action performed by others. In their study, participants were required to execute an instructed rhythmical action (e.g., slow actions), following observation of a rhythmical distractor movie (e.g., of fast actions). They report that motor imagery during action observation, of an action synchronized to the observed rhythmic action, induces a more pronounced imitation bias compared to passive observation and also in comparison to static unsynchronized imaging. On the neural side, this observation is supported by a recent neurophysiological study (Nedelko et al. 2012) that demonstrated that simultaneous imagery of action execution during action observation activates a larger cortical motor region compared to mere observation without imagery.

A study by van Leeuwen and colleagues (2009) provides an alternate possibility for controlling motor contagions, by controlling available working memory. Working memory refers to the cognitive system that retains (a small amount of) information in an active state for use in ongoing tasks (for a review see Baddeley 2007). Working memory is also believed to influence attentional control; the capacity to focus, to divide and to switch attention (Baddeley 1996). The dorsolateral prefrontal cortex in humans has been known to be involved in inhibitory control (Aron, Robbins, and Poldrack 2004) and working memory (Courtney et al. 1998; Owen et al. 2005). In the study by Brass et al. (2003), considering the fact that patients with damage to the lateral frontal region are more prone to spontaneous imitation, the authors hypothesized that a large load on working memory could increase susceptibility to motor contagion, specifically automatic imitation. In order to test their hypothesis, they examined how participant behavior in an imitation-inhibition task was affected by a

secondary task that loaded working memory (Brass et al. 2000). As expected, a higher working memory load facilitated reaction times for congruent stimuli (i.e., facilitated automatic imitation).

5-2. Prevention of motor contagion in sports

Often in sports, coaches and teammates ask players to “avoid making the same mistakes (made by others)”, or “repeat the same action (as others)”. Is it possible to capitalize on motor contagion in order to facilitate these desired behaviors? In this section, we will summarize what the discussion in section 5-1 tells us about how one can prevent motor contagion before it occurs and how one can compensate for a motor contagion that has/will occur in sports.

Focusing on Self

Although there are few studies that have directly investigated the attenuation of motor contagion in sports, laboratory experiments that have simulated a (or part of a) sports-like scenario can give us important ideas for successful performance in sports. For example, according to Spengler et al. (2010), enhanced focus on one’s own goals and intentions might help attenuate unwanted motor contagion. This result is supported by a study (Obhi et al. 2014) which reported that individuals with high narcissistic tendencies, who tend to display an excessive self-focus and reduced concern for others, demonstrate reduced automatic imitation in an imitation-inhibition task. There is some experimental evidence to show that this procedure can also work in sports. In their study with hammer throwers (discussed in section 2-3), Takeuchi et al. (2014) demonstrated that varsity hammer-throwers mimic the predicted outcome of models they watch in a video. In the second part of their study, the authors investigated the effects of self-focus on the observed motor contagion. Hammer throwers were asked to say out loud either, “I’ll do my best!” (in the self-focus condition), or “Make a mistake!” (in the non-self-focus condition), when they viewed the video of the model hammer thrower. The authors reported that the outcome mimicry observed in their first experiment was reduced only in the self-focus condition, similar to that reported in the Spengler et al. study. While this result has not been tested for other sports, it does suggest that athletes can attenuate motor contagion by focusing on self-centered ideas and on their own performance.

Manipulation of Prior information and Planning

A recent study (Andrieux and Proteau 2016) shows that information about an observed individual’s performance ability, that is, whether he/she is a “skilled” or “unskilled” performer, facilitates the effect of observational learning. They suggest that informing the observers of what they are about to see may enable them to select whether the goal of an observation is to imitate or rather to detect errors or weaknesses in the model’s performance, and hence facilitate action adaptation processes. In combination with the results from a previous study (Cross and Iacoboni 2014), that suggested that automatic imitation can be suppressed when the automatic response is likely to interfere with a task goal (see section 5-1), this result suggests that prior information (or

maybe misinformation) about an observed individual's ability may be used to control motor contagions. Such a method may be most useful to reduce motor contagions in sports like baseball, darts, curling and archery where individuals perform immediately after observing the performance of other players (Gray and Beilock 2011).

The study with Darts professionals (Ikegami and Ganesh 2014) shows the critical importance of instructions on PDC's. PDC's are caused by a difference between the predicted and observed action features of an observed individual. Predictions about actions of an observed individual are made with the knowledge of the observed individual's goal and intention (that may be inferred from a specific situation). The study shows that a lack of information about the goal (or misinformation about it) can help attenuate PDCs. For sports like curling, darts, and golf, where the goal of an action is critically dependent on the results, athletes can avoid a goal belief (and hence PDC's) by avoiding watching the game too intently.

Working memory manipulation

It has been suggested that motor contagions are increased when working memory is occupied (van Leeuwen et al. 2009). Thus, training to increase the capacity of working memory may help attenuate motor contagion. An early model of motor learning hypothesizes that motor learning occurs in three distinct stages that differ in their cognitive demand (so called cognitive, associative, and autonomous stages) (Fitts and Posner 1967). It has been hypothesized that working memory involvement diminishes with progression in motor learning (Fitts and Posner 1967), with the autonomous stage utilizing hardly any working memory at all. Therefore, it seems reasonable to assume that simply concentrating on improving one's skills in one's sport can increase resistance to motor contagion. On the other hand, in sports, some skills rely on the use of working memory, such as tactical decision-making in football and basketball, and skills that do not rely heavily on working memory (i.e., automated sensorimotor skills such as controlling the ball or a basketball free shot). While an increase in working memory can benefit both these types of skills, obviously, developing skill can help prevent motor contagion only in the latter type.

5-3. Compensating for motor contagion in sports

Planning for contagion

Preventing motor contagion would obviously be the preferred choice for most athletes but this may not always be feasible. Another option is to anticipate contagions and compensate for them during action planning. This, however, requires a good understanding of the various forms of contagions affecting the actions, intentions and outcomes in any particular sport. Motor actions are generally agreed to involve distinct planning and execution phases (Ganesh and Burdet 2013). Roughly, planning refers to the process of selection of a particular action while execution refers to the process of generating the planned action. Due to extensive training, while action selection can

still be flexibly and promptly changed by the athletes, execution changes proceed slowly and are affected by so called motor-memory effects (Ganesh et al. 2010; Kodl, Ganesh, and Burdet 2011) or use-dependent motor processes (Diedrichsen et al. 2010; Classen et al. 1998). Therefore, when contagion is expected, or the presence of contagion is detected, it is important for the athlete to explicitly change his/her plan to compensate for the error in order to attenuate it. Plan changes may be particularly effective for single or team player sports that involve alternating or one at a time performance by individuals - like baseball, archery, darts, shooting and field athletics.

Post-action correction

Finally, in many sports settings, athletes do not know whether a positive or negative contagion would affect their actions during a competition. More importantly, the contagion may not be a simple effect on particular action features, but may present itself as multiple simultaneous and non-trivial changes in one's action features. This is particularly true for team sports involving multiple players performing at the same time, like soccer, basketball and hockey. Compensating for the contagion by means of plan changes may not be intuitive in such cases. Furthermore, athletes often suffer from pressure during competitions which affects their effective working-memory functions. Performance pressure in particular is widely known to put a heavy load on the working memory of athletes (Beilock and Gray 2007), and as described previously, working memory loads can modulate motor contagion (van Leeuwen et al. 2009). One suggestion for the attenuation of detected contagions was presented in a study (Gray and Beilock 2011) which showed that the effect of motor contagion is short-lived. In this study of baseball hitting, motor contagions affecting hit direction were eliminated after four pitches in the case of more-experienced hitters and after two pitches in the case of less-experienced hitters. These results suggest that if a negative contagion is detected, it would be advantageous for an athlete to take a break, such as a *time-out*, if possible.

6. Conclusion

In conclusion, obviously the optimal strategy for avoiding contagions in sports is to avoid watching the actions of other individuals before one's own performance. However, this is not an option in many scenarios. The next best option is to understand the various motor contagions, and their causes, and with this knowledge, develop procedures to prevent, attenuate and/or compensate for the contagions. In this regard, studies in sports science and psychology over the past decades have isolated and explained many types of motor contagions that lead to implicit imitation of the kinematics, goals, intentions and outcomes of observed human actions. In this chapter we categorized these previous findings as action-driven contagions (or ADCs), as they are caused by various features of an observed action. We then introduced a new type of motor contagion, that we call prediction-driven contagions or PDCs, that are also induced by observations of other's behaviors but differ fundamentally from ADCs in terms of their cause and effect.

Based on the available data on PDCs, we proposed a possible extension (Fig. 4) to the dual route

model to incorporate and explain the ADCs and PDCs. However, being a relatively new discovery, many features of PDC are still not well understood. Further studies are required to investigate the full range of PDCs affecting human behaviors, and how these are modulated by an observer's (athlete's) skill, visual perspective and level of attention, and the observed agent's anatomy, skill, style (as well as the observer's prior knowledge about these characteristics of the agent).

An interesting aspect of our extended model (Fig. 4) is that it shows how the discovery of PDC links motor contagion studies, that until now have viewed contagion as automatic activation in already present sensory-motor associations, and motor neuroscience studies, that have concentrated on understanding the development and adaptations of sensory-motor associations. The PDC link highlights that a collaborative approach by sports psychologists, motor neuroscientists, and social neuroscientists is required for a better understanding of the complete spectrum of motor contagions, and of how they develop and shape our behaviors in society and during sports.

References

- Abernethy, B., and K. Zawi. 2007. Pickup of essential kinematics underpins expert perception of movement patterns. *J Mot Behav* 39 (5):353-67.
- Aglioti, S. M., P. Cesari, M. Romani, and C. Urgesi. 2008. Action anticipation and motor resonance in elite basketball players. *Nat Neurosci* 11 (9):1109-16.
- Andrieux, Mathieu, and Luc Proteau. 2016. Observational learning :Tell beginners what they are about to watch and they will learn better. *Frontiers in Psychology* 7.
- Aron, A. R., T. W. Robbins, and R. A. Poldrack. 2004. Inhibition and the right inferior frontal cortex. *Trends Cogn Sci* 8 (4):170-7.
- Baddeley, Alan. 1996. Exploring the central executive. *The Quarterly Journal of Experimental Psychology: Section A* 49 (1):5-28.
- Baddely, Alan. 2007. *Working memory, thought, and action*. Vol. 45: OUP Oxford.
- Beilock, Sian L., and Rob Gray. 2007. Why Do Athletes Choke Under Pressure? In *Handbook of Sport Psychology*: John Wiley & Sons, Inc.
- Belot, Michèle, Vincent P. Crawford, and Cecilia Heyes. 2013. Players of Matching Pennies automatically imitate opponents' gestures against strong incentives. *Proceedings of the National Academy of Sciences* 110 (8):2763-2768.
- Blakemore, S. J., and J. Decety. 2001. From the perception of action to the understanding of intention. *Nat Rev Neurosci* 2 (8):561-7.
- Blakemore, S. J., and C. Frith. 2005. The role of motor contagion in the prediction of action. *Neuropsychologia* 43 (2):260-7.
- Bock, Joel R., Akhilesh Maewal, and David A. Gough. 2012. Hitting Is Contagious in Baseball: Evidence from Long Hitting Streaks. *PLoS ONE* 7 (12):e51367.
- Boss, Martin, and Jens Kleinert. 2015. Explaining social contagion in sport applying Heider's balance theory: First experimental results. *Psychology of Sport and Exercise* 16, Part 3:160-

- Brass, M., H. Bekkering, and W. Prinz. 2001. Movement observation affects movement execution in a simple response task. *Acta Psychol (Amst)* 106 (1-2):3-22.
- Brass, M., H. Bekkering, A. Wohlschlager, and W. Prinz. 2000. Compatibility between observed and executed finger movements: comparing symbolic, spatial, and imitative cues. *Brain Cogn* 44 (2):124-43.
- Brass, M., J. Derrfuss, G. Matthes-von Cramon, and D. Y. von Cramon. 2003. Imitative response tendencies in patients with frontal brain lesions. *Neuropsychology* 17 (2):265-71.
- Brass, M., R. M. Schmitt, S. Spengler, and G. Gergely. 2007. Investigating action understanding: inferential processes versus action simulation. *Curr Biol* 17 (24):2117-21.
- Brass, Marcel, and Cecilia Heyes. 2005. Imitation: is cognitive neuroscience solving the correspondence problem? *Trends in Cognitive Sciences* 9 (10):489-495.
- Brass, Marcel, Perrine Ruby, and Stephanie Spengler. 2009. Inhibition of imitative behaviour and social cognition. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364 (1528):2359-2367.
- Brown, L. E., E. T. Wilson, and P. L. Gribble. 2009. Repetitive transcranial magnetic stimulation to the primary motor cortex interferes with motor learning by observing. *J Cogn Neurosci* 21 (5):1013-22.
- Brown, L. E., E. T. Wilson, S. S. Obhi, and P. L. Gribble. 2010. Effect of trial order and error magnitude on motor learning by observing. *J Neurophysiol* 104 (3):1409-16.
- Byrne, R. W., and A. E. Russon. 1998. Learning by imitation: a hierarchical approach. *Behav Brain Sci* 21 (5):667-84; discussion 684-721.
- Castiello, U. 1999. Mechanisms of selection for the control of hand action. *Trends Cogn Sci* 3 (7):264-271.
- Castiello, U. 2003. Understanding other people's actions: intention and attention. *J Exp Psychol Hum Percept Perform* 29 (2):416-30.
- Catmur, C., V. Walsh, and C. Heyes. 2007. Sensorimotor learning configures the human mirror system. *Curr Biol* 17 (17):1527-31.
- Charny, E. J. 1966. Psychosomatic manifestations of rapport in psychotherapy. *Psychosom Med* 28 (4):305-15.
- Chartrand, T. L., and J. A. Bargh. 1999. The chameleon effect: the perception-behavior link and social interaction. *J Pers Soc Psychol* 76 (6):893-910.
- Classen, J., J. Liepert, S. P. Wise, M. Hallett, and L. G. Cohen. 1998. Rapid plasticity of human cortical movement representation induced by practice. *J Neurophysiol* 79 (2):1117-23.
- Condon, W.S., and W.D. Ogston. 1967. A segmentation of behavior. *J Psychiatric Research* 5 (3):221-235.
- Cook, R., G. Bird, C. Catmur, C. Press, and C. Heyes. 2014. Mirror neurons: from origin to function. *Behav Brain Sci* 37 (2):177-92.

- Cook, R., G. Bird, G. Lunser, S. Huck, and C. Heyes. 2012. Automatic imitation in a strategic context: players of rock-paper-scissors imitate opponents' gestures. *Proc Biol Sci* 279 (1729):780-6.
- Courtney, S. M., L. Petit, J. V. Haxby, and L. G. Ungerleider. 1998. The role of prefrontal cortex in working memory: examining the contents of consciousness. *Philosophical Transactions of the Royal Society B: Biological Sciences* 353 (1377):1819-1828.
- Craighero, L., L. Fadiga, C. A. Umiltà, and G. Rizzolatti. 1996. Evidence for visuomotor priming effect. *Neuroreport* 8 (1):347-9.
- Cross, K. A., and M. Iacoboni. 2014. To imitate or not: Avoiding imitation involves preparatory inhibition of motor resonance. *Neuroimage* 91:228-36.
- Cross, Katy A., Salvatore Torrisi, Elizabeth A. Reynolds Losin, and Marco Iacoboni. 2013. Controlling automatic imitative tendencies: Interactions between mirror neuron and cognitive control systems. *NeuroImage* 83:493-504.
- De Maeght, S., and W. Prinz. 2004. Action induction through action observation. *Psychol Res* 68 (2-3):97-114.
- Diedrichsen, J., O. White, D. Newman, and N. Lally. 2010. Use-dependent and error-based learning of motor behaviors. *J Neurosci* 30 (15):5159-66.
- Eaves, Daniel L., Martine Turgeon, and Stefan Vogt. 2012. Automatic Imitation in Rhythmic Actions: Kinematic Fidelity and the Effects of Compatibility, Delay, and Visual Monitoring. *PLoS ONE* 7 (10):e46728.
- Edwards, M. G., G. W. Humphreys, and U. Castiello. 2003. Motor facilitation following action observation: a behavioural study in prehensile action. *Brain Cogn* 53 (3):495-502.
- Fitts, P. M., and C. M. Seeger. 1953. S-R compatibility: spatial characteristics of stimulus and response codes. *J Exp Psychol* 46 (3):199-210.
- Fitts, P.M., and M.I. Posner. 1967. *Human Performance*: Brooks/Cole Publishing Company.
- Furley, Philip Alexander, and Daniel Memmert. 2010. The role of working memory in sport. *International Review of Sport and Exercise Psychology* 3 (2):171-194.
- Ganesh, G., M. Haruno, M. Kawato, and E. Burdet. 2010. Motor memory and local minimization of error and effort, not global optimization, determine motor behavior. *J Neurophysiol* 104 (1):382-90.
- Ganesh, Gowrishankar, and Etienne Burdet. 2013. Motor planning explains human behaviour in tasks with multiple solutions. *Robotics and Autonomous Systems* 61 (4):362-368.
- Ganesh, Gowrishankar, and Tsuyoshi Ikegami. 2016. Beyond Watching: Action Understanding by Humans and Implications for Motion Planning by Interacting Robots. In *Dance Notations and Robot Motion*, edited by J.-P. Laumond and N. Abe. Cham: Springer International Publishing.
- Gleissner, B., A. N. Meltzoff, and H. Bekkering. 2000. Children's coding of human action: cognitive factors influencing imitation in 3-year-olds. *Dev Sci* 3 (4):405-414.

- Gray, R., and S. L. Beilock. 2011. Hitting is contagious: experience and action induction. *J Exp Psychol Appl* 17 (1):49-59.
- Heyes, C. 2011. Automatic imitation. *Psychol Bull* 137 (3):463-83.
- Heyes, C., G. Bird, H. Johnson, and P. Haggard. 2005. Experience modulates automatic imitation. *Brain Res Cogn Brain Res* 22 (2):233-40.
- Heyes, Cecilia. 2013. 12 Imitation: Associative and Context Dependent. *Action science: Foundations of an emerging discipline*:309.
- Huys, R., R. Canal-Bruland, N. Hagemann, P. J. Beek, N. J. Smeeton, and A. M. Williams. 2009. Global information pickup underpins anticipation of tennis shot direction. *J Mot Behav* 41 (2):158-71.
- Ikegami, T., and G Ganesh. 2016. Shared mechanisms of the estimation of self-generated actions and the prediction of other's actions. Paper read at Society for the Neural Control of Movement, at Montego Bay, Jamaica.
- Ikegami, T., and G. Ganesh. 2014. Watching novice action degrades expert motor performance: Causation between action production and outcome prediction of observed actions by humans. *Sci Rep* 4:6989.
- Jackson, R. C., and P. Mogan. 2007. Advance visual information, awareness, and anticipation skill. *J Mot Behav* 39 (5):341-51.
- Kawato, M. 1999. Internal models for motor control and trajectory planning. *Curr Opin Neurobiol* 9 (6):718-27.
- Kendon, A. 1970. Movement coordination in social interaction: some examples described. *Acta Psychol (Amst)* 32 (2):100-25.
- Kilner, J. M., Y. Paulignan, and S. J. Blakemore. 2003. An interference effect of observed biological movement on action. *Curr Biol* 13 (6):522-5.
- Kodl, J., G. Ganesh, and E. Burdet. 2011. The CNS stochastically selects motor plan utilizing extrinsic and intrinsic representations. *PLoS One* 6 (9):e24229.
- LaFrance, M., and M. Broadbent. 1976. Group Rapport: Posture Sharing as a Nonverbal Indicator. *Group and Organization Studies* 1:328-333.
- Leighton, J., and C. Heyes. 2010. Hand to mouth: automatic imitation across effector systems. *J Exp Psychol Hum Percept Perform* 36 (5):1174-83.
- Mattar, A. A., and P. L. Gribble. 2005. Motor learning by observing. *Neuron* 46 (1):153-60.
- McGregor, H. R., J. G. Cashaback, and P. L. Gribble. 2016. Functional Plasticity in Somatosensory Cortex Supports Motor Learning by Observing. *Curr Biol* 26 (7):921-7.
- Meltzoff, A. N., and M. K. Moore. 1977. Imitation of facial and manual gestures by human neonates. *Science* 198 (4312):75-8.
- Nedelko, V., T. Hassa, F. Hamzei, M. A. Schoenfeld, and C. Dettmers. 2012. Action imagery combined with action observation activates more corticomotor regions than action observation alone. *J Neurol Phys Ther* 36 (4):182-8.

- Obhi, S. S., J. Hogeveen, M. Giacomin, and C. H. Jordan. 2014. Automatic imitation is reduced in narcissists. *J Exp Psychol Hum Percept Perform* 40 (3):920-8.
- Owen, A. M., K. M. McMillan, A. R. Laird, and E. Bullmore. 2005. N-back working memory paradigm: a meta-analysis of normative functional neuroimaging studies. *Hum Brain Mapp* 25 (1):46-59.
- Piaget, Jean, and Margaret Cook. 1954. *The construction of reality in the child*. New York, NY, US: Basic Books.
- Prinz, W. 1997. Perception and action planning. *European Journal of Cognitive Psychology* 9:129-154.
- Rizzolatti, G., and L. Craighero. 2004. The mirror-neuron system. *Annu Rev Neurosci* 27:169-92.
- Rizzolatti, G., and C. Sinigaglia. 2010. The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nat Rev Neurosci* 11 (4):264-74.
- Schaal, S. 1999. Is imitation learning the route to humanoid robots? *Trends Cogn Sci* 3 (6):233-242.
- Schaal, Stefan, Auke Ijspeert, and Aude Billard. 2003. Computational approaches to motor learning by imitation. *Philosophical Transactions of the Royal Society B: Biological Sciences* 358 (1431):537-547.
- Scheidt, R. A., D. J. Reinkensmeyer, M. A. Conditt, W. Z. Rymer, and F. A. Mussa-Ivaldi. 2000. Persistence of motor adaptation during constrained, multi-joint, arm movements. *J Neurophysiol* 84 (2):853-62.
- Schutz-Bosbach, S., A. Avenanti, S. M. Aglioti, and P. Haggard. 2009. Don't do it! Cortical inhibition and self-attribution during action observation. *J Cogn Neurosci* 21 (6):1215-27.
- Shadmehr, R., and F. A. Mussa-Ivaldi. 1994. Adaptive representation of dynamics during learning of a motor task. *J Neurosci* 14 (5 Pt 2):3208-24.
- Shadmehr, R., and S. P. Wise. 2005. *The computational neurobiology of reaching and pointing*. Cambridge, Massachusetts: The MIT Press.
- Shapiro, L. 2010. *Embodied Cognition*: Taylor & Francis.
- Shapiro, Lawrence A. 2013. Dynamics and Cognition. *Minds and Machines* 23 (3):353-375.
- Simon, J. R. 1969. Reactions toward the source of stimulation. *J Exp Psychol* 81 (1):174-6.
- Spengler, S., M. Brass, S. Kuhn, and S. Schutz-Bosbach. 2010. Minimizing motor mimicry by myself: self-focus enhances online action-control mechanisms during motor contagion. *Conscious Cogn* 19 (1):98-106.
- Spengler, S., D. Y. von Cramon, and M. Brass. 2009. Control of shared representations relies on key processes involved in mental state attribution. *Hum Brain Mapp* 30 (11):3704-18.
- Stahl, A. E., and L. Feigenson. 2015. Cognitive development. Observing the unexpected enhances infants' learning and exploration. *Science* 348 (6230):91-4.
- Sturmer, B., G. Aschersleben, and W. Prinz. 2000. Correspondence effects with manual gestures and postures: a study of imitation. *J Exp Psychol Hum Percept Perform* 26 (6):1746-59.
- Takeuchi, T., H. Nakamoto, S. Ikudome, and S. Mori. 2014. Cause and solution of motor contagion

- in hammer throwing. Paper read at The 65th Conference of the Japanese Society of Physical Education, Health and Sports Sciences, 2014-08-27, at Iwate University, Japan.
- Totterdell, P. 2000. Catching moods and hitting runs: mood linkage and subjective performance in professional sport teams. *J Appl Psychol* 85 (6):848-59.
- Tseng, Y. W., J. Diedrichsen, J. W. Krakauer, R. Shadmehr, and A. J. Bastian. 2007. Sensory prediction errors drive cerebellum-dependent adaptation of reaching. *J Neurophysiol* 98 (1):54-62.
- van Baaren, R. B., R. W. Holland, K. Kawakami, and A. van Knippenberg. 2004. Mimicry and prosocial behavior. *Psychol Sci* 15 (1):71-4.
- van Leeuwen, Matthijs L., Rick B. van Baaren, Douglas Martin, Ap Dijksterhuis, and Harold Bekkering. 2009. Executive functioning and imitation: Increasing working memory load facilitates behavioural imitation. *Neuropsychologia* 47 (14):3265-3270.
- Vu, K. P., and R. W. Proctor. 2004. Mixing compatible and incompatible mappings: elimination, reduction, and enhancement of spatial compatibility effects. *Q J Exp Psychol A* 57 (3):539-56.
- Wanda, P. A., G. Li, and K. A. Thoroughman. 2013. State dependence of adaptation of force output following movement observation. *J Neurophysiol* 110 (5):1246-56.
- Whiten, A., N. McGuigan, S. Marshall-Pescini, and L. M. Hopper. 2009. Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Philos Trans R Soc Lond B Biol Sci* 364 (1528):2417-28.
- Wohlschlager, A., M. Gattis, and H. Bekkering. 2003. Action generation and action perception in imitation: an instance of the ideomotor principle. *Philos Trans R Soc Lond B Biol Sci* 358 (1431):501-15.
- Wolpert, D. M., K. Doya, and M. Kawato. 2003. A unifying computational framework for motor control and social interaction. *Philos Trans R Soc Lond B Biol Sci* 358 (1431):593-602.
- Wolpert, D. M., Z. Ghahramani, and M. I. Jordan. 1995. An internal model for sensorimotor integration. *Science* 269 (5232):1880-2.
- Wolpert, D. M., and M. Kawato. 1998. Multiple paired forward and inverse models for motor control. *Neural Netw* 11 (7-8):1317-29.
- Zorzi, M., and C. Umiltà. 1995. A computational model of the Simon effect. *Psychol Res* 58 (3):193-205.

Figures

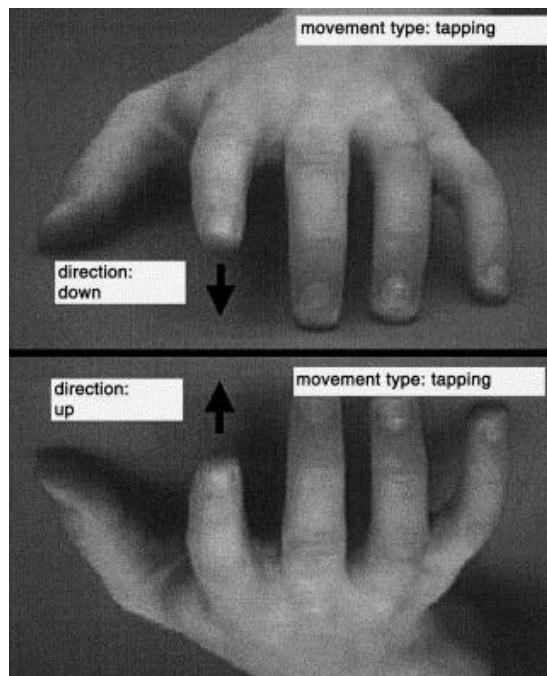


Fig. 1: Presented stimulus of normal (upper) and flipped (lower) hand orientation in the experiment by Brass, Bekkering, and Prinz (2001). During presentation of the normal hand orientation both, the topographical movement features (the finger movements shown in the stimulus) and movement direction (lift or drop of finger) in the stimulus, were congruent with the tapping movement by participants. In the flipped presentation, while the topographical movement features were still congruent, the movement direction was not, and the finger drop movement in the stimulus was now visually incongruent with a finger drop (during tapping) by the participants. The reaction time of participants was however reportedly increased during observation of the finger

drop stimulus while viewing the flipped hand orientation, even though it was visually incongruent to their tap. This result suggests that automatic imitation is modulated by the topographical movement features of observed body stimuli.

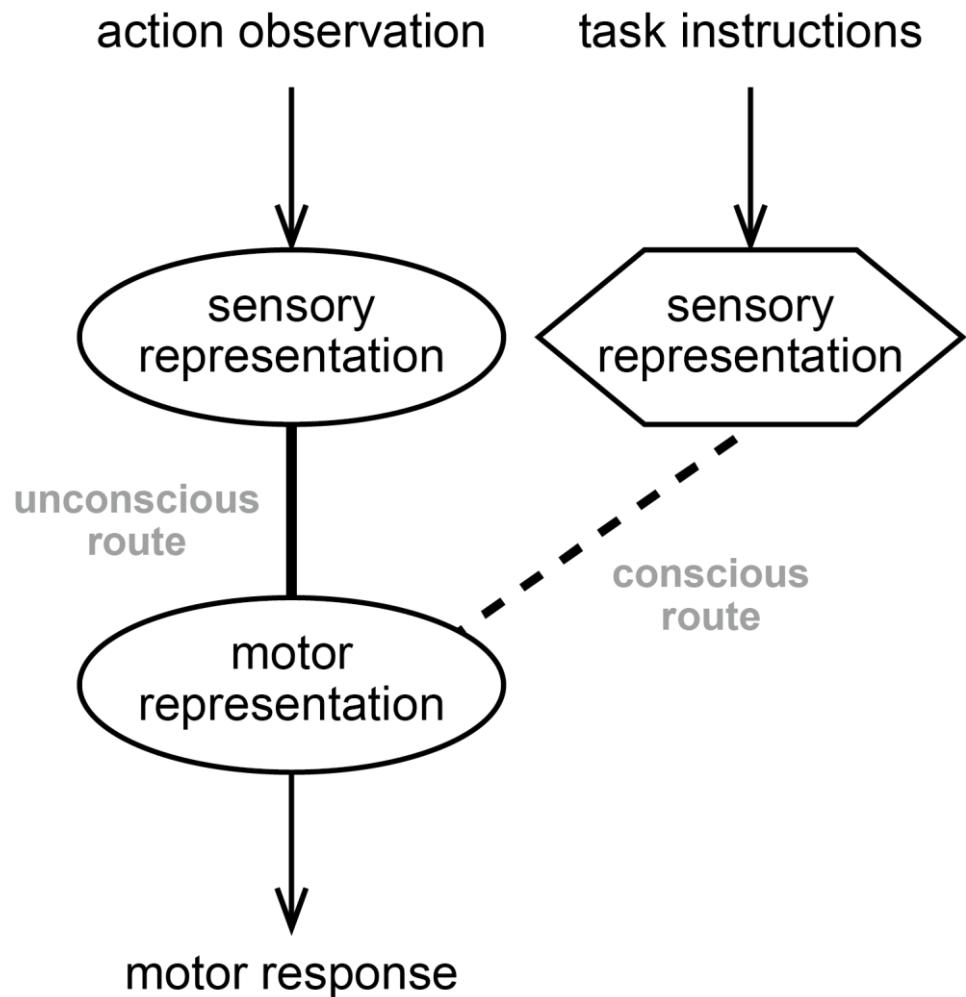


Fig. 2: The Dual Route Model suggests that motor contagions are caused by an interference between the conscious and unconscious routes of sensory-motor processing. The conscious route is driven by short-term sensorimotor associations (dashed line) which can be formed immediately based on task instructions. The unconscious route is driven by action observation and is caused by the long-term sensorimotor associations (solid line) which develop through experience or learning.

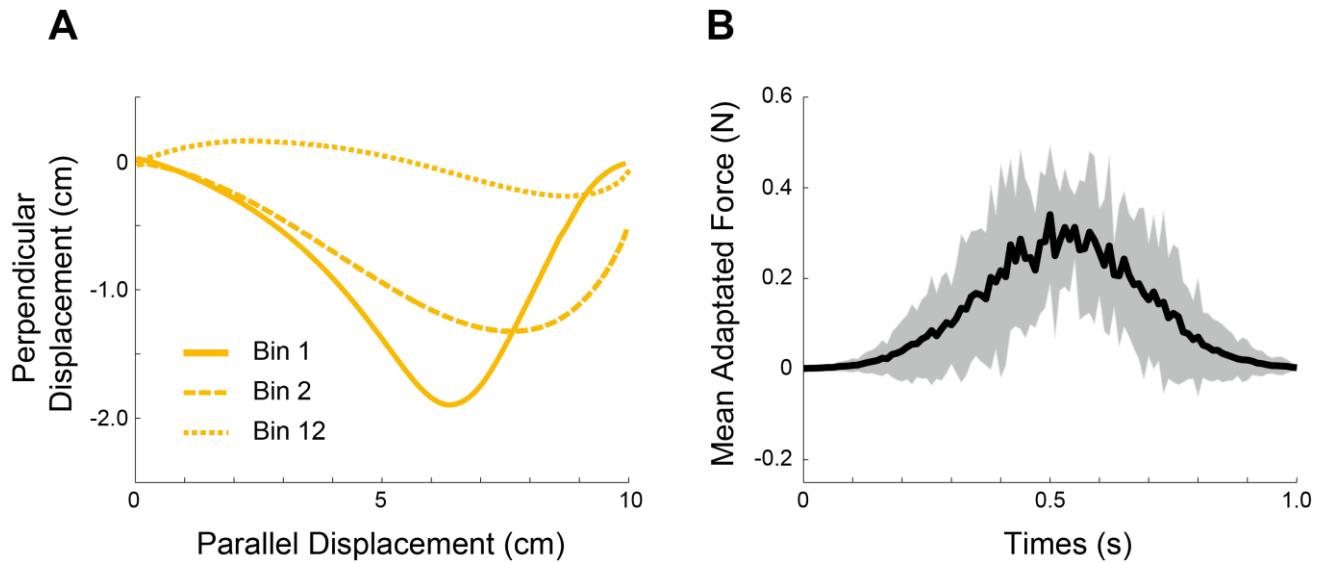


Fig. 3: Representative reproductions of figures 3 and 4 from Wanda, Li, and Thoroughman 2013. A). Participants from an *observation learning group* watched hand movements of a model actor adapting to a Viscous-curl force field before performing the task themselves. In the first learning bin (Bin 1: 1st~8th trial), the hand trajectory of the model (orange solid line) was largely distorted by the force field towards the right (downward direction in the figure). The trajectory slowly converges to a straight line as the model learns the new force environment (Bin 2: 9th~16th trial; Bin 12: 89th~96th trial). B) The mean force (black line) generated by the participants who observed the model and later worked under the ‘error clamp condition’, that allows measurement of the lateral hand forces during reaching movements. Although they had not experienced the force field themselves, they generated substantial lateral forces when they subsequently made reaching movements in the force field. These forces can be considered to be a motor contagion. Importantly, the direction of their generated forces indicates that the participants’ reaches tended to move towards the direction opposite (left) to the movements they observed in the model (compare with movement direction in A).

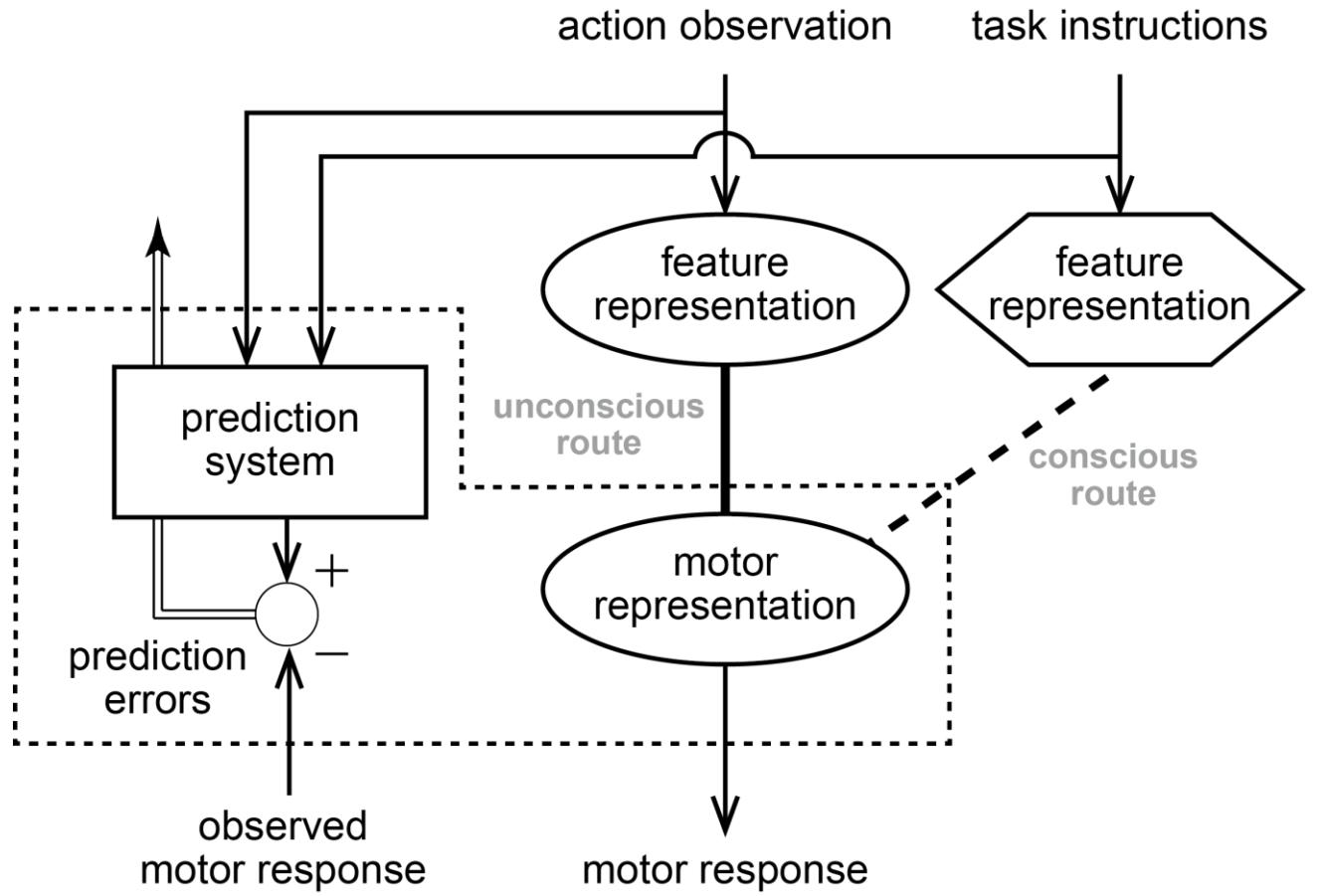


Fig. 4: Extended Dual Route Model. The prediction system is added to the original Dual Route Model. Both the action observation and task instructions are used to predict features of an observed individual's motor response. Prediction errors, differences between the predicted and actual feature/s of a motor response, change the prediction system. The model proposes that the motor system is at least partially involved in action prediction (shown by the dashed enclosure), due to which the prediction error induced changes in the prediction system can change motor representations, and in turn cause PDCs. Note that here we choose to use the term “feature representation” instead of “sensory representation” as in the original Dual Route Model (Fig. 2), to clarify the fact that the representations may include different features of an observed action (such as its kinematics, goal or intention). The above model represents only the observer, who is assumed to observe the actions of another agent and receive the same task instructions as the observed agent.