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DOI
10.1016/j.jphysparis.2015.02.003
Publication date
2015
Document Version
Final published version
Published in
Journal of Physiology - Paris
License
Article 25fa Dutch Copyright Act

Link to publication

Citation for published version (APA):
Ridderinkhof, K. R., & Brass, M. (2015). How Kinesthetic Motor Imagery works: A predictive-processing theory of visualization in sports and motor expertise. *Journal of Physiology - Paris*, *109*(1-3), 53-63. https://doi.org/10.1016/j.jphysparis.2015.02.003

Journal of Physiology - Paris 109 (2015) 53–63

Contents lists available at ScienceDirect

Journal of Physiology - Paris

journal homepage: www.elsevier.com/locate/jphysparis

Review Paper

How Kinesthetic Motor Imagery works: A predictive-processing theory of visualization in sports and motor expertise

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ARTICLE INFO

Article history:
Received 15 February 2014
Received in revised form 18 February 2015
Accepted 19 February 2015
Available online 25 March 2015

Keywords:
Motor imagery
Predictive processing
Forward modeling
Perception–action coordination
Kinesthetic visualization

ABSTRACT

Kinesthetic Motor Imagery (KMI) is an important technique to acquire and refine motor skills. KMI is widely used by professional athletes as an effective way to improve motor performance without overt motor output. Despite this obvious relevance, the functional mechanisms and neural circuits involved in KMI in sports are still poorly understood. In the present article, which aims at bridging the sport sciences and cognitive neurophysiology literatures, we give a brief overview of relevant research in the field of KMI. Furthermore, we develop a theoretical account that relates KMI to predictive motor control theories assuming that it is based on internal activation of anticipatory images of action effects. This mechanism allows improving motor performance solely based on internal emulation of action. In accordance with previous literature, we propose that this emulation mechanism is implemented in brain regions that partially overlap with brain areas involved in overt motor performance including the posterior parietal cortex, the cerebellum, the basal ganglia and the premotor cortex. Finally, we outline one way to test the heuristic value of our theoretical framework for KMI; we suggest that experience with motor performance improves the ability to correctly infer the goals of others, in particular in penalty blocking in soccer.

Contents

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http://dx.doi.org/10.1016/j.jphysparis.2015.02.003
0928-4257/

"I actually shoot in imagery because it is important not just to hold up the gun, but also to imagine the shot going off. [...] I see myself inside myself, shooting in regular motion. I can feel the initial pressure of the trigger, and then I'm looking at the sight, and the shot goes off itself."

[Olympic marksman, quoted in Orlick and Partington, 1988, p. 112]

1. Motor imagery in sports

The power of imagination is an enthralling capacity that humans can use to vividly experience virtual sensations. Motor imagery (MI) is the cognitive ability that allows an individual to perform and experience motor actions in the mind, without actually executing such actions through the activation of muscles (Moran et al., 2012). MI thus enables one to practice movements without needing to physically perform them. For this reason, MI has proven valuable in a variety of circumstances, such as athlete's or musician's training, training of surgical skills, and rehabilitation after stroke (Schuster et al., 2011). MI may be particularly useful in conditions where practical limitations constrain physical training, such as biomechanical rigidity, limited physical strength, pain, fatigue, risk of injury, limited access to equipment, *etcetera*.

MI has grown exceedingly popular among athletes in a variety of sports contexts, often under the head of 'visualization'. Estimates of the prevalence of MI among elite athletes range from 70% to 99%. Athletes consider MI to be an effective, valuable, and enjoyable technique as an adjunct to physical practice, and performance improvements have been reported for a wide array of sports, ranging from tennis, darts throwing, golf, and basketball shooting to gymnastics, down-hill skiing, soccer, and hockey (for review see Jones and Stuth, 1997). MI has been used successfully in closed motor skills, such as weightlifting or tennis serving, in which the technique used to perform the exercise is independent of surroundings; as well as in open motor skills, such as a soccer jinx or tennis volley, in which the movement depends on environmental cues such as the opponent's body language and feedforward estimations of ball motion or opponent movement. Moreover, MI has been shown to facilitate the learning and acquisition of motor skills, as well as the maintenance and retention of previously acquired skills (Cooper, 1985). The frequency of MI use increases with competitive level (Hall et al., 1990), differentiates professional players from amateurs (Lotze and Halsband, 2006), and distinguishes successful from unsuccessful Olympic track-and-field contenders (Ungerleider and Golding, 1991). Although MI is typically employed to complement physical training, even studies in which MI replaced physical practice altogether have found significant performance improvements in such events as golf putting, trampoline routines, and platform diving (Grouios, 1992; Isaac, 1992).

Despite its overwhelming popularity and wide application, theoretical progress with respect to the neurocognitive mechanisms underlying MI has remained surprisingly limited. Here we aim to develop an integral theoretical framework on the neurocognitive mechanisms underlying motor imagery as entertained in sports. Thus, we aim to contribute to bridging the (thus far largely disparate) literatures of sports science and cognitive neurophysiology with respect to 'visualization' and MI.

In the sections to come, we will (1) discuss the different perspectives entertained in MI, emphasizing the kinesthetic form. Next we will (2) discuss functional equivalence, a principle underlying most of the recent literature on MI. A consistent body of work in the field of cognitive neuroscience supports the notion that MI and overt action execution recruit partially overlapping neural circuits, with activation being less intense and less directly execution-geared during MI. We will then elaborate on (3) the ideomotor principle and (4) the notion of incipient ideomotor capture, arguing that these notions give rise to a need to revisit functional equivalence so that it (5) incorporates the principles of predictive processing. These theoretical schemes will then be integrated with the notions of (6) counterfactual generative models and (7) action observation in relation to MI. In the final section, we will (8) show how the integration of these various theoretical frameworks results in novel and nontrivial predictions regarding MI in soccer goalkeeping.

2. A matter of perspective

Mental imagery can be experienced from one of two 'viewpoints': a first-person perspective (1PP) or a third-person perspective (3PP). Using 3PP, the individual imagines the motor action from the position of a virtual onlooker, watching herself perform, as if on a home video. Using 1PP, by contrast, the individual imagines performing the action not only as if looking through her own eyes, but typically also as if *sensing* her own motions. During 1PP MI of the *Yurchenko vault* (in which gymnasts perform a flip over a vault box while performing a 180° body rotation, followed by a summersault before landing in standing position), gymnasts report to experience realistic kinesthetic sensations during the flight and arm-support phase of the imagined movement (Calmels et al., 2006). For this reason, the 1PP in MI is also referred to as *kinesthetic* MI (KMI; Amorim et al., 2000), whereas the 3PP is termed *visual* MI (VMI). Note that 1PP may actually entail both KMI and VMI, and there is no proper one-to-one mapping of 1PP/3PP to KMI/VMI. Which perspective is used may depend on a variety of factors, including the outcome focus: if the distal outcome of the action is relatively important it might be more adaptive to use VMI, whereas if the motor skill strongly depends on the precise kinematic properties of the movement it might be more beneficial to use KMI.

In practice, sportsmen will often combine 1PP and 3PP imagery, and the interoceptive and proprioceptive sensations involved in KMI will likely be modulated by 3PP imagery of exteroceptive (mostly visual) sensations (for review see Grush, 2004). Here, however, we will focus on the KMI aspect of 1PP imagery. Some pragmatic reasons for this choice will become apparent as we go along; more important, however, this focus was motivated by the integrative theoretical framework to be developed here, which details the mechanisms underlying KMI, but does not speak to 3PP imagery, or to the interplay between 1PP and 3PP imagery.

In a study reported in 1977, members of the U.S. Olympic team that had qualified for their respective finals all claimed to use MI, and most preferred KMI over VMI (Mahoney and Avener, 1977). Novices in dart throwing improved their performance after KMI more than after VMI (Epstein, 1980). Although VMI is often present to some variable extent in MI practice, in the present article we will focus on the mechanisms underlying KMI. The notion that KMI elicits anticipated sensory effects of imaged action, including kinesthetic, vestibular, visceral, tactile sensations, thus entails en embodied perspective, a notion that will be found key in unveiling such mechanisms.

We will consider one example in more detail. In weightlifting, optimal form is of the essence. In the one-repetition maximum deadlift, the athlete lifts up a barbell as heavy as she can possibly manage, from the floor upwards until full extension of the hips is achieved. Suboptimal form of the lift results not only in ineffective exertion of force to the bar, but potentially also in serious injuries. Because of its intense nature, its technical challenge, and its risk of injury, one-repetition maximum deadlifting is not suited for multiple attempts. An athlete can perform an accurate deadlift only once every few days, depending on her recovering abilities. Therefore, not surprisingly, KMI constitutes a welcome and extensively used opportunity to extend and complement training, allowing the athlete to practice form without the dangers and physical impact on the body (Richter et al., 2012). Note that the deadlift is a closed motor skill, with form resulting from proper body position and coordination of the limbs; the strength athlete does not have to adapt the movement to environmental cues. Thus, during the deadlift, sensory inputs arise from proprioceptive sensations, associated with movements of the limbs and body parts, and not from exteroceptive sensations from the environment. This renders the form of the deadlift essentially identical for every repetition, and allows the athlete to rehearse proprioceptive sensations from the limbs and other body parts. Hence, the athlete benefits from using the embodied KMI rather than VMI.

A key feature in connecting the sports science literature and the literature on cognitive neurophysiology is functional equivalence, the notion that KMI and overt action execution recruit partially overlapping neural circuits. We will discuss this principle in some detail in the next section; we will then revisit it after discussing some neural and neurocomputational mechanisms that may shed more light on how KMI works.

3. Functional equivalence

The notion of '*functional equivalence*' refers to the similarity between the imagined and actual performance. In this section we assess how functional equivalence is key to KMI, and how it extends to neural mechanisms underlying KMI vis-à-vis overt motor performance.

Perhaps the most widely used protocol for MI in sports training in recent years is the PETTLEP model, developed by Holmes and Collins (2001). This view holds that for maximal effectiveness of MI, the subject has to try and match actual performance in seven aspects: *Physical* (for optimal benefits, imagery should be as physical an experience as possible), *Environment* (the MI environment should be similar to the actual performance environment), *Task* (MI content should match individual skill level and be customized to the individual), *Timing* (MI timing should approximate that of real-time performance), *Learning* (MI should be adapted corresponding to the increase in skill), *Emotion* (MI should incorporate the affective experience as associated with physical performance), and *Perspective* (1PP is advisable for most sports situations). As one example, the potential gains for the speed and accuracy of one's tennis service are such that tennis players often use KMI for mental rehearsal. In novices at the game, KMI yields a substantial improvement in terms of serve form, ball speed, and accuracy (Fery and Morizot, 2000). Underlining the importance of mimicking the real situation (the Environment factor in PETTLEP), the tennis serve improves further when KMI is combined with a placebo racket (Guillot et al., 2012).

PETTLEP-based MI relies heavily on the notion of functional equivalence. All seven factors capitalize on this principle. With respect to timing, for instance, there is indeed evidence that the time to mentally complete a particular movement is similar to the time needed to execute the corresponding motor act (Decety and Michel, 1989; Jeannerod, 1994). Beyond these factors, mental motor images appear to be constrained by the same physical laws (such as speed–accuracy trade-off) that apply to movement execution (Sirigu et al., 1996).

Functional equivalence pertains also to corresponding physiological mechanisms. For instance, vegetative responses associated with actual effortful motor activity (such as increasing heart rate and blood pressure) appear to vary in the same manner during KMI (Decety et al., 1993). More important, evidence from a variety of sources now converges on the notion that patterns of neural activity, as observed during overt motor performance, are mirrored in corresponding patterns during KMI (for a schematic illustration, see Fig. 1). Recent studies using fMRI (for review see Lotze and Halsband, 2006) or EEG (for review see Neuper and Pfurtscheller, 2010; Osman et al., 2006) reported activation of the primary motor cortex contralateral to the effector involved in the movement (cM1) during KMI, even when controlling for the absence of EMG traces of muscle activity. Activation of cM1 during KMI is far from trivial, because such activity would not be expected if cM1 were a purely executional part of the motor system.

Direct comparison of KMI to overt motor performance reveals subtle differences in cM1 activation hotspots, with a more caudal focus during overt motor performance (Brodman Area 4p, central to execution of motor commands), and a more rostral focus during KMI (Brodmann Area 4a, closely connected to premotor cortex; Stippich et al., 2002). Likewise, in ipsilateral cerebellum, activation during KMI is located more caudal–ventral than during actual motor performance, due presumably to the absence of afferent information during KMI (for review see Lotze and Halsband, 2006). Similar distinctions have been reported for SMA: overt motor performance activates a more caudal portions of posterior SMA, tied relatively directly to motor initiation, whereas KMI activates more rostral portions of SMA as well as the pre-SMA, associated relatively more with action selection than execution (for review see Gerardin et al., 2000). Finally, in the basal ganglia, overt motor performance activates the posterior putamen (connected to the motor execution system), whereas KMI activates the head of the caudate nucleus (connected more to motor planning areas in pre-SMA and PFC; Gerardin et al., 2000). Thus, the contribution of the sensorimotor circuitry concerned with movement ideation and planning appears to be weighed more heavily during KMI, while the regions within the network which are closest to the motor output contribute more during overt motor performance (for review see Lotze and Halsband, 2006).

Thus, a careful comparison suggests that KMI and overt motor performance recruit partially overlapping neural circuits, with activation being less intense and less directly execution-geared. The data should not be taken to overemphasize the similarities or to conclude that activation during KMI simply corresponds to a subliminal activation of the same brain areas needed to perform that action (Dietrich, 2008). Rather, the data appear to support the notion that the activation during KMI is similar to the activation that occurs during the *preparatory planning stages* that eventually lead to the action (Jeannerod, 2006). Using multi-voxel pattern analysis, BOLD pattern classifiers might prove useful in determining further to what extent KMI and overt motor performance engage corresponding patterns of activation. Arguably the most interesting scenario would be partial correspondence; beyond identifying the stages of action that sow functional equivalence, multi-voxel pattern analysis might then help identify those conditions or individual differences (in expertise or vividness if KMI, for instance) under which similarity functional equivalence is optimal.

However, another source of evidence, deriving from transcranial magnetic stimulation (TMS), seems to emphasize that KMI affects corticospinal excitability, suggesting that brain activation exceeds beyond mere planning. The amplitude of motor-evoked potentials, as elicited by TMS of the primary motor cortex contralateral to the effector involved in the movement (cM1), and as observed in the electromyogram recorded over the involved muscles, is thought to reveal changes in the state of corticospinal excitability. Such changes reveal for instance how motor activation is modulated by response inhibition (van den Wildenberg et al., 2010) or emotional state (van Loon et al., 2010); note however that evoked-potential amplitude is completely independent of the muscle activation as triggered by the (real or imagined) movement.

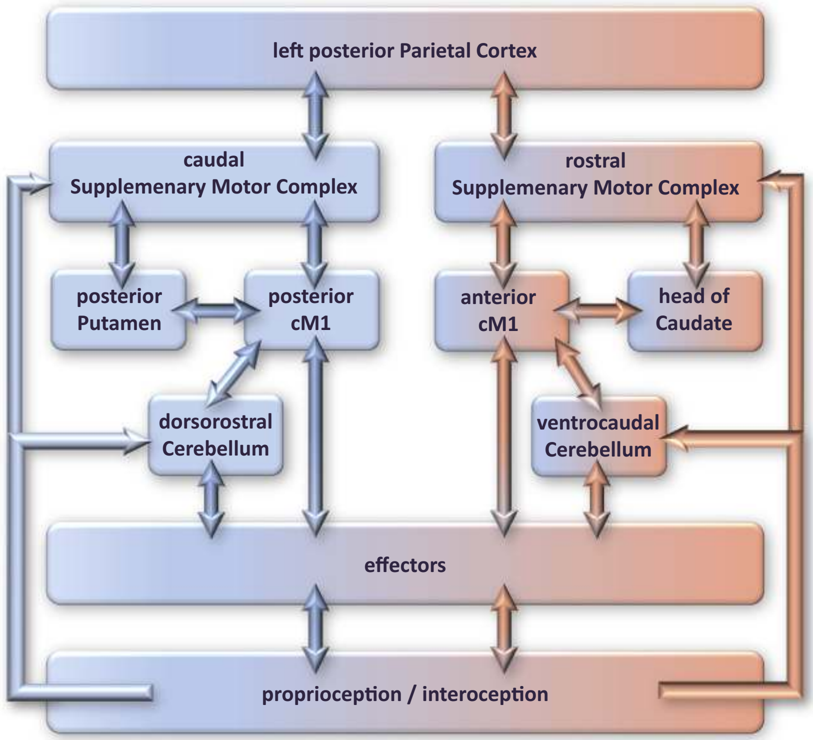

Fig. 1. Schematic illustration of the neural circuitry involved in overt motor performance (in blue, left side of figure) compared to KMI (in rose, right side of figure), based mostly on fMRI and selective lesion studies (see main text for details of individual studies). Direct comparison of KMI to overt motor performance reveals a largely similar network accompanied by subtle differences in hotspots. The left PPC provides a pragmatic representation of the emulated action which is then mapped onto a motor representation in the supplementary motor complex. The latter areas recruit portions of the dorsal striatum in movement ideation and planning. The kinematic details and precise timing parameters of the motor emulation are provided by the cerebellum. The effectors involved in the planned movement receive motor commands from contralateral primary motor cortex, but can be modulated by ipsilateral cerebellum. Proprioceptive signals are fed back into the supplementary motor complex as well as the cerebellum for updating the forward models. The contribution of the sensorimotor circuitry concerned with movement ideation and planning appears to be weighed more heavily during KMI, while the regions within the network which are closest to the motor output contribute more during overt motor performance. cM1 = contralateral primary motor cortex.

KMI (but not VMI; Stinear et al., 2006) has been shown to increase TMS-induced muscle potentials, suggesting that KMI actually engages activation in cM1 similar to such activation in actual movement (Fourkas et al., 2006; Takahashi et al., 2005; Vargas et al., 2004; for review see Stinear, 2010). The KMI-induced increase in evoked potentials was found to correlate with imagery ability as well as sports-specific expertise, with greater potential change linked to more vivid images (Williams et al., 2012) and to greater skill (Fourkas et al., 2008). Thus, functional equivalence between KMI and overt motor performance appears to depend to some extent on task experience and imagery ability.

Patients with upper limb amputation generally report vivid sensory experiences from their arm and hand, even many years after the injury (Berlucchi and Aglioti, 1997). During KMI of the phantom hand, amputees showed activation in cM1 (Lotze et al., 2001), as opposed to individuals born without the upper limb (Brugger et al., 2000). Thus, the engagement of cM1 during KMI is possible only if experience with limb movement was acquired before the injury occurred.

By definition, so it seems, KMI is a conscious and deliberate process, whereas actual motor performance involves largely implicit and nonconscious processes involved in organizing and coordinating the action. If so, this would pose a serious challenge to the notion of functional equivalence underlying most KMI research. However, consistent with the ideomotor principle, as will be argued in the next sections, KMI capitalizes on the pragmatic idea of the desired action effect. This idea will then trigger a largely unconscious process of incipient ideomotor capture and forward modeling of the sensory consequences of the action, quite similar to how things unfold in overt motor performance. Likewise, Jackson et al. (2001) concluded that internally driven images which promote the kinesthetic feeling of movements may activate nonconscious processes involved during KMI. Thus, the notion of functional equivalence between KMI and overt motor performance remains quite feasible. In the sections that follow we will explore the mechanism underlying KMI in more detail.

4. The ideomotor principle

In this section, we relate the modern notion of forward modeling and the slightly older notion of efference copies to the much older notion of ideomotor action. It will be argued that the rich literatures on these notions can be integrated to highlight a mechanism for anticipating the sensory consequences of the movement.

Goal-directed action requires, first, a pragmatic idea of the desired action effect. Based on prior experience, such an idea serves to occasion action aimed at some desired end. This pragmatic idea forms the basis of what has come to be termed *ideomotor action* (Carpenter, 1852; for a historical review see Ridderinkhof, 2014), distinguished from sensorimotor action to depict the notion that thinking of the result of an action tends to set the action in motion. A pragmatic idea consists of images of peripheral sensation associated with the action (including its direction, its extent, its strength, and its velocity, as well as the effort which it requires) and its anticipated effects on the world and on our own body (James, 1890). The ideomotor principle holds that performing a particular action generates an association between that particular action option and its sensory effects (*action–effect associations*). These associations are bidirectional; hence, the idea of an action effect can serve to retrieve the particular action that gives rise to the particular sensory effects as associated with the desired action–effect (Herwig et al., 2007). Harleß (1861/2012) used the term '*Effektbild*' to denote the consequences of actions, not only in terms of sensory effects but also in terms of the foresight of outcomes that one can learn to pursue or avoid.

Where in the brain are pragmatic ideas formed? A clue may be found in apraxia, a condition associated with deficiencies in translating the pragmatic idea of an action into overt motor performance. For instance, patients with apraxia have difficulty in generating pantomime performance of what one would stereotypically do with a hammer or comb (Clark et al., 1994), even though they can perfectly mimic the act when it is pantomimed by a model. Apraxia typically involves lesions in the left posterior parietal cortex (PPC). Work with nonhuman primates has suggested that different PPC subregions, dedicated to the planning of eye, reaching, and grasping movements, constitute an intention map (Andersen and Buneo, 2002). Direct stimulation of neurons in the human PPC activates the pragmatic idea of action, including the consciously experienced intention to produce the movement (Desmurget et al., 2009). Interestingly, at higher stimulation intensities, the patients reported not only the intention to move but also that they had actually performed the intended movement (although in reality they did not contract a muscle). Assuming that motor awareness emerges not from the movement itself but rather from forward modeling of the sensor consequences of the action (Frith et al., 2000; Haggard, 2008), as elaborated below, stimulation of PPC neurons appears to activate the network responsible for forward modeling, resulting in illusory motor awareness.

In accordance with these notions and findings, patients with left PPC damage, contrary to patients with lesions in M1, show deficits in the ability to use KMI, in particular in predicting the duration of a movement (Sirigu et al., 1996). An internal model of the projected movement, as set up in PPC, serves to predict how the movement will unfold. Indeed, KMI activates specific areas within the left PPC (Gerardin et al., 2000), supporting the specific role of this area in movement ideation; arguably, whether the action is actually performed or not should not play a role in the extent of PPC engagement. The pragmatic idea of the action may then be mapped onto premotor and motor regions to activate the corresponding motor programs (Sirigu et al., 1996; Snyder et al., 2000). Together, these circuitries may constitute an important mechanism for anticipating or *predicting the sensory consequences of the movement* (Gerardin et al., 2000). In the next section, we discuss in more detail how the notion of incipient ideomotor capture, which figured prominently in the literature a century ago, may provide a basis for such forward modeling of action effects.

5. Incipient ideomotor capture

The pragmatic idea of a desired end may awaken, at least incipiently, the actual movement which is its object: *"Such movements may be carried out to a very slight degree only; and yet they may furnish fresh kinesthetic material to fill out some links in memory and reproduction"* (Münsterberg, 1914, p.166). As we have proposed elsewhere (Ridderinkhof, 2014), this notion of incipient ideomotor capture, incited by a pragmatic idea, provides a basis for forward models of anticipated sensory, kinematic, and muscular action effects, and may serve to prepare for effecting some action that reduces the discrepancy between our current state and the desired state (Deonna and Teroni, 2012).

Stimulation of neurons in SMA/PMd evokes a strong urge to act (the incipient action may actually turn into overt action, given sufficiently intense stimulation), while failing to evoke any form of endogenous conscious intention or pragmatic idea (Desmurget et al., 2009). As a consequence, the proprioceptive volleys associated with stimulation-induced movement result in prediction error when compared to predicted lack of sensory afferents, yielding a sense of 'alien action'. Awareness of initiating and executing a movement is thus not derived from afferent inputs, but rather from the internal computations carried out in the PPC before action (Haggard, 2005). As a consequence, we are largely unaware of sensory feedback about the ongoing state of our motor system, as long as our desired action effects are accomplished (Frith et al., 2000).

Indeed, the pragmatic idea may activate the descending motor pathways at subthreshold level (e.g., Tanaka et al., 2008). Nearly a century ago, in one of the first reports on MI research, Jacobson described that the pragmatic idea of a movement is in fact routinely followed by discharges of its target muscles. He reported the use of a "string galvanometer with vacuum tube amplification", an early form of electromyography at microvolt accuracy (albeit with poor temporal resolution), to study the question whether action currents are given off by muscular contractions associated with imagery (Jacobson, 1927).

This early report, announcing preliminary positive results, was followed by a series of seven articles in 1930–1931 in *The American Journal of Physiology*, the first of which focused entirely on motor imagery (Jacobson, 1930), and which were duly summarized and discussed by the author in *The American Journal of Psychology* (Jacobson, 1932). Subjects, when lying down with their eyes closed and fully relaxed, were asked to engage in imagining that they steadily bend their right forearm, by contracting their biceps/brachial muscles. Compared to a variety of control conditions (including imagining to bend the left arm, or the right foot, or imagining these limbs relaxed, or paralyzed, or instructions to not imagine anything, or instructions to actually bend these limbs), action potentials recorded from the right biceps were identical in type with those recorded when the subjects were instructed to make slight or full actual muscular contractions, excepting only that the microvoltage is considerably less in the former instances. Similar results were observed when subjects were asked to imagine scratching their chin, combing their hair, writing their name, plucking a flower, sweeping with a broom, playing the piano, rowing a boat, or boxing. Exceptions occurred when subjects reported to imagine activating a different muscle group, or to visualize themselves performing the act without the corresponding kinesthetic experience. For these subjects, positive results were obtained when the instructions were focused more directly on performing the act: imagine lifting a cigarette or a glass of milk to one's mouth, pulling a microscope toward oneself, pulling up one's socks, grinding coffee, throwing a ball, or shifting the gear of an automobile to first speed. The best records were secured when the subjects were requested to imagine some act performed rhythmically, such as climbing a rope or pumping a bicycle tire.

The discovery that action potentials can be recorded during motor imagery lead to the question whether the muscle fibers involved actually contract. To verify this, a lever was arranged such that flexion of the arm was magnified about 80-fold and then recorded photographically. The results showed that soon after the instruction to start imagination (but not in any of the control conditions) the lever recorded flexion in the arm, suddenly returning to baseline as soon as the imagination ended. Follow-up experiments ensured that slight muscular contraction is requisite to the process of motor imagination (Jacobson, 1932). Soon afterward, it was shown that KMI of weight lifting produced motor discharges recorded from EMG over the forearm muscles, the amplitude of which co-varied linearly with the magnitude of the lifted weight (Shaw, 1940).

Even when completion of an action is prevented, the action nonetheless often takes place incipiently. *"Ideas frequently succeed one another in trains of considerable length without producing any immediate effects on conduct, without giving rise to actual movements. Nevertheless, [...] whenever ideas are vivid their motor tendencies are clearly manifested; e.g. if you vividly imagine yourself playing a part in any exciting scene or adventure, a debate, a climb, or a fight, each idea will manifest itself in incipient motions, or at least tensions of muscles"* (McDougall, 1905, p.162). This incipient ideomotor capture (Ridderinkhof, 2014) can be put to good use in a variety of ways, in particular in the interaction between partners where the quality of the interaction depends on the partners' expertise in 'reading' the other partner's expressions resulting from incipient ideomotor capture. Examples range from contact sports, such as wrestling, to intimate dance, such as tango, to classic cases of muscle-reading. *"The exhibitions of so-called mind reading, or more properly muscle reading, which have lately grown so fashionable, are based on this incipient obedience of muscular contraction to idea, even when the deliberate intention is that no contraction shall occur"* (James, 1890, vol. ii, p.525). Such illustrations serve to highlight the nontrivial (and thus far largely overlooked) principle of incipient ideomotor capture. This principle may comprise a candidate model for some mechanistic aspects of empathy (in particular, the ability to infer the intent of another person's actions).

6. Functional equivalence, revisited: forward modeling

In the preceding sections, we have argued that incipient ideomotor capture, as incited by a pragmatic idea, provides a basis for forward models of anticipated sensory, kinematic, and muscular action effects. This leads us to revisit the notion of functional equivalence, with a prominent focus on forward modeling. We first consider the potential role of the cerebellum in KMI, which informs an understanding of KMI in terms of forward modeling.

The cerebellum is involved in fine-tuning the nitty–gritty detail of actions and their timing. The cerebellum has been proposed to be a crucial component in the state estimation process that combines information from motor efferent and sensory afferent signals to produce a representation of the current state of the motor system (Kawato, 1999; Miall et al., 2007). One might argue that during KMI, there is no need for the cerebellum to stipulate all the details beforehand, let alone fine-tune them online. By contrast, however, we propose that specifying these details is of the essence for realistic KMI, such that the sensory consequences of the action can be accurately predicted, and such that the action details can be fine-tuned online (that is, if and to the extent that the anticipated action effects do not match the desired action effects). The ipsilateral cerebellar activation during KMI, as discussed in the preceding section on functional equivalence, and as reviewed in Lotze and Halsband (2006), would appear consistent with this hypothesis.

Interestingly, this view gives rise to an additional hypothesis, namely that functional equivalence, beyond neural activation and muscle discharge, also entails forward modeling of the anticipated sensory consequences of the action (Grush, 2004). This conjecture would address the somewhat challenging question how KMI can simulate overt motor performance, let alone enhance performance level, despite the lack of sensory feedback from body motion and the environment (Gentili et al., 2010). Forward models are based on corollary motor discharge; according to varieties of simulation theory, forward models simulate the expected effects in the form of efference copies, whereas according to emulation theory, forward models mimic the expected effects in terms of "mock" interoceptive and proprioceptive sensory signals (Grush, 2004). Thus, in the latter view, forward models emulate (in an embodied sense) the causal flow of the overt motor performance by predicting the ensuing sensorimotor states. During overt motor performance, the forward model relates the prepared motor commands to the sensory signals of the actual state of the effectors to predict the sensorimotor state that will result from the action; the estimated and actual sensorimotor states can be compared to refine future motor commands (Desmurget and Grafton, 2000). During KMI, although no actual movement occurs, an efference copy of the motor command is available to the forward model; and, although the state estimation derives from the forward model alone (Miall and Wolpert, 1996; Wolpert and Flanagan, 2001), the forward model provides temporal information very similar to that of actual movements, such that a training signal would still ensue, albeit less precise than during overt motor performance (for review see Gentili et al., 2010). Accordingly, sensorimotor state estimation, based on forward modeling, is a process common to overt motor performance and KMI that guides motor performance improvement (Grush, 2004). Some authors have concluded that KMI entails the inhibition of the efferent command, although this remains a controversial issue, perhaps entailing inhibition of suprathreshold signals but not necessarily of incipient capture (for review see Munzert et al., 2009).

As reviewed above, KMI relies on PPC computations. In the PPC, intentions may be processed in relation to sensory predictions; in the SMA, by contrast, intentions may be more closely related to motor commands (Desmurget and Sirigu, 2009). The cerebellum receives direct feedback from several sensory modalities, allowing for the sensorimotor integration needed for on-the-fly adjustments as the ideomotor plan unfolds (Dietrich, 2008). We propose that KMI involves the PPC and SMA as well as ipsilateral cerebellum, such that the pragmatic idea of an action entails the prediction of its sensory consequences, and such that the anticipated action effects can be fine-tuned vis-à-vis the desired action effects.

7. Theoretical synthesis

These proposals are consistent with the principles and mechanisms of perception–action coordination laid out in a recent integrative theoretical framework (*Impetus, Motivation, & Prediction in Perception–Action Coordination Theory*, or IMPPACT; Ridderinkhof, 2014). The core mechanism for ideomotor action is succinctly summarized in Fig. 2. External stimuli about the state of the world, as well as internal thoughts about desired changes in the state of the world may trigger a process of appraisal, serving to evaluate these stimuli or ideas vis-à-vis preferences and norms (for review see Frijda et al., 2014). This process gives rise to one or more motives, in the form of desired action effects that vary in urgency or strength. Action options are then evaluated in terms of their aptness for bringing about these desired action effects. Even if a particular action option has high value, this value needs to be weighed against expenditure in a cost/benefit analysis (for review see Schouppe et al., 2014). Valuation of action options is driven further by a comparison between desired and anticipated action effects. If this comparison results in discrepancy, then the ensuing prediction error (PE) will serve to update the incentive value of the action option, resulting in value learning as an integrated part of repeated action emulation (for review see Ridderinkhof, 2014).

Ideomotor action entails a further critical component: predictive processing through forward modeling. The IMPPACT framework considers the brain as a prediction pump that continually generates and tests predictions to reduce uncertainty about the effects of our actions (Friston, 2012; Kempf, 1921). Ideomotor action actively sculpt the ongoing streams of sensory (especially

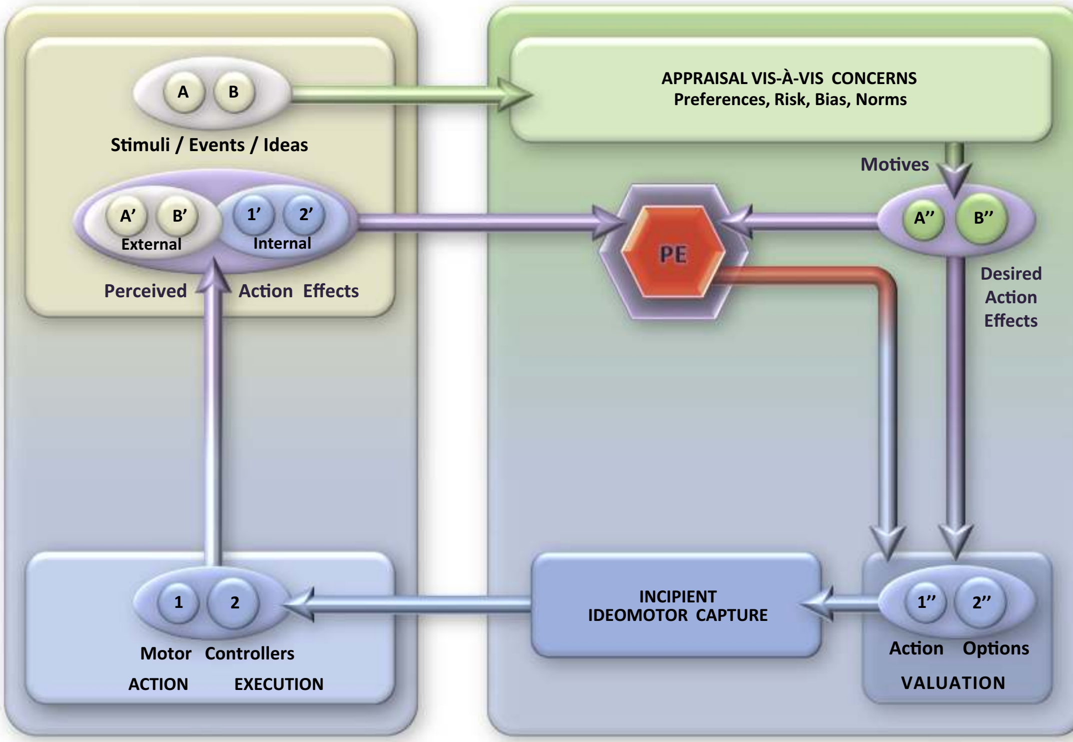

Fig. 2. Schematic architecture for ideomotor action according to the IMPPACT model. Stimuli and ideas (denoted by letters A, B, etc.) activate the corresponding motor controllers (denoted by numbers 1, 2, etc.) via a series of ideomotor processes. Appraisal of the stimuli and ideas yields motives in the form of desired action effects (denoted by letters A″, B″, etc.). Action options (denoted by numbers 1″, 2″, etc.) are valued in terms of optimal opportunity for bringing about the desired action ends. The elected course of action captures the motor system incipiently before being executed in full. Action effects (as perceived through exteroceptive senses) are fed into a comparator (symbolized by the purple-colored hexagon) to be compared against the desired action effects, giving rise (in case of discrepancy) to a prediction error (PE) which is used to re-valuate and adjust the chose action option. (Adapted from Ridderinkhof, 2014.)

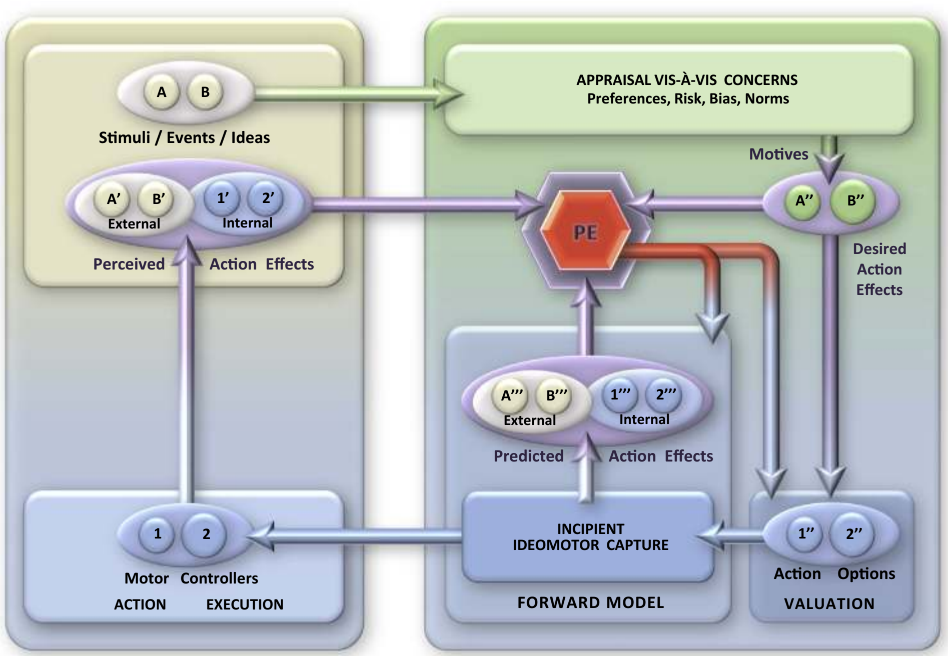

Fig. 3. Schematic architecture for ideomotor action, supplemented with a forward model (turning action selection into an action-effect prediction-and-valuation cycle), according to the IMPPACT model. The forward model calculates the predicted action effects (denoted by letters A‴, B‴, etc. for exteroceptive action effects, and numbers 1‴, 2‴, etc. for interoceptive and proprioceptive action effects), which are fed into a comparator (symbolized by the purple-colored hexagon). Predicted action effects are compared to actual action effects, giving rise (in case of discrepancy) to a prediction error (PE) which is fed back into the forward model so as to optimize its predictions. Predicted action effects are also compared to desired action effects, in which case a PE is used to re-valuate and adjust the chose action option, which is then fed into the forward model in its turn; the cycle continues until PE is minimized and the appropriate action can be executed. (Adapted from Ridderinkhof, 2014.)

proprioceptive) results that our brain predicts (Clark, 2013). Within this conjecture, predictive processing provides a neurobiological framework for understanding ideomotor action, based on the notion that we treat the desired (goal) state as if observed, and engage in forward modeling of action effects to figure out which action gets us there (see Fig. 3).

As reviewed above, forward models predict the sensory effects of the selected action program. External signals are assessed by exteroceptive inference of the causes of these signals; that is, by comparing desired to anticipated and actual sensory states (Grush, 2004). Likewise, signals from the internal milieu are assessed by interoceptive and proprioceptive inference of the causes of these signals; that is, by comparing anticipated homeostatic and kinematic effects and actual homeostatic proprioceptive state. The comparison of this prediction to the actual state yields a PE which is fed back to the forward model, allowing the prediction to be fine-tuned, after which the cycle starts again (for review see Clark, 2013; Friston et al., 2012) in order to minimize PE. Thus, practice serves to optimize the forward model. In addition to the comparison between *predicted* and *actual* sensory consequences of the action, a comparison between the *predicted* action effect and the *desired* state yields a PE that can be used to optimize the selection of those actions that are adequate for effecting the desired state (Frith et al., 2000), allowing for ideomotor action: that motor program is selected that is most likely to attain the desired action effect (Ridderinkhof, 2014). In this way, the interaction between predictors and comparators provides a circuit for internal testing (KMI) of the planned behavior prior to its initiation (Grush, 2004).

The process of comparison between action effects is schematized in the figures in terms of a single comparator. There might be a single comparator process for all comparisons, or multiple comparators; and there might be a hierarchical organization among them (in fact, in the conceptualization of Frith and colleagues, prediction error is computed in a series of hierarchically chained comparisons). For narrative simplicity, we depicted just a single process.

8. Functional equivalence, revisited once again: virtual action and counterfactual action

The notion of incipient ideomotor capture can thus be connected to computationally explicit mechanisms. Crucially, actual action is not requisite for learning of action effects: action effects can also be learned during *incipient ideomotor capture*, in the form of an association between *prepared* movement parameters and *expected* sensory action effects (Ridderinkhof, 2014). This comprises a key mechanism for KMI.

Here, we hypothesize that KMI constitutes a *virtual* action, or, rather, virtual perception–action coordination. Emulation theory states that (1) the pragmatic idea of the imagined action effect is translated into a forward model of the anticipated sensory consequences of the candidate action. Incorporated into the architecture of IMPPACT, this means further that (2) what captures the action in incipient ideomotor capture is not so much the pragmatic idea itself, but the negative PE resulting from the comparison between the desired state and the imagined state; and (3) realistic KMI through forward modeling includes in the prediction of action effects also the predicted kinesthetic as well as homeostatic effects, such as energy expenditure and biomechanical cost.

Ideomotor perception–action coordination entails selection of motor programs that will attain the desired action effect. If the PE in the comparison between the anticipated and desired action effects is minimal, then the selected motor program is invigorated; negative PE result in modification of the selected motor program or replacement by some alternative. The interaction between predictors and comparators thus provides a circuit for KMI in the form of internal testing ('mental emulation') of the planned behavior prior to its initiation. This is a useful feature from an ecological perspective: The challenges of continuously changing environments are such that the mechanisms specifying possible actions and the mechanisms for selecting between them need to operate in parallel (Cisek, 2011). The pragmatics of multiple actions are thought to be specified in parallel, and to engage in a competition that is biased by action value (Cisek and Kalaska, 2010). With repeated experience, each action choice converges on a value reflecting its integrated reinforcement history (Daw et al., 2005; Frank and Claus, 2006). These notions can be recast in predictive-processing terminology by proposing that generative models predict not only the likely sensory consequences of currently imagined courses of action, but also the likely sensory action effects predicted to occur given a large repertoire of possible alternative (counterfactual) courses of action (Seth, 2014). The vividness of KMI will depend, then, on the counterfactual richness of the corresponding generative models. By extension, we may argue that among expert sportsmen who report more vivid KMI, generative models are counterfactually richer than those of less experienced athletes.

9. Motor imagery and action observation

Predicting the actions of other individuals makes up an important part of our day-to-day interactions. Within the predictive processing framework, the most likely cause of an *observed* action can be inferred by minimizing the prediction error at all levels of the cortical hierarchy as engaged during action observation. Since mirror neurons discharge not only during action execution but also during action observation, the mirror neuron system (MNS) has been proposed to play a central role in the ability to infer intentions from actions (Kilner et al., 2007). The human MNS is thought to be comprised of premotor areas, the inferior parietal lobule, and the superior temporal sulcus (Keysers and Perrett, 2004), which are reciprocally connected. Implicit in the notion of an MNS in this context is the idea of *inversion* of the generative model. The generative model produces an estimate of the kinesthetic consequences of the kinematics of the executed action given its desired action effect). By inverting this generative model it is possible to 'read' or infer the cause or goals of an action given the observed input. An initially presumed goal of the observed action allows us to predict the associated motor commands and subsequently the associated kinematics, based on our own motor experience. The comparison of predicted and observed kinematics generates a prediction error which updates our representation of the observed motor commands; the comparison of predicted and observed motor commands generates a prediction error which updates our representation of the observed action goal (Kilner et al., 2007). The forward model is thus inverted by suppressing the prediction error generated by the forward model.

The premotor cortex is central to action planning, action imagery, and action observation (Grezes and Decety, 2001). Predictive processing has been proposed as a unifying principle (Wilson and Knoblich, 2005). By temporal occlusion of video streams of actions, Stadler et al. (2011) examined the role of PMd in predicting observed action using fMRI and disruptive rTMS (2012). The role of PMd appears to reflect prediction of sensory consequences as based on emulating the occluded portions of the observed action. The notion of real-time emulation suggests that observed actions are mentally emulated in real-time in order to achieve internal predictions (Graf et al., 2007). The correspondence between action execution and action observation indeed suggests that motor programs are activated to emulate the observed (occluded) actions (Stadler et al., 2012).

Note that, while action observation typically involves observing a third person, this does not imply that the process of emulation in motor imagery involves 3PP imagery. An important and useful role for 3PP imagery cannot be excluded; our theoretical framework specifies the mechanisms underlying KMI (here in relation to action observation) but remains mute with respect to 3PP imagery or the interplay between 1PP and 3PP imagery.

In the following section we will show how the theoretical notions deriving from various literatures, largely integrated into the IMPPACT framework, and supplemented with recent notions on action observation and counterfactual generative models in the context of predictive processing, may result in novel and non-trivial predictions.

10. The art of goal keeping

If the novel theoretical framework we have developed here for understanding KMI is to provide a meaningful scientific advance, it should be possible to derive from it empirically testable hypotheses that cannot be derived directly from existing conceptions. Although this is not the place to contrive a research agenda in any detail, we may try and sketch the outlines of a hypothetical experiment based on the notions submitted in this article. Our example will focus on how to use KMI to improve the goalkeeper's skill in stopping penalty kicks in soccer.

Penalty kicks often decide the outcome of a soccer match. However, the duel between shooter and goalkeeper is an unfair battle. Keeping the penalty kicker from scoring is in fact a rather dispiriting assignment: statistically speaking, goalkeepers manage to save the ball in less than 20% of the cases (Dohmen, 2008). Indeed, if the penalty shooter kicks well, the goalkeeper does not stand much of a chance, because she can only respond to what she sees. The time for the ball to cross the goal line and for the goalkeeper dive to a corner are roughly equal at 500–700 ms (Franks and Harvey, 1997). Thus, the goalkeeper cannot afford to lose time waiting for things to happen. She should guess direction and height before the penalty shooter even touches the ball. As a remedy to this principal disadvantage, however, the goalkeeper may try to cut a few corners by actively *predicting* what will happen.

Memmert et al. (2013) have reviewed the literature on the kinematics of penalty shooter's movements (prior to ball contact) as used by goalkeepers to anticipate ball direction. These factors include obliqueness run-up, orientation or turning of the torso, and orientation and positioning of the non-kicking foot relative to the ball. Expert goalkeepers pay more attention to the legs than novices who fixate on the torso, arm, and hip region. The orientation of the penalty taker's support foot is particularly predictive of ball direction, as it tends to point in the direction of where the ball is heading, but obviously the goalkeeper needs to wait until a very late stage for this information to become available.

Goalkeepers can potentially optimize their utilization of such advance cues through video-based training (e.g., Savelsbergh et al., 2010). For instance, when shown arrested video sequences of penalty shots, goalkeepers are to predict the direction of the interrupted penalty kick. Using such a protocol, exposure to a wide spectrum of different penalty kicks has been shown to improve goalkeepers' predictions of direction (Dicks et al., 2011). Learning can be enhanced when the goalkeepers' attention is directed to critical movement features, or even to body areas without explicating what movement feature to attend to (Savelsbergh et al., 2010).

However, the present theoretical analysis suggests that the goalkeeper not only observes the kinematic features of the penalty shooter's movement before the ball is actually kicked. Our IMPPACT-derived conjecture specifies that the goalkeeper also links these observed kinematics to the corresponding kinesthetic experience, and then mentally emulates this kinesthetic experience in the form of specific as-if sensory action affects in her own body. Through forward modeling of the action effects as anticipated *"if I were to act in this specific kinematic way"*, one can predict the corresponding bodily action effects (kinesthetic experiences) and, moreover, project the action effect in the world: which direction will the ball take. Thus, IMPPACT describes the mechanisms through which the intended action goal can be inferred from predicted sensory action effects. Since there is no time for reflective deliberation, the goalkeeper must engage in predictive processing on the fly. The kinematics of the penalty shooter must be modeled as they evolve, with as short a delay as possible since every millisecond counts. Notice how this process resembles KMI, but now online, in real-time and *in situ*.

It goes without saying that the better the goalkeeper is able to predict (or rather, emulate and infer) the shooter's intention, the better her chances of actually blocking the ball. So, what the goalkeeper needs is a rich generative model of the sensory effect of penalty kicking. Of course, just observing lots of penalty kicks will help enrich the generative model. Watching penalty kicks on video will do, and watching during actual goalkeeping (actively attempting to block the ball from going in) will do even better. But the real McCoy, according to the present theoretical analysis, is not watching, but doing. Based on the notion that the ability and vividness of KMI depends on prior experience in the action, the goalkeeper should acquire kinesthetic experience with penalty kicking herself. Kicking practice is what will enrich her generative model the most; and the more practice, the better. The more able the goalkeeper is in penalty kicking, the better she is able to accurately 'read' the kinematics of the opponent in the game. Likewise, the richer the goalkeeper's repertoire in kicking the ball at different angles and speeds, the more adequately she can match a wide variety of observed kinematics to her own, counterfactually rich generative model.

Thus, to improve goalkeeping performance, rather than closely observing the kicks of other shooters, the goalie should be kicking penalties herself. This nontrivial prediction does not follow from accounts that emphasize observation-based learning, or from PETTLEP, or from simulation theories; each of these lack the elements that allow such predictions. From IMPPACT we can in fact derive the additional prediction that goalkeeping performance can be improved by deliberate off-line KMI of penalty shooting, but only to the extent that the goalkeeper has experience in penalty shooting herself. Similar predictions may be derived for jinxing, responding to opponents' tennis serves or badminton smashes, *etcetera*. Emulation theory (Grush, 2004) could, with a few additional assumptions, be interpreted as consistent with such predictions. IMPPACT is more explicit than emulation theory in describing how learning from virtual actions could take place, but this does not seem crucial. Perhaps more important, in IMPPACT, ideomotor capture can be triggered by a variety of events, including an observed action; emulation theory lacks such a process, and hence one should assume that when observing another agent executing a specific action, this observation will produce an efference copy in the observer. Although this assumption seems far from implausible, it is not explicit or inherent to emulation theory.

11. In conclusion

In the current article we have argued that KMI is based on the activation of an anticipatory image of the sensory consequences of action. The activation of this motor representation leads to an internal emulation process of the planned motor act that has a high degree of similarity to the actual motor output. The comparison of the anticipated action effect and the internal emulation of the motor act provides an error signal that forms the basis for improving motor performance without actually performing the movement. On the neural level, a network of brain regions that is highly overlapping but not identical to the overt motor performance network is involved in KMI. The left PPC provides a pragmatic representation of the emulated action which is then mapped onto a motor representation in the premotor cortex. Premotor areas recruit portions of the basal ganglia (*vis*. the caudate nucleus) in movement ideation and planning. The kinematic details and precise timing parameters of the motor emulation are provided by the cerebellum. We suggest that one way to test the heuristic value of our theoretical framework for KMI is to investigate whether experience with motor performance improves the ability to correctly infer the goals of others on the basis of motor emulation. Thus, our novel integrative theoretical conjecture of motor imagery can have practical consequences in applied domains of motor expertise, such as penalty blocking in soccer.

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