

Motor imagery and higher-level cognition: four hurdles before research can sprint forward

Christopher R. Madan · Anthony Singhal

Received: 24 October 2011 / Accepted: 5 March 2012 / Published online: 31 March 2012
© Marta Olivetti Belardinelli and Springer-Verlag 2012

Abstract Traditionally, higher-level cognition has been described as including processes such as attention, memory, language, and decision-making. However, motor processing and motor imagery are important aspects of cognition that have typically been considered outside of the traditional view. Recent research has demonstrated that there may be a critical functional relationship between motor imagery and other higher-level cognitive processes. Here we present a review of the extant literature on motor imagery and cognition, as well as outline four hurdles that must be addressed before the field investigating the influence of motor-based processes on higher-level cognition can be moved forward. These hurdles include problems distinguishing between visual and motor processes, addressing the differences in tasks and stimuli used to evoke motor imagery, accounting for individual differences in motor imagery ability, and identifying the appropriate neural correlates. It is important that these hurdles are addressed in future research so we can sprint forward and further our knowledge about this interesting relationship.

Keywords Motor imagery · Cognition · Memory · Language · Mental imagery · Embodied cognition · Visual imagery

Motor imagery and cognition

The main focus of this paper is to provide a review of studies investigating the influence of motor imagery on higher-level cognitive processes, particularly language and memory. This is an important area of study that has implications for many areas of research.

A persisting theory in the field of ecological psychology is that some objects in our environment are more useful to our everyday lives than others, and that the information of these “affordances” is available to our basic perception and action systems automatically. This “theory of affordances” was put forward by James J. Gibson in the 1970s and still persists as an influential theory of visual perception (Gibson 1977, 1979). According to this theory, “[t]he affordances of the environment are what it offers the [observer], what it provides or furnishes, either for good or ill” (Gibson 1979, p. 127). Gibson’s theory of affordances was primarily proposed to help explain visual perception (e.g., his 1979 book is entitled “The Ecological Approach to Visual Perception”). With this in mind, one interpretation of his theory is that when an observer visually perceives an object in their environment, their perception is also influenced by the affordances of the object—the functional properties of the object. For example, a wrench can be used to tighten a bolt, a pencil can be used to write (see Chemero 2003, for a summary of Gibson’s theory of affordances). More recently, Gibson’s theory has played an important role in the development of the embodied cognition approach (Garbarini and Adenzato 2004; Wilson

C. R. Madan (✉)
Department of Psychology, University of Alberta,
Biological Sciences Building,
Edmonton, AB T6G 2E9, Canada
e-mail: cmadan@ualberta.ca

C. R. Madan
Department of Systems Neuroscience, University Medical
Center Hamburg-Eppendorf, Hamburg, Germany

A. Singhal
Department of Psychology and Centre for Neuroscience,
University of Alberta, Edmonton, AB, Canada

2002). Briefly, the basis of the embodied cognition approach is that internal mental states are closely intertwined with the external physical environment (also see Barsalou 2008; Clark 1997).

A study by Handy et al. (2003) provides support for both the Gibsonian and embodied cognition perspectives. In this study the researchers found that tools automatically recruited attention more readily than non-tools, especially when presented in the lower and right visual fields. Specifically, Handy and colleagues used a combination of both ERP and fMRI methodologies found that activation of motor cortices due to functional objects may mediate the recruitment of attention. This is further supported by the results of a study conducted by Buccino et al. (2009), which presented right-handed participants with images of objects with handles (e.g., cups and jugs). The handles of these were oriented to either be on the left-side of the container or the right-side of the container. Additionally, the handles were either intact or broken. Buccino et al. (2009) measured motor-evoked potentials in the right-hand using electromyography, while participants were shown an object and along with a word and were asked to judge if the word was or was not the name of the object. Here the researchers observed a higher motor-evoked potential when the object's handle was on the right-side and was intact, suggesting that this potential is related to the object's affordances and that visuomotor circuits can automatically transform visual information (e.g., the handle's orientation and intact/broken state) into action.

If functional properties of an object can automatically influence cognitive processes such as the recruitment of attention, it would be important to investigate the influence of motor processes on cognition. However, this topic has been severely neglected until recent, relative to other domains within cognitive psychology (see Rosenbaum 2005). This is not to say that there is no extant research on the influence of motor processing and motor imagery on cognitive processes, rather that it has been buried within studies of language and memory. However, due to the indirect nature of this research, with regards to motor imagery, numerous inconsistencies in the research methodologies of these studies, raise questions regarding the interpretation and convergence of the results of these studies. Specifically, previous research into motor imagery and cognition encountered four main hurdles: (1) issues with distinguishing between visual and motor imagery in research design and interpretation, (2) accounting for individual differences in motor imagery ability, (3) accounting for differences in paradigms used to evoke motor imagery, and (4) identifying the neural correlates of motor imagery. These hurdles will be noted throughout the review, with possible solutions outlined at the end. Without the use of appropriate methods when studying motor

imagery, we may instead be unknowingly researching other constructs, such as the influence of visual imagery on cognition. Only after these hurdles are adequately addressed in future research can we sprint forward and further our knowledge of the role of motor imagery in cognition research.

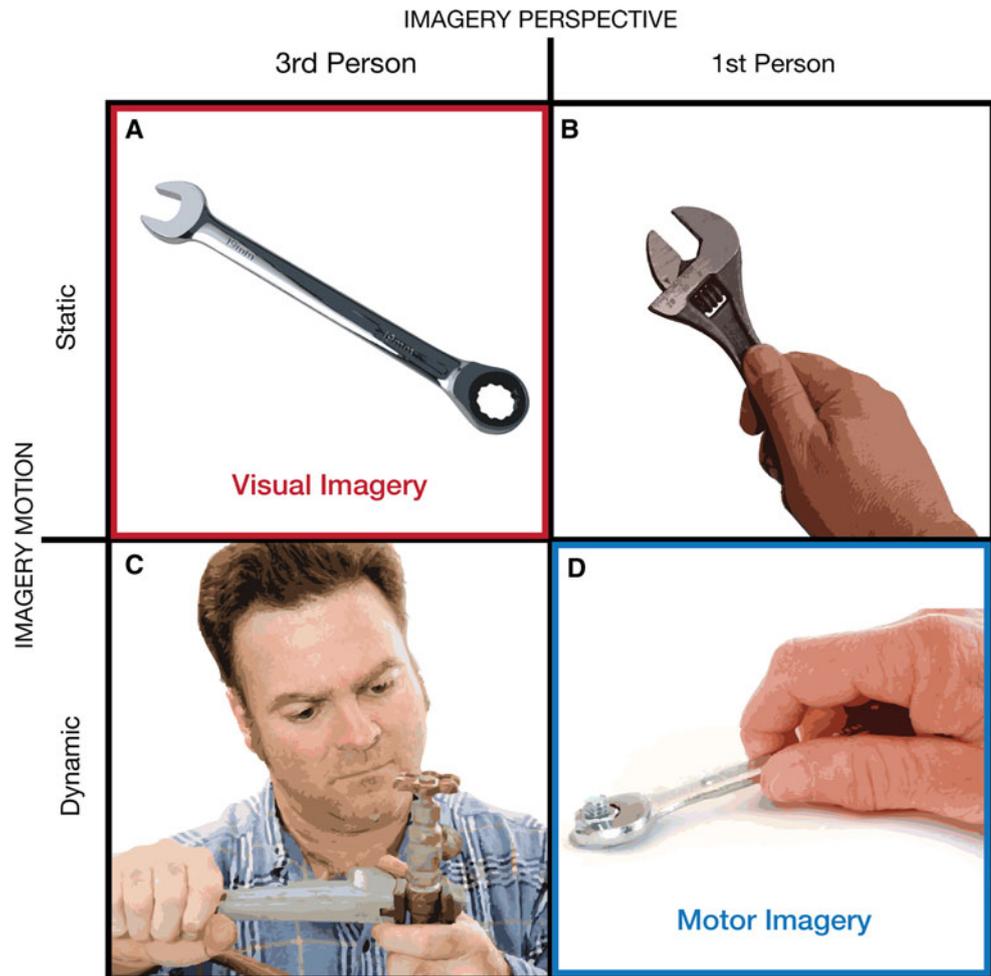
Defining motor imagery

In the psychology literature, mental imagery usually implies visual imagery. However, mental imagery also includes several other kinds of imagery: auditory, tactile, olfactory, gustatory, and motor (Betts 1909; Olivetti Belardinelli et al. 2001, 2004, 2009; Palmiero et al. 2009; Sheehan 1967).

Jeannerod and Frak (1999) define motor imagery as “a subliminal activation of the motor system, a system that appears to be involved not only in producing movements, but also in imagining actions, recognizing tools and learning by observation, as well as in understanding the behaviour of other people.” Experimentally, a prime example of a motor imagery reliant task is a mental rotation task. However, explaining a motor task, such as mental rotation, involves both motor *and* visual imagery (Annett 1995, also see the “[Mental rotation](#)” section). Specifically, visual imagery is the act of imagining an object or scene in your mind, when it is not actually in front of you. Any time you imagine an object that is not directly perceivable, you are engaging in visual imagery. Examples of visual imagery include imagining where you left your keys last or what is in your closet. Motor imagery, on the other hand, is the act of imagining a motoric action, and thus, must be a dynamic image (Engelkamp and Zimmer 1990; Decety 1996). Thus, visual imagery is usually *static* while motor imagery is *dynamic*. Many published experiments may inadvertently have studied visual imagery rather than motor imagery due to unclear task instructions (**Hurdle #1: issues with distinguishing between visual and motor imagery**). For a detailed discussion of this dissociation see McAvinue and Robertson (2007).

Another key difference between visual and motor imagery is the point-of-view (e.g., first-person versus third-person perspective; see Fig. 1). To be sure that the participant is involved in the imagery themselves, internally and egocentrically, rather than the participant externally/allogocentrically imagining a motor action being performed by another—we need to instruct the participant as to *how* to imagine the scene (Epstein 1980). A concrete example of this distinction is the difference between imagining themselves using a wrench (first-person perspective) compared to watching another person using a wrench (third-person perspective; see Fig. 1). Researchers suggest using the

Fig. 1 Examples of possible images for the word “WRENCH”. Images can either be from the 1st person or the 3rd person perspective, and either be static or dynamic in nature. Visual imagery is usually static and from a 3rd person perspective (a), while motor imagery is usually from the 1st person perspective and involves dynamic motion (d)



first-person perspective for motor imagery involves kinaesthetic feedback, where the third-person perspective is much more conducive to visual imagery (e.g., Decety et al. 1988; Epstein 1980; Jeannerod 1994; Mellet et al. 1998; Sirigu and Duhamel 2001). Providing further evidence for the embodied nature of motor imagery, Decety and Ingvar (1990) review several studies that found that engaging in motor imagery significantly increased heart rate and interacted with respiration rates, though motor imagery produced weaker effects than overt motor performance would. However, it is important to note that in the absence of kinaesthetic feedback, there is some evidence that third-person imagery may lead to better performance in some imagery tasks (White and Hardy 1995). Nonetheless, many studies do not provide clear instructions to their participants. Future studies investigating motor imagery should ensure that their imagery instructions *explicitly* ask the participants to imagine interacting with objects from a first-person perspective.

Though mental imagery comprises both visual and motor imagery, visual imagery is represented primarily

through the visual perception system, while motor imagery is reliant primarily on the motor system—two independent processes (McAvinue and Robertson 2007). While these two processes are complementary, Sirigu and Duhamel (2001) demonstrated that these processes can in fact be dissociated neurally in a lesion study. In this study, two patients—as well as several healthy controls—performed visual and motor imagery tasks. The researchers found a visual imagery deficit in the patient with inferotemporal lobe damage and a motor imagery deficit in the patient with left parietal lobe damage. While these impairments are not sufficient to suggest a sole neural correlate for their respective imagery strategies, they do indicate that the strategies are separable in a double dissociation.

Nonetheless, several hurdles exist with previous research, particularly in ensuring that motor imagery is used rather than visual imagery. Even if instructions given to the participant clearly ask for motor imagery—not everyone is equally able to imagine motoric actions (**Hurdle #2: accounting for individual differences in motor imagery ability**; see McAvinue and Robertson

2008, 2009). Using motor imagery can be difficult for some individuals, especially as it is somewhat less natural than visual imagery. Before we can look directly at the implications of motor imagery on cognitive abilities and neural substrates, we first need to account for individual variability in motor imagery ability (Annett 1995; de Lange et al. 2008). Several questionnaires have been developed to assess an individual's motor imagery ability (see McAvinue and Robertson 2008, for a review). Commonly used motor imagery ability questionnaires such as the MIQ (Hall and Pongrac 1983; most recently the MIQ-RS: Gregg, Hall and Butler 2010), VMIQ (Isaac et al. 1886; most recently the VMIQ-2: Roberts et al. 2008), and KVIQ (Malouin et al. 2007) ask participants to imagine doing the a series of overt movements and rate how vivid the imagined motor movements felt. Guillot et al. (2008) found that individuals with better motor imagery abilities activated more localized cortical regions during both motor execution and motor imagery (Fig. 2a; also see Olivetti Belardinelli et al. 2009; Palmiero et al. 2009). As some individuals are better at motor imagery than others, it is possible that these differences in ability will also interact with effects of motor imagery on other cognitive tasks.

Additionally, numerous studies have found athletes to be significantly more adept with motor imagery than individuals without extensive sport experience. For example, Mahoney and Avenier (1977) found that gymnasts who performed better used motor imagery rather than visual imagery. The better performing gymnasts also were found to have better control during mental practice. However, as pointed out by Annett (1995) athletes often regularly use mental practice to covertly rehearse sports-related actions (e.g., Driskell et al. 1994; Feltz and Landers 1983; Jones and Stuth 1997). Recent research has further tested the influence of motor imagery on sports-related motor performance. For example, an exploratory study has found that a combination of motor imagery and physical practice can improve the learning of tactical strategies in basketball more than either motor imagery or physical practice alone (Guillot et al. 2009). Recent studies have also investigated the differences between novice and expert athletes in mental practice ability in basketball players (Cummings et al. 2004), volleyball players (Tomasino et al. 2012), archers (Chang et al. 2011), golfers (Bernier and Fournier 2010), high jumpers (Olsson et al. 2008), gymnasts (Mahoney and Avenier 1977; Naito 1994), soccer players (O and Munroe-Chandler 2008), ice skaters (Arvinen-Barrow et al. 2008), speed skaters (Oishi and Maeshima 2004), martial artists (Babiloni et al. 2010; Moreau et al. 2010), and horse jockeys (Callow and Waters 2005). While much of this research is exploratory, numerous studies have shown mental practice (specifically motor imagery) to be a promising indicator of an athlete's success.

Automaticity of motor imagery

Research into motor imagery can be divided into several experimental paradigms, including mental imagery questionnaires (described above), imagined finger movements (e.g., Deiber et al. 1998; Hanakawa et al. 2008; Guillot et al. 2008), mental rotation (Shepard and Metzler 1971; Vandenberg and Kuse 1978), mental chronometry (e.g., Decety 1996; Jeannerod and Frak 1999; Jeannerod 2006; Guillot et al. 2008), hand laterality (e.g., Coslett et al. 2010; Parsons et al. 1995), grip selection (e.g., Johnson 1998), and imagined tool-use (Decety et al. 1988; Higuchi et al. 2007). See McAvinue and Robertson (2008) for more detailed discussions of these tasks. All of these tasks are based on deliberate motor imagery, where participants intentionally imagine motor actions. In these studies, motor imagery is very similar to motor planning (e.g., Hanakawa et al. 2008). For example, consider if an individual closed their eyes and vividly imagined a sequence of motor movements, such as in shooting a basketball. Similar brain regions should become active in this imagined activity compared to if the individual was actually planning to shoot a basketball. Specifically, one possible purpose of motor imagery is to “prepare the organism for a potential action” (Jeannerod 2006, p. 60). In other words, motor imagery should activate motor-related brain regions, but to a lesser degree than actual overt motor activity (discussed further in “Neural correlates of motor imagery”). Nikulin et al. (2008) developed a further intermediate between motor imagery and motor execution, called quasi-movements. Briefly, in the quasi-movement condition, the experimenters asked participants to perform a movement, but to minimize the strength of the movement such that it would be undetectable with electromyograph (EMG) recordings. As a result here participants may be “imagining” the motor action even more vividly than they would in motor imagery itself, leading to a more intense proprioceptive sensation and a greater degree of activation in motor cortices. As a result, quasi-movements may prove to be a beneficial training strategy for athletes.

In contrast to studies of deliberate motor imagery and quasi-movements, numerous studies have also suggested that motor imagery can be evoked *automatically*, without conscious intent. For example, Chao and Martin (2000) report that viewing images of graspable objects (tools) activates premotor cortex, while images of faces, houses, and animals did not. Prior to this study, Martin et al. (1996) conducted a similar study but only used tools and animals and came to similar conclusions. Similarly, processing of words that are conducive to motor imagery, such as functionally manipulable nouns and action verbs, have been shown to activate motor-related brain regions (see the sections “Motor imagery and language” and “Neural

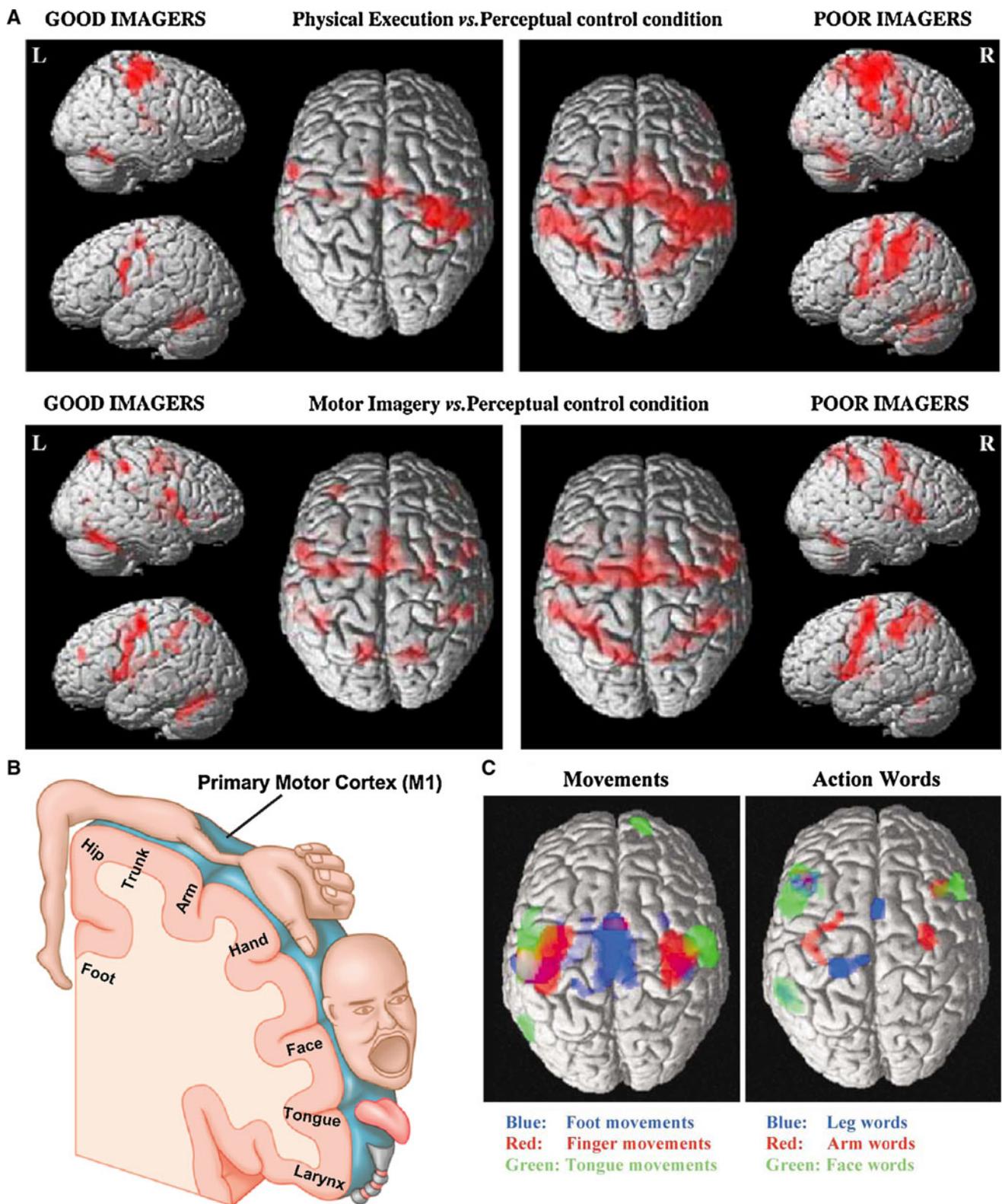


Fig. 2 Activation of primary motor cortex (M1) from motor execution and motor imagery. **a** Neural activation due to motor execution and motor imagery in both good and poor imagers. Reprinted from Guillot et al. (2008), with permission. Copyright 2008, Elsevier. **b** Illustration of the somatotopic organization of the motor cortex (after Penfield and

Rasmussen 1950). Modified, with permission. Copyright 2010, Posit Science. **c** Hemodynamic activation during either tongue, finger, and foot movements (*left*), or during reading action words related to face, arm, and leg movements (*right*). Reprinted from Hauk et al. (2004) with permission. Copyright 2004, Elsevier

correlates of motor imagery” for discussions of these studies). Importantly, these studies demonstrated that motor imagery can occur automatically, but, it is possible that this is a different form of motor imagery than is used in more deliberate motor imagery tasks. This is of particular interest in our review, as this automatic form of motor imagery is likely to be related to the influence of motor imagery on higher-level cognition.

Taken together, this brief overview of motor imagery studies separates motor imagery studies into two categories: (a) deliberate motor imagery through comparisons with motor execution, and (b) automatic motor imagery based on stimuli properties. In light of this, we also observe an additional hurdle—**Hurdle #3: accounting for differences in paradigms used to evoke motor imagery**. These differences need to be kept in mind when evaluating an assortment of motor imagery studies.

Motor imagery and language

Motor imagery can occur automatically, and is not confined to procedures that lead to deliberate and intentional motor imagery. Specifically, motor imagery can also occur automatically as a component of everyday language processing (Pulvermüller 2005; Zwaan and Taylor 2006). Most motor imagery studies involving words tend to use verbs as motor imagery stimuli, as they are ‘action words’ (e.g., Pulvermüller et al. 2001).

Providing strong evidence for an influence of motor imagery in language processing, Hauk et al. (2004) found that passively reading action words (e.g., LICK, KICK, PICK) somatotopically activated M1 cortex (see Fig. 2b, c). Similarly, Tettamanti et al. (2005) demonstrated that passively listening to action-related sentences activated the somatotopically appropriate region of primary motor cortex. For example, hearing “I kick the ball.” activated leg regions of M1, while “I grasp the knife” activated arm regions of the cortex.

Hauk et al. (2004) and Tettamanti et al. (2005) demonstrated that passive reading and listening, respectively, of action phrases can somatotopically activate primary motor cortex. Hauk et al. (2004) directly state that “word-meaning processing elicits activity patterns in frontocentral action-related areas, including motor and premotor cortex”. An ERP study by van Elk et al. (2010) also suggests that activation of primary motor and premotor cortices occurs automatically when processing the meaning of action phrases. van Elk et al. (2010) provided participants with motor imagery phrases involving either humans or animals. One hypothesis is that they may observe stronger activation of M1 for human phrases as these phrases are likely easier to process. Alternatively, stronger M1

activation may be observed for the animal phrases as there is a higher cloze probability for these phrases (more limited lexical-semantic choice). In this study, van Elk et al. (2010) found greater M1 activation for the animal phrases suggesting that M1 activation is driven more by the cloze probability than the familiarity of the action. This result provides further evidence of the interplay between action and language.

Neuroimaging research in the last decade has found many instances where language and motor performance intertwine. As an example of semantic recognition interfering with motor processing, Creem and Proffitt (2001) found that a semantic dual-task impaired object grasping significantly more than a spatial dual-task. Here the researchers directly suggest that semantic information of an object’s identity may need to be retrieved before it can be used appropriately, suggesting that a semantic-functional identity may be a necessary step prior to motor interaction with the object. From this point of view, Gibson’s affordances may be mediated by this stored semantic-functional identity, and thus by memory itself. This logic also may be related to the ‘what’ versus ‘how’ visual streams proposed by Goodale and Milner (1992). Additional evidence can also be found by Boulenger et al. (2008), finding that subliminal processing of action phrases interfered with motor performance. Taking this one step further, TMS has been used to activate the arm and leg regions of M1, significantly interfered with response time in a lexical decision task (Pulvermüller et al. 2005). A similar TMS study has also been conducted by Buccino et al. (2005) using hand- and foot-action-related sentences. Furthermore, motor lesions have also been shown to impair motor-related lexical abilities (Arévalo et al. 2007).

In a recent fMRI study, Rueschemeyer et al. (2010) used a lexical decision task to investigate differences between functionally and volumetrically manipulable object words. Rueschemeyer et al. (2010) suggest that ‘manipulability’ as used in previous studies is vague and additional specifications are needed. To be precise, functional manipulation is when the named object can be interacted with in a tool-like fashion (e.g., WRENCH, ROPE, HAMMER). A volumetric object cannot be used as a tool, but is still volumetrically manipulable (e.g., BRICK, VASE, STATUE). The results of this study suggest that neural representations of object names can be differentiated by the functional versus volumetric distinction and are differentially processed by inferior parietal cortex as well as the pre-SMA. Rueschemeyer et al. (2010) also present a detailed overview of the motor imagery and language literature. The effect of manipulability on lexical processing has also been investigated less directly in several other studies (e.g., Arévalo et al. 2007; Bub et al. 2008; Buxbaum and Saffran 2002; Just et al. 2010; Saccuman et al. 2006).

Converging with studies of manipulability, Glover et al. (2004) asked participants to silently read a word presented on a computer screen and then to grasp a wooden block that had been placed in front of the participant. They found that if the presented word represented a large graspable object (e.g., APPLE), relative to the block, participants would have larger grip aperture early in the movement. Similarly, if the word represented a small graspable object (e.g., GRAPE), participants would have a smaller grip aperture at the beginning of the movement. However, as the participant's hand approached the block, this difference decreased. These findings suggest that automatic semantic processing of the presented word interfered with initial motor planning of the block grasping, though action execution mechanisms were able to automatically correct for this interference as the participant's hand advanced towards the block. In other words, Glover et al. (2004) found that automatic semantic processing of manipulable object nouns utilized similar neural regions as overt motor execution, resulting in semantic processing interfering with the action planning (grip aperture).

Investigating motor imagery through nouns and verbs

Most studies of motor imagery and language either use (a) words that involve different body parts (several of the studies described in the section “[Motor imagery and language](#)”), or (b) motor words relative to non-motor words – using action verbs as motor words, but concrete nouns as the non-motor words (e.g., Boulenger et al. 2008; Frak et al. 2010; Nazir et al. 2008, several memory studies by Engelkamp discussed in the sections “[Memory for items](#)” and “[Memory for associations](#)”). While it is true that action verbs generally will lead to more motor imagery than concrete nouns, this comparison is potentially confounded by differences between nouns and verbs, which have been previously shown to be processed differently (Federmeier et al. 2000; Neinger and Pulvermüller 2001; Shapiro and Caramazza 2003).

To avoid this issue of contrasting verbs and nouns to research the effects of motor imagery on language, recent studies have used one of three options: (a) Used only verbs, comparing manual (hand-related) verbs with non-manual verbs (e.g., Papeo et al. 2009; Willems et al. 2011). (b) Used only nouns. In response to memory studies that also had this issue, Saltz (1988) suggests that one way to avoid this the inconsistency caused by using verbs (e.g., HOP) is to use semantically related nouns instead (e.g., RABBIT). While this partially solves the noun/verb issue, the results of recent neuroimaging studies can be employed to more directly address this hurdle, by comparing functionally manipulable (‘manipulable’) nouns with volumetrically manipulable (‘non-manipulable’) nouns (both of which are subsets of concrete nouns; e.g., Bub et al. 2008;

Buxbaum and Saffran 2002; Just et al. 2010; Rueschmeyer et al. 2010). (c) Used *both* nouns and verbs, through the inclusion of at least four conditions (both manual and non-manual verbs, and both manipulable and non-manipulable nouns; e.g., Arévalo et al. 2007; Bedny et al. 2008, 2012; Saccuman et al. 2006). This issue additionally contributes to **Hurdle #3 (paradigm differences)**, as motor imagery evoked by nouns, verbs, and most importantly nouns versus verbs, may each lead to different behavioural and neuroimaging results.

Paivio's dual-coding hypothesis

Another way to investigate how different item-properties influence cognitive processing of words is through memory performance (this approach was particularly helpful before the advent of modern neuroimaging). In the memory literature, it is well known that more imageable or concrete words are remembered better than less imageable or abstract words in tests of item memory (such as free recall). Paivio's dual-coding theory (1971, 1986, 2007) explains this result by suggesting that abstract words can only be encoded using a ‘verbal’ code. Concrete words can be encoded using both a verbal code as well as a ‘image’ code—due to the imageable properties inherit to concrete words. The premise of this theory is that while both abstract and concrete words rely on verbal processing, concrete words also involved imaginal processing—possibly leading to the memory enhancement for imageability. Neurally, while the verbal (language) system is largely lateralized to the left hemisphere in most individuals, image-based processing involves both hemispheres—as predicted by Paivio (Binder et al. 2005). Returning to motor imagery, Engelkamp and Zimmer (1984) suggest an extension of Paivio's dual-coding theory to incorporate an additional ‘motor’ code. Thus, it is possible that materials conducive to motor imagery (e.g., object and action words) could potentially activate three distinct representation systems. This hypothesis would further support the notion that memory for action-based representations are the initial purpose of the memory system and that these representations are more resilient to memory impairments. However, the literature is not clear if it is possible for the visual and motor code to work in parallel, or if only one coding may be activated at a given time (see **Hurdle #1: visual versus motor imagery**). For an example of possible features within a given processing system, see Fig. 3.

Motor imagery and memory

It has been suggested that memory evolved to help serve perception and action (Glenberg 1997). From this view, it

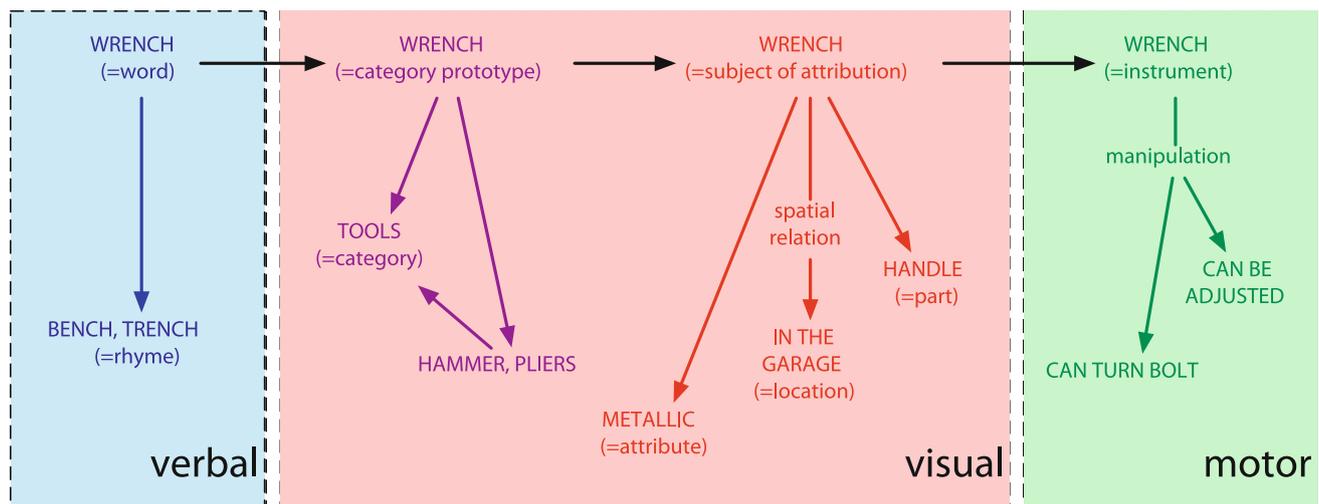


Fig. 3 Example word properties associated with verbal, visual, and motor codings of the word “WRENCH” (Inspired by Alywin 1990, Fig. 2)

can be proposed that the memory system should be better suited for encoding and retrieving action-based material, rather than more abstract concepts. Thus, memory for action-based representations (e.g., objects and actions) should have better recall performance than for other representations. For example, manipulable objects, such as tools, should be remembered easily due to their implied functional properties for action (‘affordance’). As an example of the role of affordances in memory, Boschker et al. (2002) demonstrated that expert wall climbers are better able to correctly recall the position and orientation of handgrips from a studied climbing wall. However, the expert climbers only exhibited enhanced memory for functionally relevant aspects of the climbing wall, due to their better ability to recognize functional affordances of the wall; while inexperienced participants largely reported general structural features of the wall. Here the researchers propose that this difference in memory performance can be largely accounted for by the expert climbers having a more developed understanding of the functional affordances of the wall and thus encoded functional chains of holds (the climbing path), rather than functionally irrelevant information such as the shape of the holds (smooth, irregular, round, moon-like, etc...) and information about the various notches and grooves in the wall that are not relevant when climbing. If functional affordances and action-based representations can enhance memory—it can also be hypothesized that memory for action-based representations should also be more resilient to common memory impairments such as aging, brain lesions, and attentional constraints (e.g., short presentation/exposure time and distractions). Stemming from this perspective, memory for motor imagery (‘manipulable’) stimuli should be enhanced relative to visual imagery (‘concrete’/‘imageable’) stimuli with no motor component and ‘abstract’ stimuli. Motor imagery

mnemonic strategies should also prove more effective, as they are closer to the origin of memory’s initial purpose.

Returning to Paivio’s dual-coding theory (1971, 1986, 2007) which described verbal and visual representations of verbal stimuli, as previously discussed, this theory can be expanded to also encompass a motor code (Engelkamp and Zimmer 1984, 1989, but also see Lichtheim 1885). Engelkamp and Zimmer (1989) review the then-current literature and highlight the importance of imagery modality (e.g., motor vs. visual; see Fig. 1), suggesting that encoding strategy plays an important role in memory performance. Furthermore, Nilsson and Kormi-Nouri (2001) suggested that while Paivio used the picture superiority effect to support his dual coding theory, and Engelkamp used an enactment effect as evidence for another distinct memory system—all three of the discussed encoding strategy systems (verbal, visual, and motor) are components of the Tulving’s (1985) episodic memory system.

However, Perrig (1988) suggests that the encoding nature of stimuli should not modulate memory retrieval—and that instead memory should be encoding amodal concept representations. Specifically, Perrig (1988) found that in a free recall memory task, performance was not modulated by imaginal versus motor encoding strategies. While this result runs directly contrary to a multi-code representation approach, many published findings do not agree with this result (and are discussed in the following sections).

While motor imagery in general has been shown to activate various motor-related neural correlates (e.g., primary motor cortex), Naito et al. (2002) specifically suggest that these motor areas could be associated with the memory retrieval process—providing further evidence that encoding strategy supports memory performance.

Memory can be broken down into several categories, including memory for items, memory for associations, and

memory for order (see Murdock 1974). To properly examine the influence of motor imagery on memory, these three categories of memory tasks should be looked at separately.

Memory for items

Originally studies investigating memory for action focused directly on the effect of overt action on memory performance. In a review, Engelkamp and Cohen (1991) outline several findings suggesting that recall for enacted action phrases is superior to action phrases without enactment. Cohen (1983) and Zimmer and Saathoff (1997) also provide evidence that enacted item-memory is more resilient. Enactment also has been shown to improve free recall performance more than visual imagery (Engelkamp and Cohen 1991). In general, ‘doing’ is a more effective memory strategy than listening, seeing, or imagining (Engelkamp 1988). This has been further demonstrated using neuroimaging techniques (Nyberg et al. 2001). In this study, the researchers found that motor imagery improved memory performance more than visual imagery, but less than enactment. Additionally, the neuroimaging results suggested that memory retrieval may rely on reactivation of the motor cortex. Recently it has also been shown that gesturing during memory encoding can lead to enhanced recall, even when the amount of speech produced was controlled for (Cook et al. 2010). Furthermore, this memory enhancement effect was produced regardless of whether the participant chose to gesture spontaneously or if they were instructed to gesture by the experimenter, providing further evidence that motor processes may be able to enhance memory.

As discussed earlier, visual imagery is also known to enhance memory (see Paivio 1971). It is not clear if visual and motor imagery can occur in parallel (e.g., using one encoding strategy may prevent use of the other strategy concurrently; Helstrup 1989). Research also suggests that enactment and motor imagery may be an effortless and automatic encoding strategy—whereas verbal strategies and visual imagery are known to be an effortful and elaborative in nature (Cohen 1983; Engelkamp and Zimmer 1990; Zimmer and Saathoff 1997). Kormi-Nouri and Nilsson (2001) hypothesize that motor memory strategies may be more effective as the encoding experience is more self-involved, resulting in enhanced memory. Kormi-Nouri and Nilsson (2001) suggest that this may be further evidence that motor memory is evolutionarily older than verbal encoding (converging with Glenberg 1997).

In a more every-day situation, Martin and Jones (1998) presented participants with images of road-signs (‘road works’ and ‘pedestrian crossing’) and later asked orientation details about them (e.g., in the ‘road works’ sign,

which way was the shovel pointing). Recall performance was found to be significantly influenced by handedness, where right-handed participants were more accurate at identifying the direction of the ‘road works’ sign (left-facing), whereas left-handed participants were more accurate at identifying the direction of the ‘pedestrian crossing’ sign (right-facing). Participants performed at chance for the same-facing sign. Martin and Jones (1998) suggested that the difference they observed in recall performance may be a result of the manner in which participants would prefer to draw the figures, where right-handed participants preferred to draw left-facing profiles. Thus, they proposed that the asymmetric recall performance is related to handedness, but mediated by motor imagery. To test this, participants were asked to draw figures for a person ‘digging’ and ‘walking’ in a follow-up experiment. Participants performed as expected, showing similar results to the sign recall task. Thus, it may be the case that motor imagery automatically evoked in drawing a person doing an action mediates memory for the orientation of the common, everyday road-sign.

Memory for order

Motor imagery has been shown to improve sequence-learning and motor performance (Jackson et al. 2003). Stoter et al. (2008) have shown that motor imagery and enactment influence sequence-learning similarly in a pattern repeating task (akin to the game “Simon”) and found that performance was not affected by age.

While little research has been done directly on the effect of motor imagery on memory for order, a large body of research exists on one specific mnemonic strategy that is highly imagery-dependant—the ‘method of loci’. The method of loci (sometimes referred to as ‘memory palace’, see Spence 1984) is a highly imaginal memory technique where one imagines walking through a familiar environment, usually their home, and places the to-be-remembered items in various locations (or loci) within the environment. When later attempting to recall the objects, one imagines being in the familiar environment again and mentally walks by the various loci, walking in the same route as during study—thus recalling the items again but also retaining the correct order/sequence of the items. This mnemonic strategy is credited as being an ancient memory strategy and was first developed by a Greek poet named Simonides of Ceos, circa 500 B.C. (see Yates 1966, for an in-depth discussion of the origin of the method of loci). Furthermore, the method of loci has been shown to be a particularly effective memory strategy and has been found to be employed by the world’s best mnemonists (Maguire et al. 2003)—and does not necessarily rely on visual memory (Raz et al. 2009). Interestingly, unlike other memory

strategies that often involve a visual imagery component, the method of loci also invokes motor imagery (e.g., walking through the imagined environment). This additional motor imagery aspect is likely the reason the method of loci has been found to be particularly effective—a connection that has not been previously made.

Memory for associations

While the motor system has been shown to improve item-specific information, many studies by Engelkamp and colleagues suggest that motor encoding impairs associative learning (e.g., Denis et al. 1991; Engelkamp 1986; Engelkamp et al. 1989, 1991)—see Engelkamp (1995) for a review. However, visual (interactive) imagery has been shown by many studies to enhance association-memory (e.g., Madan et al. 2010; Paivio 1971). Engelkamp (1986) demonstrated a strong interaction between encoding strategies (motor vs. visual) for free recall and cued recall. However, many of Engelkamp's studies use action verbs as the 'items' in his studies. Thus, motor encoding pairs would consist of verb-verb pairings. Saltz (1988) suggests that this would further make learning item-specific as the pairs would consist of two acts, rather than an act and actor. Specifically, nouns are easier to integrate than verbs (Helstrup 1989). Thus, much of the research into motor versus visual imagery strategies is confounded by the use of nouns and verbs as stimuli. However, recently there is also evidence that enactment can enhance associative learning (Karantzoulis et al. 2006)

Neural correlates of motor imagery

While it is generally thought that motor imagery involves similar brain regions as motor execution, there is evidence that motor imagery involves subliminal activation of motor pathways, as well as some distinct regions that are not involved in overt movements (Dietrich 2008). Here we provide an overview of the extant literature on the neural correlates of motor imagery. Specifically, several brain regions associated with motor imagery include the primary motor cortex, cerebellum, parietal cortex, prefrontal cortex, and supplementary motor area.

Primary motor cortex (M1)

While motor imagery generally evokes the same neural correlates as overt motor execution, one region still debated is the role of primary motor cortex (M1) in motor imagery (see Jeannerod 2006, for a review). Ehrsson et al. (2003) explains that earlier PET studies do not report M1 activation due to motor imagery for several possible

reasons, including: (a) PET may not be sensitive enough to detect M1 activity, whereas fMRI has much better resolution; (b) possible mis-localization between M1 and premotor cortex; and (c) subjects may have used visual imagery strategies rather than the intended motor imagery (see Hurdles #1 and 2, and section “[Mental rotation](#)”)

While classically M1 has been thought to serve as an intermediate in communicating motor execution messages from the cortex to the body, recent experimental evidence suggests that M1 is also important in cognition itself (Jeannerod 2006). Specifically, Jeannerod (1994) suggests that motor imagery is part of action planning and should engage prefrontal regions more than in motor execution—therefore regions specifically associated with motor execution should be less active in imagery, but still more active in motor imagery than in a baseline condition (e.g., Lotze et al. 1999; Porro et al. 1996; Rao et al. 1993). Ehrsson et al. (2003) report that activity in M1 due to motor imagery follows the same organization as actual motor movement (also Szameitat et al. 2007). Several further studies have reinforced the notion that motor imagery activity at M1 is somatotopically organized (see Fig. 2b), but that it can also occur automatically, even when no motor action is consciously intended. Three of these studies were discussed previously: (a) Chao and Martin (2000) found greater M1 activation when participants viewed images of tools, than if they viewed images of faces, houses, or animals (also see Martin et al. 1996). (b) Hauk et al. (2004) found passive reading of action words somatotopically activated M1 (Fig. 2c). (c) Tettamanti et al. (2005) found M1 to be somatotopically activated when participants passively listened to action-related sentences (see the sections “[Automaticity of motor imagery](#)” and “[Motor imagery and language](#)” for more detailed discussions of these studies). A recent motor imagery study also suggests that motor expertise (e.g., sporting ability) affects processing of related action phrases at a neural-level (Beilock et al. 2008). Specifically, individuals with more experience and expertise were able to more reliably recruit premotor and primary motor cortex when processing the meaning of the presented action phrases. These results suggest that expertise influences the vividness of motor imagery—further supporting the notion that M1 is involved in motor cognition rather than simply as a raw output of motor execution commands from the brain to the rest of the body (see **Hurdle #2 (individual differences)**).

Nonetheless, numerous studies found that M1 was not activated due to motor imagery (though secondary motor regions were activated). These studies include motor imagery of finger movements (e.g. Rao et al. 1993; Tyszka et al. 1994), hand-object interactions (Lorey et al. 2010), as well as imagined body movements (e.g., walking; Olivetti Belardinelli et al. 2004). Of particular interest is

that the majority of motor imagery neuroimaging studies do not use electromyography (EMG) monitoring to exclude muscle contractions during the fMRI session, though this is done in some studies (e.g., Alkadhi et al. 2005; Ehrsson et al. 2003; Lorey et al. 2010).

Mental rotation

While many neuroimaging studies of motor imagery have found significant activation in motor imagery conditions, and many have not found significant activation, a survey of the literature indicates that mental rotation does not activate M1.

Windischberger et al. (2003) found that M1 was activated in a mental rotation task, but attributed the activation to button press responses and thus is simply an artifact, rather than the being associated with mental rotation task itself. Cohen et al. (1996) did not find M1 activation due to the mental rotation task, and instead suggest that it is a visual/spatial imagery task, rather than a motor imagery task. However, Tomasino and colleagues have demonstrated that intracranial cortical stimulation of primary motor cortex can impair motor performance in a mental rotation task (Tomasino et al. 2005). Similarly, research has shown that repetitive TMS (rTMS) to inhibit the primary motor cortex can also cause impairments in a mental rotation task (Ganis et al. 2000; Tomasino et al. 2005).

While some of these differences in results may be attributed to the stimuli used in the task, where some studies use the original Shepard and Metzler (1971) images (e.g., Cohen et al. 1996), some use other abstract images (e.g., Windischberger et al. 2003), and others use hand images (e.g., Ganis et al. 2000; Tomasino et al. 2005; Tomasino, et al., 2005). Thus, it appears that M1 is involved in mental rotation studies using hand images, but not with abstract stimuli, further highlighting the importance of **Hurdle #3 (paradigm differences)**.

See Annett (1995), McAvinue and Robertson (2006, 2007), and Munzert, Lorey, and Zentgraf (2009) for further discussions of mental rotation.

Based on current results, M1 does not appear to be reliably activated (or left unactivated) due to motor imagery. It is possible that M1 is only recruited in specific motor imagery-based tasks. However, if this is the case, the boundary conditions regarding this task specificity have yet to be determined.

Cerebellum

It is unclear what role the cerebellum plays in motor imagery—some studies report cerebellar activity while others do not. Dietrich (2008) suggests that the cerebellum may only be needed for online fine-tuning of movement,

and thus should not be needed in motor imagery processing. Additionally, Aleman et al. (2005) found that silent articulation of verbal stimuli may be mediated by the SMA and lateral cerebellum—and thus the cerebellar activity may be produced as a task-irrelevant artifact in motor imagery studies.

In contrast, tool use and motor learning have been shown to produce cerebellar activity in patterns suggesting that it is involved in motor cognition (Decety 1996; Jeannerod 2006), as well as motor execution (Imamizu et al. 2003; Obayashi et al. 2001). Current research also suggests that while both parietal and cerebellar networks are activated in imagery of tool use, we are currently unable to determine if these two systems are working in parallel with each other or independently (Higuchi et al. 2007). Nonetheless, there is strong evidence that the cerebellum is important in motor imagery, particularly in the PET literature. Frings et al. (2006) report that the cerebellum is involved in verb generation—a task that unarguably does not necessitate motor simulation in the ‘classic’ sense of *intentional* motor imagery (also see Petersen et al. 1989). Narrative imagery (e.g., storytelling) also has been shown to involve brain regions similar to motor imagery, including the cerebellum (Sabatinelli et al. 2006). Timmann and Daum (2007) further outline recent research that suggest that the cerebellum plays an important role in non-motor cognitive function.

Several researchers have also suggested that the cerebellum should be regionally activated by motor imagery, possibly in an inhibitory role (i.e., to prevent motor imagery from becoming motor execution). In this case, we would expect to find greater cerebellar activation in motor imagery than for motor execution (e.g., Lotze et al. 1999). However, there currently is disagreement as to the particular cerebellar regions associated with motor imagery within the cerebellum. Many studies by Decety and colleagues have found that the cerebellum plays an important role in motor imagery—including two studies directly focused on the localizing the cerebellar activation due to motor imagery (Decety et al. 1990; Ryding et al. 1993). The results of these studies suggest that motor imagery is likely reliant on the lateral regions of the cerebellum. Similarly, Jeannerod (2006) suggested that the anterior/lateral cerebellum is involved in overt motor execution, with the posterior cerebellum being distinctly important in motor cognition. However, other research groups have found the opposing finding, with lateral regions being more activated during motor execution, rather than motor imagery (Grafton et al. 1996; Parsons et al. 1995). Imamizu et al. (2003) directly suggested the opposite assignment of roles as Jeannerod (2006), with medial regions being associated with motor functions and lateral regions being associated with cognitive function. Additionally, it is

unclear whether motor imagery would correspond to being a motor or a cognitive function, or a combination of the two.

Based on current research, it is difficult to evaluate if the cerebellum is involved in motor imagery. The role of the cerebellum in motor imagery is clearly an important area for further research. However, it is also worth noting that the role of the cerebellum in motor execution is still unclear (Chan et al. 2009; Manto et al. in press), and this likely needs to be resolved before we can directly focus on the role of the cerebellum in motor imagery.

Parietal cortex

As aforementioned when contrasting visual and motor imagery, the results of Sirigu and Duhamel (2001) suggest that motor imagery necessitates parietal lobe function (also see Sirigu et al. 1996). Specifically, Sirigu and Duhamel (2001) propose that the parietal cortex may either be necessary for accessing kinaesthetic representations in motor simulations, or that parietal cortex can anticipate intended movements and monitor motor outflow—however, the exact function of parietal cortex in motor processing, at least in the case of imagery, is still unclear. See Culham et al. (2006) for a comprehensive review summarizing the extant literature on the parietal cortex and action in both humans and monkeys.

In a summary report, Crammond (1997) further elucidate the purpose of the parietal lobe in motor processes by suggesting that parietal cortex is activated in motor tasks regardless of overt execution (e.g., Stephan et al. 1995). This reasoning may also suggest why most motor imagery studies do not specifically mention parietal cortex as it is not limited to motor imagery but rather is integral to motor processes in general. Patients with parietal damage are not simply impaired in imagining motor tasks, but rather are not limited by normal physiological constraints when engaging in motor imagery (Crammond 1997). Similarly, damage to the parietal cortex may result in ideomotor apraxia (see Wheaton and Hallet 2007, for a review), where patients are unable to pantomime the use of tools. Deiber et al. (1998) also suggest that the pre-SMA has access to visual information through the inferior parietal cortex, while the SMA proper does not.

Admittedly, the parietal cortex is a broad brain region with many segregated streams of information processing, including pathways that have been functionally identified for action execution and action perception (Rizzolatti and Matelli 2003), but not for action-related imagery. Current research has not yet been able to conclusively suggest a more localized region within the parietal cortex, most likely related to Hurdles #1, 2, and 3. Similar statements can also be made about other regions, such as the prefrontal cortex.

Prefrontal cortex

Numerous studies have suggest that the prefrontal cortex is involved in motor planning and have found it to be activated more in motor imagery than in motor execution (e.g., Stephan et al. 1995). While imagery and execution both involve motor planning, motor imagery must involve inhibition of the actual movement, though Decety et al. (1994) and Decety (1996) point out that this would still appear as activation in neuroimaging methods. The particular locus of this inhibition is unclear thus far, but possible neural substrates include the prefrontal cortex (e.g., inferior frontal cortex) and the lateral cerebellum.

In a recent review article, Dietrich (2008) suggests that motor imagery activates the prefrontal cortex while motor execution instead deactivates the region. However, this finding is not only a limitation in linking motor imagery and overt actions, but instead suggests that imagery and action are at opposite ends of a process. While the implications of this proposition are up for debate, future research should take a much closer look at the role of the prefrontal cortex in motor imagery.

Supplementary motor area (SMA)

Another difference between motor imagery and motor execution is the region of neural activation within the SMA. Brain activity during motor imagery is found to be more rostral, and is in the pre-SMA region, while activity during motor execution is localized to the SMA proper (Stephan et al. 1995; Tyszka et al. 1994). In a review, Mellet et al. (1998) explain that the pre-SMA appears to be involved specifically in motor imagery, while evidence suggests that the SMA proper is only activated in overt motor execution. Nonetheless, Deiber et al. (1998) found activation of the pre-SMA during visual imagery (imagining motor actions from a third-person perspective). In short, the pre-SMA appears to show differential activation for motor imagery and motor execution.

In sum

The aforementioned brain regions outline our current knowledge of the neural correlates of motor imagery. However, as discussed throughout, there are still many ambiguities regarding the specifics of these neural correlates (**Hurdle #4: identifying the neural correlates of motor imagery**). Jeannerod (2006, p. 24) posits that the “content of motor images extends far beyond what can consciously be accessed by the agent”—further suggesting that many brain regions are likely involved in motor imagery.

Summary

The reviewed literature outlines several key aspects regarding motor imagery: (a) Motor imagery is different than visual imagery in both the perspective of imagery and in the use of motion. (b) Viewing action words or words representing manipulable objects can induce automatic motor imagery, and activate M1 somatotopically. (c) Motor imagery has been shown to enhance memory for items and order, but may impair memory for associations. (d) Much is still to be discovered regarding motor encoding as a memory strategy. (e) Motor imagery relies on several brain regions, likely including pre-SMA, M1, parietal cortex, and possibly the cerebellum.

Proposed solutions

While future research is necessary to overcome the presented hurdles, we offer some suggestions below as to *how* these hurdles can be addressed:

Hurdle #1: issues with distinguishing between visual and motor imagery

While both visual and motor imagery are similar—they are dissociable. Visual imagery is often done from a third-person, external, or allocentric, perspective and is ‘static’ in nature. On the contrary, motor imagery must be done from a first-person, egocentric, perspective and involve dynamic actions. Moreover, visual imagery is usually associated with visual perception systems, while motor imagery relies on the motor system. Nonetheless, motor imagery does incorporate visual aspects, perhaps building on top of visual imagery processes (Engelkamp and Zimmer 1984; Jeannerod 1994). One example of this can be observed in the findings of Sirigu and Duhamel (2001), where a patient with parietal damage was impaired in motor imagery tasks but unaffected in visual imagery tasks. Furthermore, the results suggest that the patient used visual imagery strategies in the motor imagery task, presumably because the lesion impeded his ability to use motor imagery. Providing participants with clear instructions defining motor imagery should help ensure participants use motor imagery, rather than visual imagery.

Recent research by Tomasino et al. (2007) found that neural activation of M1 during mental imagery of action phrases during silent reading was not influenced by perspective, but was solely mediated by the motority of the action phrase. Nonetheless, from a Gibsonian affordances and the embodied cognition perspective, it is more logical that motor imagery is done from a first-person perspective (e.g., seeing yourself using a wrench) as this is more likely

to also involve kinaesthetic imagery. In contrast, visual imagery is more the imagination of a scene (e.g., seeing a wrench lying on a table). Thus, despite the findings of Tomasino et al. (2007), an important distinction between motor and visual imagery strategies—where motor imagery is a more embodied and engaged imagery strategy. Again, providing clear instructions elucidating the first-person perspective intrinsic to motor imagery should address this hurdle.

In an attempt to elucidate the differences between visual and motor imagery for future research, we propose the following definitions:

Visual imagery: The imagining a single object or scene, such as a wrench or a waterfall. Visual imagery does not involve any agents with the objects (‘static’) and is viewed from a third-person/external/allocentric perspective.

Movement imagery: The imagining of motor movements, either of yourself from a first-person/internal perspective, or of another person from a third-person/external perspective. Motor imagery is a type of movement imagery.

Motor imagery: The imagining of *yourself* acting out a series of motor movements. Motor imagery often involves the imagining of yourself interacting with objects dynamically within a scene and is viewed from a first-person/internal/egocentric perspective. Kinaesthetic imagery is a subcomponent of motor imagery.

Kinaesthetic imagery: The imagining of motor movements through proprioception alone. Kinaesthetic imagery involves imagining how it feels (e.g., tactile sensations) to make motor movements and interact with objects on a moment-to-moment basis. Like motor imagery, kinaesthetic imagery is done from a first-person/internal/egocentric perspective. However, unlike motor imagery, kinaesthetic imagery is focused on portions of body image and specific body-object interactions, rather than imagery of the whole body over a series of movements. Thus, kinaesthetic imagery is an integral component within motor imagery.

While the above two definitions do not capture all possible mental images (e.g., imagining someone else using a wrench, Fig. 1c), these images could be described as a *combination* of both visual and motor imagery. Nonetheless, we believe these definitions provide a solid framework for the advancement of further research.

Hurdle #2: accounting for differences in motor imagery ability

In studies of motor imagery, it is essential that participants are using motor imagery rather than visual imagery. However, depending on the instructions researchers provide to participants, it may not be clear which method the

participants are actually using (Dietrich 2008). Additionally, even if instructions are clear, McAvinue and Robertson (2007) suggest that visual imagery may still be used if the participant has poor motor imagery abilities (e.g., individual differences). Cui et al. (2007) have demonstrated that it is possible to measure vividness of visual imagery using neuroimaging methods, however, it is unclear how a similar procedure could be designed for motor imagery as current research has not yet localized the essential neural substrates involved in motor imagery (see **Hurdle #4: neural correlates**).

McAvinue and Robertson (2008) outline several different questionnaires and tasks designed to objectively evaluate motor imagery ability. One such test is the Controllability of Motor Imagery test (Nishida et al. 1986), which athletes have been shown to perform better on (Naito 1994). Note, however, that using the definitions proposed to address Hurdle #1, this questionnaire is a test of movement imagery, rather than motor imagery, as it uses a third-person perspective

Ideally, future research would first measure an individual's motor imagery ability prior to the actual task of interest, as individual differences in ability and therefore BOLD response during the fMRI study. Additionally, participants could be trained to reach a criterion of motor imagery ability prior to undergoing the proposed study, ensuring that all participants are equally skilled and comfortable with motor imagery. Without motor imagery training, participants may be using visual imagery since motor imagery is a more effortful encoding strategy (Annett 1995; de Lange et al. 2008). While we consider this to currently be a hurdle that needs to be addressed, several recent neuroimaging studies of motor imagery have included measures of individual motor imagery ability (e.g., Ehrsson et al. 2003; Naito et al. 2002; Olivetti Belardinelli et al. 2004, 2009; Palmiero et al. 2009).

Hurdle #3: accounting for paradigm differences

Different motor imagery paradigms evoke motor imagery either automatically or deliberately. This difference also influences task complexity, where deliberate imagery paradigms are more involved/effortful for the participant, and automatic imagery paradigms are much less demanding for the participant (as they occur passively, without much less conscious intention). While not a 'hurdle' per se, differences in paradigms need to be accounted for and are essential when comparing findings across studies. In particular, some tasks may be more complex for the participant and this likely also contributes to the ambiguities present when pinpointing the neural correlates of motor imagery.

To be clear, we are not suggesting that only a handful of paradigms should be used when researching motor imagery, rather, a multitude of paradigms should be utilized to study motor imagery. However, researchers should pay careful attention to paradigm differences between their current study and prior research when formulating integrative theories of motor imagery. For example, future research should investigate differences in motor imagery when motor processing is automatically or deliberately evoked (see Meiser 2011, for a detailed discussion of this issue, directed to experimental psychology as a whole.)

Though previous research has investigated cognition for visual or motor stimuli—words used as 'visual' stimuli were often nouns, while verbs were often used as 'motor' stimuli (see "[Investigating motor imagery through nouns and verbs](#)"). Though attempts have been made to suggest that word class (noun or verb) was not driving the differences in memory between the two conditions (see Engelkamp 1986), not everyone was convinced (e.g., Saltz 1988). Drawing from recent neuroimaging results, it is possible to have motor nouns in the form of object nouns of manipulable objects (e.g., tools)—though earlier researchers likely did not know of this possibility (see Engelkamp and Zimmer 1990). Additionally, Rueschemeyer et al. (2010) outline measures for rating the imageability and manipulability of object nouns. To adequately investigate the effect of motor imagery on memory performance, it is essential to remove all other possible confounding variables (including grammatical class)

Hurdle #4: identifying neural correlates of motor imagery

It will be of critical importance to the motor imagery literature to elucidate the complex nature of the underlying neural correlates. As described earlier, it will be important to identify the degree to which the neural circuitry of motor imagery is similar to that of motor preparation and execution. It is likely that there is overlap, but the full extent of this is not yet known. The neuroimaging literature has thus far been very useful in identifying action networks in humans, and will continue to play an important role in uncovering the neural correlates of motor imagery.

Additionally, some of the variability in neural activation due to motor imagery in the primary motor cortex and cerebellum may be due to the variety of methods used in these studies (e.g., automaticity), and in particular to due Hurdles #1, 2, and 3. If more consistent instructions (e.g., first-person perspective) and individual motor imagery ability are taken into consideration when conducting future research, a much clearer picture of the neural basis for motor imagery should arise.

Future research should also take a closer look at the role of the parietal cortex, prefrontal cortex, and SMA. In particular, additional research should be done to pinpoint how active these regions are in motor imagery relative to motor execution.

Conclusion

Given the ubiquitous nature of motor imagery, it is important that we gain a firm understanding of its contribution to human cognition. However, before this field can substantially move forward, it is critical that future studies use consistent and precise methods to avoid the hurdles have been previously encountered. The studies outlined throughout this review, and in particular the proposed solutions, lay the foundation for discovering the role of motor imagery on higher-level cognition and for future research into embodied cognition.

The hurdles outlined in this review suggest that researchers should exercise caution when drawing conclusions when using problematic findings as precedents for their current studies (e.g., such as using the mental rotation task to research motor imagery). As previously described, neuroimaging studies have encountered difficulties in pinpointing the neural correlates of motor imagery. This is likely due to differences in motor imagery ability in the study participants. Just like visual imagery (Cui et al. 2007), there are differences in how well individuals are able to produce motor imagery (Guillot et al. 2008; Olivetti Belardinelli et al. 2009; Palmiero et al. 2009). Specificity in the researcher's instructions may also be an issue; motor imagery should be described as imagining motor interactions from a first-person perspective and should clearly differentiate motor imagery from visual imagery. Current research also suggests that some influential prior studies regarding motor imagery and memory may need to be re-evaluated. For example, Engelkamp (1986) suggested that motor imagery impairs association-memory. However, in this study, Engelkamp (1986) used action verbs as the to-be-remembered content, while in the visual imagery manipulation, concrete nouns were studied. We now know that concrete nouns can be either manipulable or non-manipulable and that these are processed differently in the brain (e.g., Rueschemeyer et al. 2010). Using a more controlled experimental design, it is possible that motor imagery may actually enhance association-memory. However, we cannot know for sure until the study is conducted.

From a Gibsonian and embodied cognition perspective, processing the functionality of objects around us is essential to our day-to-day lives. Everyday life involves situations where we are actively interacting with our environment—exemplifying the ecological value of a more embodied

approach to cognition. Wilson (2002) suggests that embodied cognition consists of six key claims. However, a close examination of these claims suggests that several aspects of embodied cognition are fundamentally driven by the interaction of the individual with their environment through motor processes. Thus, for us to gain a better understanding of embodied cognition as a perspective on everyday human behaviour, we must understand the influence of motor imagery on higher-level cognition.

Acknowledgments We thank Chris Westbury for constructive feedback on an earlier version of the manuscript. This research was partly funded by a Discovery grant from the National Science and Engineering Research Council of Canada held by AS.

References

- Aleman A, Formisano E, Koppenhagen H, Hagoort P, de Haan EHF, Kahn RS (2005) The functional neuroanatomy of metrical stress evaluation of perceived and imagined spoken words. *Cereb Cortex* 15:221–228
- Alkadhi H, Brugger P, Boendermaker SH, Crelier G, Curt A, Hepp-Reymond M-C et al (2005) What disconnection tells about motor imagery: evidence from paraplegic patients. *Cereb Cortex* 15:131–140
- Annett J (1995) Motor imagery: perception or action? *Neuropsychologia* 33:1395–1417
- Arevalo A, Perani D, Cappa SF, Butler A, Bates E, Dronkers N (2007) Action and object processing in aphasia: from nouns and verbs to the effect of manipulability. *Brain Lang* 100:79–94
- Arvinen-Barrow M, Weigand DA, Hemmings B, Walley M (2008) The use of imagery across competitive levels and time of season: a cross-sectional study among synchronized skaters in Finland. *Eur J Sport Sci* 8:135–142
- Aylwin S (1990) Imagery and affect: big questions, little answers. In: Hampson PJ, Marks DE, Richardson JTE (eds) *Imagery: current developments*, International Library of Psychology, New York
- Babiloni C, Marzano N, Infarinato F, Iacoboni M, Rizza G, Aschieri P, Cibelli G et al (2010) “Neural efficiency” of experts' brain during judgment of actions: a high-resolution EEG study in elite and amateur karate athletes. *Behav Brain Res* 207:466–475
- Barsalou LW (2008) Grounded cognition. *Annu Rev Psychol* 59: 617–645
- Bedny M, Caramazza A, Grossman E, Pascual-Leone A, Saxe R (2008) Concepts are more than percepts: the case of action verbs. *J Neurosci* 28:11347–11353
- Bedny M, Caramazza A, Pascual-Leone A, Saxe R (2012) Typical neural representations of action verbs develop without vision. *Cereb Cortex* 22:286–293
- Beilock SL, Lyons IM, Mattarella-Micke A, Nusbaum HC, Small SL (2008) Sports experience changes the neural processing of action language. *Proc Natl Acad Sci USA* 105:13269–13273
- Bernier M, Fournier JF (2010) Functions of mental imagery in expert golfers. *Psychol Sport Exerc* 11:444–452
- Betts GH (1909) *The distribution and functions of mental imagery*. Teachers College, Columbia University, New York
- Binder JR, Westbury CF, McKiernan KA, Possing ET, Medler DA (2005) Distinct brain systems for processing concrete and abstract concepts. *J Cogn Neurosci* 17:905–917
- Boschker MSJ, Bakker FC, Michaels CF (2002) Memory for the functional characteristics of climbing walls: perceiving affordances. *J Mot Behav* 34:25–36

- Boulenger V, Silber BY, Roy AC, Paulignan Y, Jeannerod M, Nazir TA (2008) Subliminal display of action words interferes with motor planning: a combined EEG and kinematic study. *J Physiol Paris* 102:130–136
- Bub DN, Masson MEJ, Cree GS (2008) Evocation of functional and volumetric gestural knowledge by objects and words. *Cognition* 106:27–58
- Buccino G, Riggio L, Melli G, Binkofski F, Gallese V, Rizzolatti G (2005) Listening to action-related sentences modulates the activity of the motor system: a combined TMS and behavioral study. *Cogn Brain Res* 24:355–363
- Buccino G, Sato M, Cattaneo L, Roda F, Riggio L (2009) Broken affordances, broken objects: a TMS study. *Neuropsychologia* 47:3074–3078
- Buxbaum LJ, Saffran EM (2002) Knowledge of object manipulation and object function: dissociations in apraxic and nonapraxic subjects. *Brain Lang* 82:179–199
- Callow N, Waters A (2005) The effect of kinesthetic imagery on the sport confidence of flat-race horse jockeys. *Psychol Sport Exerc* 6:443–459
- Chan RCK, Huang J, Di X (2009) Dexterous movement complexity and cerebellar activation: a meta-analysis. *Brain Res Rev* 59:316–323
- Chang Y, Lee J-J, Seo J-H, Song H-J, Kim Y-T, Lee HJ et al (2011) Neural correlates of motor imagery for elite archers. *NMR Biomed* 24:366–372
- Chao LL, Martin A (2000) Representation of manipulable man-made objects in the dorsal stream. *Neuroimage* 12:478–484
- Chemero A (2003) The outline of a theory of affordances. *Ecol Psychol* 15:181–195
- Clark A (1997) *Being there: putting brain, body, and world together again*. MIT Press, Cambridge
- Cohen MS, Kosslyn SM, Breiter HC, DiGirolamo GJ, Thompson WL, Anderson AK et al (1996) Changes in cortical activity during mental rotation: a mapping study using functional magnetic resonance imaging. *Brain* 119:89–100
- Cohen RL (1983) The effect of encoding variables on the free recall of words and action events. *Mem Cognit* 11:575–582
- Cook SW, Yip TK, Goldin-Meadow S (2010) Gesturing makes memories that last. *J Mem Lang* 63:465–475
- Coslett HB, Medina J, Kliot D, Burkey AR (2010) Mental motor imagery indexes pain: the hand laterality task. *Eur J Pain* 14:1007–1013
- Crammond DJ (1997) Motor imagery: never in your wildest dream. *Trends Neurosci* 20:54–57
- Creem SH, Proffitt DR (2001) Grasping objects by their handles: a necessary interaction between cognition and action. *J Exp Psychol Hum Percept Perform* 27:218–228
- Cui X, Jeter CB, Yang D, Montague PR, Eagleman DM (2007) Vividness of mental imagery: individual variability can be measured objectively. *Vis Res* 47:474–478
- Culham JC, Cavina-Pratesi C, Singhal A (2006) The role of parietal cortex in visuomotor control: what have we learned from neuroimaging? *Neuropsychologia* 44:2668–2684
- Cummings J, Hall C, Shambrook C (2004) The influence of an imagery workshop on athletes' use of imagery. *Athl Insight* 6:52–73
- de Lange FP, Roelofs K, Toni I (2008) Motor imagery: a window into the mechanisms and alterations of the motor system. *Cortex* 44:494–506
- Decety J (1996) The neurophysiological basis of motor imagery. *Behav Brain Res* 77:45–52
- Decety J, Ingvar DH (1990) Brain structures participating in mental simulation of motor behavior: a neuropsychological interpretation. *Acta Psychol* 73:13–34
- Decety J, Perani D, Jeannerod M, Bettinardi V, Tadary B, Woods R et al (1994) Mapping motor representations with positron emission tomography. *Nature* 371:600–602
- Decety J, Philippon B, Ingvar DH (1988) rCBF landscapes during motor performance and motor ideation of a graphic gesture. *Eur Arch Psychiatry Neurol Sci* 238:33–38
- Decety J, Sjöholm H, Ryding E, Stenberg G, Ingvar DH (1990) The cerebellum participates in mental activity: tomographic measurements of regional cerebral blood flow. *Brain Res* 535:313–317
- Deiber M-P, Ibanez V, Honda M, Sadato N, Raman R, Hallett M (1998) Cerebral processes related to visuomotor imagery and generation of simple finger movements studied with positron emission tomography. *Neuroimage* 7:73–85
- Denis M, Engelkamp J, Mohr G (1991) Memory of imagined actions: Imagining oneself or another person. *Psychol Res* 53:246–250
- Dietrich A (2008) Imaging the imagination: the trouble with motor imagery. *Methods* 45:319–324
- Driskell JE, Copper C, Moran A (1994) Does mental practice enhance performance? *J Appl Psychol* 79:481–492
- Ehrsson HH, Geyer S, Naito E (2003) Imagery of voluntary movement of fingers, toes, and tongue activates corresponding body-part-specific motor representations. *J Neurophysiol* 90:3304–3316
- Engelkamp J (1986) Nouns and verbs in paired-associate learning: instructional effects. *Psychol Res* 48:153–159
- Engelkamp J (1988) Modality-specific encoding and word class in verbal learning. In: Grueberg MM, Morris RE, Sykes RN (eds) *Practical aspects of memory: current research and issues*, Wiley, New York
- Engelkamp J (1995) Visual imagery and enactment of actions in memory. *Br J Psychol* 86:227–240
- Engelkamp J, Cohen RL (1991) Current issues in memory of action events. *Psychol Res* 53:175–182
- Engelkamp J, Mohr G, Zimmer HD (1991) Pair-relational encoding of performed nouns and verbs. *Psychol Res* 53:232–239
- Engelkamp J, Zimmer HD (1984) Motor programme information as a separable memory unit. *Psychol Res* 46:283–299
- Engelkamp J, Zimmer HD (1989) Memory for action events: a new field of research. *Psychol Res* 51:153–157
- Engelkamp J, Zimmer HD (1990) Imagery and action: differential encoding of verbs and nouns. In: Hampson PJ, Marks DE, Richardson JTE (eds) *Imagery: current developments*, International Library of Psychology, New York
- Engelkamp J, Zimmer HD, Denis M (1989) Paired associate learning of action verbs with visual- or motor-imaginal encoding instructions. *Psychol Res* 50:257–263
- Epstein ML (1980) The relationship of mental imagery and mental rehearsal to performance of a motor task. *J Sport Psychol* 2:211–220
- Federmeier KD, Segal JB, Lombrozo T, Kutas M (2000) Brain responses to nouns, verbs, and class-ambiguous words in context. *Brain* 123:2552–2566
- Feltz DL, Landers DM (1983) The effects of mental practice on motor skill learning and performance: a meta-analysis. *J Sport Psychol* 5:25–27
- Frak V, Nazir T, Goyette M, Cohen H, Jeannerod M (2010) Grip force is part of the semantic representation of manual action verbs. *PLoS ONE* 5:e9728
- Frings M, Dimitrova A, Schorn CF, Elles H-G, Hein-Kropp C, Gizewski ER et al (2006) Cerebellar involvement in verb generation: an fMRI study. *Neurosci Lett* 409:19–23
- Ganis G, Keenan JP, Kosslyn SM, Pascual-Leone A (2000) Transcranial magnetic stimulation of primary motor cortex affects mental rotation. *Cereb Cortex* 10:175–180

- Garbarini F, Adenzato M (2004) At the root of embodied cognition: cognitive science meets neurophysiology. *Brain Cognit* 56:100–106
- Gibson JJ (1977) The theory of affordances. In: Shaw R, Bransford J (eds) *Perceiving, acting, and knowing: toward an ecological psychology*, Lawrence Erlbaum, Hillsdale, pp 67–82
- Gibson JJ (1979) *The ecological approach to visual perception*. Houghton Mifflin, Boston
- Glenberg AM (1997) What memory is for. *Behav Brain Sci* 20:1–55
- Glover S, Rosenbaum DA, Graham J, Dixon P (2004) Grasping the meaning of words. *Exp Brain Res* 154:103–108
- Goodale MA, Milner AD (1992) Separate visual pathways for perception and action. *Trends Neurosci* 15:20–25
- Grafton ST, Arbib MA, Fadiga L, Rizzolatti G (1996) Localization of grasp representations in humans by positron emission tomography. 2. Observation compared with imagination. *Exp Brain Res* 112:103–111
- Gregg M, Hall C, Butler A (2010) The MIQ-RS: a suitable option for examining movement imagery ability. *Evid Based Complement Alternat Med* 7:249–257
- Guillot A, Colle C, Nguyen VA, Malouin F, Richards C, Doyon J (2008) Functional neuroanatomical networks associated with expertise in motor imagery. *Neuroimage* 41:1471–1483
- Guillot A, Nadrowska E, Collet C (2009) Using motor imagery to learn tactical movements in basketball. *J Sport Behav* 32:189–206
- Hall C, Pongrac J (1983) *Movement imagery questionnaire*. University of Western Ontario, London
- Hanakawa T, Dimyan MA, Hallett M (2008) Motor planning, imagery, and execution in the distributed motor network: a time-course study with functional MRI. *Cereb Cortex* 18:2775–2788
- Handy TC, Grafton ST, Shroff NM, Ketay S, Gazzaniga M (2003) Graspable objects grab attention when the potential for action is recognized. *Nat Neurosci* 6:421–427
- Hauk O, Johnsrude I, Pulvermüller F (2004) Somatotopic representation of action words in human motor and premotor cortex. *Neuron* 41:301–307
- Helstrup T (1989) Memory for performed and imaged noun pairs and verb pairs. *Psychol Res* 50:237–240
- Higuchi S, Imamizu H, Kawato M (2007) Cerebellar activity evoked by common tool-use execution and imagery tasks: an fMRI study. *Cortex* 43:350–358
- Imamizu H, Kuroda T, Miyauchi S, Yoshioka T, Kawato M (2003) Modular organization of internal models of tools in the human cerebellum. *Proc Natl Acad Sci USA* 100:5461–5466
- Isaac A, Marks DF, Russell DG (1986) An instrument for assessing imagery of movement: the vividness of movement imagery questionnaire (VMIQ). *J Ment Imag* 10:23–30
- Jackson PL, Lafleur MF, Malouin F, Richards CL, Doyon J (2003) Functional cerebral reorganization following motor sequence learning through mental practice with motor imagery. *Neuroimage* 20:1171–1180
- Jeannerod M (1994) The representing brain: neural correlates of motor intention and imagery. *Behav Brain Sci* 17:187–245
- Jeannerod M (2006) *Motor cognition: what actions tell the self*. Oxford University Press, New York
- Jeannerod M, Frak V (1999) Mental imaging of motor activity in humans. *Curr Opin Neurobiol* 9:735–739
- Johnson SH (1998) Cerebral organization of motor imagery: contralateral control of grip selection in mentally represented prehension. *Psychol Sci* 8:219–222
- Jones L, Stuth G (1997) The uses of mental imagery in athletics: an overview. *Appl Prev Psychol* 6:101–115
- Just MA, Cherkassky VL, Aryal S, Mitchell TM (2010) A neurosemantic theory of concrete noun representation based on the underlying brain codes. *PLoS ONE* 5:e8622
- Karantzoulis S, Rich JB, Mangels JA (2006) Subject-per formed tasks improve associative learning in amnesic mild cognitive impairment. *J Int Neuropsychol Soc* 12:493–501
- Kormi-Nouri R, Nilsson L-G (2001) The motor component is not crucial! In: Zimmer HD, Cohen RL, Guynn MJ, Engelkamp J, Kormi-Nouri R, Foley MA (eds) *Memory for action: a distinct form of episodic memory?*, Oxford University Press, New York, pp 97–111
- Lichtheim L (1885) On aphasia. *Brain* 7:433–484
- Lorey B, Pilgramm S, Walter B, Stark R, Munzert J, Zentgraf K (2010) Your mind's hand: motor imagery of pointing movements with different accuracy. *Neuroimage* 49:3239–3247
- Lotze M, Montoya P, Erb M, Hulsmann E, Flor H, Klose U et al (1999) Activation of cortical and cerebellar motor areas during executed and imagined hand movements: an fMRI Study. *J Cogn Neurosci* 11:491–501
- Madan CR, Glaholt MG, Caplan JB (2010) The influence of item properties on association-memory. *J Mem Lang* 63:46–63
- Maguire EA, Valentine ER, Wilding JM, Kapur N (2003) Routes to remembering: the brains behind superior memory. *Nat Neurosci* 6:90–95
- Mahoney MJ, Avenier M (1977) Psychology of the elite athlete: a exploratory study. *Cognit Ther Res* 1:135–141
- Malouin F, Richards CL, Jackson PL, Lafleur MF, Durand A, Doyon J (2007) The kinesthetic and visual imagery questionnaire (KVIQ) for assessing motor imagery in persons with physical disabilities: a reliability and construct validity study. *J Neurol Phys Ther* 31:20–29
- Manto M, Bower JM, Conforto AB, Delgado-Garcia JM, da Guarda SNF, Gerwig M et al (in press) Consensus paper: roles of the cerebellum in motor control: the diversity of ideas on cerebellar involvement in movement. *Cerebellum*
- Martin A, Wiggs CL, Ungerleider LG, Haxby JV (1996) Neural correlates of category-specific knowledge. *Nature* 379:649–652
- Martin M, Jones GV (1998) Generalizing everyday memory: signs and handedness. *Mem Cognit* 26:193–200
- McAvinue LP, Robertson IH (2006) Measuring visual imagery ability: a review. *Imagn Cogn Pers* 26:191–211
- McAvinue LP, Robertson IH (2007) Relationship between visual and motor imagery. *Percept Mot Skills* 104:823–843
- McAvinue LP, Robertson IH (2008) Measuring motor imagery ability: a review. *Eur J Cogn Psychol* 20:232–251
- McAvinue LP, Robertson IH (2009) Motor imagery: a multidimensional ability. *J Ment Imag* 33:99–120
- Meiser T (2011) Much pain, little gain? Paradigm-specific models and methods in experimental psychology. *Perspect Psychol Sci* 6:183–191
- Mellet E, Petit L, Mazoyer B, Denis M, Tzourio N (1998) Reopening the mental imagery debate: lessons from functional anatomy. *Neuroimage* 8:129–139
- Moreau D, Clerc J, Mansy-Dannay A, Guerrien A (2010) Assessing movement imagery ability: self-report questionnaires versus performance-based tests. *Eur J Psychol* 4:93–109
- Munzert J, Lorey B, Zentgraf K (2009) Cognitive motor processes: the role of motor imagery in the study of motor representations. *Brain Res Rev* 60:306–326
- Murdoch BB (1974) *Human memory: theory and data*. Wiley, New York
- Naito E (1994) Controllability of motor imagery and transformation of visual imagery. *Percept Mot Skills* 78:479–487
- Naito E, Kochiyama T, Kitada R, Nakamura S, Matsumura M, Yonekura Y et al (2002) Internally simulated movement sensations during motor imagery activate cortical motor areas and the cerebellum. *J Neurosci* 22:3683–3691
- Nazir TA, Boulenger V, Roy A, Silber B, Jeannerod M, Paulignan Y (2008) Language-induced motor perturbations during the execution of a reaching movement. *Q J Exp Psychol* 61:933–943

- Neininger B, Pulvermüller F (2001) The right hemisphere's role in action word processing: a double case study. *Neurocase* 7: 303–317
- Nikulin VV, Hohlefeld FU, Jacobs AM, Curio G (2008) Quasi-movements: a novel motorcognitive phenomenon. *Neuropsychologia* 46:727–742
- Nilsson L-G, Kormi-Nouri R (2001) What is the meaning of a memory-systems approach? Comments on Engelkamp. In: Zimmer HD, Cohen RL, Guynn MJ, Engelkamp J, Kormi-Nouri R, Foley MA (eds) *Memory for action: a distinct form of episodic memory?*, Oxford University Press, New York, pp 136–143
- Nishida T, Katube A, Inomata K, Okazawa Y, Ito M, Kayama S et al (1986) A new test for controllability of motor imagery: the examination of its validity and reliability. *Jap J Phys Educ* 31: 13–22
- Nyberg L, Petersson KM, Nilsson L-G, Sandblom J, Aberg C, Ingvar M (2001) Reactivation of motor brain areas during explicit memory for actions. *Neuroimage* 14:521–528
- O J, Munroe-Chandler KJ (2008) The effects of image speed on the performance of a soccer task. *Sport Psychol* 22:1–17
- Obayashi S, Suhara T, Kawabe K, Okauchi T, Maeda J, Akine Y et al (2001) Functional brain mapping of monkey tool use. *Neuroimage* 14:853–861
- Oishi K, Maeshima T (2004) Autonomic nervous system activities during motor imagery in elite athletes. *J Clin Neurophysiol* 21: 170–179
- Olivetti Belardinelli M, Del Gratta C, Di Matteo R, De Nicola A, Ferretti A, Tartaro A et al (2001) Sensory image generation: a comparison between different sensory modalities with fMRI. *Neuroimage* 13:S394
- Olivetti Belardinelli M, Di Matteo R, Del Gratta C, De Nicola A, Ferretti A, Tartaro A et al (2004) Intermodal sensory image generation: an fMRI analysis. *Eur J Cogn Psychol* 16:729–752
- Olivetti Belardinelli M, Palmiero M, Sestieri C, Nardo D, Di Matteo R, Londei A et al (2009) An fMRI investigation on image generation in different sensory modalities: the influence of vividness. *Acta Psychol* 132:190–200
- Olsson C-J, Jonsson B, Nyberg L (2008) Internal imagery training in active high jumpers. *Scand J Psychol* 49:133–140
- Paivio A (1971) *Imagery and verbal processes*. Holt, Rinehart, and Winston, New York
- Paivio A (1986) *Mental representations: a dual coding approach*. Oxford University Press, New York
- Paivio A (2007) *Mind and its evolution: a dual coding theoretical approach*. Lawrence Erlbaum Associates, Mahwah
- Palmiero M, Olivetti Belardinelli M, Nardo D, Sestieri C, Di Matteo R, D'Ausilio A et al (2009) Mental imagery generation in different modalities activates sensory-motor areas. *Cogn Process* 10(Suppl 2):S268–S271
- Papeo L, Vallesi A, Isaja A, Rumiati RI (2009) Effects of TMS on different stages of motor and non-motor verb processing in the primary motor cortex. *PLoS ONE* 4:e4508
- Parsons LM, Fox PT, Downs JH, Glass T, Hirsch TB, Martin CC et al (1995) Use of implicit motor imagery for visual shape discrimination as revealed by PET. *Nature* 375:54–58
- Penfield W, Rasmussen T (1950) *The cerebral cortex of man*. Macmillan, New York
- Perrig WJ (1988) On the distinction of memory codes: image versus motor encoding. In: Denis M, Engelkamp J, Richardson JTE (eds) *Cognitive and neuropsychological approaches to mental imagery*, Martinus Nijhoff, Boston
- Petersen SE, Fox PT, Posner ML, Mintun M, Raichle ME (1989) Positron emission tomographic studies of single words. *J Cogn Neurosci* 1:153–170
- Porro CA, Francescato MP, Cettolo V, Diamond ME, Baraldi P, Zuiani C et al (1996) Primary motor and sensory cortex activation during motor performance and motor imagery: a functional magnetic resonance imaging study. *J Neurosci* 16: 7688–7698
- Pulvermüller F (2005) Brain mechanisms linking language and action. *Nat Rev Neurosci* 6:576–582
- Pulvermüller F, Harle M, Hummel F (2001) Walking or talking?: Behavioral and neurophysiological correlates of action verb processing. *Brain Lang* 78:143–168
- Pulvermüller F, Hauk O, Nikulin VV, Ilmoniemi RJ (2005) Functional links between motor and language systems. *Eur J Neurosci* 21:793–797
- Rao SM, Binder JR, Bandettini PA, Hammeke TA, Yetkin FZ, Jesmanowicz A et al (1993) Functional magnetic resonance imaging of complex human movements. *Neurology* 43:2311–2318
- Raz A, Packard MG, Alexander GM, Buhle JT, Zhu H, Yu S et al (2009) A slice of π : an exploratory neuroimaging study of digit encoding and retrieval in a superior memorist. *Neurocase* 15: 361–372
- Rizzolatti G, Matelli M (2003) Two different streams form the dorsal visual system: anatomy and functions. *Exp Brain Res* 153:146–157
- Roberts R, Callow N, Hardy L, Markland D, Bringer J (2008) Movement imagery ability: development and assessment of a revised version of the vividness of movement imagery questionnaire. *J Sport Exerc Psychol* 30:200–221
- Rosenbaum DA (2005) The Cinderella of psychology: the neglect of motor control in the science of mental life and behavior. *Am Psychol* 60:308–317
- Rueschemeyer S-A, van Rooij D, Lindemann O, Willems R, Bekkering H (2010) The function of words: distinct neural correlates for words denoting differently manipulable objects. *J Cogn Neurosci* 22:1844–1851
- Ryding E, Decety J, Sjöholm H, Stenberg G, Ingvar DH (1993) Motor imagery activates the cerebellum regionally. A SPECT rCBF study with ^{99m}Tc -HMPAO. *Cogn Brain Res* 1:94–99
- Sabatinelli D, Lang PJ, Bradley MM, Flaisch T (2006) The neural basis of narrative imagery: emotion and action. *Prog Brain Res* 156:93–103
- Saccuman MC, Cappa SF, Bates EA, Arevalo A, Rosa PD, Danna M et al (2006) The impact of semantic reference on word class: an fMRI study of action and object naming. *Neuroimage* 32:1865–1878
- Saltz E (1988) The role of motoric enactment (M-processing) in memory for words and sentences. In: Grueberg MM, Morris RE, Sykes RN (eds) *Practical aspects of memory: current research and issues*, Wiley, New York
- Shapiro KA, Caramazza A (2003) The representation of grammatical categories in the brain. *Trends Cogn Sci* 7:201–206
- Sheehan PW (1967) A shortened form of Betts' questionnaire upon mental imagery. *Clin Psychol* 23:386–389
- Shepard RN, Metzler J (1971) Mental rotation of three-dimensional objects. *Science* 171:701–703
- Sirigu A, Duhamel J-R (2001) Motor and visual imagery as two complementary but neurally dissociable mental processes. *J Cogn Neurosci* 13:910–919
- Sirigu A, Duhamel J-R, Cohen L, Pillon B, Dubois B, Agid Y (1996) The mental representation of hand movements after parietal cortex damage. *Science* 273:1564–1568
- Spence JD (1984) *The memory palace of Matteo Ricci*. Viking Penguin, New York
- Stephan KM, Fink GR, Passingham RE, Silbersweig D, Ceballos-Baumann AO, Frith CD et al (1995) Functional anatomy of the mental representation of upper extremity movements in healthy subjects. *J Neurophysiol* 73(1):373–386
- Stoter AJR, Scherder EJA, Kamsma YPT, Mulder T (2008) Rehearsal strategies during motor-sequence learning in old age: execution versus motor imagery. *Percept Mot Skills* 106:967–978

- Szameitat AJ, Shen S, Sterr A (2007) Motor imagery of complex everyday movements: an fMRI study. *Neuroimage* 34:702–713
- Tettamanti M, Buccino G, Saccuman MC, Gallese V, Danna M, Scifo P et al (2005) Listening to action-related sentences activates fronto-parietal motor circuits. *J Cogn Neurosci* 17:273–281
- Timmann D, Daum I (2007) Cerebellar contributions to cognitive functions: a progress report after two decades of research. *Cerebellum* 6:159–162
- Tomasino B, Borroni P, Isaja A, Rumiati RI (2005) The role of the primary motor cortex in mental rotation: a TMS study. *Cogn Neuropsychol* 22:348–363
- Tomasino B, Budai R, Mondani M, Skrap M, Rumiati RI (2005) Mental rotation in a patient with an implanted electrode grid in the motor cortex. *Neuroreport* 16:1795–1800
- Tomasino B, Guatto E, Rumiati RI, Fabbro F (2012) The role of volleyball expertise in motor simulation. *Acta Psychol* 139:1–6
- Tomasino B, Werner CJ, Weiss PH, Fink GR (2007) Stimulus properties matter more than perspective: an fMRI study of mental imagery and silent reading of action phrases. *Neuroimage* 36:T128–T141
- Tulving E (1985) How many memory systems are there? *Am Psychol* 40:385–398
- Tyszka JM, Grafton ST, Chew W, Woods RP, Colletti PM (1994) Parceling of mesial frontal motor areas during ideation and movement using functional magnetic resonance imaging at 1.5 Tesla. *Ann Neurol* 35:746–749
- van Elk M, van Schie HT, Zwaan RA, Bekkering H (2010) The functional role of motor activation in language processing: motor cortical oscillations support lexical-semantic retrieval. *Neuroimage* 50:665–677
- Vandenberg SG, Kuse AR (1978) Mental rotations: a group test of three-dimensional spatial visualization. *Percept Mot Skills* 47:599–604
- Wheaton LA, Hallet M (2007) Ideomotor apraxia: a review. *J Neurol Sci* 260:1–10
- White A, Hardy L (1995) Use of different imagery perspectives on the learning and performance of different motor skills. *Br J Psychol* 86:169–180
- Willems RM, Labruna L, D'Esposito M, Ivry R, Casasanto D (2011) A functional role for the motor system in language understanding: evidence from theta-burst transcranial magnetic stimulation. *Psychol Sci* 22:849–854
- Wilson M (2002) Six views of embodied cognition. *Psychon Bull Rev* 9:625–636
- Windischberger C, Lamm C, Bauer H, Moser E (2003) Human motor cortex activity during mental rotation. *Neuroimage* 20:225–232
- Yates FA (1966) *The art of memory*. University of Chicago Press, Chicago
- Zimmer HD, Saathoff J (1997) The influence of enactment on short-term recognition. *Acta Psychol* 95:85–95
- Zwaan RA, Taylor LJ (2006) Seeing, acting, understanding: motor resonance in language comprehension. *J Exp Psychol Gen* 135:1–11