



# The format of mental imagery: from a critical review to an integrated embodied representation approach

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## Abstract

The issue of the format of mental imagery is still an open debate. The classical analogue (depictive)—propositional (descriptive) debate has not provided definitive conclusions. Over the years, the debate has shifted within the frame of the embodied cognition approach, which focuses on the interdependence of perception, cognition and action. Although the simulation approach still retains the concept of representation, the more radical line of the embodied cognition approach emphasizes the importance of action and clearly disregards the concept of representation. In particular, the enactive approach focuses on motor procedures that allow the body to interact with the environment, whereas the sensorimotor approach focuses on the possession and exercise of sensorimotor knowledge about how the sensory input changes as a function of movement. In this review, the embodied approaches are presented and critically discussed. Then, in an attempt to show that the format of mental imagery varies according to the ability and the strategy used to represent information, the role of individual differences in imagery ability (e.g., vividness and expertise) and imagery strategy (e.g., object vs. spatial imagers) is reviewed. Since vividness is mainly associated with perceptual information, reflecting the activation level of specific imagery systems, whereas the preferred strategy used is mainly associated with perceptual (e.g., object imagery) or amodal and motor information (e.g., spatial imagery), the format of mental imagery appears to be based on dynamic embodied representations, depending on imagery abilities and imagery strategies.

**Keywords** Imagery · Dynamic · Perception · Semantic · Motor · Neuroimaging · Neuropsychology · Embodied cognition

## Introduction

Mental imagery is one of the most evident introspective aspects of human thought. It arises in the mind as mental

representations of stimuli and events in the absence of sensory inputs. Mental imagery plays a key role in different cognitive operations, such as memory (Paivio 1986), planning for the future (Moulton and Kosslyn 2009), spatial orientation (Palermo et al. 2008; Piccardi et al. 2017), navigational planning (Bocchi et al. 2017) and creativity (Finke et al. 1992; Palmiero et al. 2011, 2015, 2016a, b; Zaidel 2014). However, despite the introspective evidence of mental imagery and its importance for cognition, it is difficult to clarify its exact format.

Traditionally, the format of mental imagery has been debated in terms of depictive (analogue) and descriptive (propositional) approaches. The depictive approach is based on visual imagery (Finke 1989; Kosslyn 1980, 1994; Kosslyn et al. 2006). The core assumption is that mental imagery shares with perception common processes and mechanisms to a significant degree and functions as a modal analogue of perception. For Kosslyn (1980, 1994), mental images are picture-like representations. These are topographically organized at the neural level, allowing the generation of patterns of activation that make explicit geometric properties of representations

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stored in one's long-term memory (Kosslyn and Thompson 2003). Visual mental images share inherent properties of real stimuli, such as spatial extension, that would resemble arrays or matrices (Kosslyn et al. 2006) and produce the same effects as manipulating real objects. The depictive approach has also been associated with non-visual imagery modalities (Palmiero et al. 2014), although with some limitations (see the case of olfactory imagery: Stevenson and Case 2005).

In this vein, Brogaard and Gatzia (2017) proposed the quasi-pictorial (quasi-depictive) approach, positing that the mechanisms underlying vision for perception and conscious imagery do not overlap, whereas those governing vision for action and unconscious visual imagery do overlap. Vision for action relies on the dorsal stream, which is action-related and unconscious, working as the organizing principle of vision. (The ventral stream is perception-related and conscious.) According to this view, the pictorial phenomenology of visual imagery would be possible because it is processed by visual systems that also process matching visual experience. Thus, vividness of visual imagery relies on differences in the involvement of the primary visual cortex.

On the other hand, the descriptive approach (Pylyshyn 1973, 1979, 1981, 2002) assumes that mental images are descriptive representations that rely on an abstract, language-like format. A symbol system would transduce subsets of perceptual states into non-perceptual representations. Since these lose their link with perception, they become amodal and take part in representational structures that form a functional symbolic system, one characterized by a propositional format. For Pylyshyn, mental imagery does exist but has no symbolic independence. Mental images are epiphenomena involving tacit knowledge of the world. For example, mentally scanning over a distance marked as 50 miles would take longer than mentally scanning over a distance marked as 10 miles due to the individual's knowledge that more time is needed to cover longer distances. Therefore, the pattern of activation that can arise in topographically organized sensory areas is spurious.

Over the years, a new perspective on the format of mental imagery has been offered by the embodied cognition approach (Clark 1997; Gallagher 2005; Palmiero and Borsellino 2018; Varela et al. 1991; Wilson 2002). This approach is in progress and involves different views. In general, it rejects the idea that cognition works by processing abstract symbols. It focuses on the role of the body, action, environment and sensorimotor experience. The basic assumption is that perception is direct and serves to guide actions in cooperation with the environment, offering affordances of interactions in relation to the sensorimotor capacities of the organism, either for good or ill (Garbadini and Adenzato 2004; Gibson 1966, 1979). For example, a set of stairs represents an affordance that they be used for going up or down to a

human adult, but not for a crawling infant that is not yet able to walk. Thus, cognition is grounded in the body because it emerges from both the brain and the dynamic interactions between the body and its environment.

The concept of representation is addressed in different ways within the embodied cognition framework. On the one hand, the 'conservative and moderately embodied' approaches (Foglia and O'Regan 2016, p. 183) still retain the concept of representation, such as the simulation view (Barsalou 1999, 2008). On the other hand, the fully embodied approaches bypass the notion of representation, such as the enactive (Thomas 1999, 2009, 2014; Thompson 2007) and sensorimotor (Noë 2004; O'Regan and Noë 2001) views. This means that in using the lens of embodied cognition, the debate on the format of mental imagery has shifted from a representationalist to an anti-representationalist view.

The simulation, enactive and sensorimotor approaches are presented and discussed below. The goal was not to systematically review all studies, but to provide inputs in order to highlight the strengths and weaknesses of the embodied approaches to mental imagery. Next, based on insights provided by the embodied framework, the format of mental imagery is reviewed and discussed in terms of individual differences in imagery ability and imagery strategy.

## The simulation approach and mental imagery

This approach posits that cognition works on the basis of modal simulations that rely on the partial reactivation of perceptual, motor and introspective states, underlying past sensorimotor experience (Barsalou 1999, 2008). The 'perceptual symbol system' (Barsalou 1999) assumes that selective attention allows one to extract schematic representations of perceptual experience (e.g., the color green), which are subsequently stored in memory to function as symbols. The result is that these symbols are modal in nature because they are neural representations that reside in sensory-motor areas. Across different experiences, related perceptual symbols become integrated into a simulator that produces limitless simulations of the percept (e.g., simulations of green). Simulators also develop aspects of proprioception and introspection. They implement a fully conceptual system, allowing representation, categorization, productivity, abstraction, etc. At the neural level, associated brain areas capture bottom-up patterns of activation in sensory-motor areas. Afterward, association areas partially reactivate sensory-motor areas to implement perceptual symbols in a top-down manner. According to Barsalou, different kinds of simulations are possible. Mental imagery is the best-known case of non-automatic simulation of perceptual symbols. Since neural states underlying simulations of perceptual symbols arise

across the sensory modalities, proprioception and introspection, this approach also supports the generation of multimodal images. In general, this approach implies that mental imagery is based on simulations of sensorimotor processes through the reactivation of the same neural regions that are recruited in actual perception.

This approach is supported by studies that revealed interference (Craver-Lemley and Reeves 1992; Craver-Lemley et al. 1999; Ishai and Sagi 1997b; Perky 1910; Segal and Fusella 1970) and facilitation (Ishai and Sagi 1995, 1997a) of visual imagery on a subsequent visual detection task, because they account for common mechanisms at an early perceptual level (Wu et al. 2012). On the other hand, studies showing the interference and facilitation effects (Finke 1986; Cabeza et al. 1997; Wu et al. 2012) of visual imagery on subsequent visual identification tasks would account for interactions at later stages of the visual information processing stream, being more content-specific (Wu et al. 2012). In this vein, interference (Okada and Matsuoka 1992; Segal and Fusella 1970) and facilitation (Farah and Smith 1983) effects revealed using auditory detection tasks and interference effects of olfactory images using the odor detection task (Djordjevic et al. 2004) also show interactions between imagery and perception at an early stage of the information processing stream.

Behavioral evidence in support of the simulation approach also comes from studies of mental rotation (Borst et al. 2011; Shepard and Metzler 1971), scaling (D'Angiulli and Reeves 2007), scanning (Kosslyn et al. 1978; Borst and Kosslyn 2008) and inspection (Thompson et al. 2008), as they reveal that visual imagery preserves spatial properties. Interestingly, auditory images of environmental sounds were also found to preserve the structural properties of auditory stimuli, such as temporal-like characteristics (Halpern 1988) and pitch information (Elkin and Leuthold 2011; Intons-Peterson et al. 1992). Olfactory images of pleasant stimuli were found to involve larger sniffing than imagery of unpleasant odors, as in perception (Bensafi et al. 2003). Motor images resulted in the preservation of the total timing properties (duration) of actual movements (Papaxantis et al. 2002). However, structural and functional overlaps between visual imagery and visual perception have been questioned, given that visual images of objects (Intons-Peterson and Roskos-Ewoldsen 1989), mental scanning and mental rotation (Pylyshyn 1981) were found to be affected by the implicit knowledge of the physical laws that govern the world.

In addition, the neuroimaging evidence also leads one to question the extent to which mental imagery and perception share common neural areas (see Olivetti Belardinelli et al. 2009, 2011). Indeed, various studies have found activations of primary sensory cortices in visual (Amedi et al. 2005; Olivetti Belardinelli et al. 2009), tactile (Yoo et al.

2003), olfactory (Bensafi et al. 2007), gustatory (Kikuchi et al. 2005) and motor (Porro et al. 1996) imagery modalities. However, numerous other studies failed to detect the activation of the primary cortices during visual (Daselaar et al. 2010; Olivetti Belardinelli et al. 2004a, b), auditory (Bunzeck et al. 2005), olfactory (Olivetti Belardinelli et al. 2004a, 2009) and motor (Hanakawa et al. 2003) imagery modalities.

In summary, the simulation approach seems to account for the overlap between imagery and perception better at later than at earlier stages of the information processing stream.

## The enactive approach and mental imagery

This approach posits that cognition is based on dynamic interactions between an organism and its environment (Varela et al. 1991). The word 'enactive' refers to the concept of embodied action, which has two implications: (a) Cognition depends on the experience that derives from the body characterized by different sensorimotor capacities embedded in a biological, psychological and cultural context (Varela et al. 1991); and (b) perception and action are inseparable (Thomas 1999, 2009; Varela et al. 1991). Thus, there is no external representation of the world, but rather an inner generation of a system of meanings by actions and interactions that the individual establishes within the world. In addition, perception is a form of active action (Thomas 2014) that uses sensory systems in order to actively search for specific information needed at a specific moment (Thomas 1999). Different procedures are applied to extract specific information as a sort of ongoing activity of schemata-guided perceptual exploration of the environment (Thomas 1999). Consequently, during mental imagery, perceptual exploration would also be almost as active as during perception in order to search for specific information (Thomas 1999). The perceptual acts that are executed when the subject actually perceives are also partially executed when the subject imagines (Thomas 2014). This view implies that the visuospatial recollections of stimuli stored in long-term memory are not schematic spatial mental models, but rather correspond to visuospatial behavior that is guided by overt attention shifts (eye movements) according to the levels of visuospatial processing (Sima 2011). Therefore, internal representations are not necessary for mental imagery because there is no experience of mental pictures (Thomas 1999, 2009). The peculiarities of the body and the types of interactions with the environment can give rise to different mental images in terms of phenomenological and functional properties. In general, according to this approach, imagery depends on action and on the body interacting with the environment.

This approach is also supported by studies that showed the interference and facilitation effects of imagery on subsequent perceptual detection or identification tasks. However, through the lens of the enactive approach, these effects are explained by considering the allocation of attentional resources (Farah 1989), given that the active search for information needed at that particular moment is a form of selective attention. Sakai and Miyashita (1994) proposed that visual imagery relies on the interaction between memory retrieval and focal attention mechanisms. Thus, the attentional resources devoted to the visual images of the target would impair visual perception when images and targets are different, whereas they would facilitate visual perception if images and target were similar.

Neuropsychological evidence related to representational neglect (the failure to represent and pay attention to the personal and extrapersonal contralesional space, following a lesion involving the right hemisphere, especially the right temporoparietal junction—Bartolomeo et al. 1994; Bisiach and Luzzatti 1978; Committeri et al. 2015; Guariglia et al. 1993; 2013) also supports the enactive approach in terms of allocation of attentional resources. Indeed, although representational neglect indicates that the left sides of mental images (and percepts) are not appropriately processed, items located contralesionally may be recalled when located ipsilesionally to the imagined vantage point (Bisiach and Luzzatti 1978). Moreover, representational symptoms improve when external attention is manipulated. Meador et al. (1987) showed that when a neglect patient's head/eye orientation was physically shifted from the right to the left hemisphere, the recall for items imagined in the left hemisphere improved. Rode et al. (2001) also revealed that during a short adaptation period to a prismatic shift of the visual field to the right, two neglect patients were able to fully recover the left-sided information from the mental image of a map of France.

The enactive approach is also supported by studies of motor behavior occurring during imagery. In visual imagery, eye movements are considered motor processes that occur during active exploration of the environment, reflecting the content and spatial features of visual inputs (Laeng and Teodorescu 2002). However, according to Johansson et al. (2010), eye movements relieved working memory load during visual imagery, especially when the task complexity increased. Indeed, maintaining central fixation while inspecting a scene or hearing a scene description did not affect eye movements during subsequent recall; eye movements were spread out, reflecting the spatial positions and directions within the picture (Johansson et al. 2010). Moreover, restricting fixation during recall impaired the retrieval of the scene regardless of the type of encoding (visual or auditory) (Johansson et al. 2012). The involvement of motor processes during imagery has also been demonstrated by studies of mental rotation (Voyer and Jansen 2017; Wexler

et al. 1998; Wohlschläger 2001). Even olfactory imagery was found to be associated with motor activity (the typical act of sniffing) (Bensafi et al. 2003). The olfactomotor activity during perception and imagery of olfactory stimuli are similar in terms of respiratory volume and temporal characteristics (Kleemann et al. 2008). In general, the recruitment of motor cortices (e.g., premotor area and/or supplementary cortex) was found in all mental imagery modalities (Djordjevic et al. 2005; Halpern et al. 2004; Kobayashi et al. 2004; Palmiero et al. 2009; Yoo et al. 2003; Winlove et al. 2018).

In summary, these findings show that the enactive approach entails the involvement of motor processes during imagery, as a sort of allocation of attentional resources.

## The sensorimotor approach and mental imagery

This approach posits that perception depends on practical (sensorimotor) knowledge of possibilities for action (Noë 2004, 2010; O'Regan and Noë 2001). Sensorimotor knowledge is a set of rules of covariations between stimulation (input) and movement (output). Therefore, perception is a mode of exploration that is mediated by the mastery and exercise of implicit and practical sensorimotor knowledge (O'Regan and Noë 2001). Bearing this in mind, mental imagery is also characterized by the conscious use of practical knowledge of laws that explain the relationships between sensory input and motor output (Foglia and O'Regan 2016). In particular, mental imagery requires tuning (attunement) to previously learned sensorimotor laws. The attunement to sensorimotor laws is a state that changes continuously to determine the contingency between sensory inputs and movement outputs. In this way, mental imagery relies on a state of familiarity and harmony with sensorimotor laws, without rehearsing the exploration mechanisms of the environment. What is being activated during imagery is ultimately the knowledge of the potential applicability of the law that describes the event corresponding to the content of imagery (Foglia and O'Regan 2016). In general, this approach entails two basic factors: (1) the possession and exercise of sensorimotor know-how; and (2) no reenactment of perceptual experience is required, but rather the expectation as to how the sensory input changes as a function of movements.

This approach is also partially supported by neuroimaging studies, which reveal epiphenomenal effects enabled by the sensorimotor knowledge (Foglia and O'Regan 2016). In this vein, studies revealing the interference and facilitation effects of imagery on subsequent perceptual detection tasks can also account for the sensorimotor approach. If the evidence showing that perception and imagery activate the same neural structures (e.g., the early visual cortex) does

not go against the sensorimotor approach, then the interference and facilitation effects between imagery and perceptual detection should also be considered as epiphenomenal effects enabled by the sensorimotor knowledge (Foglia and O'Regan's 2016). However, considering that neuroimaging results are contradictory and that the interference/facilitation effects of imagery on perception can rely on interactions at later stages of the information processing stream, mastery of the sensorimotor knowledge is not necessarily processed at early perceptual levels.

In addition, the sensorimotor approach is also supported by studies that developed the analogue-propositional imagery debate. Most of these studies showed that imagery draws upon the physical laws of the external world, even though the set of rules for covariations between stimulation (input) and movement (output) was not explicitly entailed. Specifically, mental rotation has been related to motor processes (e.g., Jansen and Kellner 2015; Wexler et al. 1998; Wohlschläger 2001). Even motor expertise plays a key role in mental rotation (Pietsch and Jansen 2012; Voyer and Jansen 2017), especially in the egocentric transformation condition (Feng et al. 2017; Kaltner et al. 2014). This latter finding supports a better integration of proprioceptive information (Lorey et al. 2009), being based on left–right judgments about single fixed objects while the observer's point of view rotates in relation to the object or to the environment. As shown above, mental imagery can also adhere to the sensorimotor contingencies in non-visual imagery modalities (e.g., Bensafi et al. 2003; Elkin and Leuthold 2011; Papaxantis et al. 2002). In this vein, the lack of a complete overlap between imagery and perception would depend on the lack of bodily processes that mediate the interaction with the environment when imagining (Degenaar and O'Regan 2015).

In summary, these findings show that the possession and use of the sensorimotor knowledge (Kaltner et al. 2014; Voyer and Jansen 2017) explains the ability to tune into sensorimotor laws while generating and manipulating mental images in different sensory modalities.

### The limits of the embodied cognition approaches to mental imagery

Regarding the simulation approach, the reenactment thesis of perceptual symbols seems to suffer from the same problems that affected the original depictive approach. Indeed, it is unclear the extent to which imagery and sensorimotor processing share common mechanisms and neural structures. In addition, even the observation that imagery and perception activate the psychological system in a similar manner appears to be an insufficient argument for establishing the successful shift of the imagery debate within the framework

of the embodied cognition approach. Such a shift in the imagery debate requires the presence of the body interacting with the external world, rather than the reenactment of past experience. This point has not been sufficiently addressed by the simulation approach. Studies of spatial cognition have shown that the motor-dependent perceptual system is involved in the perception of peripersonal space (Delevoye-Turrell et al. 2010). This leads to the assumption that mental imagery does not necessarily consist in the reenactment of sensorimotor experience but can be predictive of action preparation (Gallese 2009) while the body interacts with an object. The emulation theory proposed that motor areas drive an emulator of the body to produce imagery (Grush 2004). In other words, assuming that spatial perception depends on representations of potential actions in the environment, it is possible to assume that spatial imagery also depends on representations of motor processes.

As for the enactive approach, the most problematic issue is the concept of representation. It is difficult to imagine, dream, plan, etc., without being supported by mental representations (Foglia and O'Regan 2016). In addition, when solving problems (e.g., mental rotation), the reenactment of corresponding exploratory behaviors is insufficient; an internal model to which active behavior must be directed (Foglia and Grush 2011) is also necessary. Following Gładziejewski (2016, p. 576), this internal model represents an object that would '...guide action by constituting map-like internal stand-ins for worldly states of affairs.' Even though some forms of basic imaginings can be apparently understood without the aid of representational content (see Hutto and Myin 2017), an internal mental model including content is always necessary and needs to be corrected continuously in order to carry out the task (e.g., adjust the rotating imaging shape if it does not match the perceived shape) (Roelofs 2018).

In terms of the sensorimotor approach, the weakest point also refers to the concept of representation. The issue is that the mastery of the laws of contingencies between sensory input and motor output is a form of knowledge that must be stored somehow (Di Paolo et al. 2017), especially if this mastery is assumed to support mental imagery. Kosslyn et al. (2005) found that visual images generated by both memorized verbal descriptions of segments and memorized visual segments yielded similar cortical activations rather than different activations as guided by different types of sensorimotor know-how. This finding supports the notion that mental images are representations generated by information stored in memory rather than by the active exercise of the mastery of sensorimotor knowledge. In addition, the issue of the conscious possession and exercise of sensorimotor know-how is also questionable. According to Brogaard and Gatzia (2017), the dorsal-stream processes, which basically correspond

to sensorimotor know-how, do not constitute the conscious phenomenology of mental imagery because they are largely unconscious.

Given these limits, it appears that the simulation approach cannot account for the format of imagery because it focuses on the reenactment thesis and neglects the role of action, whereas the enactive and sensorimotor approaches highlight the key role of the body and action while sacrificing the concept of representation, which is undoubtedly a central element of any theory of mental imagery. With this in mind, an integrative view of the format of mental imagery, one that combines a representation-based approach with an action-based approach, seems possible and increasingly required. It is possible to refer to this view as the ‘integrated embodied representation approach.’ The basic idea is that imagery relies on mental representations that encompass both perceptual and motor components, which are intrinsically related to specific experiences (e.g., seeing a book that involves both the perceptual details of the book and the action of seeing). When one generates a mental image, perceptual and motor components that have been stored together in long-term memory are recollected, activating a unique representation.

Since mental images generally rely on representations of things that are not actually present to senses, their activation vary widely according to two characteristics: the individual ability to evoke subjective perceptual and motor experiences manifested in terms of differences in the vividness of images, and the strategy preferentially used in the individual processing of the related sensory information. This does not mean that imagery ability and imagery strategy are involved into organizing principles and mechanisms of imagery, but that they are fundamental characteristics of imagery that can be also added on the top of the integrated embodied representation approach. The study of individual differences in imagery ability and imagery strategy can help to address the extent to which perceptual and motor components contribute to mental imagery.

## The role of individual differences in imagery ability and imagery strategy

Hereafter, the way in which perceptual and motor information is activated and represented is reviewed in terms of individual differences in (1) mental imagery abilities (e.g., the level of vividness) and (2) cognitive strategies (e.g., object vs. spatial imagers).

### (1) Individual differences in imagery ability: the role of vividness

Imagery ability has been defined as ‘an individual’s capability of forming vivid, controllable images and retaining

them for sufficient time to effect the desired rehearsal’ (Morris et al. 2005, p. 37). Traditionally, individual differences in imagery abilities have been explored using self-report questionnaires aimed at measuring the vividness (e.g., Betts 1909; Galton 1880; Marks 1973; Sheehan 1967) and control (e.g., Gordon 1949) of images.

In particular, the vividness of mental imagery has been associated with the preservation of perceptual information. For Reeder (2017), the pictorial content of visual images varies according to individual differences in vividness. Indeed, visual vivid imagers were found to report significantly more colors and details than non-vivid imagers (Hishitani and Murakami 1992) and to recruit brain areas more selectively, as if they accessed more visual (perceptual) sources of knowledge than low-vividness imagers (Fulford et al. 2018). This finding indicates that the vividness of visual mental images plays a key role in the retrieval of sensory traces from long-term memory (D’Angiulli et al. 2013) and allows more visual sensory information to be available within the visuospatial sketchpad of working memory (Baddeley and Andrade 2000). Similarly, the vividness of images of sounds also seems to rely on the strength of representation of auditory information contained within the phonological loop of working memory (Baddeley and Andrade 2000). Interestingly, good perceivers of odors were also found to rely on the vividness of olfactory images to evaluate their olfactory performance (Kollndorfer et al. 2015). High-vividness imagers in the motor domain (classified on the basis of the sum of the rating scales used in both the vividness of visual and motor imagery questionnaires) were also revealed to significantly take advantage of a mental practice program with respect to low-vividness imagers, regardless of the level of expertise (trampolinists vs. novices) (Isaac 1992). Vividness of kinesthetic motor imagery was associated with sensorimotor event-related desynchronization shared by motor (kinesthetic) imagery and motor execution, as if the corticospinal excitability during motor imagery was similar to that during motor execution in the presence of the high vividness of kinesthetic imagery (Toriyama et al. 2018).

Moreover, subjective measures of vividness in modality-specific imagery were found to yield activations in the early visual (e.g., Cui et al. 2007; Olivetti Belardinelli et al. 2009), tactile/proprioceptive, gustatory and motor (Olivetti Belardinelli et al. 2009) cortices. Other studies showed that vividness of modality-specific imagery yielded no activation of the early sensory cortices, but rather found increased activity in higher-order visual (Fulford et al. 2018), auditory (Herholz et al. 2012) and motor (Lorey et al. 2011) cortices. These results do not invalidate the idea that vividness is correlated with perceptual information, given that neuroimaging studies still show modality-specific brain activations in high-vividness compared to low-vividness imagers.

Vividness of imagery has also been associated with expertise, which generally refers to the highest level of

performance on a specific task or within a specific domain (Bourne et al. 2014). Morrison and Wallace (2001) showed that individuals with higher visual art involvement reported higher visual imagery vividness scores compared to individuals with lower visual art involvement. Hishitani (2009) reported that musical experience was associated with higher vividness of auditory imagery, suggesting that participants with more musical experience were able to retain more auditory perceptual information than non-musicians. The generation of olfactory images is also profoundly affected by the level of expertise (Bensafi et al. 2007; Plailly et al. 2012). In other studies, high-level athletes reported higher levels of vividness of motor imagery (Eton et al. 1998; Isaac and Marks 1994; Zhang et al. 2018).

In line with this evidence, vividness of imagery is barely related to semantic information. Although a general association between visual imagery vividness and picture-naming in different categories was found, no association between the vividness of modality-specific imagery and naming in different categories emerged (Laws 2002). This finding indicates that low-vividness imagers are probably more supported by semantic information. This idea is consistent with Olivetti Belardinelli et al. (2009), who found that low-vividness imagers activated a different neural network compared to high-vividness imagers, probably because, in their attempt to generate mental images, they relied on semantic representations rather than on sensory-modality representations.

In summary, these results suggest that high-vividness imagery in different sensory (and motor) modalities preserves more perceptual and motor components than semantic ones, reflecting the activation level of specific imagery systems. The extent to which the vividness of non-motor imagery is also associated with motor components is not clear. That is, motor components seem to play a key role in imagery regardless of vividness. Using a mental rotation task, Logie et al. (2011) showed that high-vividness imagers revealed more activity in the visual and premotor cortices than did low-vividness imagers, which in turn relied more on the frontoparietal control network, including the supplementary motor area. For the authors, high and low imagers activated different neural networks, including different motor cortices, because high-vividness imagers simulated the rotation of the object in view, whereas low-vividness imagers used a more self-referential strategy because they could not use an adequate mental representation of external stimuli. Using object tasks, Dijkstra et al. (2017) also revealed that the overlap between visual imagery and visual perception, regardless of vividness, extended beyond the visual cortex to the parietal and premotor cortices. The idea that motor components are required regardless of the vividness of imagery is consistent with those studies that revealed the participation of motor cortices in all mental imagery modalities (Djordjevic et al. 2005; Halpern et al. 2004; Kobayashi

et al. 2004; Palmiero et al. 2009; Yoo et al. 2003; Winlove et al. 2018).

## (2) Individual differences in imagery strategy

Traditionally, people have been classified as either visualizers (also called imagers), who process information relying primarily on mental images and holistic strategies, or verbalizers, who process information relying primarily on verbal and analytical strategies (e.g., Paivio 1971; Richardson 1977). In terms of visualizers, visual imagery has actually been considered to comprise two distinct subsystems that encode and process visual information in different ways (Blajenkova et al. 2006; Blazhenkova and Kozhevnikov 2009, 2010): on the one hand, object imagery strategy, which relies on pictorial representations of visual stimuli, defined by specific attributes, such as shape, size, color and brightness; and on the other hand, spatial imagery strategy, which relies on relatively abstract representations of visual stimuli, defined by specific spatial attributes, such as relations among objects or parts of objects, location of objects in space and movements of objects. Object imagers process visual information globally, whereas spatial imagers do so analytically and sequentially (Kozhevnikov et al. 2005). Interestingly, Blajenkova et al. (2006) revealed that visual artists rely on object imagery, whereas scientists and humanities professionals rely on spatial imagery. Blazhenkova (2016) also found that object imagery and spatial imagery are supported by separate dimensions of vividness: pictorial details and schema or 3D structures in details, respectively.

Consistent with this evidence, properties of shapes, which support object imagery, were found mostly related to activations in the early visual cortex (Kosslyn and Thompson 2003). In addition, object imagery is also associated with the verbal system, favoring dual coding of information (Paivio 1986; Paivio and Yuille 1969). Neuroimaging evidence confirmed that object mental images cued by verbal descriptions can activate both visual and language brain areas (Mazoyer et al. 2002). This means that object imagery relies not only on visual features but also on semantic information, which is presumably attached to the visual attributes of the object itself, and which also comprises categorical, functional and associative information.

On the other hand, spatial imagery is more readily associated with motor components. Different studies have shown that mental rotation is improved by motor expertise (Kaltner et al. 2014; Voyer and Jansen 2017), even when it is based on object-based transformations (Moreau et al. 2012; Pietsch and Jansen 2012). Spatial imagery (e.g., mental rotation) was also found supported by motor cortices (e.g., medial superior precentral cortex) under conditions that favor motor simulation (Zacks 2008), or by the portions of the parietal lobe near the junction of the superior and inferior lobules,

that may play a key role in spatial-transformation processes (Thompson et al. 2009). In this vein, the premotor cortex would serve as a relay station, projecting to the parietal cortex during spatial imagery (Sack et al. 2008). To comply with motor demands, spatial imagery can also be encoded and processed independently from visual experience. Ricciardi et al. (2017) revealed that when the affording object (a small ball) was visually or auditorily cued within both the subjects' reach and another's peripersonal space, sighted and congenitally blind participants showed a comparable spatial alignment effect. Sighted and blind participants also showed comparable performances in terms of object identification and manipulation in the surrounding space (Postma et al. 2007), suggesting that tool use relied on the contextual motor demands of the peripersonal space (Serino et al. 2007). This evidence supports the amodal hypothesis of spatial imagery (Delogu et al. 2010; Giudice et al. 2011). Yet spatial imagery cued by verbal descriptions can also activate both spatial and language brain areas, although the latter are recruited less diffusely and at a lesser extent compared with object imagery (Mazoyer et al. 2002). In general, given that spatial and verbal processing might interfere in some cases, reflecting modes of operations that serve as alternative strategies to approach the same problem, spatial imagers can simply use spatial skills more frequently than verbal strategy and vice versa (Blazhenkova and Kozhevnikov 2009).

In summary, these results suggest that object imagery strategy relies mostly on perceptual and semantic components, whereas spatial imagery strategy relies on amodal components with the involvement of motor components.

The extent to which object imagery strategy is also associated with motor components must be fully addressed. The literature shows that motor imagery can also be disentangled in different modalities of execution. On the one hand, there is the visual motor imagery modality, which requires one to self-visualize a movement from a first-person (internal perspective; the individual takes part in the action him/herself) perspective, and a third-person (external perspective; the individual observes someone else performing the movement) perspective (Guillot et al. 2009). On the other hand, there is the kinesthetic motor imagery modality, which requires one to mentally feel the movement from a first-person perspective (Guillot et al. 2009; White and Hardy 1995). Visual motor imagery, both internal and external perspectives, supports closed (Hardy and Callow 1999) and open sports (Yu et al. 2016). The external perspective is more useful to improve learning the movement throughout mental observation, especially for novices (Montuori et al. 2018), whereas the internal perspective, being more self-oriented and kinesthetic-based, is more useful for higher-skill-level athletes, regardless of the sport (Yu et al. 2016), serving to train or to revise a gesture already internalized (Montuori et al. 2018). Kinesthetic motor imagery is more associated

with motor processing than with visual motor imagery. It was found to modulate cortico-motor excitability (Stinear et al. 2006) and facilitate the performance of complex movements that rely on the use of forms in a relatively stable environment (e.g., closed sports such as diving, gymnastics) (Guillot et al. 2004; White and Hardy 1995), especially in high-level performers, contributing an additional beneficial effect to performance (Hardy and Callow 1999). In addition, subjective vividness of kinesthetic motor imagery was associated with cortical circuits corresponding to those of motor execution (Toriyama et al. 2018). In the presence of the low vividness of kinesthetic motor imagery, the primary visual cortex is recruited, indicating that visual motor imagery is inevitably used for the less vivid kinesthetic motor imagery of difficult whole-body movements (Mizugochi et al. 2016).

### Interactions between imagery ability and imagery strategy

From the literature reviewed, it appears that mental imagery is supported by mental representations. The extent to which perceptual and motor components are part of the format of mental imagery depends on both imagery ability (e.g., vividness) and imagery strategy (e.g., object vs. spatial style). In this view, semantic components should also be considered, because mental images are penetrable by conceptual processing. Specifically, (1) a high ability of sensory mental imagery preserves mostly perceptual components, whereas a high ability of motor mental imagery preserves mostly motor components; the semantic component is also preserved, although it is expected to be mostly used in the presence of the low ability of mental imagery. The motor information seems to be involved in imagery regardless of vividness; however, its involvement can take different forms according to the imagery ability and the task carried out. (2) The imagery strategy relies on different types of components (e.g., object imagery mainly relies on pictorial and semantic components, whereas spatial imagery relies on amodal and motor components).

With this in mind, it is important to point out that the interaction between imagery ability (high and low) and imagery strategy (object and spatial) can give rise to different combinations of integrated embodied representations in support of mental imagery (see Table 1).

For example, the combination of high vividness and object imagery strategy is supposed to support mental images based mostly on the following: details about the visual appearance of the object (shape, color, brightness, etc.); motor components, which refer mainly to the action of seeing the object (e.g., eye movements), but also include hand movements, associated with the object use (Belardinelli et al. 2015, 2016a, b), as well as to body position

**Table 1** Basic interactions between imagery ability and imagery strategy

Imagery ability	Imagery strategy		Component
	Object	Spatial	
High	Object details (e.g., shape, color, brightness)	Spatial details (e.g., relations among objects, object location)	Perceptual
	Action of seeing (e.g., eye movements), and hand movements, body position changes for object use.	Action of seeing, and activity aimed at complying with the spatial task	Motor
	Conceptual relations to sensory attributes of the object (e.g., color = red); general conceptual information (e.g., categorical, functional, encyclopedic, semantically explicable relationships between stimulus and movement)	Relations to general conceptual information	Semantic
Low	Few object details	Few spatial details	Perceptual
	Action of seeing and activity for object use	Action of seeing and activity for the spatial task	Motor
	High general conceptual information	High general conceptual information	Semantic

changes; semantic components, which are related to both the sensory attributes of the object itself (rectangular shape, red color, etc.), and more general conceptual information (categorical, functional, encyclopedic information, semantically explicable relationships between stimulation and movement). Following this reasoning, the combination of high vividness and spatial imagery strategy should rely less on the sensory attributes of the object and mostly on detailed spatial structures (spatial attributes, relations among objects, location of the object in space) and motor components that include the action of seeing mostly spatial attributes, as well as the actions aimed at complying with the imagery task in the surrounding space, and general conceptual information. On the other hand, the combination of low vividness and object imagery strategy should rely scarcely on details about the visual appearance of the object and even less on details of spatial structure, but mostly on motor components and general semantic components, whereas the combination of low vividness and spatial imagery strategy would support mental imagers based mostly on the following: low details of spatial structures and even lower sensory attributes of objects; motor components, which are mostly associated with the action of seeing and the manipulation of the object in the surrounding space; semantic components, which are barely related to the sensory attributes of the object, but highly related to general conceptual information. In all cases, mental images are underpinned by integrated embodied representations.

Of course, further study is necessary to clarify this view and to precisely identify the way in which imagery ability and imagery strategy interact while generating mental images in different modalities. This would help to understand the contribution of perceptual, semantic and motor components to mental imagery. It might be useful to investigate individual differences in quantitatively measured perceptual, semantic and motor components with respect to a modality-specific

imagery task and clarify the extent to which these components are mediated by imagery abilities and imagery strategies.

When proper mental images cannot be generated (Faw 2009, Zeman et al. 2015, 2016), especially when people are asked to generate olfactory images (see Stevenson and Case, 2005, for a review), it might be that semantic knowledge of the principles that govern the sensory system is used. The result is a mental representation quite free of olfactory perceptual information and probably partially supported by motor processes. Indeed, olfactory stimuli may be partly encoded by non-olfactory means, for instance, processing a picture of the odor's source (Lyman and McDaniel 1990) or using semantic information about the odor with the possibility of an alternative encoding, which might affect the format of olfactory imagery itself. In addition, according to Royet et al. (2013), memory, sniffing, attention and odor expectation can also elicit confounding effects, as they can contribute to activating the primary olfactory cortex in non-experts, even if mental images of odors are not actually generated. On the other hand, when olfactory images are successfully generated, expertise (Bensafi et al. 2007; Plailly et al. 2012), facility to name odors (Stevenson et al. 2007) and sniffing activate sensorial-type representations stored in long-term memory.

## Conclusions

This review highlighted the importance of combining representation with action, or more broadly with both perceptual and motor components, without diminishing the contribution of semantic components. This integrative view could give rise to an integrated embodied representational approach that is shaped according to individual differences in imagery ability and imagery strategy. In other words, mental imagery should be considered a dynamic embodied representation that adapts and reorganizes itself according

to different cognitive and personality factors. Studying the links between mental imagery and these factors through the lens of an integrative view such as that outlined above can be a starting point for understanding the format of mental imagery.

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

## References

- Amedi A, Malach R, Pascual-Leone A (2005) Negative BOLD differentiates visual imagery and perception. *Neuron* 5:859–872
- Baddeley AD, Andrade J (2000) Working memory and the vividness of imagery. *J Exp Psychol Gen* 129:126–145
- Barsalou LW (1999) Perceptual symbol systems. *Behav Brain Sci* 22:577–660
- Barsalou LW (2008) Grounded cognition. *Ann Rev Psychol* 59:1–14
- Bartolomeo P, D’Erme P, Gainotti G (1994) The relationship between visuospatial and representational neglect. *Neurology* 44:1710–1714
- Belardinelli A, Herbot O, Butz MV (2015) Goal-oriented gaze strategies afforded by object interaction. *Vis Res* 106:47–57
- Belardinelli A, Barabas M, Himmelbach M, Butz MV (2016a) Anticipatory eye fixations reveal tool knowledge for tool interaction. *Exp Brain Res* 234:2415–2431
- Belardinelli A, Stepper M, Butz MV (2016b) It’s in the eyes: planning precise manual actions before execution. *J Vis* 16:18
- Bensafi M, Porter J, Pouliot S, Mainland J, Johnson B, Zelano C et al (2003) Olfactory motor activity during imagery mimics that during perception. *Nat Neurosci* 6:1142–1144
- Bensafi M, Sobel N, Khan RM (2007) Hedonic-specific activity in piriform cortex during odor imagery mimics that during odor perception. *J Neurophysiol* 98:3254–3262
- Betts GH (1909) The distribution and functions of mental imagery (Contribution to Education, No. 26). Columbia University, Teachers College, New York
- Bisiach E, Luzzatti C (1978) Unilateral neglect of representational space. *Cortex* 14:129–133
- Blajenkova O, Kozhevnikov M, Motes MA (2006) Object-spatial imagery: a new self-report imagery questionnaire. *Appl Cogn Psychol* 20:239–263
- Blazhenkova O (2016) Vividness of object and spatial imagery. *Percept Mot Skills* 122:490–508
- Blazhenkova O, Kozhevnikov M (2009) The new object-spatial-verbal cognitive style model: theory and measurement. *Appl Cogn Psychol* 23:638–663
- Blazhenkova O, Kozhevnikov M (2010) Visual-object ability: a new dimension of non-verbal intelligence. *Cognition* 117:276–301
- Bocchi A, Carrieri M, Lancia S, Quaresima V, Piccardi L (2017) The key of the Maze: the role of mental imagery and cognitive flexibility in navigational planning. *Neurosci Lett* 651:146–150
- Borst G, Kosslyn SM (2008) Visual mental imagery and visual perception: structural equivalence revealed by scanning processes. *Mem Cogn* 36:849–862
- Borst G, Kievit RA, Thompson WL, Kosslyn SM (2011) Mental rotation is not easily cognitively penetrable. *J Cogn Psychol* 23:60–75
- Bourne LE Jr, Kole JA, Healy AF (2014) Expertise: defined, described, explained. *Front Psychol* 5:186
- Brogaard B, Gatzia DE (2017) Unconscious imagination and the mental imagery debate. *Front Psychol* 8:799
- Bunzeck N, Wuestenberg T, Lutz K, Heinze HJ, Jancke L (2005) Scanning silence: mental imagery of complex sounds. *NeuroImage* 26:1119–1127
- Cabeza R, Burton AM, Kelly SW, Akamatsu S (1997) Investigating the relation between imagery and perception: evidence from face priming. *Q J Exp Psychol A* 50:274–289
- Clark A (1997) Being there: Putting brain, body, and world together again. MIT Press, Cambridge
- Committeri G, Piccardi L, Galati G, Guariglia C (2015) Where did you ‘left’ Piazza del Popolo? At your ‘right’ temporo-parietal junction. *Cortex* 73:106–111
- Craver-Lemley C, Reeves A (1992) How visual imagery interferes with vision. *Psychol Rev* 99:633–649
- Craver-Lemley C, Arterberry ME, Reeves A (1999) ‘Illusory’ illusory conjunctions: the conjoining of features of visual and imagined stimuli. *J Exp Psychol Hum Percept Perform* 25:1036–1049
- Cui X, Jeter CB, Yang PD, Montague R, Eagleman DM (2007) Vividness of mental imagery: individual variability can be measured objectively. *Vis Res* 47:474–478
- D’Angiulli A, Reeves A (2007) The relationship between self-reported vividness and latency during mental size scaling of everyday items: phenomenological evidence of different types of imagery. *Am J Psychol* 120:521–551
- D’Angiulli A, Runge M, Faulkner A, Zakizadeh J, Chan A, Morcos S (2013) Vividness of visual imagery and incidental recall of verbal cues, when phenomenological availability reflects long-term memory accessibility. *Front Psychol* 4:1
- Daselaar SM, Porat Y, Huijbers W, Pennartz CM (2010) Modality-specific and modality-independent components of the human imagery system. *NeuroImage* 52:677–685
- Degenaar J, O’Regan JK (2015) Sensorimotor theory of consciousness. *Scholarpedia* 10:4952
- Delevoeye-Turrell Y, Bartolo A, Coello Y (2010) Motor representation and the perception of space. In: Gangopadhyay N (ed) Perception, action and consciousness. Oxford University Press, New York
- Delogu F, Palmiero M, Federici S, Zhao H, Plaisant C, Olivetti Belardinelli M (2010) Non-visual exploration of geographic maps: does sonification help? *Disabil Rehabil Assist Technol* 5:164–174
- Di Paolo E, Buhmann T, Barandiaran X (2017) Sensorimotor life: an enactive proposal. Oxford University Press, New York
- Dijkstra N, Bosch SE, van Gerven MAJ (2017) Vividness of visual imagery depends on the neural overlap with perception in visual areas. *J Neurosci* 37:1367–1373
- Djordjevic J, Zatorre RJ, Petrides M, Jones-Gotman M (2004) The mind’s nose: effects of odor and visual imagery on odor detection. *Psychol Sci* 15:143–148
- Djordjevic J, Zatorre RJ, Petrides M, Boyle JA, Jones-Gotman M (2005) Functional neuroimaging of odor imagery. *Neuroimage* 24:791–801
- Elkin J, Leuthold H (2011) The representation of pitch in auditory imagery: evidence from S-R compatibility and distance effects. *J Cogn Psychol* 23:76–91
- Eton DT, Gilner FH, Munz DC (1998) The measurement of imagery vividness: a test of the reliability and validity of the vividness of visual imagery questionnaire and the vividness of movement imagery questionnaire. *J Ment Imag* 22:125–136
- Farah MJ (1989) Mechanisms of imagery-perception interaction. *J Exp Psychol Hum Percept Perform* 15:203–211
- Farah MJ, Smith AF (1983) Perceptual interference and facilitation with auditory imagery. *Percept Psychophys* 33:475–478

- Faw B (2009) Conflicting intuitions may be based on differing abilities: evidence from mental imaging research. *J Conscious Stud* 16:45–68
- Feng T, Zhang Z, Ji Z, Jia B, Li Y (2017) Selective effects of sport expertise on the stages of mental rotation tasks with object-based and egocentric transformations. *Adv Cogn Psychol* 13:248–256
- Finke R (1986) Some consequences of visualization in pattern identification and detection. *Am J Psychol* 99:257–274
- Finke RA (1989) *Principles of mental imagery*. The MIT Press, Cambridge
- Finke RA, Ward TM, Smith SM (1992) *Creative cognition: theory, research, and applications*. MIT Press, Cambridge
- Foglia L, Grush R (2011) The limitations of a purely enactive (non-representational) account of imagery. *J Conscious Stud* 18:35–43
- Foglia L, O'Regan KJ (2016) A new imagery debate: enactive and sensorimotor accounts. *Rev Philos Psychol* 7:181–196
- Fulford J, Milton F, Salas D et al (2018) The neural correlates of visual imagery vividness—an fMRI study and literature review. *Cortex* 105:26–40
- Gallagher S (2005) *How the body shapes the mind*. Oxford University Press, Oxford
- Gallesse V (2009) Motor abstraction: a neuroscientific account of how action goals and intentions are mapped and understood. *Psychol Res* 73:486–498
- Galton F (1880) Statistics of mental imagery. *Mind* 5:301–318
- Garbadini F, Adenzato M (2004) At the root of embodied cognition: cognitive science meets neurophysiology. *Brain Cogn* 56:100–106
- Gibson JJ (1966) *The senses considered as perceptual systems*. Houghton Mifflin, Boston
- Gibson JJ (1979) *The ecological approach to visual perception*. Houghton Mifflin, Boston
- Giudice NA, Betty MR, Loomis JM (2011) Functional equivalence of spatial images from touch and vision: evidence from spatial updating in blind and sighted individuals. *Exp Psychol Learn Mem Cogn* 37:621–634
- Gładziejewski P (2016) Predictive coding and representationalism. *Synthese* 193:559–582
- Gordon R (1949) An investigation into some of the factors that favor the formation of stereotyped images. *Br J Psychol* 39:156–167
- Grush R (2004) The emulation theory of representation: motor control, imagery, and perception. *Behav Brain Sci* 27:377–396
- Guariglia C, Padovani A, Pantano P, Pizzamiglio L (1993) Unilateral neglect restricted to visual imagery. *Nature* 364:235–237
- Guariglia C, Palermo L, Piccardi L, Iaria G, Incoocia C (2013) Neglecting the left side of a city square but not the left side of its clock: prevalence and characteristics of representational neglect. *PLoS ONE* 8:e67390
- Guillot A, Collet C, Dittmar A (2004) Relationship between visual vs. kinesthetic imagery, field dependence-independence and complex motor skills. *J Psychophysiol* 18:190–199
- Guillot A, Collet C, Nguyen VA, Malouin F, Richards C, Doyon J (2009) Brain activity during visual versus kinesthetic imagery: an fMRI study. *Hum Brain Mapp* 30:2157–2172
- Halpern AR (1988) Mental scanning in auditory imagery for songs. *J Exp Psychol Learn Mem Cogn* 14:193–202
- Halpern AR, Zatorre RJ, Bouffard M, Johnson JA (2004) Behavioral and neural correlates of perceived and imagined musical timbre. *Neuropsychologia* 42:1281–1292
- Hanakawa T, Immisch I, Toma K, Dimyan MA, Van Gelderen P, Hallett M (2003) Functional properties of brain areas associated with motor execution and imagery. *J Neurophysiol* 89:989–1002
- Hardy L, Callow N (1999) Efficacy of external and internal visual imagery perspectives for the enhancement of performance on tasks in which form is important. *J Sport Exerc Psychol* 21:95–112
- Herholz SC, Halpern AR, Zatorre RJ (2012) Neuronal correlates of perception, imagery and memory for familiar tunes. *J Cogn Neurosci* 6:1382–1397
- Hishitani S (2009) Auditory imagery questionnaire: its factorial structure, reliability, and validity. *J Mental Imagery* 33:63–80
- Hishitani S, Murakami S (1992) What is the vividness of imagery? The characteristics of vivid visual imagery. *Percept Mot Skills* 75:1291–1307
- Hutto D, Myin E (2017) *Evolving enactivism: basic minds meet content*. MIT Press, Cambridge
- Intons-Peterson MJ, Roskos-Ewoldsen BB (1989) Sensory perceptual qualities of images. *J Exp Psychol Learn Mem Cogn* 15:188–199
- Intons-Peterson MJ, Russell W, Dressel S (1992) The role of pitch in auditory imagery. *J Exp Psychol Hum Percept Perform* 18:233–240
- Isaac A (1992) Mental practice: does it work in the field? *Sport Psychol* 6:192–198
- Isaac AR, Marks DF (1994) Individual differences in mental imagery experience: developmental changes and specialization. *Br J Psychol* 85:479–500
- Ishai A, Sagi D (1995) Common mechanisms of visual imagery and perception. *Science* 268:1772–1774
- Ishai A, Sagi D (1997a) Visual imagery facilitates visual perception: psychophysical evidence. *J Cogn Neurosci* 9:476–489
- Ishai A, Sagi D (1997b) Visual imagery: effects of short- and long-term memory. *J Cogn Neurosci* 9:734–742
- Jansen P, Kellner J (2015) The role of rotational hand movements and general motor ability in children's mental rotation performance. *Front Psychol* 6:984
- Johansson R, Holšánová J, Holmqvist K (2010) Eye movements during mental imagery are not reenactments of perception. In: Ohlsson S, Catrambone R (eds) *Proceedings of the 32nd annual conference of the cognitive science society*. Cognitive Science Society
- Johansson R, Holšánová J, Dewhurst R, Holmqvist K (2012) Eye movements during scene recollection have a functional role, but they are not reinstatements of those produced during encoding. *J Exp Psychol Hum Percept Perform* 38:1289–1314
- Kaltner S, Riecke B, Jansen P (2014) Embodied mental rotation: a special link between transformation and the bodily self. *Front Psychol* 5:505
- Kikuchi S, Kubota F, Nisijima K, Washiya S, Kato S (2005) Cerebral activation focusing on strong tasting food: a functional magnetic resonance imaging study. *NeuroReport* 16:281–283
- Kleemann AM, Koppitz R, Albrecht J, Schoepf V, Pollatos O, Schreder T et al (2008) Investigation of breathing parameters during odor perception and olfactory imagery. *Chem Senses* 34:1–9
- Kobayashi M, Takeda M, Hattori N, Fukunaga M, Sasabe T, Inoue N et al (2004) Functional imaging of gustatory perception and imagery: top-down processing of gustatory signals. *NeuroImage* 23:1271–1282
- Kollndorfer K, Kowalczyk K, Nell S, Krajnik J, Mueller CA, Schöpf V (2015) The inability to self-evaluate smell performance. How the vividness of mental images outweighs awareness of olfactory performance. *Front Psychol* 6:627
- Kosslyn SM (1980) *Image and mind*. Harvard University Press, Cambridge
- Kosslyn SM (1994) *Image and brain: the resolution of the imagery debate*. MIT Press, Cambridge
- Kosslyn SM, Thompson WL (2003) When is early visual cortex activated during visual mental imagery? *Psychol Bull* 129:723–746
- Kosslyn SM, Ball TM, Reiser BJ (1978) Visual images preserve metric spatial information: evidence from studies of image scanning. *J Exp Psychol Hum Percept Perform* 4:47–60
- Kosslyn SM, Thompson WL, Sukel KE, Alpert NM (2005) Two types of image generation: evidence from PET. *Cogn Affect Behav Neurosci* 5(1):41–53

- Kosslyn SM, Thompson WL, Ganis G (2006) The case for mental imagery. Oxford University Press, New York
- Kozhevnikov M, Kosslyn SM, Shepard J (2005) Spatial versus object visualizers: a new characterization of visual cognitive style. *Mem Cogn* 33:710–726
- Laeng B, Teodorescu DS (2002) Eye scanpaths during visual imagery reenact those of perception of the same visual scene. *Cogn Sci* 26:207–231
- Laws KR (2002) Category-specific naming and modality-specific imagery. *Brain Cogn* 48:418–420
- Logie RH, Pernet CR, Buonocone A, Della Sala S (2011) Low and high imagers activate networks differentially in mental rotation. *Neuropsychologia* 49:3071–3077
- Lorey B, Bischoff M, Pilgramm S, Stark R, Munzert J, Zentgraf K (2009) The embodied nature of motor imagery: the influence of posture and perspective. *Exp Brain Res* 194:233–243
- Lorey B, Pilgramm S, Bischoff M, Stark R, Vaitl D, Kindermann S et al (2011) Activation of the parieto-premotor network is associated with vivid motor imagery—a parametric fMRI study. *PLoS ONE* 6:e20368
- Lyman B, McDaniel M (1990) Memory for odors and odor names: modalities of elaboration and imagery. *J Exp Psychol Learn Mem Cogn* 16:656–664
- Marks DF (1973) Visual imagery differences in the recall of pictures. *Br J Psychol* 64:17–24
- Mazoyer B, Tzourio-Mazoyer N, Al Mazard, Denis M, Mellet E (2002) Neural bases of image and language interactions. *Int J Psychol* 37:204–208
- Meador KJ, Loring DW, Bowers D, Heilman KM (1987) Remote memory and neglect syndrome. *Neurology* 37:522–526
- Mizuguchi N, Nakata H, Kanosue K (2016) Motor imagery beyond the motor repertoire: activity in the primary visual cortex during kinesthetic motor imagery of difficult whole body movements. *Neuroscience* 315:104–113
- Montuori S, Curcio G, Sorrentino P, Belloni L, Sorrentino G, Foti F, Mandolesi L (2018) Functional role of internal and external visual imagery: preliminary evidences from pilates. *Neural Plast*. <https://doi.org/10.1155/2018/7235872>
- Moreau D, Clerc J, Mansy-Dannay A, Guerrin A (2012) Enhancing spatial ability through sport practice: evidence for an effect of motor training on mental rotation performance. *J Individ Differ* 33:83–88
- Morris T, Spittle M, Watt AP (2005) Imagery in sport. *Human Kinetics, Campaign*
- Morrison GR, Wallace B (2001) Imagery vividness, creativity and the visual arts. *J Ment Imag* 25:135–152
- Moulton ST, Kosslyn SM (2009) Imagining predictions: mental imagery as mental emulation. *Philos Trans R Soc Lond B Biol Sci* 364:1273–1280
- Noë A (2004) Action in perception. The MIT Press, Cambridge
- Noë A (2010) Vision without representation. In: Gangopadhyay N, Madary M, Spicer F (eds) Perception, action, and consciousness: sensorimotor dynamics and two visual systems. Oxford University Press, Oxford, pp 245–256
- O'Regan JK, Noë A (2001) A sensorimotor account of vision and visual consciousness. *Behav Brain Sci* 24:883–917
- Okada H, Matsuoka K (1992) Effects of auditory imagery on the detection of a pure tone in white noise: experimental evidence of the auditory Perky effect. *Percept Mot Skills* 74:443–448
- Olivetti Belardinelli M, Di Matteo R, Del Gratta C, De Nicola A, Ferretti A, Tartaro A, Bonomo L, Romani GL (2004a) Intermodal sensory image generation: an fMRI analysis. *Eur J Clin Pharmacol* 16:729–752
- Olivetti Belardinelli M, Di Matteo R, Del Gratta C, De Nicola A, Ferretti A, Romani GL (2004b) Communalities between visual imagery and imagery in other modalities: an investigation by means of fMRI. In: Carsetti A (ed) Seeing, thinking and knowing. Kluwer, Dordrecht, pp 203–218
- 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
- Olivetti Belardinelli M, Palmiero M, Di Matteo R (2011) How fMRI technology contributes to the advancement of research in mental imagery: A review. In: Peres JFP (eds) Neuroimaging for clinician—combining research and practice. InTech Open Access Publisher, Rijeka (Croatia), pp 329–346
- Paivio A (1971) Imagery and verbal processes. Holt, Rinehart & Winston, Oxford
- Paivio A (1986) Mental representations: a dual coding approach. Oxford University Press, New York
- Paivio A, Yuille JC (1969) Changes in associative strategies and paired-associate learning over trials as a function of work imagery and type of learning set. *J Exp Psychol* 79:458–463
- Palermo L, Iaria G, Guariglia C (2008) Mental imagery skills and topographical orientation in humans: a correlation study. *Behav Brain Res* 192:248–253
- Palmiero M, Borsellino MC (2018) Embodied cognition: Comprendere la mente incarnata. ARAS Edizioni, Fano (Pu)
- Palmiero M, Olivetti Belardinelli M, Nardo D, Sestieri C, Di Matteo R, D'Ausilio A, Romani GL (2009) Mental imagery generation in different modalities activates sensory-motor areas. *Cogn Process* 10:268–271
- Palmiero M, Cardi V, Olivetti Belardinelli M (2011) The role of vividness of visual mental imagery on different dimensions of creativity. *Creat Res J* 23:372–375
- Palmiero M, Di Matteo R, Olivetti Belardinelli M (2014) The representation of conceptual knowledge: visual, auditory, and olfactory imagery compared with semantic processing. *Cogn Process* 15:143–157
- Palmiero M, Nori R, Aloisi V, Ferrara M, Piccardi L (2015) Domain-specificity of creativity: a study on the relationship between visual creativity and visual mental imagery. *Front Psychol* 6:1870
- Palmiero M, Nori R, Piccardi L (2016a) Visualizer cognitive style enhances visual creativity. *Neurosci Lett* 615:98–101
- Palmiero M, Piccardi L, Nori R, Palermo L, Salvi C, Guariglia C (eds) (2016b) Creativity and mental imagery. *Frontiers Media, Lausanne*
- Papaxantis C, Scieppati M, Gentili R, Pozzo T (2002) Imagined and actual arm movements have similar durations when performed under different conditions of direction and mass. *Exp Brain Res* 143:447–452
- Perky CW (1910) An experimental study of imagination. *Am J Psychol* 21:422–452
- Piccardi L, Bocchi A, Palmiero M, Verde P, Nori R (2017) Mental imagery skills predict the ability in performing environmental directional judgements. *Exp Brain Res* 235:2225–2233
- Pietsch S, Jansen P (2012) Different mental rotation performance in students of music, sports and education science. *Learn Individ Differ* 2:159–163
- Plailly J, Delon-Martin C, Royet JP (2012) Experience induces functional reorganization in brain regions involved in odor imagery in perfumers. *Hum Brain Mapp* 33:224–234
- 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
- Postma A, Zuidhoek S, Noordzij ML, Kappers AM (2007) Differences between early-blind, late-blind, and blindfolded-sighted people in haptic spatial-configuration learning and resulting memory traces. *Perception* 36:1253–1265

- Pylyshyn ZW (1973) What the mind's eye tells the mind's brain: a critique of mental imagery. *Psychol Bull* 80:1–24
- Pylyshyn ZW (1979) The rate of “mental rotation” of images: a test of a holistic analogue hypothesis. *Mem Cognit* 7:19–28
- Pylyshyn ZW (1981) The imagery debate: analogue media versus tacit knowledge. *Psychol Rev* 87:16–45
- Pylyshyn ZW (2002) Mental imagery: in search of a theory. *Behav Brain Sci* 25:157–237
- Reeder RR (2017) Individual differences shape the content of the visual representations. *Vision Res* 141:266–281
- Ricciardi E, Menicagli D, Leo A, Costantini M, Pietrini P, Sinigaglia C (2017) Peripersonal space representation develops independently from visual experience. *Sci Rep* 7:17673
- Richardson A (1977) Verbalizer-visualizer: a cognitive style dimension. *J Ment Imag* 1:109–125
- Rode G, Rossetti Y, Boisson D (2001) Prism adaptation improves representational neglect. *Neuropsychologia* 39:1250–1254
- Roelofs L (2018) Why Imagining requires content: a reply to a reply to an objection to radical enactive cognition. *Thought J Philos*. <https://doi.org/10.1002/tht3.393> (ahead of publication)
- Royet JP, Delon-Martin C, Plailly J (2013) Odor mental imagery in non-experts in odors: a paradox? *Front Hum Neurosci* 7:87
- Sack AT, Jacobs C, De Martino F, Staeren N, Goebel R, Formisano E (2008) Dynamic premotor-to-parietal interaction during spatial imagery. *J Neurosci* 28:8417–8429
- Sakai K, Miyashita Y (1994) Neuronal tuning to learned complex forms in vision. *NeuroReport* 5:829–832
- Segal SJ, Fusella V (1970) Influence of imaged pictures and sounds on detection of visual and auditory signals. *J Exp Psychol* 83:458–464
- Serino A, Bassolino M, Farne A, Ladavas E (2007) Extended multisensory space in blind cane users. *Psychol Sci* 18:642–648
- Sheehan PW (1967) A shortened form of Betts' questionnaire upon mental imagery. *J Clin Psychol* 23:386–389
- Shepard RN, Metzler J (1971) Mental rotation of three-dimensional objects. *Science* 171:701–703
- Sima JF (2011) The format of mental images—an integrative computational theory. In: Carlson L, Holscher C, Shipley T (eds) Proceedings of the 33rd annual meeting of the cognitive science society. Cognitive Science Society, Austin, TX, pp 2878–2883
- Stevenson RJ, Case TI (2005) Olfactory dreams: phenomenology, relationship to volitional imagery and odor identification. *Imagin Cogn Pers* 24:69–90
- Stevenson RJ, Case TI, Mahmut M (2007) Difficulty in evoking odor images: the role of odor naming. *Mem Cognit* 35:578–589
- Stinear CM, Byblow WD, Steyvers M, Levin O, Swinnen SP (2006) Kinesthetic, but not visual, motor imagery modulates corticomotor excitability. *Exp Brain Res* 168:157–164
- Thomas NJT (1999) Are theories of imagery theories of imagination? An active perception approach to conscious mental content. *Cogn Sci* 23:207–245
- Thomas NJT (2009) Visual imagery and consciousness. In: Banks WP (ed) *Encyclopedia of consciousness*, vol 2. Elsevier/Academic Press, Oxford, pp 445–457
- Thomas NJT (2014) The multidimensional spectrum of imagination: images, dreams, hallucinations, and active, imaginative perception. *Humanities* 3(2):132–184
- Thompson E (2007) *Mind in life: biology, phenomenology, and the sciences of mind*. Harvard University Press, Cambridge
- Thompson WL, Kosslyn SM, Hoffman MS, van Der Kooij K (2008) Inspecting visual mental images: can people “see” implicit properties as easily in imagery and perception? *Mem Cognit* 36:1024–1032
- Thompson WL, Slotnick SD, Burrage MS, Kosslyn SM (2009) Two forms of spatial imagery: neuroimaging evidence. *Psychol Sci* 20:1245–1253
- Toriyama H, Ushiba J, Ushiyama J (2018) Subjective vividness of kinesthetic motor imagery is associated with the similarity in magnitude of sensorimotor event-related desynchronization between motor execution and motor imagery. *Front Hum Neurosci* 12:295
- Varela F, Thompson E, Rosch E (1991) *The embodied mind: cognitive science and human experience*. MIT Press, Cambridge
- Voyer D, Jansen P (2017) Motor expertise and performance in spatial tasks: a meta-analysis. *Hum Mov Sci* 54:110–124
- Wexler M, Kosslyn SM, Berthoz A (1998) Motor processes in mental rotation. *Cognition* 68:77–94
- 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
- Wilson M (2002) Six views of embodied cognition. *Psychon Bull Rev* 9:625–636
- Winlove C, Milton F, Ranson J, Fulford J, Mackisack M, Macpherson F, Zeman A (2018) The neural correlates of visual imagery: a coordinate-based meta-analysis. *Cortex*. <https://doi.org/10.1016/j.cortex.2017.12.014>
- Wohlschläger A (2001) Mental object rotation and the planning of hand movements. *Percept Psychophys* 63:709–718
- Wu J, Duan H, Tian X, Wang P, Zhang K (2012) The effects of visual imagery on face identification: an ERP study. *Front Hum Neurosci* 6:305
- Yoo SS, Freeman DK, McCarthy JJ, Jolesz FA (2003) Neural substrates of tactile imagery: a functional MRI study. *NeuroReport* 14:581–585
- Yu QH, Fu ASN, Kho A, Li J, Sun XH, Chan CCH (2016) Imagery perspective among young athletes: differentiation between external and internal visual imagery. *J Sport Health Sci* 5:211–218
- Zacks J (2008) Neuroimaging studies of mental rotation: a meta-analysis and review. *J Cogn Neurosci* 20:1–19
- Zaidel DW (2014) Creativity, brain, and art: biological and neurological considerations. *Front Hum Neurosci* 8:389
- Zeman A, Dewar M, Della Sella S (2015) Lives without imagery e congenital aphantasia. *Cortex* 73:378–380
- Zeman A, Dewar M, Della Sella S (2016) Reflections on aphantasia. *Cortex* 74:336–337
- Zhang L, Pi Y, Zhu H, Shen C, Zhang J, Wu Y (2018) Motor experience with a sport-specific implement affects motor imagery. *PeerJ* 6:e4687

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