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The effects of healthy aging on mental imagery as revealed by egocentric and allocentric mental spatial transformations

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ABSTRACT

Previous studies suggest that mental rotation can be accomplished by using different mental spatial transformations. When adopting the allocentric transformation, individuals imagine the stimulus rotation referring to its intrinsic coordinate frame, while when adopting the egocentric transformation they rely on multisensory and sensory-motor mechanisms. However, how these mental transformations evolve during healthy aging has received little attention. Here we investigated how visual, multisensory, and sensory-motor components of mental imagery change with normal aging. Fifteen elderly and 15 young participants were asked to perform two different laterality tasks within either an allocentric or an egocentric frame of reference. Participants had to judge either the handedness of a visual hand (egocentric task) or the location of a marker placed on the left or right side of the same visual hand (allocentric task). Both left and right hands were presented at various angular departures to the left, the right, or to the center of the screen. When performing the egocentric task, elderly participants were less accurate and slower for biomechanically awkward hand postures (i.e., lateral hand orientations). Their performance also decreased when stimuli were presented laterally. The findings revealed that healthy aging is associated with a specific degradation of sensory-motor mechanisms necessary to accomplish complex effector-centered mental transformations. Moreover, failure to find a difference in judging left or right hand laterality suggests that aging does not necessarily impair non-dominant hand sensory-motor programs.

1. Introduction

Mental imagery (MI) is the distinctive human ability to create and transform mental representations of self and external objects. The debate on the underlying cognitive mechanisms of MI has emphasized the relevance of different classes of mental transformations (see Zacks & Michelon, 2005). A mental image can be mentally transformed, for instance, in order to process its visual features without the need for the observer to physically move the object or himself. In this case, an allocentric transformation, based on the updating of the object's intrinsic coordinate frame, is applied. It is also possible to use MI in order to transform our whole body image rotating or translating in the space. This latter process constitutes a form of egocentric transformation that involves the updating of the observer's reference frame (i.e., eye and head centered) like, for instance, during perspective taking tasks. When MI is applied to a specific body part, an effector-based transformation based on the effector reference frame (e.g., hand centered) is applied. This different form of egocentric transformation updates the coordinate frame of a specific body part relative to an object, to another body part or to the environment frame of reference making use of sensory-motor brain mechanisms that occur also during action planning and rehearsal (e.g., Michelon, Vettel, & Zacks, 2006; Parsons et al., 1995).

One very fruitful way of studying MI has been trough mental rotation (MR) paradigms. MR has been first systematically explored by Shepard and Metzler (1971) in a series of experiments in which they visually presented participants with identical or mirror-image pairs of solid objects and recorded reaction times (RTs) for same-different judgments. They found that participants' RTs monotonically increased with the increase of angular disparity between the two objects and argued that, in order to decide whether they are the same or different, participants mentally rotated one of the objects until it matched the position of the other. Similar results have been documented using laterality judgment about mirror-symmetric visual stimuli. For example in the "hand laterality task" observers were shown with a rotated picture of a hand and were asked to decide if the stimulus represents a left hand or a right hand. To perform this task it typically takes longer for larger hand rotations (Sekiyama, 1982; Parsons, 1987). However, it has also been shown that, differently from MR of solid abstract objects, MR of hands is strongly influenced by body part's somatic and kinesthetic aspects (Sekiyama, 1982; Parsons, 1987, 1994). Indeed, the hand laterality

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judgment takes longer when hands are rotated away from the body's midsagittal plane (i.e., lateral orientations) than when hands are rotated toward it (i.e., medial orientations). RTs associated with hand laterality judgments of left hand stimuli and right hand stimuli are asymmetric relative to 180° of stimulus angular departure. This non-monotonic distribution of RTs seems to reflect the physical constraints of the forearm and wrist movements toward the lateral side of the body midline, as the forearm movements crossing toward the body midline are easier to be executed. It has been argued that MR of hands is performed by mentally simulating one's own hand rotating it until it reaches the same position as the displayed hand stimulus (Cooper & Shepard, 1975; Gentilucci, Daprati, & Gangitano, 1998; Parsons, 1987). Parsons (1994) also showed that the time needed to make the left–right judgment is comparable to the time needed to actually move the hand into the same displayed hand posture. However, the medial–lateral RT difference also indicates the existence of a preferred tuning between the angular departure of the hand stimulus and its handedness. Indeed for some combinations of stimulus view, stimulus angular departure, and stimulus handedness, the laterality judgment is much faster than for others. This phenomenon is consistent with the idea that, for some given orientations (i.e., medial), participants rely less on sensory-motor processes (i.e., the mental transformation) and more on a direct proprioceptive-visual matching between the observer's felt hand and the visually presented hand. Coherently, RTs for medial hand orientations do not necessarily follow a linear relation with the stimulus angular departures (Parsons, 1994; ter Horst, Jongsma, Janssen, van Lier, & Steenbergen, 2012). In this sense, the difference between medial and lateral orientation response latencies for correct trials reflects the general degree of sensory-motor processing necessary to accomplish the mental spatial transformation. Indeed, when the stimulus angular departure and the stimulus view are not coherent with the observer's felt hand, the decision relies on sensory-motor mechanisms that are reflected in the typical RT-orientation dependent distribution observed during MR of hands.

Hand laterality judgment is strongly influenced by the observer's hand posture during the task (Ionta & Blanke, 2009; Ionta, Fourkas, Fiorio, & Aglioti, 2007; Parsons, 1987; Shenton, Schwoebel, & Coslett, 2004), while individuals with congenital limb absence (Funk & Brugger, 2008), upper limb amputees (Nico, Daprati, Rigal, Parsons, & Sirigu, 2004), and chronic pain patients (Coslett, Medina, Kliot, & Burkey, 2010; Moseley, 2004; Schwoebel, Friedman, Duda, & Coslett, 2001) are impaired in performing this task. These findings suggest that proprioception and peripheral factors influence imagery and that sensory-motor mechanisms are essential in order to accomplish egocentric mental spatial transformations. The key role of the brain sensory-motor areas in supporting MR of hands has been recently demonstrated in a study in which patients with damage to the cortical somato-motor hand representation were selectively impaired in performing MR of hands but not MR of objects (Tomasino, Skrap, & Rumiati, 2011). In brain-damaged patients, dissociations between egocentric and allocentric transformations can be observed depending on the lesion site. For instance, Tomasino and Rumiati (2004) described patients whose abilities to perform MR based on “the visual strategy” or “the motor strategy” double dissociated as a consequence of a lesion either of the right- or left-hemisphere respectively. More specifically, right-hemisphere damaged patients were impaired when MR was based on the object reference frame but were able to perform egocentric-based MR, while left-hemisphere damaged patients showed the opposite pattern. This distinction has also received support from another neuropsychological study revealing a double dissociation between the two strategies (Sirigu & Duhamel, 2001).

Neuroimaging studies show that egocentric and allocentric transformations are supported by two complementary brain networks (see Zacks, 2008, for a recent review). In particular, the posterior parietal, the occipital and the superior temporal cortex are activated during allocentric transformations (e.g., Wraga, Shephard, Church, Inati, & Kosslyn, 2005; Zacks, Vettel, & Michelon, 2003). In addition, areas normally engaged in programming and executing movements (e.g., the supplementary motor area, the primary motor, premotor and parietal cortices, the cerebellum and the basal ganglia) are activated when the MR task is performed using an egocentric reference frame (e.g., Alivisatos & Petrides, 1997; Bonda, Petrides, Frey, & Evans, 1995; Kosslyn, DiGirolamo, Thompson, & Alpert, 1998; Kosslyn, Thompson, Wraga, & Alpert, 2001). Moreover, relative to objects, MR of hands was found to elicit stronger activity in the cortical motor areas (de Lange, Hagoort, & Toni, 2005; Kosslyn et al., 1998; Wraga, Thompson, Alpert, & Kosslyn, 2003; Wraga et al., 2005), and transcranial magnetic stimulation (TMS) applied over the motor cortex selectively impairs MR of hands (Ganis, Keenan, Kosslyn, & Pascual-Leone, 2000), but not MR of letters (Tomasino, Borroni, Isaja, & Rumiati, 2005). It has been demonstrated that within this wide brain network supporting MI, dissociation between egocentric and allocentric mental transformations can be found at the level of the posterior parietal cortex. Indeed, repetitive transcranial magnetic stimulation (rTMS) applied over the superior parietal lobule alters MR of letters while rTMS over the supramarginal gyrus impairs MR of hands (Pelgrims, Andres, & Olivier, 2009).

Like other cognitive abilities, MR seems to slowly degrade in elderly individuals. Age-related changes have been reported for MR of objects and alphanumeric characters (Berg, Hertzog, & Hunt, 1982; Cerella, Poon, & Fozard, 1981; Dror & Kosslyn, 1994; Gaylord & Marsh, 1975; Hertzog & Rypma, 1991; Kemps & Newson, 2005; Puglisi & Morrell, 1986; Sharps & Gollin, 1987), and MR of hands (Devlin & Wilson, 2010; Saimpont, Pozzo, & Papaxanthis, 2009). Elderly individuals have also been found to be slower than younger controls at explicitly imagining movements in a Fitts' like task (Personnier, Ballay, & Papaxanthis, 2010; Skoura, Papaxanthis, Vinter, & Pozzo, 2005), particularly when they imagined movements of the non-dominant hand (Skoura, Personnier, Vinter, Pozzo, & Papaxanthis, 2008). In this task, the time needed to imagine one's hand movement to a target increases with the distance and decreases with the size of the target, following the same physical law that regulates goal directed actions (Jeannerod, 1995). This is also consistent with their being less accurate and slower at executing movements with the non-dominant hand in highly demanding tasks (Francis & Spirduso, 2000; Mitrushina, Fogel, D'Elia, Uchiyama, & Satz, 1995; Teixeira, 2008).

However it remains unclear whether the age-related decline in MI hides a more specific deficit in applying either an egocentric mental transformation or an allocentric mental transformation. Indeed, the relationship between the type of stimulus and the mental transformation employed is not always necessarily so direct. Many studies suggest that MR of abstract objects can, to some extent, share the same cognitive and neural sources employed during egocentric transformations (e.g., de Lange et al., 2005; Wexler, Kosslyn, & Berthoz, 1998; Wraga et al., 2003). Thus, to date, the literature on the effect of normal aging on MR failed to clearly disentangle between potential differential effects of aging on the two mental transformation processes. Hence, the main purpose of the present study was to clarify the impact of normal aging on MR using either an egocentric (i.e., effector-centered) or an allocentric (i.e., object-centered) mental transformation. Differently from previous research, the paradigm employed in the present study allowed us to directly compare the two complementary mental spatial transformations by holding constant the stimuli to be mentally rotated and the type of response required. If the two classes of mental transformation differently decline with age, then we expected the group of elderly participants to perform worse in one of the two tasks. Instead, if healthy aging generally affects MR, then we expected impairments in both the egocentric and the allocentric task.

Since the functionality of the non-dominant hand changes with age (see e.g., Mitrushina et al., 1995; Francis & Spirduso, 2000; Teixeira, 2008), all our right-handed participants were asked to respond with their dominant hand (i.e., the right hand) irrespective of whether the response was left or right. This is at variance with Saimpont et al. (2009), in which elderly participants responded with the left hand or