Review article

Embodiment in the aging mind

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ABSTRACT

Bodily awareness is a central component of human sensation, action, and cognition. The human body is subject to profound changes over the adult lifespan. We live in an aging society: the mean age of people living in industrialized countries is currently over 40 years, and further increases are expected. Nevertheless, there is a lack of comprehensive knowledge that links changes in embodiment that occur with age to neuronal mechanisms and associated sensorimotor and cognitive deficits in older adults. Here, we synthesize existing evidence and introduce the NFL Framework of Embodied Aging, which links basic neuronal (N) mechanisms of age-related sensorimotor decline to changes in functional (F) bodily impairments, including deficits in higher-level cognitive functions, and impairments in daily life (L). We argue that cognitive and daily life impairments associated with old age are often due to deficits in embodiment, which can partly be linked to neuronal degradation at the sensorimotor level. The framework may encourage the development of novel approaches to improve autonomous living for older adults.

1. Introduction

Body perception and bodily awareness play central roles in human sensation, action, and cognition (Gallagher, 2005; Pfeifer et al., 2007). Research that is conducted on embodiment typically investigates interactions between perceptual, motor, and cognitive processes and how they influence our daily living. Bodily processes, mediated by peripheral receptors, muscles, and associated neuronal pathways, indeed influence many aspects of our daily life, such as the way we interact with our peers (Buccino et al., 2001; Rizzolatti and Craighero, 2004; Rizzolatti and Fabbri-Destro, 2008), the way we perceive and evaluate our spatial environment (van der Hoort et al., 2011), the way we make important decisions (Damásio, 1994; Reimann et al., 2012; Selen et al., 2012) and feel about their outcomes (Brassen et al., 2012), and the way we memorize events (Bergouignan et al., 2014).

However, the various and complex changes the human body undergoes over the lifespan are not taken into account in most current theories on embodiment. But we live in an aging society: the mean age of people living in industrialized countries is currently over 40 years, and further increases are expected (Vaupel, 2010). Nevertheless, so far, little attention has been paid to age-related changes in embodiment, the associated sensory, motor, and cognitive abilities, and the underlying neuronal mechanisms determining these effects. Critically, the lack of a comprehensive framework discussing the effects of bodily changes on sensory, motor, and cognitive processes and their influence on daily life can lead to an underestimation of the importance of changes in embodiment for cognitive disorders and sensorimotor deficits that are specific for older adults. This can slow down the development of treatment strategies to counteract these deficits and improve autonomous living for older adults. In addition, it leads to a limited basic understanding of the neuronal mechanisms that underlie age-related changes in cognitive functions. A better understanding of these changes may help policy makers to ensure that people aged 65 and older continue to play an integral role in their community.

Here, we take a first step in filling this current knowledge gap. We review the available empirical evidence on age-related changes in embodiment and synthesize it to introduce the NFL Framework of Embodied Aging. This novel theoretical framework clusters age-related changes in embodiment into three basic categories: neuronal mechanisms (N), functional consequences (F), and daily life relevance (L). The framework highlights the interactions between these levels, supported by empirical evidence. We refer to each category (N, F, and L) in the text and summarize the framework in Fig. 1. To increase readability, we have structured our review according to standard classification schemes
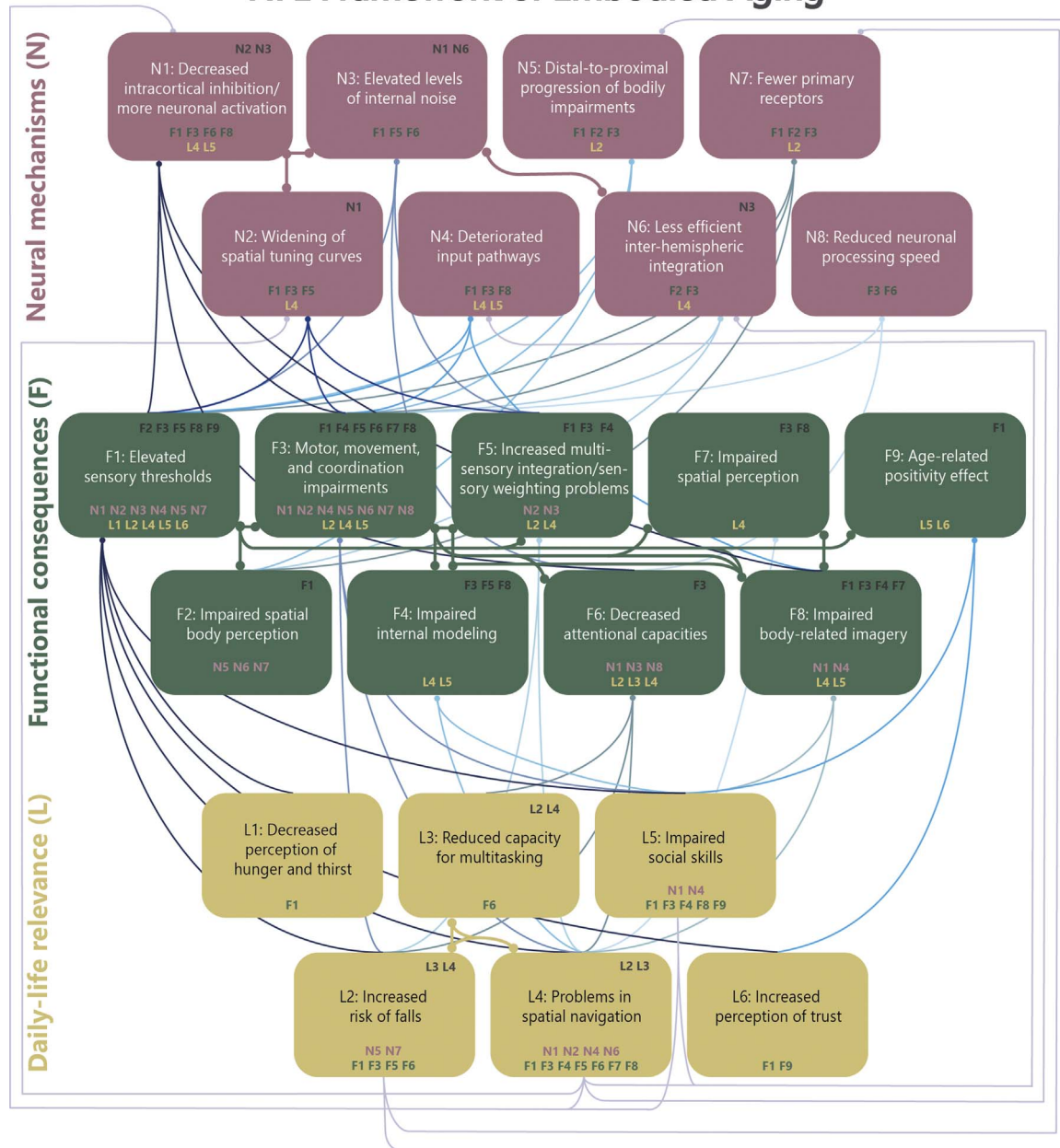
Fig. 1. NFL Framework of Embodied Aging. Displayed are interactions between neuronal mechanisms (N), functional consequences (F), and consequences for every-day life (L) of body-related impairments in older adults. Similar to the colored lines, the small letter-number pairs inside the boxes indicate relationships between different elements, which are explained in the text. Black pairs = relationships between elements within same level; red, green, yellow pairsom = relationships between elements across levels.

(e.g., touch, proprioception, interoception). Each category (N, F, and L) therefore appears in each of the specific sections. The NFL Framework of Embodied Aging was developed to allow a more detailed understanding of the interactions between age-related neuronal changes, age-related changes in perception, motor control, and cognition, and daily life experiences by older adults. The framework allows linking different research fields that have so far often been studied in isolation. Two reviews target similar issues (Vallet, 2015; Loeffler et al., 2016): Vallet et al. (2015) summarizes interactions between sensorimotor deficits and cognitive impairments in older adults, whereas Loeffler et al. (2016) provide a lifespan perspective on embodiment including literature both on children and on older adults. Our review extends this literature by (i) introducing specific neuronal mechanisms that may underlie age-related changes in embodiment, (ii) discussing a variety of modalities (e.g., touch, proprioception, interoception) and cognitive

functions (e.g., spatial cognition, social cognition), and (iii) integrating existing evidence into a novel framework.

We focus on published studies in the field of human cognitive and clinical neuroscience that either introduce changes in basic sensorimotor processing in older adults, or have established or supported links between age-related changes in basic sensorimotor processes on the one hand and age-related changes in higher cognitive processes on the other hand. The basic neuronal mechanisms we identified are summarized in Table 1, and the NFL Framework of Embodied Aging is summarized in Fig. 1. We included higher-level cognitive functions whenever published research indicated a link between age-dependent deficits in basic bodily processing and cognitive functions. Due to this subjective approach, neither these links nor the cognitive functions included can be exhaustive. We expect that future research will expand our initial framework. We note that although the plasticity of bodily processes and

Table 1

Overview over empirical evidence that supports the eight neuronal mechanisms as integrated into the NFL Framework of Embodied Aging (see Fig. 1).

Empirical finding	References	Neuronal mechanism (N)
• Decreased inhibitory responses in somatosensory system after repeated tactile stimulation	Sebastián and Ballesteros (2012), Cheng and Lin (2013), Heise et al. (2013), Strömmer et al. (2014), Cheng et al. (2015)	1. Decreased intracortical inhibition/more neuronal activation
• Enlarged cortical representations in somatosensory system during tactile stimulation, and haptic recognition	Kalisch et al. (2009), Brodoehl et al. (2013), Pleger et al. (2016)	
• Increased neuronal activation in motor cortex when performing motor movements	Peinemann et al. (2001), Ward and Frackowiak (2003), Wu and Hallett (2005), Riecker et al. (2006), Bernard and Seidler (2012)	
• Decreased (GABA-ergic) intracortical inhibition	Lenz et al. (2012), Levin et al. (2014), Lich and Bremmer (2014)	
• Increased sensory stimulus persistence	Botwinick (1978), Humes et al. (2009)	
• Decrease of GABAergic interneurons, and inhibitory synapses	Poe et al. (2001), Lehmann et al. (2012)	
• Widening of spatial tuning curves in the firing pattern of neurons	Engle et al. (2013), Strömmer et al. (2014)	2. Widening of spatial tuning curves
• Receptive fields of somatosensory neurons in rats increase with age, and overlap with the receptive fields of other neurons coding for different areas on the skin	Spengler et al. (1995), David-Jürgens et al. (2008)	
• Worse tactile amplitude discrimination close to noise level	Gescheider et al. (1996)	3. Elevated levels of internal noise
• Increased signal-to-noise ratio during bilateral integration of proprioceptive information	Schaap et al. (2015)	
• Impairments in the suppression of irrelevant stimuli	Poliakoff et al. (2006a), Hugenschmidt et al. (2009), Vallesi and Stuss (2010), Anguera and Gazzaley (2012), Sebastian et al. (2013), Strömmer et al. (2014)	
• Decreased proprioceptive feedback at the central level	Goble et al. (2011)	4. Deteriorated input pathways
• Primary interoceptive cortex shows decreased BOLD signal change during soft touch stimulation	May (2004)	
• Axonal loss and demyelinization in different brain areas	Gong et al. (2014), Betts et al. (2016)	
• Less evident tactile sensory impairments at lower arm and calf, stronger at hands and face, strongest at feet	Stevens and Choo (1996), Stevens et al. (2003), Shaffer and Harrison (2007)	5. Distal-to-proximal progression of bodily impairments
• Proprioceptive differences particularly apparent in the lower limbs and the hand	Karanjia and Ferguson (1983), Ferrell et al. (1992), Verschueren et al. (2002), Pickard et al. (2003), Madhavan and Shields (2005), Schrager et al. (2008), Baltich et al. (2015), Schaap et al. (2015), Yeh et al. (2015), Wang et al., (2012), Boisgontier and Nougier (2013), Schmidt et al. (2013), Boisgontier and Swinnen (2015)	
• Differences in the speed of tactile integration across hemispheres	Brown and Sainsbury (2000)	6. Less efficient inter-hemispheric integration
• Proprioceptive differences in bilateral integration	Schaap et al. (2015)	
• Particular impairment in performing bimanual movements where both hands are performing conflicting movements	Bangert et al. (2010)	
• Less responsivity of the corpus callosum during tactile stimulation, reduced size of corpus callosum	Fling et al. (2011), Brodoehl et al. (2013)	
• Semicircular canals show profound degeneration in older age	Rauch et al. (2001)	7. Fewer primary receptors
• Degradation of peripheral mechanoreceptors in the muscle, skin, and joints	Shaffer and Harrison (2007)	
• Proprioceptive differences most prominent under time pressure	Wu and Hallett (2005), Boisgontier et al. (2013)	8. Reduced neuronal processing speed
• Delayed neuronal response as measured by EEG beta activity during passive ankle movements	Toledo et al. (2016a, 2016b)	
• Delayed reaction times	Cespón et al. (2013)	
• Prioritizing of accuracy over speed	Salthouse and Somberg (1982), Goggin and Stelmach (1990), Smith and Brewer (1995)	
• Reduced preparatory changes in corticospinal facilitation in go/no-go task	Fujiyama et al. (2012)	
• Longer latency of P300 component	Reuter et al. (2013)	

associated changes in cognitive function and behaviour are relevant, particularly in light of the need to develop training techniques for older adults, the inclusion of plasticity mechanisms would have gone beyond the scope of our review. Instead, our review aims at providing a framework that may help to interpret past and future research results and to draw the readers' attention to the need to conduct multi-level and multi-disciplinary studies on embodied aging.

2. Bodily perception and action

Here, we will focus on age-related changes in bodily perception and action by introducing eight neuronal mechanisms (N1-N8; see Table 1 for an overview) and four functional consequences (F1-F4; see Fig. 1) that have been associated with age-related changes in embodiment. The list of eight neuronal mechanisms is not exhaustive. The mechanisms, introduced in modality-specific sections, provide the critical neurobiological links between age-related changes in perception and action on the one hand and age-related changes in cognition on the other hand, as will be discussed in later sections (see Sections 4–8).

2.1. Touch

Touch is fundamental to our internal and external sense of reality. It is essential for motor coordination and object handling, and it allows a direct and immediate interaction with the world around us. Tactile information can be transported both via myelinated A-beta mechanoreceptive afferents (discriminative touch) and non-myelinated C tactile (CT) afferents (affective touch). In this section, we focus only on discriminative touch, as pleasant touch will be discussed in a later section (2.3. Interoception).

Age seems to negatively affect sensory tactile abilities (F1: *Elevated sensory thresholds*; see Fig. 1). For example, performance on the two-point discrimination task, which tests the ability to spatially distinguish two needles applied to the skin surface, decreases with age (Cole, 1991; Desrosiers et al., 1999; Ranganathan et al., 2001; Kalisch et al., 2009; Lenz et al., 2012; Bowden and McNulty, 2013a,b; Vieira et al., 2016). Performance on the grating orientation task, where participants have to judge the orientation of objects that vary in groove width applied to their skin, also declines with age (Sathian et al., 1997; Remblay et al.,

2000). Similarly, older adults are impaired in their ability to perform tactile time judgments, such as the detection of small temporal gaps within trains of tactile stimuli (Van Doren et al., 1990; Humes et al., 2009), the discrimination of two subsequent touches on the skin (Hoshiyama et al., 2004; Ramos et al., 2016), and the determination which of two subsequently applied tactile stimuli came first (Brown and Sainsbury, 2000).

Decreased intracortical inhibition and the associated expansion of neuronal representations in older adults is one neuronal mechanism that has frequently been related to increased spatial and temporal tactile discrimination thresholds in older adults (N1: *Decreased intracortical inhibition/more neuronal activation*; see Fig. 1 and Table 1). This view is supported by decreased inhibitory responses in the somatosensory system of older adults after repeated tactile stimulation (Sebastián and Ballesteros, 2012; Cheng and Lin, 2013; Heise et al., 2013; Strömmer et al., 2014; Cheng et al., 2015), enlarged cortical representations in the primary somatosensory cortex when perceiving touch (Kalisch et al., 2009; Brodoehl et al., 2013; Pleger et al., 2016, but see Reuter et al., 2013), and during haptic recognition (Sebastián et al., 2011). Decreased intracortical inhibition also correlates with impairments in tactile abilities (Pellicciari et al., 2009; Lenz et al., 2012), and increased stimulus persistence is regarded as one reason for the reduced temporal discrimination thresholds in older adults (Botwinick, 1978; Humes et al., 2009). Finally, the number of GABAergic interneurons declines with age (Lehmann et al., 2012), as do presumptive inhibitory synapses in cortical layer II of the primary somatosensory cortex (Poe et al., 2001).

A widening of spatial tuning curves in the firing pattern of neurons also seems to play a role in the degraded tactile abilities in older adults (N2: *Widening of spatial tuning curves*; see Fig. 1 and Table 1), and it partly explains the enlarged neuronal representations (Engle et al., 2013; Strömmer et al., 2014). For example, the receptive fields of somatosensory neurons in rats increase with age and overlap with the receptive fields of other neurons coding for different areas on the skin (Spengler et al., 1995; David-Jürgens et al., 2008). Age-related widening of neuronal tuning curves has also been observed for neurons in visual (Schmolesky et al., 2000) and auditory cortices (Juarez-Salinas et al., 2010; Engle et al., 2013) in monkeys. Additionally, the increased sharpening of tuning curves from primary to secondary areas, as observed in young animals, is dramatically reduced in older animals (Juarez-Salinas et al., 2010). The prevalence of this phenomenon across different modalities and species suggests a general mechanism underlying some of the functional changes that occur with age (Engle et al., 2013).

The ability to differentiate two tactile stimuli that vary in *intensity* seems to be preserved in older adults, at least when stimuli are adjusted to individual tactile detection thresholds (Gescheider et al., 1996). This motivated the hypothesis that there are elevated levels of internal neuronal noise in the sensory system of older adults than among younger adults (N3: *Elevated levels of internal noise*; see Fig. 1) (Gescheider et al., 1996). Elevated levels of internal neuronal noise would explain age-related difficulties in discriminating stimuli with amplitudes close to noise levels, and increased detection thresholds of mechanical forces and vibration with age, but preserved amplitude discrimination abilities when stimuli are presented at stronger forces (cf., F1; see Fig. 1).

Tactile detection abilities on the index finger significantly worsen with age, even over a period of three years (Desrosiers et al., 1999). Similarly, the ability to detect mechanical forces using fine hair stimuli declines with age (Bowden and McNulty, 2013a,b), and when vibratory stimulation is applied to the skin surface, older adults have significantly higher detection thresholds than younger adults (Goble et al., 1996; Perry, 2006; Humes et al., 2009). The latter effect seems to be stronger for high- than for low-stimulation frequencies (Humes et al., 2009). In addition to elevated levels of internal neuronal noise, as discussed above (cf., N3), deteriorated input pathways due to neuronal loss and/

or demyelination may also be responsible for these effects (N4: *Deteriorated input pathways*; see Fig. 1) (Gong et al., 2014; Betts et al., 2016).

Age-related decline in tactile sensitivity seems to differ across body parts. Tactile sensory impairments in older age are less evident at the lower arm and calf, stronger at the hands and face, and strongest at the feet (Stevens and Choo, 1996; Stevens et al., 2003). This is in line with the observation that neuronal receptive fields in the somatosensory cortex of old rats are increased for the hindpaws, while those for the forepaws are not affected by age (Godde et al., 2002), which is in accordance with the distal-to-proximal hypotheses of sensory aging (N5: *Distal-to-proximal progression of impairments;* see Fig. 1). This hypothesis states that due to the reduced rate of information transfer along axons, distal body parts are more impaired in sensory perception than proximal body parts in older adults (Shaffer and Harrison 2007). This hypothesis relates to different sensory and motor qualities, as will be discussed below (Section 2.4, 2.6, 5.1).

Aging also seems to impair the ability to *localize* touch on the body (F2: *Impaired spatial body perception*; see Fig. 1). In one study, the ability to localize seven locations on the arm was compared between older and younger participants. Group differences appeared when tactile stimulation was applied to the middle of the arm but disappeared when it was applied closer to major anatomical landmarks, such as the elbow or the wrist (Cholewiak and Collins, 2003).

Older adults also seem to present differences in the *speed* of tactile integration across hemispheres (N6: *Less efficient inter-hemispheric integration*; see Fig. 1). In Brown and Sainsbury (2000), participants judged whether or not pairs of tactile stimuli that were applied to the left and right index fingers or to the index and middle fingers of one hand were delivered simultaneously. The authors calculated inter-hemispheric transfer times by taking the difference between the means of the bimanual condition and the combined means of the unimanual conditions. Older participants had longer inter-hemispheric transfer times than younger participants, which was interpreted as a slowing of tactile neuronal transfer across hemispheres. This finding accords with the reduced responsivity of the corpus callosum in older adults, compared with younger adults, during tactile stimulation (Brodoehl et al., 2013). Altered inter-hemispheric inhibition in older adults seems to be linked to different sensory, motor, and cognitive deficits, as will be outlined below (Section 2.4, 2.5, 5.1; see Fig. 1 for an overview).

2.2. Vestibular processing

The vestibular system has its primary receptors in the inner ear, and it detects body position and self-motion in three-dimensional space. The vestibular system conveys signals with respect to body position and head position to the perceiver, and it plays important roles in the reflexive control of eye gaze, head movement, and body position. The degeneration of the vestibular system with age is not uniform, and well-controlled studies on the underlying causal neuronal mechanisms, behavioural consequences, and clinical implications are currently lacking (Brosel et al., 2016; Martins et al., 2016). Here, we provide a brief overview of available evidence.

The semicircular canals, which sense angular head rotation, seem to show the most profound degeneration in older age. The hair cells in all canals decrease 40% by age 80 (Rauch et al., 2001), but the saccule and utricle experience only a 25% reduction with age (Matheson et al., 1999) (N7: *Fewer primary receptors*; see Fig. 1). Accordingly, older adults show particular impairments in sensing head direction as evidenced by impairments in the vestibular-ocular reflex (Baloh et al., 1993; Baloh et al., 2001). The vestibular-ocular reflex measures stable vision during head motion by rotating the eyes in the direction opposite to head rotation. Hsieh et al. (2014) measured age-related declines in the vestibular system by cross-correlating eye velocity and head velocity during head movements in different age groups (Hsieh et al., 2014). They found reduced cross-correlation coefficients in older adults (particularly when they had their eyes open) and significant correlations

proprioceptive tasks sometimes occur only when participants are forced to execute movements fast and not when they are allowed to conduct them in their own pace (Wu and Hallett, 2005; Boisgontier et al., 2013). This relates to another neuronal mechanism that changes with age, i.e., the speed of neuronal information processing (N8: *Reduced neuronal processing speed;* see Fig. 1). In the proprioceptive system, this idea is supported by a delayed N1 component, as measured by event-related potentials (ERPs) during passive ankle movements in older adults (Toledo et al., 2016a, 2016b). There is also evidence for a delayed processing speed in other domains, as discussed below (Sections 2.5, 4; see Fig. 1).

2.5. Manual motor control

Older adults show declined dexterity in a number of manual tasks, which can lead to problems carrying out even simple everyday movements (Bowden and McNulty, 2013a,b) (F3; see Fig. 1). Muscle co-contraction, for example, describes the tendency of aged individuals to activate more muscles around the joints than would be necessary to carry out a movement, for example during grip tasks (Diermayr et al., 2011), or while standing (Cenciarini et al., 2010). It is still under debate whether muscle co-contraction can be explained by decreased proprioceptive abilities (Madhavan and Shields, 2005) and/or may be a compensatory strategy in older adults to overcome the limitations of tactile feedback (cf., N4, N7, F1; see Fig. 1) (Nowak et al., 2001; Diermayr et al., 2011; Craig et al., 2016; see also Tremblay et al., 2005; Bowden and McNulty, 2013a,b).

As previously mentioned, another neuronal mechanism that may explain decreased manual dexterity in older adults is their stronger inter-hemispheric coupling or decreased inter-hemispheric inhibition (cf., N6; see Fig. 1) (Talelli et al., 2008; Levin et al., 2014). During unimanual hand movements, associated activity in the non-moving hand is higher in older compared to younger adults (Ward and Frackowiak, 2003; Naccarato et al., 2006; Riecker et al., 2006; Ward et al., 2008; McGregor et al., 2011; Davidson and Tremblay, 2013; McGregor et al., 2013; Zapparoli et al., 2013; Heetkamp et al., 2014; Solesio-Jofre et al., 2014), and the characteristic asymmetric desynchronization, which arises contralateral to the responding hand, is largely reduced in older adults (Vallesi et al., 2010). In addition, older adults are particularly impaired in performing bimanual tasks where both hands are performing conflicting movements, such as when the two hands are moving out-of-phase (Bangert et al., 2010). Fling et al. (2011) showed that better performance in a bimanual task where both hands moved asynchronously was associated with a larger size and more intact microstructure in the corpus callosum of older adults (Fling et al., 2011). The authors suggested that structural changes in the corpus callosum are accompanied by decreased inter-hemispheric inhibition, which leads to decreased performance on bimanual tasks. Similarly, Solesio-Jofre et al. (2014) indicated that degraded abilities to carry out a bimanual visuo-motor task, where participants were asked to track a target with their hands occluded from view, correlated with increased inter-hemispheric coupling between sensorimotor cortices (Solesio-Jofre et al., 2014).

Muscle co-contraction and less efficient inter-hemispheric coupling are neuronal mechanisms that partly overlap with the concept of increased neuronal dedifferentiation (cf., N1; see Fig. 1) (Bernard and Seidler, 2012). Neuronal dedifferentiation is often evidenced in the motor cortex by a higher neuronal activation among older participants than among younger participants when performing motor movements (Peinemann et al., 2001; Ward and Frackowiak, 2003; Wu and Hallett, 2005; Riecker et al., 2006; Bernard and Seidler, 2012), even if the task is matched in difficulty (Heuninckx et al., 2005). This elevated activity during simple motor movements correlates positively with reaction times in a visuo-motor task (Bernard and Seidler, 2012; see also Riecker et al., 2006 for a similar point). In addition, decreased GABAergic inhibition has been related to problems with inhibiting motor responses

in older adults (Levin et al., 2014). However, there is also evidence that increased activity in the motor system during bimanual movements improves coordinative abilities in older adults, which would suggest compensatory activation rather than dedifferentiation as a reason for the elevated activation (Goble et al., 2010).

Finally, similar to other modalities, motor responses are slowed in the aging population (cf., N8; see Fig. 1), causing slower reaction times during motor tasks. Reaction times and delayed motor movements increase linearly with age (Cespón et al., 2013). This may be due in part to differences in preparatory action planning between older and younger adults: Older adults seem to prioritize accuracy over speed (Salthouse and Somberg, 1982; Goggin and Stelmach, 1990; Smith and Brewer, 1995), and show reduced preparatory changes in corticospinal facilitation in go/no-go tasks (Fujiyama et al., 2012).

2.6. Gait and walking impairments

Very common motor deficits in older adults are problems with controlling gait while standing and walking (Owings and Grabiner, 2004) (cf., F3: *Motor, movement, and coordination impairments;* see Fig. 1). Interestingly, also here, impaired bodily sensory abilities can sometimes explain impaired motor control. One causal mechanism for decreased motor skills in older adults is their impaired sensitivity to detecting vestibular signals (cf., N4, N7, F1; see Fig. 1). Loss of vestibular function has been related in particular to dizziness, walking impairments, and increased risks of falls, a major factor that reduces autonomous living (L2: *Increased risks of falls;* see Fig. 1) (Fife and Baloh, 1993; Pothula et al., 2004; Murray et al., 2005; Ekvall Hansson and Magnusson, 2013; Liston et al., 2014; Chau et al., 2015; Semenov et al., 2016). Vestibular dysfunction seems in this respect to be highly relevant for autonomous living in older adults and should perhaps be attended more by basic and applied research. As a possible compensatory mechanism for the reduced vestibular input, older adults may show a higher head-trunk correlation while walking than young people because this may reduce the complexity of postural control (Deshpande and Patla, 2007).

In addition to vestibular degeneration, reduced lower limb proprioception (cf., N5: *Distal-to-proximal progression of bodily impairments;* see Fig. 1) has been related to fall accidents (cf., L2; see Fig. 1) (Lord et al., 1999), and balance problems (Madhavan and Shields 2005). Tactile deficits also seem to relate to gait and walking impairments: Widened tuning in neurons coding for the hindpaws of rats is related to impaired walking behaviour (Spengler et al., 1995).

2.7. Internal inverse and forward modeling

Age-related differences in motor control and sensory perception may partly be linked to difficulties in action planning and adapting to sensorimotor perturbations. To plan, control, and learn actions efficiently, multiple internal inverse and forward models are used to simulate the behaviour of the body and the environment (Wolpert and Kawato, 1998; Wolpert and Flanagan, 2001; Wolpert et al., 2011). The inverse model provides the motor commands that would be necessary to carry out a certain action. The corresponding forward model represents a prediction about the sensory consequences of that action for which an efference copy of the respective motor command is used. These predictions are supported by learned regularities. For example, during object lifting, information about the characteristics of an object (e.g., size and texture) is used to generate a prediction about its weight.

Bernard and Seidler (2014) proposed that forward modeling is particularly affected by aging, although inverse modeling may also be modified (F4: *Impaired internal modeling;* see Fig. 1). The authors link age-related difficulties in the formation of new internal models and/or the degradation of existing models to age-related changes in cerebellar functioning and/or a disruption of its connections to cortical motor areas, and the basal ganglia. Age-related deficits in sensorimotor

adaptation have further been associated with changes in striatal functioning, which is thought to be responsible for the retrieval of appropriate sensorimotor representations after changes in the environment (King et al., 2013). For example, functional connectivity between the striatum and sensory or motor cortices has been shown to change with age, which was negatively correlated with performance on a motor learning task (Marchand et al., 2011).

Other evidence suggests that internal modeling may remain relatively preserved with age as long as it concerns simple movement sequences, whereas it becomes imprecise in conditions of higher task complexity or when flexible adaptations to changes in the environment are required (Saimpont et al., 2013). For example, older adults in their mid-sixties exert comparable levels of anticipatory grip force control during self-initiated object lifting and holding, but only for simple tasks such as two-digit grasps, whereas age group differences emerge when more fingers are involved, or when new information needs to be incorporated (Diermayr et al., 2011).

The adaptation to visual or visuo-motor distortions is impaired in older compared to younger adults, although both groups show similar levels of sensorimotor recalibration (Buch et al., 2003; Bock, 2005; Seidler 2006; Hegele and Heuer, 2010). Recalibration in these paradigms has been typically defined as the magnitude of after-effects following removal of visuo-motor distortion, and therefore, it relates to the modification of internal (inverse) models. Thus, age-related declines in sensorimotor adaptation appear to rely on difficulties in other task components such as movement corrections and updating based on visual feedback. Older adults also exhibit a higher number of corrective sub-movements during a self-timed motor task in order to attain the level of performance observed in younger adults (Boisgontier and Nougier, 2013; see also Sarlegna, 2006). Additionally, the mismatch negativity is attenuated and delayed in older adults (Strömmer et al., 2014). The mismatch negativity is typically measured with event-related potentials (ERPs), and measures the ERP elicited by a deviant tactile stimulus in a background of homogenous tactile stimuli.

From a neurocomputational modeling perspective, these changes might be taken as an indicator of a brain that progressively optimizes its internal models over the lifespan, leading to a complexity reduction (higher generalization, or dedifferentiation, cf., N1; see Fig. 1), and an attenuation of bottom-up error signals used to update internal models (Moran et al., 2014). In constant and/or familiar environments, older adults' internal (forward) models may be appropriate to predict sensorimotor contingencies in an efficient manner, whereas the younger brain is more accurate in accommodating subtle or short-term changes in sensory input and forming new internal models in response to novel sensory input. This has consequences for a number of behaviours, such as inhibiting motor plans that have been primed beforehand, with which older adults have been shown to have problems (cf., F3; see Fig. 1) (Potter and Grealy, 2006; Rossit and Harvey, 2008; Trewartha et al., 2009), but also more complex cognitive skills as will be outlined below (see Fig. 1 for an overview).

3. Integration of bodily signals

Above, we have considered age-related changes in bodily perception for single modalities, such as touch, the vestibular sense, interoception, and proprioception, and for the motor domain. By introducing eight neuronal mechanisms (N1-N8) and four functional consequences (F1-F4), and by highlighting the relevance of these deficits for daily living (L1-L2), we have introduced the basic building blocks of the NFL Framework of Embodied Aging (summarized in Fig. 1). Next, we will introduce age-related changes in bodily cue integration while referring to the neuronal mechanisms described above.

3.1. Multisensory integration

Age-related increases in temporal discrimination thresholds occur for multimodal stimuli in the same way as they do for unimodal stimuli

(Poliakoff et al., 2006a,b). In a study by Poliakoff et al. (2006b), for example, discrimination thresholds (just noticeable differences) between visuo-tactile stimuli were higher for older than for younger participants. This suggests a widened window for the integration of body-related signals across space and time (F5: *Increased multisensory integration/sensory weighting problems*; see Fig. 1). Indeed, experiments revealed an enhanced integration of visual and tactile stimuli in older adults (Poliakoff et al., 2006b), especially when the spatial integration window was tested (Poliakoff et al., 2006a; Couth et al., 2016). This pattern is similar to the enhanced integration between (non-body) auditory and visual cues in older adults (Diederich et al., 2008; Diaconescu et al., 2013) and may be due to an age-related widening of spatial tuning curves at the neuronal level (cf., N2; see Fig. 1). Importantly, increased integration of visual and tactile stimuli correlates with the frequencies of falls (cf., L2: *Increased risk of falls*; see Fig. 1), indicating that altered multimodal integration in older adults may be a potential risk factor that is relevant for health care (Mahoney et al., 2014a).

Brodoehl et al. (2015) suggested that increased multisensory integration in older adults (cf., F5) is an epiphenomenon of decreased unisensory processing capacities, such as of tactile cues (cf., N4, F1; see Fig. 1). Also Diederich et al. (2008) and Diaconescu et al. (2013) argued that increased multisensory integration serves as a compensating function for decreased processing of unisensory stimuli in older adults. Diaconescu et al. (2013) detected a correlation between age-related increases in multisensory integration and increased activation in the posterior parietal and medial prefrontal areas, which are possible neuronal substrates for this effect.

A different explanation for enhanced multisensory integration in older adults was proposed by Mozolic et al. (2012). According to them, older participants have difficulty in suppressing irrelevant background noise, which is related to a neuronal mechanism introduced earlier (cf., N3; see also Fig. 1). According to this view, background stimuli are automatically processed and integrated with relevant information, which may lead to increased multisensory integration. Finally, the idea that increased multisensory integration is related to deficits in attention (see Section 4) is corroborated by Hugenschmidt et al. (2009), who found that multisensory integration can be reduced by focusing attentional resources on one specific modality.

3.2. Weighting of bodily cues

In addition to an apparently sometimes widened window for multisensory integration, older adults have difficulties adjusting the sensory weights of different bodily signals according to the principle of optimal sensory integration (cf., F5; see Fig. 1). In one study, younger and older participants were asked to lift different objects. The colour of the object indicated to them which weights or surface properties the objects had. Young participants were able to use the colour code to scale their grip force to the respective object, whereas older adults did not take advantage of the colour coding; rather, they made use of a default scaling scheme (Cole and Rotella, 2002). This may indicate less weighting of vision in a proprioceptive/motor task in older adults, when the integration of visual cues would have in fact been beneficial.

There is also evidence that older adults do not decrease the weight of sensory input even when those senses become deteriorated. Zhang and Deshpande (2016) investigated whether older adults reduce the weighting of discordant vestibular input and use available visual information to compensate for vestibular disturbances while walking. Although age-related differences were small, they found that older adults showed reduced abilities to downweight disrupted vestibular input to control head stability. Similarly, Deshpande and Patla (2007) found that young people showed no further increase in path deviation when vestibular disturbance was increased, whereas older adults did. The authors suggested that young participants reweight the vestibular input in favour of visual input when disturbances increase, whereas

older adults do not. Similarly, in a proprioceptive-motor task, younger and older participants were asked to control their balance while standing on a platform. When visual feedback in the standing position was delayed, older adults were more affected than young participants, which was interpreted as a tendency among older adults to rely on visual feedback even when vision is disrupted (Yeh et al., 2014; see also Camicioli et al., 1997; Bugnariu and Fung, 2007).

There are different reasons why older adults may be impaired in adjusting sensory weights based on Bayesian principles. One reason may again be their impaired sensory processing capacities (cf., F1, N4; see Fig. 1). For example, the impaired modulation of vestibular input despite deterioration was interpreted as compensatory strategy: Older adults may increase their sensitivity to vestibular input to compensate for age-related peripheral structural degeneration (Pyykkö et al., 1990; Kobayashi et al., 2002; Sun et al., 2014). This would lead to decreased abilities to lower sensory weight when necessary. Jahn et al. (2003) suggested that this age-related increase in vestibular weighting may even change over time: Whereas earlier vestibular disturbances that are related to hair cell loss (cf., N7; see Fig. 1) would lead to increased weighting of vestibular cues, later in life, when nerve fibres degenerate, this compensatory sensitivity may break down, which then results in a decreased weighting of the vestibular sense (Jahn et al., 2003). This would explain higher weighting of vestibular cues in the early phases of degeneration but the lower weighting of vestibular cues in later phases of degeneration.

A second possible explanation of difficulties in sensory weighting, albeit not excluding the first, is that older adults may a have particular difficulty in rapidly reorganizing the hierarchy of the sensory inputs when required, which may relate to their internal modeling deficits (cf., F4; see Fig. 1) (Hay et al., 1996). This hypothesis was developed based on the finding that older adults are able to adjust postural control when vision is absent. That is, they increase the weights of the proprioceptive system when necessary, but when another sensory modality is added (e.g., proprioception to vision-only), older adults appear less able to rapidly integrate this new information to adjust weights and increase performance (Hay et al., 1996). Age-related atrophy in the association cortex, such as the posterior and inferior parietal cortex (Salat et al., 2004) and the brainstem (Tang et al., 2001) have been discussed as potential underlying neuronal substrates for these difficulties.

4. Bodily attention

In the first two sections, we focused on age-related impairments in bodily perception and action taking single-cue conditions (Section 2) and multi-cue conditions (Section 3) into account. We introduced eight neuronal mechanisms (N1-N8) and five functional consequences (F1-F5) associated with these impairments, and we highlighted the relevance of these impairments for daily living (L1-L2). In the following section, we will focus on age-related changes in bodily attention, and integrate these insights into the NFL framework (see Fig. 1).

Evidence regarding attention deficits in older adults (F6: *Decreased attentional capacities*) has typically pointed to impairments in the suppression of irrelevant stimuli. The decreased capabilities of older adults to inhibit non-attended cues is apparent in different modalities (Guerreiro et al., 2014), including those where signals stem from the body. For example, Bolton and Staines (2012) applied tactile stimulation either to the index finger or to the small finger of younger and older participants. When comparing attended with non-attended sensory evoked potentials (SEPs), older participants showed a reduced P100 suppression of the non-attended finger than younger participants. Similarly, Valeriani et al. (2003) demonstrated that the N140 component was identifiable in young participants only when an electrical stimulus was attended to, while older adults showed the N140 component irrespective of whether the stimuli was attended to or not.

The ability of older adults to suppress irrelevant information has also been tested in studies using secondary attention-demanding tasks.

Poliakoff et al. (2006a) tested several age groups in a visuo-tactile selective attention task, where participants were required to attend to one of either modality. Performance of older adults worsened significantly when attending to tactile stimuli and ignoring visual distractors but not in the reverse condition. The authors suggested that a reduced signal-to-noise ratio of the tactile modality in older adults (cf., N3) could explain these selective attention deficits. This may interact with the reduced capacity of older adults to inhibit irrelevant information (see also Hugenschmidt et al., 2009; Mozolic et al., 2012), and older adults' general impairments in intracortical inhibition (cf., N1; see Fig. 1) (Poliakoff et al., 2006a; Vallesi and Stuss, 2010; Anguera and Gazzaley, 2012; Sebastian et al., 2013; Strömmer et al., 2014). Basic sensory processing deficits are therefore often interlinked with more cognitive, attention-related deficits. To provide another example, Boisgontier et al. (2014) used a proprioceptive matching task in which participants had to imitate the movements of one hand (passive) with the opposite hand (active). Both participant groups performed better when directing their attention towards the passive limb, but when their attention was drawn towards the active limb, older adults showed higher impairments than young participants.

Performing a demanding secondary task also deteriorates postural control in older adults more than in younger adults (cf., F3; see Fig. 1) (Teasdale et al., 1993; Shumway-Cook et al., 1997; Brown et al., 1999; Brauer et al., 2001; Redfern et al., 2001). For instance, Goble et al. (2012) divided older adults into high and low attention/working memory groups based on their performance on a digit span task (Goble et al., 2012). Performance on a subsequent proprioceptive matching task, where participants had to solve an additional cognitive test, was significantly worse for the low attention/working memory group than for the high attention/working memory group. Simultaneous performance of a postural task and a secondary task, however, may not lead to worse performance in older adults if the postural task is executed automatically. Age-related deficits are more likely to become apparent when postural control requires further central processing (Ruffieux et al., 2015). This suggests deficits in recruiting attentional resources in older adults and may partly explain their problems with multi-tasking in everyday life (L3: *Reduced capacity for multitasking*; see Fig. 1).

Older adults also invest more attentional resources in motor control than young people (Maki et al., 2001; Huxhold et al., 2006). This has often been explained as a compensatory strategy to overcome decreased task-specificity, i.e., neuronal de-differentiation (cf., N1; see Fig. 1) (Cabeza 2002; Logan et al., 2002; Reuter-Lorenz, 2002; Buckner, 2004). For instance, Vallesi and Stuss (2010) used a task with two levels of no-go trials: high-conflict trials and low-conflict trials. Participants were required to give a response by pressing a key with either hand. The authors calculated the lateralized readiness potential (LRP) using EEG as a measure of unilateral preparation. Although older and younger participants were matched in performance, older participants demonstrated a greater LRP not only in high-conflict conditions but also in low-conflict no-go conditions. Moreover, older participants with larger LRPs during no-go trials were quicker to respond in go trials, which suggests that this additional recruitment of attentional resources is needed for successful task performance (see also Li et al., 2001). This has consequences for daily life: Divided attention or dual task-paradigms are able to predict the risk of falling (Verghese et al., 2002; Springer et al., 2006), in addition to neuropsychological studies that link deficits in executive attention with the risk of falling (cf., L2; see Fig. 1) (Holtzer et al., 2007).

Decreased attentional capacities in older adults could also explain their slower sensory processing (cf., N8; see Fig. 1). For example, the P300 component is regarded as a marker of processing speed (Gaál et al., 2007; Riis et al., 2009), and its latency seems to be longer in older than in middle-aged and younger adults (Reuter et al., 2013) when elicited by tactile stimulation of the fingertip. In light of the evidence presented above, the reduced sensorimotor processing speed could be partially explained by the difficulties that older adults face in applying

focused attention or controlling their attentional focus to increase the saliency of pertinent sensory stimuli (cf., N3; see Fig. 1).

5. Body and space

Above, we were concerned with age-related impairments in embodiment, taking single-cue conditions (Section 2) and multi-cue conditions (Section 3) into account. We also highlighted the multiple interactions between associated neuronal mechanisms and deficits in bodily attention and as well as functional consequences (Section 4). So far, eight neuronal mechanisms (N1-N8) and six functional consequences (F1-F6) were described, and we highlighted the relevance of these impairments for daily living (L1-L3). In the NFL Framework of Embodied Aging (see Fig. 1), these categories link age-related changes in embodiment to neurobiological mechanisms, functional consequences, and everyday life impairments. In the current section, we addressed the relevance of age-related changes in embodiment as introduced above to more complex cognitive functions such as the perception of space.

5.1. Spatial reference frames

Our body influences the way we perceive the environment. In particular, stimuli close to the body are processed differently from stimuli that are more distant from the body, which may relate to an increased readiness for potential incoming hazards (Graziano and Cooke, 2006). This area of enhanced processing ('peripersonal space') can be defined as the space immediately accessible around our hands and body, whereas 'extrapersonal space' would refer to the area that is not within the reach of the arm (Rizzolatti et al., 1997; Holmes and Spence, 2004).

Prior studies have noted an expanded representation of peripersonal space in older adults (cf., F2; see Fig. 1) (Gabbard et al., 2011, but see Gabbard and Cordova, 2013). In particular, Poliakoff et al. (2006a) showed that the visuo-tactile congruency effect, which is normally restricted to the space near the hand, was found in older adults also when visual distractors were presented near the unstimulated hand, in the contralateral hemispace (Poliakoff et al., 2006a; see also Mahoney et al., 2014b). This spatially extended congruency effect does not occur when visual distractors are presented farther away at the ipsilateral side (Couth et al., 2016). Thus, in older adults, there seems to be a specific expansion of peripersonal space to the contralateral hemisphere, which may be related to their decreased inter-hemispheric inhibition (cf., N6; see Fig. 1). More research is needed to support this idea. In addition, older adults do not experience changes in their perceived distance to targets as a result of tool use as young adults do, which suggests that older people may be impaired in their capacity to perform visuo-motor remapping (Caçola et al., 2013; Costello et al., 2015).

Current evidence also depicts age-related differences in the anchor points of reference frames between younger and older participants. Bloesch et al. (2013) conducted an experiment where participants were seated in front of a screen and were instructed to reach for targets turning green. A distractor was presented simultaneously, and the researchers evaluated at which spatial locations the distractor was most effective: While younger participants exhibited an increased response latency whenever the distractor was placed along the movement path of the hand, older adults exhibited increases in reaction times when the distractor was close to their body irrespective of the starting position of the hand. The researchers concluded that younger and older participants used different reference frames: Whereas young people may have used a 'hand-centred' reference frame, older people may have used a 'body-centred' reference frame. This switch may be caused by a degeneration of the neural mechanisms that support the perihand spatial representation, motivating the change towards a broader, trunk-based reference frame. This may relate to the distal-to-proximal hypothesis of sensory aging (cf., N5; see Fig. 1): Because sensory impairments are greater in distal than in proximal body parts, the latter may be used by older adults as spatial anchor points.

5.2. Distance perception

The perceived distance between one's own body and a static, external object is usually underestimated. Bian and Andersen (2013) demonstrated, however, that older adults outperform younger adults in the judgment of body-object distances (egocentric distances) between 4 and 12 m because older people showed this compression of space to a lesser extent than young participants. Sugovic and Witt (2013) interpreted this finding in terms of higher anticipated effort for reaching an object among older adults. Indeed, in contrast to those of younger participants, the distance judgments of older participants are influenced by the ground surface material they would have to traverse to reach the object, which supports the idea that age-related changes in the perception of egocentric distances are grounded in altered bodily capacities (Sugovic and Witt, 2013; Kandula et al., 2016). According to this view, distances appear longer as it becomes more difficult to traverse them.

This view is corroborated by studies showing intact perception of surface slant and depth cues in old age (Norman et al., 2004; Norman et al., 2009), which are important cues for distance perception. In addition, Norman et al. (2015) showed that the differences in perceived distance between younger and older participants do not generalize to allocentric distances. The perception of egocentric distances between the observer and an object is subject to age-related changes, while the perception of allocentric distances between two external objects is not (see also Philbeck and Witt, 2015).

5.3. Perspective taking and body-related imagery

Older adults seem to have a diminished capacity to perform body-related imagery tasks (F8: *Impaired body-related imagery*; see Fig. 1), such as mental rotation of body parts, or perspective taking. For example, age-specific deficits do arise when people imagine simple movements or rotations of limbs but sometimes do not arise when they imagine the movement of objects (Saimpont et al., 2009; De Simone et al., 2013; Zapparoli et al., 2013; Wallwork et al., 2015). These deficits are evidenced by increased reaction times of older adults in performing spatial body-related transformations (Zapparoli et al., 2013). This difference usually increases when the amount of rotation increases and when the movements become more difficult to simulate (Saimpont et al., 2009). There are also reports showing a loss of correspondence between the timing of actual movements and mentally simulated movements in older adults, frequently involving arm or hand movements (Skoura et al., 2005; Personnier et al., 2010; Zapparoli et al., 2013). This indicates deficits simulating those movements correctly.

Older adults seem to be particularly impaired in performing motor imagery tasks from a first-person perspective (Mulder et al., 2007), and a growing body of evidence reveals age-related deficits in mental perspective-taking (Inagaki et al., 2002; Joanisse et al., 2008; Borella et al., 2014; Meneghetti et al., 2015; Montefinese et al., 2015; Zancada-Menendez et al., 2016). For example, Inagaki et al. (2002) used two variants of Piaget's Three Mountain Task, where subjects either mentally rotate objects or imagine changes in their perspective to solve the task. Here, older adults showed greater impairments in the latter condition, while the ability to mentally rotate objects seemed relatively preserved (see Devlin and Wilson, 2010 for a similar point, but see De Beni et al., 2007; Watanabe and Takamatsu, 2014).

Reduced tactile and proprioceptive input during real movements (cf., F1: *Elevated sensory thresholds*; see Fig. 1) could underlie the specific deficit in body-related mental rotation abilities in older adults. It may simply cause deficits to vividly simulate movements in mental rotation tasks that one has difficulty performing oneself (Mulder et al., 2007; Skoura et al., 2008; Saimpont et al., 2009). In addition, impairments in motor control (cf., F3) and internal modeling (cf., F4) could explain difficulties in simulating motor movements correctly (Saimpont et al., 2009).

Another explanation for the degraded body-related mental rotation and perspective-taking abilities in older adults is their use of visual compensatory strategies that account for degraded sensory and motor representations. This theory is supported by an over-recruitment of visual areas during imagined movements (Zapparoli et al., 2013; Zapparoli et al., 2016), and by decreased BOLD signal changes in the supplementary motor area and precentral gyrus during motor imagery tasks (Wang et al., 2014). The abovementioned time disparity between actual and simulated movements also correlated with activity in occipitoparietal areas, instead of motor areas, in older adults (Zapparoli et al., 2013, but see Malouin et al., 2010).

Impaired inhibition of sensorimotor signals may also contribute to deficits in perspective-taking, as the conflict between current and imagined perspectives results in interfering sensorimotor codes that must be suppressed to perform optimally (May, 2004; Kelly et al., 2007; Avraamides and Kelly, 2010, but see Kessler and Thomson, 2010). For example, impairments in the inhibition of bodily cues seem to explain the differential performance between age groups in tasks where subjects must ignore physical body rotation and point to target objects as if they were in their original position (Joanisse et al., 2008). In addition, older adults may experience deficits in perspective-taking due to vestibular degeneration (see Section 2.2), as recent reports highlight the importance of vestibular input for this task (Gardner et al., 2017).

6. Spatial navigation

Aging is accompanied by impaired spatial perception and decreased spatial navigation abilities, which severely affect daily living (Lester et al., 2017) (F7: *Impaired spatial perception*, L4: *Problems in spatial navigation*; see Fig. 1). Spatial navigation – the ability to find one's way in complex environments – relies on deriving spatial information from multiple sensory cues, such as idiothetic cues that provide information about bodily movements. Idiothetic cues include those derived from motor efference copies, vestibular feedback, and proprioceptive cues, all of which can be used to keep track of one's own position and orientation and have been discussed above with respect to age-related changes (see Sections 2.2, 2.4, 2.6). Following primary sensory processing, these cues are first integrated in brainstem nuclei to yield estimates of angular and linear movement velocity. In primates, self-motion information is further processed in parietal/superior temporal cortices (i.e., areas MST, VIP and 7a). The second type of cues are so-called allothetic or environmental cues that are external to the organism. Allothetic cues mainly comprise stable objects, such as landmarks and extended boundaries, that can be used to determine one's position and orientation relative to the environment. In primates, these cues are predominantly derived from visual perception, but other species also make heavy use of non-visual cues (i.e., auditory, olfactory and tactile stimuli). Finally, optic flow is a special type of allothetic cue as it provides visual self-motion information to the organism, similar to idiothetic cues. For this reason, it is unsurprising that areas MST and VIP are known to be multisensory structures that integrate optic flow and body-based cues to provide an integrated percept of self-motion (Gu et al., 2008). The NFL Framework of Embodied Aging (see Fig. 1) may therefore be a useful framework also to explain age-related impairments in higher-level cognitive functions such as spatial navigation, as will be discussed below.

6.1. Self-motion perception and path integration

Clinical studies have shown that lesions to the vestibular system affect performance on path integration tasks in which participants have to use body-based cues to keep track of their position and orientation in space (Metcalfe and Gresty, 1992; Cohen, 2000; Péruch et al., 2005). As aging is known to severely affect, for example, the integrity of the semicircular canals (cf., N7: *Fewer primary receptors*; see Fig. 1), older adults should be particularly impaired in measuring self-motion.

Consistent with this prediction, older adults commit more errors in perceiving the direction and speed of self-motion and are also impaired in using this information to regulate their walking speed (Ball and Sekuler, 1986; Warren et al., 1989; Berard et al., 2009; Roditi and Crane, 2012; Lalonde-Parsi and Lamontagne, 2015).

Impaired perception of optic flow and body-based motion cues should result in deficits in judging the length of travelled distances and ultimately in reduced spatial orientation. In a virtual environment, Harris and Wolbers (2012) asked their participants to reproduce the distance of a visually presented forward motion (i.e., by covering the same distance twice). They reported a restricted range for responses in older adults, which resulted in an increased tendency to under-reproduce travelled distances (i.e., to stop too early). The same was found when participants were asked to reproduce turns by rotating the viewing perspective, which suggested a general deficit in path integration mechanisms (Harris and Wolbers, 2012). It is important that many studies on spatial navigation in old age employ virtual reality animations in which path integration is based only on visual cues. In such paradigms, participants need to actively simulate their own movements through an environment (i.e., walking) and to overcome the mismatch between body-based and visual cues. As discussed previously (cf., F4, Sections 2.7, 5.3), older adults show difficulties in the mental simulation of movements (Schott and Munzert, 2007; Personnier et al., 2010), which might contribute to the deficit in estimating the length of a travelled distance in virtual reality.

Nevertheless, age-related deficits in path integration were also found when participants were deprived of visual and proprioceptive cues, i.e., when they were passively transported in a wheelchair and asked to return to the starting location from the end of an outbound journey (Allen et al., 2004; Adamo et al., 2012). In addition to changes in primary vestibular processing, such deficits in self-motion perception have also been linked to cortical changes such as neuron loss or reduced GABAergic inhibition in multisensory areas VIP and MT/MST (cf., N1) (Lich and Bremmer, 2014). These changes can increase the level of noise, as discussed before (cf., N3; see Fig. 1), and broaden the directional tuning of motion-sensitive neurons (cf., N2; see Fig. 1), as shown in aged monkeys (Liang et al., 2010). Importantly, however, path integration deficits are strongly attenuated when the outbound path is experienced via active walking (Allen et al., 2004; Adamo et al., 2012), which suggests that motor efference copies and/or proprioceptive feedback can at least partially compensate for the impaired vestibular processing. This would be consistent with the notion that internal models of easy motor movements are preserved with age (cf., F4, Section 2.6). Furthermore, path integration performance under conditions of reduced vision (i.e., greater reliance on proprioceptive and vestibular information) differentiates between healthy and fall-prone older adults, which highlights the important role of multisensory integration deficits (cf., F5, L2; see Fig. 1) for autonomous living (Barrett et al., 2013).

6.2. Cognitive mapping and route learning

Self-motion perception and path integration not only are relevant for maintaining orientation relative to one's immediate surroundings but also support the learning of unfamiliar environments. This process, often termed cognitive mapping, is more difficult for older adults (Iaria et al., 2009); this difficulty has been attributed to changes in hippocampal processing (i.e., reduced synaptic plasticity). However, vestibular deficits and altered processing of bodily cues (cf., N4, F1; see Fig. 1) are also contributing factors. Patients with vestibular lesions show structural changes in brain areas beyond the primary vestibular system, such as the hippocampus (Brandt et al., 2005). Such changes (i) could be driven by the downstream effects of altered vestibular input on the head direction system, which provides a key spatial input to the entorhinal-hippocampal system, and (ii) should lead to general navigational deficits that would also affect navigation based on external cues (i.e., landmarks, optic flow). Patients with vestibular lesions

indeed show deficits in visual navigation tasks (Brandt et al., 2005; Kremmyda et al., 2016). Thus, altered vestibular processing in older adults could contribute to the well-established alterations in hippocampal processing and navigation based on visual cues. Recent work by Previc et al. (2014) provides initial evidence for such a link between impaired vestibular processing and impaired topographical memory in older adults.

A second mechanism by which vestibular changes could impair spatial navigation involves problems (cf. N4; see Fig. 1) with balance and postural control, which makes avoiding obstacles more difficult and increases the risk of falling (cf., N2; see Fig. 1). To counteract such deficits, older adults often employ more conservative adaptation strategies by taking slow, short and multiple steps (Caetano et al., 2016) and by prioritizing walking control over concurrent cognitive tasks (Simieli et al., 2015). As a consequence, a reduced amount of attentional resources may be allocated to keeping track of both idiothetic and allothetic cues, which could result in reduced path integration and cognitive mapping performance. The above-outlined difficulties that older adults face in allocating attentional resources (cf., F6; see Fig. 1) and multitasking (cf., L3; see Fig. 1) could hence also increase the impairments in spatial navigation abilities (cf., L4; see Fig. 1).

A further mechanism contributing to problems with cognitive mapping could be deficits in simulating movements in virtual environments (Schott and Munzert, 2007; Personnier et al., 2010). Yamamoto and colleagues showed that older adults are especially impaired in generating cognitive maps when required to actively explore the layout of an environment in virtual reality (i.e., without bodily movements), which suggests that a general deficit in action simulation (cf., F4; see Fig. 1) may often contribute to age-related navigational deficits (Yamamoto and Degirolamo, 2012).

Importantly, in humans, arguably the most frequent navigation task is not cognitive mapping (representing an environment's layout) but route navigation (repeating or retracing a previously walked route). Route knowledge is considered a form of procedural knowledge, and several studies have demonstrated declines in route learning in older adults (Barrash, 1994; Wilkniss et al., 1997; Moffat et al., 2001; Head and Isom, 2010; Wiener et al., 2012). Successful route navigation requires the recognition of landmarks and places encountered during learning, knowledge about the sequence in which they were encountered, the selection of landmarks that are navigationally relevant (i.e., those at decision points), and the association of specific motor behaviours with these landmarks (e.g., turn right at the bakery). While the ability to freely recall or recognize objects or landmarks seen along a route is comparatively spared in old age (Cushman et al., 2008; Head and Isom, 2010; Zhong and Moffat, 2016), aging has been associated with less accurate binding of motor decisions to landmarks (Head and Isom, 2010; Liu et al., 2011; Wiener et al., 2012; Zhong and Moffat, 2016), which could be related to a more general deficit in stimulus-response binding (Naveh-Benjamin et al., 2007; Naveh-Benjamin et al., 2009). Importantly, stimulus response learning is thought to involve basal ganglia structures such as the caudate nucleus, which is indeed critically involved in route navigation (Hartley et al., 2003; Head and Isom, 2010). Given that the caudate shows age-related volumetric and neurodegenerative changes at similar rates to the hippocampus (Betts et al., 2007; Raz et al., 2015), altered stimulus-response binding in the caudate is likely to contribute to declines in route navigation.

Age-related deficits in embodied perspective taking (cf., F8, Section 5.3; see Fig. 1) are also highly relevant here because retracing a taken route necessarily requires the processing of landmarks and decision points from different viewpoints (Wiener et al., 2012). The association between a stimulus (e.g., church) and a response (e.g., turn left) that was learned during the outbound path has to be adjusted according to the changed perspective during the inbound path. Indeed, tasks involving perspective taking have been shown to predict navigational skills (Kozhevnikov et al., 2006), but direct evidence for a link between age-related perspective taking problems and deficits with route navigation is missing at present.

7. Social embodiment

The following section will address the implications of age-related deficits in embodiment as discussed above (N1-N8, F1-F8; see Fig. 1) for age-related changes in social cognition. Social cognition is an important component of everyday life and a prerequisite for an independent and satisfying lifestyle. Preserving social skills in older adults is therefore an important component to maintain high quality-of-life.

7.1. Inferring and anticipating the actions of others

Impaired internal modeling in older adults (cf. F4; see Fig. 1) seems to have direct consequences for social perception and social interaction. During action observation, internal forward models are used to generate predictions that are compared to the actual sensory input to infer and anticipate actions performed by others (Wolpert et al., 2003; Friston et al., 2011). In this way, the perceiver exploits the sensorimotor system to reduce ambiguities and adapts to changes in the social environment. In older adults, the efficacy of this internal matching process seems to be compromised, particularly for more complex action sequences (see Section 2.7).

For example, the detection and discrimination of biological motion seems to be relatively preserved in older adults, particularly in conditions with natural and highly familiar motion patterns, such as walking (Norman et al., 2004; Pilz et al., 2010). This indicates that older adults also rely on their sensorimotor experience (i.e., internal models) when discriminating biological motion, which may allow them to partly compensate for declines in low-level information processing (e.g., F1: *Elevated sensory thresholds*; see Fig. 1). However, age-related group differences emerge in more complex task conditions requiring, for example, higher spatiotemporal control (see Saimpont et al., 2013 for review).

With respect to inferring the actions of others, Maguinness et al. (2013) showed that compared to younger adults, older adults were less sensitive in judging the perceived weight of a box lifted by a person, which reflects impaired abilities to take over the perspective of the observed person (L5: *Impaired social skills*; see Fig. 1). The impairment diminished, however, when more visual information about the box's weight was made available. Older adults were also less precise in predicting the time-course of actions partly occluded from view, which indicates difficulties in correctly anticipating forthcoming actions. However, their performance benefited from sensorimotor experience with the observed actions (Diersch et al., 2012), which highlights that motor experience (cf., F3; see Fig. 1) shapes the ability to anticipate the actions of others and that internal forward modeling that becomes less efficient with age (cf., F4; see Fig. 1) impacts both action execution and action observation. With respect to the latter, compared to younger adults, older adults may exhibit lower sensitivity (or higher uncertainty) towards others' action trajectories or goals and a greater reliance on visual cues in social interactions as a consequence (see also Section 5.3).

Action observation and action execution result in overlapping activity in sensorimotor cortices in the frontal and parietal regions of the brain (Caspers et al., 2010; Grosbras et al., 2012). Using multi-voxel pattern analysis (MVPA), Carp and colleagues showed that motor as well as perceptual representations during action observation become less distinct with advancing age (Carp et al., 2011a,b). This relates to the concept of neuronal dedifferentiation, which assumes less distinct representations in the aging brain (cf., N1; see Fig. 1). Additionally, Léonard and Tremblay (2007) showed that corticomotor facilitation in relevant muscles is more widespread in older than in younger adults during action observation, imagery, and imitation. Moreover, Nedelko et al. (2010) showed that older adults recruit additional brain regions during action observation and imagery. Similar over-activations, predominantly located in sensory cortices, have been reported in subsequent studies examining age-related differences in neural activity

during motor imagery tasks (Zwergal et al., 2012; Zapparoli et al., 2013). During the prediction of actions that are partly occluded from view, older adults engage more regions in visual cortices during task performance (Diersch et al., 2013), and increasing age has been linked to activity shifts from posterior to more anterior parts in the frontal and superior temporal regions (Diersch et al., 2016). Lower precision in action prediction, as tested behaviourally, was further found to modulate the BOLD response in the caudate within older adults (Diersch et al., 2016). If internal models are indeed optimized over the lifespan and consequently become more generalized as suggested above (Section 2.7) (Moran et al., 2014), fine-grained differences or changes in observed actions, such as those typically employed in the above-mentioned studies, might not be appropriately represented in the aging brain and therefore are no longer reliably detectable.

7.2. Social perception and empathy

There seems to be an age-related positivity effect in the processing of non-social but also social emotions in older adults (F9: *Age-related positivity effect*; see Fig. 1) (Reed et al., 2014), which manifests in different tasks: Older adults prefer to fixate more on positive or neutral emotional stimuli (Allard and Isaacowitz, 2008) and are less distracted by negative emotional stimuli in Stroop tasks than younger adults (Ashley and Swick, 2009). Older adults are also less distracted by visual stimuli printed on negative faces (Ebner and Johnson, 2010), show decreased visually evoked potentials in response to angry faces (Mienaltowski et al., 2011), show attentional biases away from negative faces (Mather and Carstensen, 2003), and respond faster to a visual stimulus when presented behind a neutral face rather than a negative face (Knight et al., 2007). Similar effects are also apparent in memory-recall tests (Charles et al., 2003; Mather and Carstensen, 2003; Denburg et al., 2003; Fernandes et al., 2008). It is worth noting that the specific emotions that can elicit the age-related positivity effect are still debated, sadness or disgust for example do not always elicit the effect (Tsai et al., 2000; Birditt and Fingerman, 2003; Rothermund and Brandtstädter, 2003; Charles and Carstensen, 2008; Ruffman et al., 2008; Stone et al., 2010; Mienaltowski et al., 2011; Kunzmann et al., 2013; Kunzmann and Thomas, 2014).

The reason for the age-related positivity effect is still debated. In older adults, the amygdala is more responsive to positive than to negative stimuli than it is in younger adults (Mather et al., 2004; Leclerc and Kensinger, 2011; Waldinger et al., 2011; Kehoe et al., 2013; Ge et al., 2014). Moreover, specific differences in the processing of negative emotions, particularly anger and regret, could relate to different cognitive control mechanisms (Nashiro et al., 2012) and/or different motivational goals. The former aspect is supported by studies that indicate a causal role of medial prefrontal cortex/anterior cingulate cortex activity – areas that are known for their role in cognitive control – in the occurrence of the positivity effect in older adults (Sakaki et al., 2013). The latter aspect is proposed by the socioemotional selectivity theory (Carstensen, 1992a,b; Carstensen et al., 1999; Reed and Carstensen, 2012). According to this theory, with age, there is a shift in goals related to emotional gratification and emotionally fulfilling situations. Increased activity in the anterior cingulate cortex has been assumed to be the neuronal basis for this process (Brassen et al., 2011; Brassen et al., 2012). However, other studies found no differences in emotion regulation of negative stimuli in older adults (Kunzmann et al., 2005; Mather 2016).

Age-related emotional differences in social perception are not restricted to the observation of static faces; they also occur when recognizing facial expressions from faces that changed their expressions dynamically from neutral to happy or from neutral to angry. Older adults were, for example, faster in recognizing happy than angry facial expressions, whereas this was not the case for younger adults (Di Domenico et al., 2015). The age-related positivity effect also generalizes to situations where emotions are judged based not on facial expressions but on observed body cues, such as point-like-walker movements (Spencer et al., 2016) or body parts in pain (Chen et al., 2014). Observing hands and feet in pain activated the right anterior insula less among older adults than among younger adults. This may relate to the decreased interoceptive awareness of older adults (cf., F1, N4; see Fig. 1), including their reduced sensitivity to pain, which may transfer to the perception of empathic pain.

Facial expression recognition in older adults can be facilitated when faces are accompanied by bodily cues, i.e., when a face is presented not in isolation but as attached to a body. Facilitated emotional face recognition when bodily cues are present also occurs in younger adults, but the effect is significantly stronger in older adults (Noh and Isaacowitz, 2013). Older adults even outperformed younger adults in continuous emotion judgment tasks when dynamic, multimodal social stimuli were provided (videotaped interactions) rather than single faces (Sze et al., 2012), which indicates a strong effect of contextual bodily cues on social perception in older adults. Perhaps contextual body perception can to a certain extent compensate for age-related differences in cortical inhibition (cf., N1; see Fig. 1) and attention (cf., F6; see Fig. 1). The increased reliance on visual cues of older adults as described above (Section 7.1) may also be relevant.

There is also evidence that older adults assign higher pleasantness ratings to slow tactile stroking stimulation than do younger adults (Section 2.3). This may imply that the positivity bias in older adults exists not only for visual body perception, such as the perception of faces and bodies, but also for the tactile perception of others during gentle stroking. In addition, interactions between individual tactile discrimination thresholds and the attitude towards social touch have been suggested (Vieira et al., 2016). More work is needed to investigate these aspects further.

An interesting link also emerges between the above-outlined deficits in older adults in intracortical inhibition (cf., N1; see Fig. 1) and empathy. This link was drawn by a study of Bailey and Henry (2008). They tested younger and older participants in a false belief task where participants were asked to report another person's specific knowledge, which required suppressing their own knowledge. Older participants performed worse than younger participants only when strong inhibitory demands were placed on their own knowledge, for example, when the information in the room that later had to be suppressed was actually shown to them. Difficulties to take over another person's perspective may therefore be linked to a lack of inhibitory control of self-perspective (Bailey and Henry, 2008). This may also be linked to deficits of older adults in mental rotation (cf., F8; see Fig. 1).

It is also worth noting that there are studies that find no selective bias of older adults towards positive emotions (Sullivan and Ruffman, 2004; Rakoczy et al., 2012); rather, they suggest a more general age-related decline in emotion recognition. Additionally, when verbal material is used, older adults are sometimes not impaired in decoding emotions (Happé et al., 1998; Phillips et al., 2002; Keightley et al., 2006), and performance in theory-of-mind stories often remains stable (Phillips et al., 2002; Keightley et al., 2006) or is even improved in older adults (Happé et al., 1998, but see Maylor et al., 2002; Sullivan and Ruffman, 2004; Rakoczy et al., 2012).

7.3. The perception of trust

Judging another person as trustworthy or untrustworthy affects daily decision making and social behaviour, such as when making monetary investments or when lending money or goods to other people. Older adults are reduced in their capabilities to identify non-trustworthy faces (L6: *Increased perception of trust*; see Fig. 1). Castle et al. (2012) showed pictures of trustworthy, neutral, or non-trustworthy faces to younger and older participants. The authors did not find age-related differences in the perception of trustworthiness in trustworthy and neutral faces but found that older adults perceived non-trustworthy faces as significantly more trustworthy than young participants. Older

adults also rated those faces as more approachable than younger adults, which is in line with their positivity bias in social perception as discussed above (cf., F9; see Fig. 1) (see also Kiiski et al., 2016). In addition, older adults rated people as generally more dominant and more competent than young people did (Kiiski et al., 2016), and they tended to rate trustworthy faces as more trustful than young people did even after interactions where those people proved to be non-trustworthy (Suzuki, 2016).

When perceiving non-trustworthy faces, older adults showed less BOLD signal change in the anterior insula than young participants (Castle et al., 2012). No other brain area was sensitive to this contrast. Interoceptive awareness, which is mediated by the anterior insula and is impaired in older adults (see Section 2.3), has been associated with a "gut feeling" that signals emotions and guides decision making (Naqvi et al., 2006; Weierich et al., 2011). Castle et al. (2012) hypothesized that the reduced ability to identify non-trustworthy faces in older adults may relate to their reduced "gut feelings" in social situations, particularly when confronted with non-trustworthy people or risky situations (Bechara et al., 1996). Similarly, in the "maturational dualism" hypothesis, Mendes (2010) reports that with age, the ability of people to use internal states to guide their decisions and behaviour is impaired. The author argues that older people rely more on external rather than body-based cues during decision making and emotion perception, which may shape their tendency to place more trust in non-trustworthy people.

Because the financial consequences of misplaced trust by older adults reach almost 3 billion dollars per year in the United States of America alone (Company, 2011), the development of training paradigms and educational campaigns that target decreased interoceptive sensitivity and help older adults to compensate for this loss seems to be essential to reduce financial losses among older adults in the future.

8. Neurodegenerative diseases

A wide variety of neurodegenerative diseases have complex relations with age-related changes in embodiment. Here, we focus on selected literature that has been published on the relationship between Parkinson's disease/Alzheimer's disease and disease-related impairments in embodied perception and action in order to provide novel inspiration for the development of treatment strategies for neurodegenerative diseases.

People with Parkinson's disease are severely affected in their motor abilities. In addition to suffering from tremor, they are often impaired in movement control even of simple actions. One study compared mental rotation abilities in Parkinson's patients between non-body cues and body cues (faces), and indicated that Parkinson's patients face selective impairments in performing body-related mental imagery (cf., F8; see Fig. 1) (Conson et al., 2014). Patients with Parkinson's disease also show impairments in movement simulation tasks (cf., F4, F8; see Fig. 1). When patients judge the weight of lifted boxes, the real weight and the guessed weight are significantly related, but the slope value of this relationship is lower than it is among age-matched controls (Poliakoff et al., 2010). Parkinson's patients are also impaired in facial emotion recognition and theory-of-mind tasks (Narme et al., 2013).

Motor imagery abilities in Parkinson's disease, however, can be enhanced by external cueing (Heremans et al., 2012). It has therefore been argued that motor imagery may be an efficient way to train Parkinson's patients during rehabilitation (Heremans et al., 2011). Other approaches are to selectively train visual strategies that Parkinson's patients often apply in mental rotation to compensate for their deficits (Poliakoff, 2013), or to use action observation to restore motor control in Parkinson patients (see Caligiore et al., 2017 for review). The latter approach seems promising particularly in light of apparently intact motor resonance in Parkinson's disease (Bek et al., 2017).

In contrast to Parkinson's patients, patients with Alzheimer's disease usually do not have strong motor deficits; their impairments manifest

first at the cognitive level. This may be one reason why patients with Alzheimer's disease often show preserved abilities in many tasks that require embodied processes, such as voluntary motor imitation (Bisio et al., 2012), motor resonance responses during observed movements (Bisio et al., 2012), and musical memory that involves motor areas (Jacobsen et al., 2015). In contrast to Parkinson's patients, there is also no strong evidence that Alzheimer's patients involve more visual strategies during social perspective taking (Ruby et al., 2009). Finally, while deficits in spatial navigation are frequently reported in Alzheimer's patients (Serino et al., 2014), a potential contribution of embodied processes has not been systematically explored.

Whereas processes that involve embodied simulations are hence sometimes preserved in Alzheimer's disease, patients show impairments in body-related processing when cognitive functions are involved, such as age estimation of faces (Moyse et al., 2015). Impairments in the ability to recognize emotional faces have also been described in relation to Alzheimer's disease (Phillips et al., 2010). Therefore, with respect to training social or mental abilities, strategies for Alzheimer's and Parkinson's patients are almost orthogonal, which should be taken into account when developing strategies to increase their quality of life.

9. Conclusions and outlook

The body is an essential part of human experience. Bodily features, action abilities, and bodily signals such as tactile, proprioceptive, vestibular, and visceral sensations have a great impact on our perception of the environment. In recent years, influential embodiment theories have noted that higher cognitive functions are also influenced by bodily factors. In an aging society where the prevalence of neurodegenerative diseases is increasing and older adults play important roles in the economic and political spheres, it is becoming more and more relevant to delineate the cognitive and perceptual changes that are primarily caused by age-related bodily alterations and to develop effective strategies for their preservation, compensation, or at least awareness.

In this review, we introduced the NFL Framework of Embodied Aging (see Fig. 1) to link age-related decreases in embodiment to neuronal mechanisms on the one hand and functional consequences and daily life impairments on the other hand. To sum up, we introduced eight neuronal mechanisms (N1: *decreased intracortical inhibition,* N2: *widening of spatial tuning curves,* N3: *elevated levels of internal noise,* N4: *deteriorated input pathways,* N5: *distal-to-proximal progression of bodily impairments,* N6: *less efficient inter-hemispheric integration,* N7: *fewer primary receptors,* and N8: *reduced neuronal processing speed*) and linked them to nine functional consequences (F1: *elevated sensory thresholds,* F2: *impaired spatial body perception,* F3: *motor, movement, and coordination impairments,* F4: *impaired internal modeling,* F5: *increased multisensory integration,* F6: *decreased attentional capacities,* F7: *impaired spatial perception,* F8: *impaired body-related imagery,* and F9: *age-related positivity effect*) and highlighted the relevance for everyday life (L1: *decreased perception of hunger and thirst,* L2: *increased risk of falls,* L3: *reduced capacity for multitasking,* L4: *problems in spatial navigation,* L5: *impaired social skills,* and L6: *increased perception of trust*).

However, does the increasing experience with one's own body, with certain types of actions, or with emotions that naturally accompany increasing age also lead to *higher* (instead of lower) embodiment in older adults? Based on the literature reviewed above, the critical point seems to be the efficient utilization of one's own sensorimotor percepts, which often seems to be compromised in older adults. For example, less efficient forward modeling in older adults has been shown to result in difficulty perceiving the social environment under certain circumstances. Moreover, sensorimotor functioning is subject to age-related decline, which limits its potential to positively impact cognitive and social functioning. In line with this, the ability to anticipate the actions of others benefits from sensorimotor experience in both older and younger adults, but older adults rarely reach the same level of performance as their younger counterparts. Instead, the reliance on additional

sources of information, such as visual cues, seems to increase with age. On the other hand, as outlined above (see Section 7.2), older adults can sometimes compensate for their deficits in social perception by taking into account more contextual information and by making use of their prior knowledge, which can lead to superior performance in some situations. More studies should be conducted to test 'experience'- or 'wisdom'-related hypotheses in light of bodily changes and cognitive performance differences in tolder adults.

Together, the NFL Framework of Embodied Aging as introduced here offers three categories and multiple interactions between their elements, which demonstrate a strong interlinkage between bodily factors and cognitive functions in old age that influence many aspects of everyday life. The NFL Framework of Embodied Aging provides a first step towards the development of more comprehensive and detailed frameworks on the interactions between changes in bodily perception and action on the one hand and age-related changes in cognitive functions on the other hand. This and similar approaches have the potential to elucidate conditions and influencing factors for the development of neurodegenerative diseases. Some of those are associated with distorted processing of bodily stimuli and embodiment deficits (e.g., Parkinson's disease), whereas others are to a lesser extent (e.g., Alzheimer's disease). Particularly for pathological aging, an embodiment perspective can generate new directions for research and enhance our understanding of age-related cognitive and behavioural deficits.

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References

Adamo, D.E., Briceño, E.M., Sindone, J.A., Alexander, N.B., Moffat, S.D., 2012. Age differences in virtual environment and real world path integration. Front. Aging. Neurosci. 4, 26.

Allard, E.S., Isaacowitz, D.M., 2008. Are preferences in emotional processing affected by distraction? Examining the age-related positivity effect in visual fixation within a dual-task paradigm. Neuropsychol. Dev. Cogn. B. Aging. Neuropsychol. Cogn. 15, 725–743.

Allen, G.L., Kirasic, K.C., Rashotte, M.A., Haun, D.B., 2004. Aging and path integration skill: kinesthetic and vestibular contributions to wayfinding. Percept. Psychophys. 66, 170–179.

Anguera, J.A., Gazzaley, A., 2012. Dissociation of motor and sensory inhibition processes in normal aging. Clin. Neurophysiol. 123, 730–740.

Ashley, V., Swick, D., 2009. Consequences of emotional stimuli: age differences on pure and mixed blocks of the emotional Stroop. Behav. Brain. Funct. 5, 14.

Avraamides, M.N., Kelly, J.W., 2010. Multiple systems of spatial memory: evidence from described scenes. J. Exp. Psychol. Hum. Learn. 36, 635.

Bailey, P.E., Henry, J.D., 2008. Growing less empathic with age: disinhibition of the self-perspective. J. Gerontol. B Psychol. Sci. Soc. Sci. 63, 219–P226.

Ball, K., Sekuler, R., 1986. Improving visual perception in older observers. J. Gerontol. 41, 176–182.

Baloh, R.W., Jacobson, K.M., Socotch, T.M., 1993. The effect of aging on visual-vestibuloocular responses. Exp. Brain Res. 95, 509–516.

Baloh, R.W., Enrietto, J., Jacobson, K.M., Lin, A., 2001. Age-related changes in vestibular function: a longitudinal study. Ann. N. Y. Acad. Sci. 942, 210–219.

Baltich, J., von Tscharner, V., Nigg, B.M., 2015. Degradation of postural control with aging. Proc. Inst. Mech. Eng. H 229, 638–644.

Bangert, A.S., Reuter-Lorenz, P.A., Walsh, C.M., Schachter, A.B., Seidler, R.D., 2010. Bimanual coordination and aging: neurobehavioral implications. Neuropsychologia 48, 1165–1170.

Barrash, J., 1994. Age-related decline in route learning ability. Dev. Neuropsychol. 10, 189–201.

Barrett, M.M., Doheny, E.P., Setti, A., Maguinness, C., Foran, T.G., Kenny, R.A., Newell, F.N., 2013. Reduced vision selectively impairs spatial updating in fall-prone older adults. Multisens. Res. 26, 69–94.

Bechara, A., Tranel, D., Damasio, H., Damasio, A.R., 1996. Failure to respond autonomically to anticipated future outcomes following damage to prefrontal cortex. Cereb. Cortex 6, 215–225.

Bek, J., Gowen, E., Vogt, S., Crawford, T., Poliakoff, E., 2017. Action observation produces motor resonance in Parkinson's disease. J. Neurophysiol. http://dx.doi.org/10.1111/jnp.12133. (Epub ahead of print).

Benwell, C.S.Y., Thut, G., Grant, A., Harvey, M., 2014. A rightward shift in the visuospatial attention vector with healthy aging. Front. Aging. Neurosci. 6, 113.

Berard, J.R., Fung, J., McFadyen, B.J., Lamontagne, A., 2009. Aging affects the ability to use optic flow in the control of heading during locomotion. Exp. Brain Res. 194, 183–190.

Bergouignan, L., Nyberg, L., Ehrsson, H.H., 2014. Out-of-body-induced hippocampal amnesia. Proc. Natl. Acad. Sci. U. S. A. 111, 4421–4426.

Bernard, J.A., Seidler, R.D., 2012. Evidence for motor cortex dedifferentiation in older adults. Neurobiol. Aging 33, 1890–1899.

Bernard, J.A., Seidler, R.D., 2014. Moving forward: age effects on the cerebellum underlie cognitive and motor declines. Neurosci. Biobehav. Rev. 42, 193–207.

Betts, L.R., Sekuler, A.B., Bennett, P.J., 2007. The effects of aging on orientation discrimination. Vision Res. 47, 1769–1780.

Betts, M.J., Acosta-Cabronero, J., Cardenas-Blanco, A., Nestor, P.J., Duzel, E., 2016. High-resolution characterisation of the aging brain using simultaneous quantitative susceptibility mapping (QSM) and R2* measurements at 7T. Neuroimage 138, 43–63.

Bian, Z., Andersen, G.J., 2013. Aging and the perception of egocentric distance. Psychol. Aging 28, 813–825.

Birditt, K.S., Fingerman, K.L., 2003. Age and gender differences in adults' descriptions of emotional reactions to interpersonal problems. J. Gerontol. B. Psychol. Sci. Soc. Sci. 58, 237–P245.

Bisio, A., Casteran, M., Ballay, Y., Manckoundia, P., Mourey, F., Pozzo, T., 2012. Motor resonance mechanisms are preserved in Alzheimer's disease patients. Neuroscience 222, 58–68.

Björnsdotter, M., Morrison, I., Olausson, H., 2010. Feeling good: on the role of C fiber mediated touch in interoception. Exp. Brain Res. 207, 149–155.

Bloesch, E.K., Davoli, C.C., Abrams, R.A., 2013. Age-related changes in attentional reference frames for peripersonal space. Psychol. Sci. 24, 557–561.

Bock, O., 2005. Components of sensorimotor adaptation in young and elderly subjects. Exp. Brain Res. 160, 259–263.

Boisgontier, M.P., Nougier, V., 2013. Ageing of internal models: from a continuous to an intermittent proprioceptive control of movement. Age (Dordr.) 35, 1339–1355.

Boisgontier, M.P., Swinnen, S.P., 2015. Age-related deficit in a bimanual joint position matching task is amplitude dependent. Front. Aging. Neurosci. 7, 162.

Boisgontier, M.P., Beets, I.A., Duysens, J., Nieuwboer, A., Krampe, R.T., Swinnen, S.P., 2013. Age-related differences in attentional cost associated with postural dual tasks: increased recruitment of generic cognitive resources in older adults. Neurosci. Biobehav. Rev. 37, 1824–1837.

Boisgontier, M.P., Van Halewyck, F., Corporaal, S.H., Willacker, L., Van Den Bergh, V., Beets, I.A., Levin, O., Swinnen, S.P., 2014. Vision of the active limb impairs bimanual motor tracking in young and older adults. Front. Aging. Neurosci. 6, 320.

Bolton, D.A., Staines, W.R., 2012. Age-related loss in attention-based modulation of tactile stimuli at early stages of somatosensory processing. Neuropsychologia 50, 1502–1513.

Borella, E., Meneghetti, C., Ronconi, L., De Beni, R., 2014. Spatial abilities across the adult life span. Dev. Psychol. 50, 384–392.

Botwinick, J., 1978. Aging and Behavior: A Comprehensive Integration of Research Findings. Springer Pub. Co., New York.

Bowden, J.L., McNulty, P.A., 2013a. Age-related changes in cutaneous sensation in the healthy human hand. Age (Dordr.) 35, 1077–1089.

Bowden, J.L., McNulty, P.A., 2013b. The magnitude and rate of reduction in strength: dexterity and sensation in the human hand vary with ageing. Exp. Gerontol. 48, 756–765.

Brandt, T., Schautzer, F., Hamilton, D.A., Bruning, R., Markowitsch, H.J., Kalla, R., Darlington, C., Smith, P., Strupp, M., 2005. Vestibular loss causes hippocampal atrophy and impaired spatial memory in humans. Brain 128, 2732–2741.

Brassen, S., Gamer, M., Büchel, C., 2011. Anterior cingulate activation is related to a positivity bias and emotional stability in successful aging. Biol. Psychiatry 70, 131–137.

Brassen, S., Gamer, M., Peters, J., Gluth, S., Büchel, C., 2012. Don't look back in anger! Responsiveness to missed chances in successful and nonsuccessful aging. Science 336, 612–614.

Brauer, S.G., Woollacott, M., Shumway-Cook, A., 2001. The interacting effects of cognitive demand and recovery of postural stability in balance-impaired elderly persons. J. Gerontol. A Biol. Sci. Med. Sci. 56, M489–M496.

Brodoehl, S., Klingner, C., Stieglitz, K., Witte, O.W., 2013. Age-related changes in the somatosensory processing of tactile stimulation–an fMRI study. Behav. Brain. Res. 238, 259–264.

Brodoehl, S., Klingner, C., Stieglitz, K., Witte, O.W., 2015. The impact of eye closure on somatosensory perception in the elderly. Behav. Brain. Res. 293, 89–95.

Brooks, J.L., Della Sala, S., Logie, R.H., 2011. Tactile rod bisection in the absence of visuo-spatial processing in children, mid-age and older adults. Neuropsychologia 49, 3392–3398.

Brosel, S., Laub, C., Averdam, A., Bender, A., Elstner, M., 2016. Molecular aging of the mammalian vestibular system. Ageing Res. Rev. 26, 72–80.

Brown, L.N., Sainsbury, R.S., 2000. Hemispheric equivalence and age-related differences in judgments of simultaneity to somatosensory stimuli. J. Clin. Exp. Neuropsychol. 22, 587–598.

Brown, L.A., Shumway-Cook, A., Woollacott, M.H., 1999. Attentional demands and postural recovery: the effects of aging. J. Gerontol. A Biol. Sci. Med. Sci. 54, M165–M171.

Buccino, G., Binkofski, F., Fink, G.R., Fadiga, L., Fogassi, L., Gallese, V., Seitz, R.J., Zilles, K., Rizzolatti, G., Freund, H.J., 2001. Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. Eur. J. Neurosci. 13, 400–404.

Buch, E.R., Young, S., Contreras-Vidal, J.L., 2003. Visuomotor adaptation in normal aging. Learn. Mem. 10, 55–63.

Buckner, R.L., 2004. Memory and executive function in aging and AD: multiple factors

that cause decline and reserve factors that compensate. Neuron 44, 195–208.

Bugnariu, N., Fung, J., 2007. Aging and selective sensorimotor strategies in the regulation of upright balance. J. Neuroeng. Rehabil. 4, 19.

Caçola, P., Martinez, A., Ray, C., 2013. The ability to modulate peripersonal and extra-personal reach space via tool use among the elderly. Arch. Gerontol. Geriatr. 56, 383–388.

Cabeza, R., 2002. Hemispheric asymmetry reduction in older adults: the HAROLD model. Psychol. Aging 17, 85–100.

Caetano, M.J., Lord, S.R., Schoene, D., Pelicioni, P.H., Sturnieks, D.L., Menant, J.C., 2016. Age-related changes in gait adaptability in response to unpredictable obstacles and stepping targets. Gait Posture 46, 35–41.

Caligiore, D., Mustile, M., Spalletta, G., Baldassarre, G., 2017. Action observation and motor imagery for rehabilitation in Parkinson's disease: a systematic review and an integrative hypothesis. Neurosci. Biobehav. Rev. 72, 210–222.

Camicioli, R., Panzer, V.P., Kaye, J., 1997. Balance in the healthy elderly: posturography and clinical assessment. Arch. Neurol. 54, 976–981.

Carp, J., Park, J., Hebrank, A., Park, D.C., Polk, T.A., 2011a. Age-related neural ded-ifferentiation in the motor system. PLoS One 6, e29411.

Carp, J., Park, J., Polk, T.A., Park, D.C., 2011b. Age differences in neural distinctiveness revealed by multi-voxel pattern analysis. Neuroimage 56, 736–743.

Carstensen, L.L., Isaacowitz, D.M., Charles, S.T., 1999. Taking time seriously: a theory of socioemotional selectivity. Am. Psychol. 54, 165–181.

Carstensen, L.L., 1992a. Motivation for social contact across the life span: a theory of socioemotional selectivity. Nebr. Symp. Motiv. 40, 209–254.

Carstensen, L.L., 1992b. Social and emotional patterns in adulthood: support for socio-emotional selectivity theory. Psychol. Aging. 7, 331–338.

Caspers, S., Zilles, K., Laird, A.R., Eickhoff, S.B., 2010. ALE meta-analysis of action ob-servation and imitation in the human brain. Neuroimage 50, 1148–1167.

Castle, E., Eisenberger, N.I., Seeman, T.E., Moons, W.G., Boggero, I.A., Grinblatt, M.S., Taylor, S.E., 2012. Neural and behavioral bases of age differences in perceptions of trust. Proc. Natl. Acad. Sci. U. S. A. 109, 20848–20852.

Cenciarini, M., Loughlin, P.J., Sparto, P.J., Redfern, M.S., 2010. Stiffness and damping in postural control increase with age. IEEE. Trans. Biomed. Eng. 57, 267–275.

Cespón, J., Galdo-Álvarez, S., Diaz, F., 2013. Age-related changes in ERP correlates of visuospatial and motor processes. Psychophysiology 50, 743–757.

Charles, S.T., Carstensen, L.L., 2008. Unpleasant situations elicit different emotional re-sponses in younger and older adults. Psychol. Aging 23, 495–504.

Charles, S.T., Mather, M., Carstensen, L.L., 2003. Aging and emotional memory: the forgettable nature of negative images for older adults. J. Exp. Psychol. Gen. 132, 310–324.

Chau, A.T., Menant, J.C., Hubner, P.P., Lord, S.R., Migliaccio, A.A., 2015. Prevalence of vestibular disorder in older people who experience dizziness. Front. Neurol. 6, 268.

Chen, Y.C., Chen, C.C., Decety, J., Cheng, Y., 2014. Aging is associated with changes in the neural circuits underlying empathy. Neurobiol. Aging 35, 827–836.

Cheng, C.H., Lin, Y.Y., 2013. Aging-related decline in somatosensory inhibition of the human cerebral cortex. Exp. Brain Res. 226, 145–152.

Cheng, C.H., Chan, P.Y., Baillet, S., Lin, Y.Y., 2015. Age-Related reduced somatosensory gating is associated with altered alpha frequency desynchronization. Neural Plast. 2015, 302878.

Cholewiak, R.W., Collins, A.A., 2003. Vibrotactile localization on the arm: effects of place, space, and age. Percept. Psychophys. 65, 1058–1077.

Cohen, H.S., 2000. Vestibular disorders and impaired path integration along a linear trajectory. J. Vestib. Res. 10, 7–15.

Cole, K.J., Rotella, D.L., 2002. Old age impairs the use of arbitrary visual cues for pre-dictive control of fingertip forces during grasp. Exp. Brain Res. 143, 35–41.

Cole, K.J., 1991. Grasp force control in older adults. J. Mot. Behav. 23, 251–258.

Company, M.L.I., 2011. In: Company, M.L.I. (Ed.), The MetLife Study of Elder Financial Abuse: Crimes of Occasion, Desperation, and Predation Against America's Elders. MetLife Mature Marker Institute, New York.

Conson, M., Trojano, L., Vitale, C., Mazzarella, E., Allocca, R., Barone, P., Grossi, D., Santangelo, G., 2014. The role of embodied simulation in mental transformation of whole-body images: evidence from Parkinson's disease. Hum. Mov. Sci. 33, 343–353.

Costello, M.C., Bloesch, E.K., Davoli, C.C., Panting, N.D., Abrams, R.A., Brockmole, J.R., 2015. Spatial representations in older adults are not modified by action: evidence from tool use. Psychol. Aging 30, 656–668.

Couth, S., Gowen, E., Poliakoff, E., 2016. Investigating the spatial and temporal mod-ulation of visuotactile interactions in older adults. Exp. Brain Res. 234, 1233–1248.

Craig, C.E., Goble, D.J., Doumas, M., 2016. Proprioceptive acuity predicts muscle co-contraction of the tibialis anterior and gastrocnemius medialis in older adults' dy-namic postural control. Neuroscience 322, 251–261.

Craig, A.D., 2002. How do you feel? Interoception: the sense of the physiological con-dition of the body. Nat. Rev. Neurosci. 3, 655–666.

Critchley, H.D., Mathias, C.J., Dolan, R.J., 2001. Neural activity in the human brain re-lating to uncertainty and arousal during anticipation. Neuron 29, 537–545.

Cushman, L.A., Stein, K., Duffy, C.J., 2008. Detecting navigational deficits in cognitive aging and Alzheimer disease using virtual reality. Neurology 71, 888–895.

Damásio, A., 1994. Descartes' error: emotion. Reason and the Human Brain. Avon Books, New York.

David-Jürgens, M., Churs, L., Berkefeld, T., Zepka, R.F., Dinse, H.R., 2008. Differential effects of aging on fore- and hindpaw maps of rat somatosensory cortex. PLoS One 3, e3399.

Davidson, T., Tremblay, F., 2013. Age and hemispheric differences in transcallosal in-hibition between motor cortices: an ispsilateral silent period study. BMC Neurosci. 14, 62.

De Beni, R., Pazzaglia, F., Gardini, S., 2007. The generation and maintenance of visual mental images: evidence from image type and aging. Brain Cogn. 63, 271–278.

De Simone, L., Tomasino, B., Marusic, N., Eleopra, R., Rumiati, R.I., 2013. The effects of healthy aging on mental imagery as revealed by egocentric and allocentric mental spatial transformations. Acta Psychol. (Amst.) 143, 146–156.

Denburg, N.L., Buchanan, T.W., Tranel, D., Adolphs, R., 2003. Evidence for preserved emotional memory in normal older persons. Emotion 3, 239–253.

Deshpande, N., Patla, A.E., 2007. Visual-vestibular interaction during goal directed lo-comotion: effects of aging and blurring vision. Exp. Brain Res. 176, 43–53.

Desrosiers, J., Hébert, R., Bravo, G., Rochette, A., 1999. Age-related changes in upper extremity performance of elderly people: a longitudinal study. Exp. Gerontol. 34, 393–405.

Devlin, A.L., Wilson, P.H., 2010. Adult age differences in the ability to mentally transform object and body stimuli. Neuropsychol. Dev. Cogn. B Aging Neuropsychol. Cogn. 17, 709–729.

Di Domenico, A., Palumbo, R., Mammarella, N., Fairfield, B., 2015. Aging and emotional expressions: is there a positivity bias during dynamic emotion recognition? Front. Psychol. 6, 1130.

Diaconescu, A.O., Hasher, L., McIntosh, A.R., 2013. Visual dominance and multisensory integration changes with age. Neuroimage 65, 152–1166.

Diederich, A., Colonius, H., Schomburg, A., 2008. Assessing age-related multisensory enhancement with the time-window-of-integration model. Neuropsychologia 46, 2556–2562.

Diermayr, G., McIsaac, T.L., Gordon, A.M., 2011. Finger force coordination underlying object manipulation in the elderly – a mini-review. Gerontology 57, 217–227.

Diersch, N., Cross, E.S., Stadler, W., Schütz-Bosbach, S., Rieger, M., 2012. Representing others' actions: the role of expertise in the aging mind. Psychol. Res. 76, 525–541.

Diersch, N., Mueller, K., Cross, E.S., Stadler, W., Rieger, M., Schutz-Bosbach, S., 2013. Action prediction in younger versus older adults: neural correlates of motor famil-iarity. PLoS One 8, e64195.

Diersch, N., Jones, A.L., Cross, E.S., 2016. The timing and precision of action prediction in the aging brain. Hum. Brain Mapp. 37, 54–66.

Ebner, N.C., Johnson, M.K., 2010. Age-group differences in interference from young and older emotional faces. Cogn. Emot. 24, 1095–1116.

Ekvall Hansson, E., Magnusson, M., 2013. Vestibular asymmetry predicts falls among elderly patients with multi-sensory dizziness. BMC Geriatr. 13, 77.

Engle, J.R., Tinling, S., Recanzone, G.H., 2013. Age-related hearing loss in rhesus mon-keys is correlated with cochlear histopathologies. PLoS One 8, e55092.

Fernandes, M., Ross, M., Wiegand, M., Schryer, E., 2008. Are the memories of older adults positively biased? Psychol. Aging 23, 297–306.

Ferrell, W.R., Crighton, A., Sturrock, R.D., 1992. Age-dependent changes in position sense in human proximal interphalangeal joints. Neuroreport 3, 259–261.

Fife, T.D., Baloh, R.W., 1993. Disequilibrium of unknown cause in older people. Ann. Neurol. 34, 694–702.

Fling, B.W., Walsh, C.M., Bangert, A.S., Reuter-Lorenz, P.A., Welsh, R.C., Seidler, R.D., 2011. Differential callosal contributions to bimanual control in young and older adults. J. Cogn. Neurosci. 23, 2171–2185.

Friston, K., Mattout, J., Kilner, J., 2011. Action understanding and active inference. Biol. Cybern. 104, 137–160.

Fujiyama, H., Hinder, M.R., Schmidt, M.W., Tandonnet, C., Garry, M.I., Summers, J.J., 2012. Age-related differences in corticomotor excitability and inhibitory processes during a visuomotor RT task. J. Cogn. Neurosci. 24, 1253–1263.

Gaál, Z.A., Csuhaj, R., Molnár, M., 2007. Age-dependent changes of auditory evoked potentials–effect of task difficulty. Biol. Psychol. 76, 196–208.

Gabbard, C., Cordova, A., 2013. Association between imagined and actual functional reach (FR): a comparison of young and older adults. Arch. Gerontol. Geriatr. 56, 487–491.

Gabbard, C., Caçola, P., Cordova, A., 2011. Is there an advanced aging effect on the ability to mentally represent action? Arch. Gerontol. Geriatr. 53, 206–209.

Gagliese, L., 2009. Pain and aging: the emergence of a new subfield of pain research. J. Pain 10, 343–353.

Gallagher, S., 2005. How the Body Shapes the Mind. Clarendon Press, Oxford.

Gardner, M.R., Stent, C., Mohr, C., Golding, J.F., 2017. Embodied perspective-taking indicated by selective disruption from aberrant self motion. Psychol. Res. 81, 480–489.

Ge, R., Fu, Y., Wang, D., Yao, L., Long, Z., 2014. Age-related alterations of brain network underlying the retrieval of emotional autobiographical memories: an fMRI study using independent component analysis. Front. Hum. Neurosci. 8, 629.

Gescheider, G.A., Edwards, R.R., Lackner, E.A., Bolanowski, S.J., Verrillo, R.T., 1996. The effects of aging on information-processing channels in the sense of touch: III: Differential sensitivity to changes in stimulus intensity. Somatosens. Mot. Res. 13, 73–80.

Goble, A.K., Collins, A.A., Cholewiak, R.W., 1996. Vibrotactile threshold in young and old observers: the effects of spatial summation and the presence of a rigid surround. J. Acoust. Soc. Am. 99, 2256–2269.

Goble, D.J., Coxon, J.P., Wenderoth, N., Van Impe, A., Swinnen, S.P., 2009. Proprioceptive sensibility in the elderly: degeneration, functional consequences and plastic-adaptive processes. Neurosci. Biobehav. Rev. 33, 271–278.

Goble, D.J., Coxon, J.P., Van Impe, A., De Vos, J., Wenderoth, N., Swinnen, S.P., 2010. The neural control of bimanual movements in the elderly brain regions exhibiting age-related increases in activity, frequency-induced neural modulation, and task-specific compensatory recruitment. Hum. Brain Mapp. 31, 1281–1295.

Goble, D.J., Coxon, J.P., Van Impe, A., Geurts, M., Doumas, M., Wenderoth, N., Swinnen, S.P., 2011. Brain activity during ankle proprioceptive stimulation predicts balance performance in young and older adults. J. Neurosci. 31, 16344–16352.

Goble, D.J., Mousigian, M.A., Brown, S.H., 2012. Compromised encoding of proprio-ceptively determined joint angles in older adults: the role of working memory and attentional load. Exp. Brain Res. 216, 35–40.

Godde, B., Berkefeld, T., David-Jürgens, M., Dinse, H.R., 2002. Age-related changes in primary somatosensory cortex of rats: evidence for parallel degenerative and plastic-adaptive processes. Neurosci. Biobehav. Rev. 26, 743–752.

Goggin, N.L., Stelmach, G.E., 1990. Age-related differences in a kinematic analysis of precued movements. Can. J. Aging 9, 371–385.

Gong, N.J., Wong, C.S., Chan, C.C., Leung, L.M., Chu, Y.C., 2014. Aging in deep gray matter and white matter revealed by diffusional kurtosis imaging. Neurobiol. Aging 35, 2203–2216.

Good, C.D., Johnsrude, I.S., Ashburner, J., Henson, R.N., Friston, K.J., Frackowiak, R.S., 2001. A voxel-based morphometric study of ageing in 465 normal adult human brains. Neuroimage 14, 21–36.

Graziano, M.S., Cooke, D.F., 2006. Parieto-frontal interactions, personal space, and defensive behavior. Neuropsychologia 44, 845–859.

Grosbras, M.H., Beaton, S., Eickhoff, S.B., 2012. Brain regions involved in human movement perception: a quantitative voxel-based meta-analysis. Hum. Brain Mapp. 33, 431–454.

Gu, Y., Angelaki, D.E., Deangelis, G.C., 2008. Neural correlates of multisensory cue integration in macaque MSTd. Nat. Neurosci. 11, 1201–1210.

Guerreiro, M.J., Adam, J.J., Van Gerven, P.W., 2014. Aging and response interference across sensory modalities. Psychon. Bull. Rev. 21, 836–842.

Happé, F.G., Winner, E., Brownell, H., 1998. The getting of wisdom: theory of mind in old age. Dev. Psychol. 34, 358–362.

Harris, M.A., Wolbers, T., 2012. Ageing effects on path integration and landmark navigation. Hippocampus 22, 1770–1780.

Hartley, T., Maguire, E.A., Spiers, H.J., Burgess, N., 2003. The well-worn route and the path less traveled: distinct neural bases of route following and wayfinding in humans. Neuron 37, 877–888.

Hay, L., Bard, C., Fleury, M., Teasdale, N., 1996. Availability of visual and proprioceptive afferent messages and postural control in elderly adults. Exp. Brain Res. 108, 129–139.

Head, D., Isom, M., 2010. Age effects on wayfinding and route learning skills. Behav. Brain Res. 209, 49–58.

Heetkamp, J., Hortobágyi, T., Zijdewind, I., 2014. Increased bilateral interactions in middle-aged subjects. Front. Aging Neurosci. 6, 5.

Hegele, M., Heuer, H., 2010. Adaptation to a direction-dependent visuomotor gain in the young and elderly. Psychol. Res. 74, 21–34.

Heise, K.F., Zimerman, M., Hoppe, J., Gerloff, C., Wegscheider, K., Hummel, F.C., 2013. The aging motor system as a model for plastic changes of GABA-mediated intracortical inhibition and their behavioral relevance. J. Neurosci. 33, 9039–9049.

Heremans, E., Feys, P., Nieuwboer, A., Vercruysse, S., Vandenberghe, W., Sharma, N., Helsen, W., 2011. Motor imagery ability in patients with early- and mid-stage Parkinson disease. Neurorehabil. Neural Repair 25, 168–177.

Heremans, E., Nieuwboer, A., Feys, P., Vercruysse, S., Vandenberghe, W., Sharma, N., Helsen, W.F., 2012. External cueing improves motor imagery quality in patients with Parkinson disease. Neurorehabil. Neural Repair 26, 27–35.

Heuninckx, S., Wenderoth, N., Debaere, F., Peeters, R., Swinnen, S.P., 2005. Neural basis of aging: the penetration of cognition into action control. J. Neurosci. 25, 6787–6796.

Holmes, N.P., Spence, C., 2004. The body schema and multisensory representation (s) of peripersonal space. Cogn. Process. 5 (2), 94–105.

Holtzer, R., Friedman, R., Lipton, R.B., Katz, M., Xue, X., Verghese, J., 2007. The relationship between specific cognitive functions and falls in aging. Neuropsychology 21, 540–548.

Hoshiyama, M., Kakigi, R., Tamura, Y., 2004. Temporal discrimination threshold on various parts of the body. Muscle Nerve 29, 243–247.

Hsieh, L.C., Lin, H.C., Lee, G.S., 2014. Aging of vestibular function evaluated using correlational vestibular autorotation test. Clin. Interv. Aging 9, 1463–1469.

Hugenschmidt, C.E., Mozolic, J.L., Laurienti, P.J., 2009. Suppression of multisensory integration by modality-specific attention in aging. Neuroreport 20, 349–353.

Humes, L.E., Busey, T.A., Craig, J.C., Kewley-Port, D., 2009. The effects of age on sensory thresholds and temporal gap detection in hearing vision, and touch. Atten. Percept. Psychophys. 71, 860–871.

Huxhold, O., Li, S.C., Schmiedek, F., Lindenberger, U., 2006. Dual-tasking postural control: aging and the effects of cognitive demand in conjunction with focus of attention. Brain Res. Bull. 69, 294–305.

Iaria, G., Palermo, L., Committeri, G., Barton, J.J., 2009. Age differences in the formation and use of cognitive maps. Behav. Brain Res. 196, 187–191.

Igarashi, M., Reschke, M.F., Henley, C., MacDonald, S., Kohl, R., Mizukoshi, K., 1993. Salivary total protein and experimental Coriolis sickness. Acta Otolaryngol. Suppl. 504, 38–40.

Inagaki, H., Meguro, K., Shimada, M., Ishizaki, J., Okuzumi, H., Yamadori, A., 2002. Discrepancy between mental rotation and perspective-taking abilities in normal aging assessed by Piaget's three-mountain task. J. Clin. Exp. Neuropsychol. 24, 18–25.

Jacobsen, J.H., Stelzer, J., Fritz, T.H., Chételat, G., La Joie, R., Turner, R., 2015. Why musical memory can be preserved in advanced Alzheimer's disease. Brain 138, 2438–2450.

Jahn, K., Naessl, A., Schneider, E., Strupp, M., Brandt, T., Dieterich, M., 2003. Inverse U-shaped curve for age dependency of torsional eye movement responses to galvanic vestibular stimulation. Brain 126, 1579–1589.

Jewell, G., McCourt, M.E., 2000. Pseudoneglect: a review and meta-analysis of performance factors in line bisection tasks. Neuropsychologia 38, 93–110.

Joanisse, M., Gagnon, S., Kreller, J., Charbonneau, M.C., 2008. Age-related differences in viewer-rotation tasks: is mental manipulation the key factor? J. Gerontol. B Psychol. Sci. Soc. Sci. 63, P193–P200.

Juarez-Salinas, D.L., Engle, J.R., Navarro, X.O., Recanzone, G.H., 2010. Hierarchical and serial processing in the spatial auditory cortical pathway is degraded by natural aging. J. Neurosci. 30, 14795–14804.

Kalisch, T., Ragert, P., Schwenkreis, P., Dinse, H.R., Tegenthoff, M., 2009. Impaired tactile acuity in old age is accompanied by enlarged hand representations in somatosensory cortex. Cereb. Cortex 19, 1530–1538.

Kandula, M., Hofman, D., Dijkerman, H.C., 2016. Location estimation of approaching objects is modulated by the observer's inherent and momentary action capabilities. Exp. Brain Res. 234, 2315–2322.

Karanjia, P.N., Ferguson, J.H., 1983. Passive joint position sense after total hip replacement surgery. Ann. Neurol. 13, 654–657.

Kehoe, E.G., Toomey, J.M., Balsters, J.H., Bokde, A.L., 2013. Healthy aging is associated with increased neural processing of positive valence but attenuated processing of emotional arousal: an fMRI study. Neurobiol. Aging 34, 809–821.

Keightley, M.L., Winocur, G., Burianova, H., Hongwanishkul, D., Grady, C.L., 2006. Age effects on social cognition: faces tell a different story. Psychol. Aging 21, 558–572.

Kelly, J.W., Avraamides, M.N., Loomis, J.M., 2007. Sensorimotor alignment effects in the learning environment and in novel environments. J. Exp. Psychol. Learn. Mem. Cogn. 33, 1092.

Kessler, K., Thomson, L.A., 2010. The embodied nature of spatial perspective taking: embodied transformation versus sensorimotor interference. Cognition 114, 72–88.

Khalsa, S.S., Rudrauf, D., Tranel, D., 2009. Interoceptive awareness declines with age. Psychophysiology 46, 1130–1136.

Kiiski, H.S., Cullen, B., Clavin, S.L., Newell, F.N., 2016. Perceptual and social attributes underlining age-related preferences for faces. Front. Hum. Neurosci. 10, 437.

King, B.R., Fogel, S.M., Albouy, G., Doyon, J., 2013. Neural correlates of the age-related changes in motor sequence learning and motor adaptation in older adults. Front. Hum. Neurosci. 7, 142.

Knight, M., Seymour, T.L., Gaunt, J.T., Baker, C., Nesmith, K., Mather, M., 2007. Aging and goal-directed emotional attention: distraction reverses emotional biases. Emotion 7, 705–714.

Kobayashi, H., Hayashi, Y., Higashino, K., Saito, A., Kunihiro, T., Kanzaki, J., Goto, F., 2002. Dynamic and static subjective visual vertical with aging. Auris Nasus Larynx 29, 325–328.

Kozhevnikov, M., Motes, M.A., Rasch, B., Blajenkova, O., 2006. Perspective-taking vs. mental rotation transformations and how they predict spatial navigation performance. Appl. Cogn. Psychol. 20, 397–417.

Kremmyda, O., Hüfner, K., Flanagin, V.L., Hamilton, D.A., Linn, J., Strupp, M., Jahn, K., Brandt, T., 2016. Beyond dizziness: virtual navigation, spatial anxiety and hippocampal volume in bilateral vestibulopathy. Front. Hum. Neurosci. 10, 139.

Kristinsdottir, E.K., Fransson, P.A., Magnusson, M., 2001. Changes in postural control in healthy elderly subjects are related to vibration sensation, vision and vestibular asymmetry. Acta Otolaryngol. 121, 700–706.

Kuehn, E., Mueller, K., Lohmann, G., Schuetz-Bosbach, S., 2016. Interoceptive awareness changes the posterior insula functional connectivity profile. Brain Struct. Funct. 221, 1555–1571.

Kunzmann, U., Thomas, S., 2014. Multidirectional age differences in anger and sadness. Psychol. Aging 29, 16–27.

Kunzmann, U., Kupperbusch, C.S., Levenson, R.W., 2005. Behavioral inhibition and amplification during emotional arousal: a comparison of two age groups. Psychol. Aging 20, 144–158.

Kunzmann, U., Richter, D., Schmukle, S.C., 2013. Stability and change in affective experience across the adult life span: analyses with a national sample from Germany. Emotion 13, 1086–1095.

Léonard, G., Tremblay, F., 2007. Corticomotor facilitation associated with observation, imagery and imitation of hand actions: a comparative study in young and old adults. Exp. Brain Res. 177, 167–175.

Löken, L.S., Wessberg, J., Morrison, I., McGlone, F., Olausson, H., 2009. Coding of pleasant touch by unmyelinated afferents in humans. Nat. Neurosci. 12, 547–548.

Lagier, E., Delvaux, M., Vellas, B., Fioramonti, J., Bueno, L., Albarede, J.L., Frexinos, J., 1999. Influence of age on rectal tone and sensitivity to distension in healthy subjects. Neurogastroenterol. Motil. 11, 101–107.

Lalonde-Parsi, M.J., Lamontagne, A., 2015. Perception of self-motion and regulation of walking speed in young-old adults. Motor Control 19, 191–206.

Larsson, J., Miller, M., Hansson, E.E., 2016. Vestibular asymmetry increases double support time variability in a counter-balanced study on elderly fallers. Gait Posture 45, 31–34.

Lasch, H., Castell, D.O., Castell, J.A., 1997. Evidence for diminished visceral pain with aging: studies using graded intraesophageal balloon distension. Am. J. Physiol. 272, G1–3.

Leclerc, C.M., Kensinger, E.A., 2011. Neural processing of emotional pictures and words: a comparison of young and older adults. Dev. Neuropsychol. 36, 519–538.

Lehmann, K., Steinecke, A., Bolz, J., 2012. GABA through the ages: regulation of cortical function and plasticity by inhibitory interneurons. Neural Plast. 2012, 892784.

Lenz, M., Tegenthoff, M., Kohlhaas, K., Stude, P., Höffken, O., Gatica Tossi, M.A., Kalisch, T., Kowalewski, R., Dinse, H.R., 2012. Increased excitability of somatosensory cortex in aged humans is associated with impaired tactile acuity. J. Neurosci. 32, 1811–1816.

Lester, A.W., Moffat, S.D., Wiener, J.M., Barnes, C.A., Wolbers, T., 2017. The aging navigational system. Neuron 95, 1019–1035.

Levin, O., Fujiyama, H., Boisgontier, M.P., Swinnen, S.P., Summers, J.J., 2014. Aging and motor inhibition: a converging perspective provided by brain stimulation and imaging approaches. Neurosci. Biobehav. Rev. 43, 100–117.

Li, K.Z., Lindenberger, U., Freund, A.M., Baltes, P.B., 2001. Walking while memorizing: age-related differences in compensatory behavior. Psychol. Sci. 12, 230–237.

Liang, Z., Yang, Y., Li, G., Zhang, J., Wang, Y., Zhou, Y., Leventhal, A.G., 2010. Aging affects the direction selectivity of MT cells in rhesus monkeys. Neurobiol. Aging 31, 863–873.

Lich, M., Bremmer, F., 2014. Self-motion perception in the elderly. Front. Hum. Neurosci. 8, 681.

Liston, M.B., Bamiou, D.E., Martin, F., Hopper, A., Koohi, N., Luxon, L., Pavlou, M., 2014. Peripheral vestibular dysfunction is prevalent in older adults experiencing multiple non-syncopal falls versus age-matched non-fallers: a pilot study. Age Ageing 43, 38–43.

Liu, I., Levy, R.M., Barton, J.J., Iaria, G., 2011. Age and gender differences in various topographical orientation strategies. Brain Res. 1410, 112–119.

Loeffler, J., Raab, M., Cañal-Bruland, R., 2016. A lifespan perspective on embodied cognition. Front. Psychol. 7 (845), 1–6. http://dx.doi.org/10.3389/fpsyg.2016.00845.

Logan, J.M., Sanders, A.L., Snyder, A.Z., Morris, J.C., Buckner, R.L., 2002. Under-recruitment and nonselective recruitment: dissociable neural mechanisms associated with aging. Neuron 33, 827–840.

Lord, S.R., Rogers, M.W., Howland, A., Fitzpatrick, R., 1999. Lateral stability, sensorimotor function and falls in older people. J. Am. Geriatr. Soc. 47, 1077–1081.

Madhavan, S., Shields, R.K., 2005. Influence of age on dynamic position sense: evidence using a sequential movement task. Exp. Brain Res. 164, 18–28.

Maguinness, C., Setti, A., Roudaia, E., Kenny, R.A., 2013. Does that look heavy to you? Perceived weight judgment in lifting actions in younger and older adults. Front. Hum. Neurosci. 7, 795.

Mahoney, J.R., Holtzer, R., Verghese, J., 2014a. Visual-somatosensory integration and balance: evidence for psychophysical integrative differences in aging. Multisens. Res. 27, 17–142.

Mahoney, K., Cayea, D., Li, Q.K., Gelber, A.C., 2014b. A handy clue: palmar fasciitis and polyarthritis syndrome. Am. J. Med. 127, 116–118.

Maki, B.E., Zecevic, A., Bateni, H., Kirshenbaum, N., McIlroy, W.E., 2001. Cognitive demands of executing postural reactions: does aging impede attention switching? Neuroreport 12, 3583–3587.

Malouin, F., Richards, C.L., Durand, A., 2010. Normal aging and motor imagery vividness: implications for mental practice training in rehabilitation. Arch. Phys. Med. Rehabil. 91, 1122–1127.

Marchand, W.R., Lee, J.N., Suchy, Y., Garn, C., Johnson, S., Wood, N., Chelune, G., 2011. Age-related changes of the functional architecture of the cortico-basal ganglia circuitry during motor task execution. Neuroimage 55, 194–203.

Martins, E.S.D.C., Bastos, V.H., de Oliveira Sanchez, M., Nunes, M.K., Orsini, M., Ribeiro, P., Velasques, B., Teixeira, S.S., 2016. Effects of vestibular rehabilitation in the elderly: a systematic review. Aging Clin. Exp. Res. 28, 599–606.

Mather, M., Carstensen, L.L., 2003. Aging and attentional biases for emotional faces. Psychol. Sci. 14, 409–415.

Mather, M., Canli, T., English, T., Whitfield, S., Wais, P., Ochsner, K., Gabrieli, J.D., Carstensen, L.L., 2004. Amygdala responses to emotionally valenced stimuli in older and younger adults. Psychol. Sci. 15, 259–263.

Mather, M., 2016. The affective neuroscience of aging. Annu. Rev. Psychol. 67, 213–238.

Matheson, A.J., Darlington, C.L., Smith, P.F., 1999. Dizziness in the elderly and age-related degeneration of the vestibular system. N. Z. J. Psychol. 28, 10–16.

May, M., 2004. Imaginal perspective switches in remembered environments: transformation versus interference accounts. Cogn. Psychol. 48, 163–206.

Maylor, E.A., Moulson, J.M., Muncer, A.M., Taylor, L.A., 2002. Does performance on theory of mind tasks decline in old age? Br. J. Psychol. 93, 465–485.

McGregor, K.M., Zlatar, Z., Kleim, E., Sudhyadhom, A., Bauer, A., Phan, S., Seeds, L., Ford, A., Manini, T.M., White, K.D., Kleim, J., Crosson, B., 2011. Physical activity and neural correlates of aging: a combined TMS/fMRI study. Behav. Brain Res. 222, 158–168.

McGregor, K.M., Nocera, J.R., Sudhyadhom, A., Patten, C., Manini, T.M., Kleim, J.A., Crosson, B., Butler, A.J., 2013. Effects of aerobic fitness on aging-related changes of interhemispheric inhibition and motor performance. Front. Aging Neurosci. 5, 66.

Mendes, W.B., 2010. Weakened links between mind and body in older age: the case for maturational dualism in the experience of emotion. Emot. Rev. 2, 240–244.

Meneghetti, C., Pazzaglia, F., De Beni, R., 2015. Mental representations derived from spatial descriptions: the influence of orientation specificity and visuospatial abilities. Psychol. Res. 79, 289–307.

Metcalfe, T., Gresty, M., 1992. Self-controlled reorienting movements in response to rotational displacements in normal subjects and patients with labyrinthine disease. Ann. N. Y. Acad. Sci. 656, 695–698.

Mienaltowski, A., Corballis, P.M., Blanchard-Fields, F., Parks, N.A., Hilimire, M.R., 2011. Anger management: age differences in emotional modulation of visual processing. Psychol. Aging 26, 224–231.

Moffat, S.D., Zonderman, A.B., Resnick, S.M., 2001. Age differences in spatial memory in a virtual environment navigation task. Neurobiol. Aging 22, 787–796.

Montefinese, M., Sulpizio, V., Galati, G., Committeri, G., 2015. Age-related effects on spatial memory across viewpoint changes relative to different reference frames. Psychol. Res. 79, 687–697.

Moran, R.J., Symmonds, M., Dolan, R.J., Friston, K.J., 2014. The brain ages optimally to model its environment: evidence from sensory learning over the adult lifespan. PLoS. Comput. Biol. 10, e1003422.

Morrison, I., Löken, L.S., Minde, J., Wessberg, J., Perini, I., Nennesmo, I., Olausson, H., 2011. Reduced C-afferent fibre density affects perceived pleasantness and empathy for touch. Brain 134, 1116–1126.

Moyse, E., Bastin, C., Salmon, E., Bredart, S., 2015. Impairment of age estimation from faces in Alzheimer's disease. J. Alzheimers Dis. 45, 631–638.

Mozolic, J.L., Hugenschmidt, C.E., Peiffer, A.M., Laurienti, P.J., 2012. Multisensory integration and aging. In: Murray, M.M., Wallace, M.T. (Eds.), The Neural Bases of Multisensory Processes. CRC Press, Boca Raton (FL), pp. 381–392.

Mulder, T., Hochstenbach, J.B., van Heuvelen, M.J., den Otter, A.R., 2007. Motor imagery: the relation between age and imagery capacity. Hum. Mov. Sci. 26, 203–211.

Mulligan, C., Moreau, K., Brandolini, M., Livingstone, B., Beaufrère, B., Boirie, Y., 2002. Alterations of sensory perceptions in healthy elderly subjects during fasting and re-feeding. A pilot study. Gerontology 48, 39–43.

Murray, K.J., Hill, K., Phillips, B., Waterston, J., 2005. A pilot study of falls risk and vestibular dysfunction in older fallers presenting to hospital emergency departments. Disabil. Rehabil. 27, 499–506.

Naccarato, M., Calautti, C., Jones, P.S., Day, D.J., Carpenter, T.A., Baron, J.C., 2006. Does healthy aging affect the hemispheric activation balance during paced index-to-thumb opposition task? An fMRI study. Neuroimage 32, 1250–1256.

Naqvi, N., Shiv, B., Bechara, A., 2006. The role of emotion in decision making: a cognitive neuroscience perspective. Curr. Dir. Psychol. Sci. 15, 260–264.

Narme, P., Mouras, H., Roussel, M., Duru, C., Krystkowiak, P., Godefroy, O., 2013. Emotional and cognitive social processes are impaired in Parkinson's disease and are related to behavioral disorders. Neuropsychology 27, 182–192.

Nashiro, K., Sakaki, M., Mather, M., 2012. Age differences in brain activity during emotion processing: reflections of age-related decline or increased emotion regulation? Gerontology 58, 156–163.

Naveh-Benjamin, M., Cowan, N., Kilb, A., Chen, Z., 2007. Age-related differences in immediate serial recall: dissociating chunk formation and capacity. Mem. Cognit. 35, 724–737.

Naveh-Benjamin, M., Shing, Y.L., Kilb, A., Werkle-Bergner, M., Lindenberger, U., Li, S.C., 2009. Adult age differences in memory for name-face associations: the effects of intentional and incidental learning. Memory 17, 220–232.

Nedelko, V., Hassa, T., Hamzei, F., Weiller, C., Binkofski, F., Schoenfeld, M.A., Tüscher, O., Dettmers, C., 2010. Age-independent activation in areas of the mirror neuron system during action observation and action imagery. A fMRI study. Restor. Neurol. Neurosci. 28, 737–747.

Noh, S.R., Isaacowitz, D.M., 2013. Emotional faces in context: age differences in recognition accuracy and scanning patterns. Emotion 13, 238–249.

Norman, J.F., Payton, S.M., Long, J.R., Hawkes, L.M., 2004. Aging and the perception of biological motion. Psychol. Aging 19, 219–225.

Norman, J.F., Crabtree, C.E., Bartholomew, A.N., Ferrell, E.L., 2009. Aging and the perception of slant from optical texture motion parallax, and binocular disparity. Atten. Percept. Psychophys. 71, 116–130.

Norman, J.F., Adkins, O.C., Pedersen, L.E., Reyes, C.M., Wulff, R.A., Tungate, A., 2015. The visual perception of exocentric distance in outdoor settings. Vision Res. 117, 100–104.

Nowak, D.A., Hermsdörfer, J., Glasauer, S., Philipp, J., Meyer, L., Mai, N., 2001. The effects of digital anaesthesia on predictive grip force adjustments during vertical movements of a grasped object. Eur. J. Neurosci. 14, 756–762.

Olausson, H., Lamarre, Y., Backlund, H., Morin, C., Wallin, B.G., Starck, G., Ekholm, S., Strigo, I., Worsley, K., Vallbo, A.B., Bushnell, M.C., 2002. Unmyelinated tactile afferents signal touch and project to insular cortex. Nat. Neurosci. 5, 900–904.

Owings, T.M., Grabiner, M.D., 2004. Step width variability, but not step length variability or step time variability, discriminates gait of healthy young and older adults during treadmill locomotion. J. Biomech. 37, 935–938.

Péruch, P., Borel, L., Magnan, J., Lacour, M., 2005. Direction and distance deficits in path integration after unilateral vestibular loss depend on task complexity. Brain Res. Cogn. Brain Res. 25, 862–872.

Peinemann, A., Lehner, C., Conrad, B., Siebner, H.R., 2001. Age-related decrease in paired-pulse intracortical inhibition in the human primary motor cortex. Neurosci. Lett. 313, 33–36.

Pellicciari, M.C., Miniussi, C., Rossini, P.M., De Gennaro, L., 2009. Increased cortical plasticity in the elderly: changes in the somatosensory cortex after paired associative stimulation. Neuroscience 163, 266–276.

Perry, S.D., 2006. Evaluation of age-related plantar-surface insensitivity and onset age of advanced insensitivity in older adults using vibratory and touch sensation tests. Neurosci. Lett. 392, 62–67.

Personnier, P., Kubicki, A., Laroche, D., Papaxanthis, C., 2010. Temporal features of imagined locomotion in normal aging. Neurosci. Lett. 476, 146–149.

Pfeifer, R., Bongard, J., Grand, S., 2007. How the Body Shapes the Way We Think: a New View of Intelligence. MIT Press, Cambridge (MA).

Philbeck, J.W., Witt, J.K., 2015. Action-specific influences on perception and post-perceptual processes: present controversies and future directions. Psychol. Bull. 141, 1120–1144.

Phillips, L.H., MacLean, R.D., Allen, R., 2002. Age and the understanding of emotions: neuropsychological and sociocognitive perspectives. J. Gerontol. B Psychol. Sci. Soc. Sci. 57, 526–P530.

Phillips, L.H., Scott, C., Henry, J.D., Mowat, D., Bell, J.S., 2010. Emotion perception in Alzheimer's disease and mood disorder in old age. Psychol. Aging 25, 38–47.

Pickard, C.M., Sullivan, P.E., Allison, G.T., Singer, K.P., 2003. Is there a difference in hip joint position sense between young and older groups? J. Gerontol. A Biol. Sci. Med. Sci. 58, 631–635.

Pilz, K.S., Bennett, P.J., Sekuler, A.B., 2010. Effects of aging on biological motion discrimination. Vision Res. 50, 211–219.

Pleger, B., Wilimzig, C., Nicolas, V., Kalisch, T., Ragert, P., Tegenthoff, M., Dinse, H.R., 2016. A complementary role of intracortical inhibition in age-related tactile degradation and its remodelling in humans. Sci. Rep. 6, 27388.

Poe, B.H., Linville, C., Brunso-Bechtold, J., 2001. Age-related decline of presumptive

inhibitory synapses in the sensorimotor cortex as revealed by the physical disector. J. Comp. Neurol. 439, 65–72.

Poliakoff, E., Ashworth, S., Lowe, C., Spence, C., 2006a. Vision and touch in ageing: crossmodal selective attention and visuotactile spatial interactions. Neuropsychologia 44, 507–517.

Poliakoff, E., Shore, D.I., Lowe, C., Spence, C., 2006b. Visuotactile temporal order judgments in ageing. Neurosci. Lett. 396, 207–211.

Poliakoff, E., Galpin, A.J., Dick, J.P., Tipper, S.P., 2010. Does Parkinson's disease affect judgement about another person's action? Exp. Brain Res. 204, 327–331.

Poliakoff, E., 2013. Representation of action in Parkinson's disease: imagining, observing, and naming actions. J. Neuropsychol. 7, 241–254.

Pothula, V.B., Chew, F., Lesser, T.H., Sharma, A.K., 2004. Falls and vestibular impairment. Clin. Otolaryngol. Allied Sci. 29, 179–182.

Potter, L.M., Grealy, M.A., 2006. Aging and inhibitory errors on a motor shift of set task. Exp. Brain Res. 171, 56–66.

Previc, F.H., Krueger, W.W., Ross, R.A., Roman, M.A., Siegel, G., 2014. The relationship between vestibular function and topographical memory in older adults. Front. Integr. Neurosci. 8, 46.

Pyykkö, I., Jäntti, P., Aalto, H., 1990. Postural control in elderly subjects. Age Ageing 19, 215–221.

Rakoczy, H., Harder-Kasten, A., Sturm, L., 2012. The decline of theory of mind in old age is (partly) mediated by developmental changes in domain-general abilities. Br. J. Psychol. 103, 58–72.

Ramos, V.F., Esquenazi, A., Villegas, M.A., Wu, T., Hallett, M., 2016. Temporal discrimination threshold with healthy aging. Neurobiol. Aging 43, 174–179.

Ranganathan, V.K., Siemionow, V., Sahgal, V., Yue, G.H., 2001. Effects of aging on hand function. J. Am. Geriatr. Soc. 49, 1478–1484.

Rauch, S.D., Velazquez-Villaseñor, L., Dimitri, P.S., Merchant, S.N., 2001. Decreasing hair cell counts in aging humans. Ann. N. Y. Acad. Sci. 942, 220–227.

Rayner, C.K., MacIntosh, C.G., Chapman, I.M., Morley, J.E., Horowitz, M., 2000. Effects of age on proximal gastric motor and sensory function. Scand. J. Gastroenterol. 35, 1041–1047.

Raz, N., Daugherty, A.M., Bender, A.R., Dahle, C.L., Land, S., 2015. Volume of the hippocampal subfields in healthy adults: differential associations with age and a pro-inflammatory genetic variant. Brain Struct. Funct. 220, 2663–2674.

Redfern, M.S., Jennings, J.R., Martin, C., Furman, J.M., 2001. Attention influences sensory integration for postural control in older adults. Gait Posture 14, 211–216.

Reed, A.E., Carstensen, L.L., 2012. The theory behind the age-related positivity effect. Front. Psychol. 3, 339.

Reed, A.E., Chan, L., Mikels, J.A., 2014. Meta-analysis of the age-related positivity effect: age differences in preferences for positive over negative information. Psychol. Aging 29, 1–15.

Reimann, M., Feye, W., Malter, A.J., Ackerman, J.M., Castaño, R., Garg, N., Kreuzbauer, R., Labroo, A.A., Lee, A.Y., Morrin, M., Nenkov, G.Y., Nielsen, J.H., Perez, M., Pol, G., Rosa, J.A., Yoon, C., Zhong, C., 2012. Embodiment in judgment and choice. J. Neurosci. Psychol. Econ. 5, 104–123.

Remblay, F., Backman, A., Cuenco, A., Vant, K., Wassef, M.A., 2000. Assessment of spatial acuity at the fingertip with grating (JVP) domes: validity for use in an elderly population. Somatosens. Mot. Res. 17, 61–66.

Reuter, A.E., Voelcker-Rehage, C., Vieluf, S., Winneke, A.H., Godde, B., 2013. A parietal-to-frontal shift in the P300 is associated with compensation of tactile discrimination deficits in late middle-aged adults. Psychophysiology 50, 583–593.

Reuter-Lorenz, P., 2002. New visions of the aging mind and brain. Trends Cogn. Sci. (Regul. Ed.) 6, 394.

Riecker, A., Gröschel, K., Ackermann, H., Steinbrink, C., Witte, O., Kastrup, A., 2006. Functional significance of age-related differences in motor activation patterns. Neuroimage 32, 1345–1354.

Riis, J.L., Chong, H., McGinnnis, S., Tarbi, E., Sun, X., Holcomb, P.J., Rentz, D.M., Daffner, K.R., 2009. Age-related changes in early novelty processing as measured by ERPs. Biol. Psychol. 82, 33–44.

Rizzolatti, G., Craighero, L., 2004. The mirror-neuron system. Annu. Rev. Neurosci. 27, 169–192.

Rizzolatti, G., Fabbri-Destro, M., 2008. The mirror system and its role in social cognition. Curr. Opin. Neurobiol. 18, 179–184.

Rizzolatti, G., Fadiga, L., Fogassi, L., Gallese, V., 1997. The space around us. Science 277, 190–191.

Roditi, R.E., Crane, B.T., 2012. Directional asymmetries and age effects in human self-motion perception. J. Assoc. Res. Otolaryngol. 13, 381–401.

Rossit, S., Harvey, M., 2008. Age-related differences in corrected and inhibited pointing movements. Exp. Brain Res. 185, 1–10.

Rothermund, K., Brandtstädter, J., 2003. Coping with deficits and losses in later life: from compensatory action to accommodation. Psychol. Aging 18, 896–905.

Ruby, P., Collette, F., D'Argembeau, A., Péters, F., Degueldre, C., Balteau, E., Luxen, A., Maquet, P., Salmon, E., 2009. Perspective taking to assess self-personality: what's modified in Alzheimer's disease? Neurobiol. Aging 30, 1637–1651.

Ruffieux, J., Keller, M., Lauber, B., Taube, W., 2015. Changes in standing and walking performance under dual-task conditions across the lifespan. Sports Med. 45, 1739–1758.

Ruffman, T., Henry, J.D., Livingstone, V., Phillips, L.H., 2008. A meta-analytic review of emotion recognition and aging: implications for neuropsychological models of aging. Neurosci. Biobehav. Rev. 32, 863–881.

Saimpont, A., Pozzo, T., Papaxanthis, C., 2009. Aging affects the mental rotation of left and right hands. PLoS One 4, e6714.

Saimpont, A., Malouin, F., Tousignant, B., Jackson, P.L., 2013. Motor imagery and aging. J. Mot. Behav. 45, 21–28.

Sakaki, M., Nga, L., Mather, M., 2013. Amygdala functional connectivity with medial

prefrontal cortex at rest predicts the positivity effect in older adults' memory. J. Cogn. Neurosci. 25, 1206–1224.

Salat, D.H., Buckner, R.L., Snyder, A.Z., Greve, D.N., Desikan, R.S., Busa, E., Morris, J.C., Dale, A.M., Fischl, B., 2004. Thinning of the cerebral cortex in aging. Cereb. Cortex 14, 721–730.

Salthouse, T.A., Somberg, B.L., 1982. Isolating the age deficit in speeded performance. J. Gerontol. 37, 59–63.

Sarlegna, F.R., 2006. Impairment of online control of reaching movements with aging: a double-step study. Neurosci. Lett. 403, 309–314.

Sathian, K., Zangaladze, A., Green, J., Vitek, J.L., DeLong, M.R., 1997. Tactile spatial acuity and roughness discrimination: impairments due to aging and Parkinson's disease. Neurology 49, 168–177.

Schaap, T.S., Gonzales, T.I., Janssen, T.W., Brown, S.H., 2015. Proprioceptively guided reaching movements in 3D space: effects of age, task complexity and handedness. Exp. Brain Res. 233, 631–639.

Schmidt, L., Depper, L., Kerkhoff, G., 2013. Effects of age, sex and arm on the precision of arm position sense-left-arm superiority in healthy right-handers. Front. Hum. Neurosci. 7, 915.

Schmolesky, M.T., Wang, Y., Pu, M., Leventhal, A.G., 2000. Degradation of stimulus selectivity of visual cortical cells in senescent rhesus monkeys. Nat. Neurosci. 3, 384–390.

Schott, N., Munzert, J., 2007. Temporal accuracy of motor imagery in older women. Int. J. Sport Psychol. 38S, 304–320.

Schrager, M.A., Kelly, V.E., Price, R., Ferrucci, L., Shumway-Cook, A., 2008. The effects of age on medio-lateral stability during normal and narrow base walking. Gait Posture 28, 466–471.

Sebastián, M., Ballesteros, S., 2012. Effects of normal aging on event-related potentials and oscillatory brain activity during a haptic repetition priming task. Neuroimage 60, 7–20.

Sebastián, M., Reales, J.M., Ballesteros, S., 2011. Ageing affects event-related potentials and brain oscillations: a behavioral and electrophysiological study using a haptic recognition memory task. Neuropsychologia 49, 3967–3980.

Sebastian, A., Baldermann, C., Feige, B., Katzev, M., Scheller, E., Hellwig, B., Lieb, K., Weiller, C., Tuscher, O., Kloppel, S., 2013. Differential effects of age on sub-components of response inhibition. Neurobiol. Aging 34, 2183–2193.

Sehlstedt, I., Ignell, H., Backlund Wasling, H., Ackerley, R., Olausson, H., Croy, I., 2016. Gentle touch perception across the lifespan. Psychol. Aging. 31, 176–184.

Seidler, R.D., 2006. Differential effects of age on sequence learning and sensorimotor adaptation. Brain Res. Bull. 70, 337–346.

Selen, L.P.J., Shadlen, M.N., Wolpert, D.M., 2012. Deliberation in the motor system: reflex gains track evolving evidence leading to a decision. J. Neurosci. 32, 2276–2286.

Semenov, Y.R., Bigelow, R.T., Xue, Q.L., du Lac, S., Agrawal, Y., 2016. Association between vestibular and cognitive function in U.S. adults: data from the national health and nutrition examination survey. J. Gerontol. A Biol. Sci. Med. Sci. 71, 243–250.

Serino, S., Cipresso, P., Morganti, F., Riva, G., 2014. The role of egocentric and allocentric abilities in Alzheimer's disease: a systematic review. Ageing Res. Rev. 16, 32–44.

Serrador, J.M., Lipsitz, L.A., Gopalakrishnan, G.S., Black, F.O., Wood, S.J., 2009. Loss of otolith function with age is associated with increased postural sway measures. Neurosci. Lett. 465, 10–15.

Shaffer, S.W., Harrison, A.L., 2007. Aging of the somatosensory system: a translational perspective. Phys. Ther. 87, 193–207.

Shumway-Cook, A., Woollacott, M., Kerns, K.A., Baldwin, M., 1997. The effects of two types of cognitive tasks on postural stability in older adults with and without a history of falls. J. Gerontol. A Biol. Sci. Med. Sci. 52, M232–M240.

Simieli, L., Barbieri, F.A., Orcioli-Silva, D., Lirani-Silva, E., Stella, F., Gobbi, L.T., 2015. Obstacle crossing with dual tasking is a danger for individuals with Alzheimer's disease and for healthy older people. J. Alzheimers Dis. 43, 435–441.

Skoura, X., Papaxanthis, C., Vinter, A., Pozzo, T., 2005. Mentally represented motor actions in normal aging: I. Age effects on the temporal features of overt and covert execution of actions. Behav. Brain Res. 165, 229–239.

Skoura, X., Personnier, P., Vinter, A., Pozzo, T., Papaxanthis, C., 2008. Decline in motor prediction in elderly subjects: right versus left arm differences in mentally simulated motor actions. Cortex 44, 1271–1278.

Smith, G.A., Brewer, N., 1995. Slowness and age: speed-accuracy mechanisms. Psychol. Aging 10, 238–247.

Solesio-Jofre, E., Serbruyns, L., Woolley, D.G., Mantini, D., Beets, I.A., Swinnen, S.P., 2014. Aging effects on the resting state motor network and interlimb coordination. Hum. Brain Mapp. 35, 3945–3961.

Spencer, J.M., Sekuler, A.B., Bennett, P.J., Giese, M.A., Pilz, K.S., 2016. Effects of aging on identifying emotions conveyed by point-light walkers. Psychol. Aging 31, 126–138.

Spengler, F., Godde, B., Dinse, H.R., 1995. Effects of ageing on topographic organization of somatosensory cortex. Neuroreport 6, 469–473.

Springer, S., Giladi, N., Peretz, C., Yogev, G., Simon, E.S., Hausdorff, J.M., 2006. Dual-tasking effects on gait variability: the role of aging, falls, and executive function. Mov. Disord. 21, 950–957.

Stevens, J.C., Choo, K.K., 1996. Spatial acuity of the body surface over the life span. Somatosens. Mot. Res. 13, 153–166.

Stevens, J.C., Alvarez-Reeves, M., Dipietro, L., Mack, G.W., Green, B.G., 2003. Decline of tactile acuity in aging: a study of body site, blood flow, and lifetime habits of smoking and physical activity. Somatosens. Mot. Res. 20, 271–279.

Stone, A.A., Schwartz, J.E., Broderick, J.E., Deaton, A., 2010. A snapshot of the age distribution of psychological well-being in the United States. Proc. Natl. Acad. Sci. U. S. A. 107, 9985–9990.

Strömmer, J.M., Tarkka, I.M., Astikainen, P., 2014. Somatosensory mismatch response in young and elderly adults. Front. Aging Neurosci. 6, 293.

Sugovic, M., Witt, J.K., 2013. An older view on distance perception: older adults perceive

walkable extents as farther. Exp. Brain Res. 226, 383–391.

Sullivan, S., Ruffman, T., 2004. Social understanding: how does it fare with advancing years? Br. J. Psychol. 95, 1–18.

Sun, D.Q., Zuniga, M.G., Davalos-Bichara, M., Carey, J.P., Agrawal, Y., 2014. Evaluation of a bedside test of utricular function – the bucket test – in older individuals. Acta Otolaryngol. 134, 382–389.

Suzuki, A., 2016. Persistent reliance on facial appearance among older adults when judging someone's trustworthiness. J. Gerontol. Ser. B. http://dx.doi.org/10.1093/geronb/gbw034. gbw034, Published: 30 March 2016.

Sze, J.A., Goodkind, M.S., Gyurak, A., Levenson, R.W., 2012. Aging and emotion recognition: not just a losing matter. Psychol. Aging 27, 940–950.

Takio, F., Koivisto, M., Tuominen, T., Laukka, S.J., Hämäläinen, H., 2013. Visual rightward spatial bias varies as a function of age. Laterality 18, 44–67.

Talelli, P., Waddingham, W., Ewas, A., Rothwell, J.C., Ward, N.S., 2008. The effect of age on task-related modulation of interhemispheric balance. Exp. Brain Res. 186, 59–66.

Tang, Y., Lopez, I., Baloh, R.W., 2001. Age-related change of the neuronal number in the human medial vestibular nucleus: a stereological investigation. J. Vestib. Res. 11, 357–363.

Teasdale, N., Bard, C., LaRue, J., Fleury, M., 1993. On the cognitive penetrability of posture control. Exp. Aging Res. 19, 1–13.

Toledo, D.R., Barela, J.A., Manzano, G.M., Kohn, A.F., 2016a. Age-related differences in EEG beta activity during an assessment of ankle proprioception. Neurosci. Lett. 622, 1–5.

Toledo, D.R., Manzano, G.M., Barela, J.A., Kohn, A.F., 2016b. Cortical correlates of response time slowing in older adults: ERP and ERD/ERS analyses during passive ankle movement. Clin. Neurophysiol. 127, 655–663.

Tremblay, F., Mireault, A.C., Dessureault, L., Manning, H., Sveistrup, H., 2005. Postural stabilization from fingertip contact II. Relationships between age, tactile sensibility and magnitude of contact forces. Exp. Brain Res. 164, 155–164.

Trewartha, K.M., Endo, A., Li, K.Z., Penhune, V.B., 2009. Examining prepotent response suppression in aging: a kinematic analysis. Psychol. Aging 24, 450–461.

Tsai, J.L., Levenson, R.W., Carstensen, L.L., 2000. Autonomic, subjective, and expressive responses to emotional films in older and younger Chinese Americans and European Americans. Psychol. Aging 15, 684–693.

Valeriani, M., Ranghi, F., Giaquinto, S., 2003. The effects of aging on selective attention to touch: a reduced inhibitory control in elderly subjects? Int. J. Psychophysiol. 49, 75–87.

Vallesi, A., Stuss, D.T., 2010. Excessive sub-threshold motor preparation for non-target stimuli in normal aging. Neuroimage 50, 1251–1257.

Vallesi, A., McIntosh, A.R., Kovacevic, N., Chan, S.C., Stuss, D.T., 2010. Age effects on the asymmetry of the motor system: evidence from cortical oscillatory activity. Biol. Psychol. 85, 213–218.

Vallet, G.T., 2015. Embodied cognition of aging. Front. Psychol. 6, 463.

van der Hoort, B., Guterstam, A., Ehrsson, H.H., 2011. Being barbie: the size of one's own body determines the perceived size of the world. PLoS One 6, e20195.

Van Doren, C.L., Gescheider, G.A., Verrillo, R.T., 1990. Vibrotactile temporal gap detection as a function of age. J. Acoust. Soc. Am. 87, 2201–2206.

Vaupel, J.W., 2010. Biodemography of human ageing. Nature 464, 536–542.

Verghese, J., Buschke, H., Viola, L., Katz, M., Hall, C., Kuslansky, G., Lipton, R., 2002. Validity of divided attention tasks in predicting falls in older individuals: a preliminary study. J. Am. Geriatr. Soc. 50, 1572–1576.

Verschueren, S.M., Brumagne, S., Swinnen, S.P., Cordo, P.J., 2002. The effect of aging on dynamic position sense at the ankle. Behav. Brain Res. 136, 593–603.

Vieira, A.I., Nogueira, D., de Azevedo Reis, E., da Lapa Rosado, M., Vania Nunes, M., Castro-Caldas, A., 2016. Hand tactile discrimination, social touch and frailty criteria in elderly people: a cross sectional observational study. Arch. Gerontol. Geriatr. 66, 73–81.

Waldinger, R.J., Kensinger, E.A., Schulz, M.S., 2011. Neural activity, neural connectivity, and the processing of emotionally valenced information in older adults: links with life satisfaction. Cogn. Affect. Behav. Neurosci. 11, 426–436.

Wallwork, S.B., Butler, D.S., Wilson, D.J., Moseley, G.L., 2015. Are people who do yoga any better at a motor imagery task than those who do not? Br. J. Sports Med. 49, 123–127.

Walther, L.E., Westhofen, M., 2007. Presbyvertigo-aging of otoconia and vestibular sensory cells. J. Vestib. Res. 17, 89–92.

Wang, L., Sutter, C., Müsseler, J., Dangel, R.J., Disselhorst-Klug, C., 2012. Perceiving one's own limb movements with conflicting sensory feedback: the role of mode of movement control and age. Front. Psychol. 3, 289.

Wang, L., Qiu, M., Liu, C., Yan, R., Yang, J., Zhang, J., Zhang, Y., Sang, L., Zheng, X., 2014. Age-specific activation of cerebral areas in motor imagery–a fMRI study. Neuroradiology 56, 339–348.

Ward, N.S., Frackowiak, R.S., 2003. Age-related changes in the neural correlates of motor performance. Brain 126, 873–888.

Ward, N.S., Swayne, O.B.C., Newton, J.M., 2008. Age-dependent changes in the neural correlates of force modulation: an fMRI study. Neurobiol. Aging 29, 1434–1446.

Warren Jr., W.H., Blackwell, A.W., Morris, M.W., 1989. Age differences in perceiving the direction of self-motion from optical flow. J. Gerontol. 44, 147–P153.

Watanabe, M., Takamatsu, M., 2014. Spatial perspective taking is robust in later life. Int. J. Aging Hum. Dev. 78, 277–297.

Weierich, M.R., Kensinger, E.A., Munnell, A.H., Sass, S.A., Dickerson, B.C., Wright, C.I., Barrett, L.F., 2011. Older and wiser? An affective science perspective on age-related challenges in financial decision making. Soc. Cogn. Affect. Neurosci. 6, 195–206.

Wiener, J.M., Kmecova, H., de Condappa, O., 2012. Route repetition and route retracing: effects of cognitive aging. Front. Aging Neurosci. 4, 7.

Wilkniss, S.M., Jones, M.G., Korol, D.L., Gold, P.E., Manning, C.A., 1997. Age-related differences in an ecologically based study of route learning. Psychol. Aging 12, 372–375.

Wolpert, D.M., Flanagan, J.R., 2001. Motor prediction. Curr. Biol. 11, R729–732.

Wolpert, D.M., Kawato, M., 1998. Multiple paired forward and inverse models for motor control. Neural Netw. 11, 1317–1329.

Wolpert, D.M., Doya, K., Kawato, M., 2003. A unifying computational framework for motor control and social interaction. Philos. Trans. R. Soc. Lond. B Biol. Sci. 358, 593–602.

Wolpert, D.M., Diedrichsen, J., Flanagan, J.R., 2011. Principles of sensorimotor learning. Nat. Rev. Neurosci. 12, 739–751.

Wu, T., Hallett, M., 2005. The influence of normal human ageing on automatic movements. J. Physiol. 562, 605–615.

Yamamoto, N., Degirolamo, G.J., 2012. Differential effects of aging on spatial learning through exploratory navigation and map reading. Front. Aging. Neurosci. 4, 14.

Yeh, T.T., Cluff, T., Balasubramaniam, R., 2014. Visual reliance for balance control in older adults persists when visual information is disrupted by artificial feedback delays. PLoS One 9, e91554.

Yeh, T.T., Cinelli, M.E., Lyons, J.L., Lee, T.D., 2015. Age-related changes in postural control to the demands of a precision task. Hum. Mov. Sci. 44, 134–142.

Young, J., Inouye, S.K., 2007. Delirium in older people. BMJ 334, 842–846.

Zancada-Menendez, C., Sampedro-Piquero, P., Lopez, L., McNamara, T.P., 2016. Age and gender differences in spatial perspective taking. Aging Clin. Exp. Res. 28, 289–296.

Zapparoli, L., Invernizzi, P., Gandola, M., Verardi, M., Berlingeri, M., Sberna, M., De Santis, A., Zerbi, A., Banfi, G., Bottini, G., Paulesu, E., 2013. Mental images across the adult lifespan: a behavioural and fMRI investigation of motor execution and motor imagery. Exp. Brain Res. 224, 519–540.

Zapparoli, L., Saetta, G., De Santis, C., Gandola, M., Zerbi, A., Banfi, G., Paulesu, E., 2016. When I am (almost) 64: the effect of normal ageing on implicit motor imagery in young elderlies. Behav. Brain Res. 303, 137–151.

Zhang, F., Deshpande, N., 2016. Sensory interactions for head and trunk control in space in young and older adults during normal and narrow-base walking. Motor Control 20, 21–32.

Zhong, J.Y., Moffat, S.D., 2016. Age-related differences in associative learning of landmarks and heading directions in a virtual navigation task. Front. Aging Neurosci. 8.

Zwergal, A., Linn, J., Xiong, G., Brandt, T., Strupp, M., Jahn, K., 2012. Aging of human supraspinal locomotor and postural control in fMRI. Neurobiol. Aging 33, 1073–1084.