Motion perception as a model for perceptual aging

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Research on functional changes across the adult lifespan has been dominated by studies related to cognitive processes. However, it has become evident that a more comprehensive approach to behavioral aging is needed. In particular, our understanding of age-related perceptual changes is limited. Visual motion perception is one of the most studied areas in perceptual aging and therefore, provides an excellent domain on the basis of which we can investigate the complexity of the aging process. We review the existing literature on how aging affects motion perception, including different processing stages, and consider links to cognitive and motor changes. We address the heterogeneity of results and emphasize the role of individual differences. Findings on age-related changes in motion perception ultimately illustrate the complexity of functional dynamics that can contribute to decline as well as stability during healthy aging. We thus propose that motion perception offers a conceptual framework for perceptual aging, encouraging a deliberate consideration of functional limits and resources emerging across the lifespan.

Introduction

Life expectancy in developed countries is steadily rising. In Europe, for example, it has increased by approximately four years over the last decade; in addition, birth rates have been decreasing since the 60s (Eurostat, 2016). As a consequence, the mean age of the population has dramatically increased and will continue to do so. In order to meet the needs of an aging society, but also to appreciate their resources appropriately, research on functional changes across the adult lifespan has become an important topic in many different research areas. However, there are two fundamental biases in aging research that dominate our understanding of functional changes.

First, the primary focus of aging research still lies with specific cognitive functions, such as working memory, attention, inhibition, or processing speed. Research within the last decades has yielded seminal theories about age-related changes that share an emphasis on general functional decline (Baltes, Staudinger, & Lindenberger, 1999; Craik & Byrd, 1982; Salthouse, 1996). Only recently, an awareness for evidence regarding stability, preserved resources, and functional adaptivity during aging has begun to emerge (see Michel, 2017; Monge & Madden, 2016; Park & McDonough, 2013). Second, age-related diseases such as dementia represent the highest source of overall disease burden in the high-income countries (Mathers, Fat, & Boerma, 2008), and therefore, it comes as no surprise that most aging research concentrates on pathological processes. Indeed, the demarcation between healthy aging and disease processes might be not well defined and gradual transitions have been proposed (e.g., Gauthier et al., 2006). However, the majority of older adults are aging without any form of neurodegenerative diseases, e.g., only five to eight percent of people over the age of 65 are suffering from dementia (Prince et al., 2013).

In this review, we will extend prevalent views on age-related functional changes by focusing on perceptual rather than cognitive abilities and by emphasizing changes related to healthy aging rather than concentrating on pathological ones. Investigating healthy aging of perceptual abilities provides an opportunity to shed light on the dynamics of decline, stability, and adaptivity during aging. Perception is often considered to be the most basic function of the human mind because it provides the fundamental interface to our environment (Hoffman, Singh, & Prakash, 2015). At the same time, perception is a highly complex process in which sensory information is interpreted and shaped by elaborate mechanisms. This "making sense of the senses" depends on different interconnected processing stages, spanning from early signal processing in the primary sensory cortices to higher level processing that involves cognitive, motivational, and predictive mechanisms (for a review, see Gilbert & Li, 2013).

Citation: Billino, J., & Pilz, K. S. (2019). Motion perception as a model for perceptual aging. *Journal of Vision*, *19*(4):3, 1–28, https://doi.org/10.1167/19.4.3.

https://doi.org/10.1167/19.4.3 Received September 13, 2018; published April 3, 2019 ISSN 1534-7362 Copyright 2019 The Authors

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Motion perception provides a particularly well-suited framework within which the complexity of perceptual changes can be explored. No other visual ability has attracted more efforts to understanding its principles, and seminal models have been proposed to describe the discrete processing steps involved (for reviews see Burr & Thompson, 2011; Nakayama, 1985). Although the notion of general age-related decline has also been considered for perceptual aging (e.g., Trick & Silverman, 1991), evidence from visual perception clearly supports highly specific age-related changes (for reviews see Andersen, 2012; Owsley, 2011). Similarly, age effects on motion perception have been found to be dissociated from other changes in visual perception (e.g., Porter et al., 2017; Shaqiri et al., 2015), and even within the domain of motion perception differential effects have been observed (e.g., Billino, Bremmer, & Gegenfurtner, 2008; Pilz, Bennett, & Sekuler, 2010). Most importantly, motion perception has been shown to be highly sensitive to gradual age-related changes across adulthood (Billino et al., 2008; Bogfjellmo, Bex, & Falkenberg, 2013; Tran, Silverman, Zimmerman, & Feldon, 1998; Trick & Silverman, 1991). In addition, these changes have been specifically linked to healthy aging and can be differentiated from pathological processes, e.g., related to dementia (Kavcic, Vaughn, & Duffy, 2011; Mapstone, Dickerson, & Duffy, 2008; Wilkins, Gray, Graska, & Winterbottom, 2013). Therefore, motion perception offers an ideal example for perceptual aging that captures fundamental principles of lifespan development and allows insights into functional dynamics. At the same time, it highlights critical questions that still need to be explored in order to understand the complexity of functional aging. Given the hitherto prevalent neglect of perceptual aging, motion perception can be used as a conceptual model that provides efficient guidance for approaching a theoretical understanding of age-related changes in perception (compare Kalmar & Sternberg, 1988; Marx & Goodson, 1976).

We will start with a comprehensive overview of age-related changes in visual motion perception that involves different processing stages and complements behavioral evidence by current knowledge on putative neuronal correlates. We will discuss how a detailed consideration of perceptual changes challenges the often-postulated view of general functional decline with increasing age, and scrutinize how differential age effects question processing hierarchies or point to substantial processing plasticity. We will further review selected examples of how the described perceptual changes are interlinked with other functional domains. In particular, we will describe individual differences in aging of motion perception, findings on perceptual learning, and the role of motion perception for action. In the concluding remarks, we will highlight that our knowledge on development of motion perception across the adult lifespan encourages a stronger consideration of perceptual aging in order to understand the complexity of functional changes during healthy aging.

Vulnerability of motion perception on different processing stages

The domain of visual motion perception plays an outstanding role in research on perceptual mechanisms. Sensing movement represents a vital prerequisite for interacting with the dynamic environments we are continuously confronted with. It enables us to keep track of the position of ourselves and other objects in space, allows us to plan and carry out actions smoothly, to anticipate upcoming changes or events, and to interpret facial expressions and body language in social situations. Several processing stages contribute to these specialized perceptual capacities (compare e.g., Culham, He, Dukelow, & Verstraten, 2001). In order to review specific age effects, we will differentiate between three main stages: an early sensory stage, a low-/mid-level perceptual stage, and a high-level perceptual stage. Although there is no generally agreed upon definition of these stages and transitions seem often not well demarcated, this tentative differentiation allows us to classify age-related changes into functional mechanisms related to motion perception. Figure 1 provides a coarse illustration of neural correlates linked to the different processing stages and gives the basic outline of our review.

The sensory stage, as the first level of processing, takes place in the eye, where light enters the pupil, hits the retina, and is transferred into meaningful neural signals. The retinal ganglion cells are the origin of the two parallel visual pathways to the lateral geniculate nucleus (LGN), i.e., the magno- and the parvocellular pathways. There is evidence that in particular the magnocellular system is functionally specialized for motion processing (Maunsell, Nealey, & DePriest, 1990). However, both pathways provide inputs to cortical motion areas (Callaway, 2005; Nassi, Lyon, & Callaway, 2006).

The low-/mid-level perceptual stage refers to the processing of visual signals in early visual areas that process the input based on basic features such as orientation, edges, luminance, and simple motion signals. These local visual signals are further integrated in order to allow for inferences to be made about global changes in our environment. While V1 neurons are already selective for specific motion directions, a whole network of early visual areas has been identified to be involved in motion processing, including areas V5/MT,

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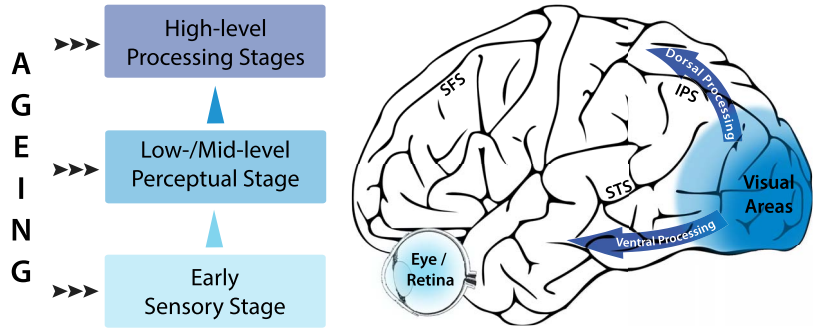

Figure 1. Stages of motion processing that are subject to age-related functional changes. Please note that the neural correlates highlighted on the lateral view of the left hemisphere provide only a coarse outline that is elaborated in the text. Major sulci that are critical for motion processing pathways beyond visual cortical areas are labelled as landmarks, i.e., superior temporal sulcus (STS), intraparietal sulcus (IPS), superior frontal sulcus (SFS).

V3A, and V6 (Braddick et al., 2001; Pitzalis, Fattori, & Galletti, 2012; Sunaert, van Hecke, Marchal, & Orban, 1999; Zeki et al., 1991). In particular area V5/MT, located at the temporo-parieto-occipital junction, plays a prominent functional role. Neurophysiological evidence shows that almost all V5/MT neurons exhibit directional selectivity and accomplish the integration of local motion signals.

The fundamental distinction between the dorsal and the ventral processing streams shapes the high-level perceptual stage (Goodale & Milner, 1992). Motion processing is generally acknowledged as a distinguishing feature of the dorsal stream which provides a key contribution to the control of visually guided actions and spatial attention (Kravitz, Saleem, Baker, & Mishkin, 2011). This functional role of the dorsal stream is reflected by several motion-responsive areas along the intraparietal sulcus and in frontal areas relevant for attentional control. However, motion signals also qualify as a significant input to the ventral stream since they often convey form information. Motion-responsive areas are documented in particular in the superior temporal sulcus, in particular involved in processing of motion information related to faces and bodies (Giese & Poggio, 2003). Overall, high-level motion perception can be assumed to be substantially modulated by cognitive processes, e.g., predictions, motivation, attention, or memory, which help to assess and interpret the visual input. It has been suggested that the dorsal stream is particularly vulnerable during child development (Atkinson, 2017; Braddick, Atkinson, & Wattam-Bell, 2003). A corresponding vulnerability during aging still awaits clarification.

The described stages of processing are foremost hierarchical in nature, but strong feedback connections exist between the LGN and cortical areas as well as between different cortical areas (Ahissar, Nahum, Nelken, & Hochstein, 2009; Bullier, Hupé, James, & Girard, 2001; Ghazanfar & Schroeder, 2006; Hegde & Felleman, 2007; Hochstein & Ahissar, 2002).Thus, age-related changes at advanced processing stages might closely interact, and an evaluation at large seems indicated.

Age-related changes in early sensory processing

The most fundamental interface between the visual world and the brain is the eye. The origin of motion perception lies within the retinal photoreceptors which convert the physical signals of light into neural signals that can be further interpreted by the brain. Indeed, this processing stage is subject to a variety of age-associated dysfunctions (for a review, see Lin, Tsubota, & Apte, 2016).

The most common disorders at this stage relate to optical problems that complicate focusing light on the retina, such as presbyopia or decrease retinal illuminance. Presbyopia, or age-related far-sightedness can usually be compensated comprehensively by appropriate glasses (Petrash, 2013). In contrast, only incomplete treatment is available for age-related decrease in retinal illumination. With increasing age, the light entering the pupil is substantially reduced due to three main factors: decreased pupil size, clouding of the lens that can lead to cataracts, and drusen, i.e., an accumulation of extracellular material under the retina (Karanjia, ten Hove, & Coupland, 2011; Khan et al., 2016; Sperduto, 1994).

Although age effects on the optics of the eye clearly represent a major constraint on visual processing, there is consensus that they cannot account for altered motion perception across the adult lifespan, as a more uniform impairment of perceptual performance would be expected (Owsley, 2011; Spear, 1993; Weale, 1987). However, age-related deficits in motion perception appear highly specific with regard to the exact pattern of motion information, e.g., speed (Atchley & Andersen, 1998; Billino et al., 2008; Snowden & Kavanagh, 2006). Moreover, there is evidence that impairments

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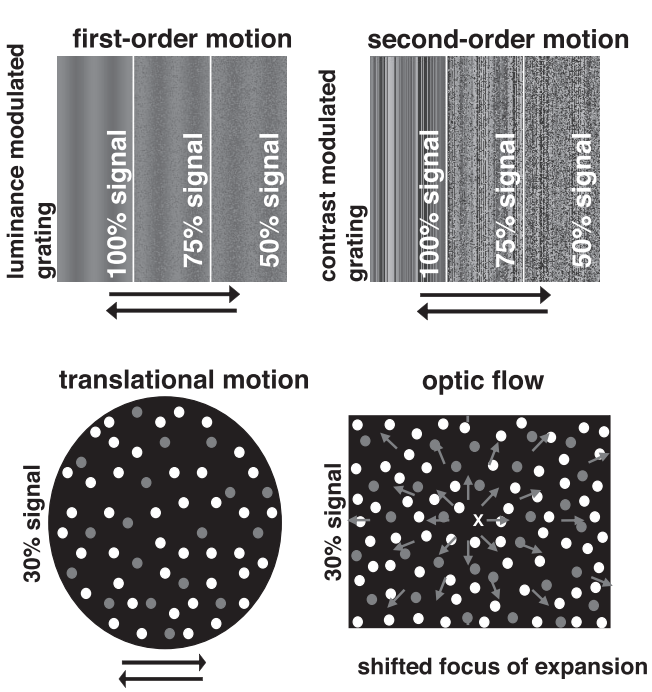

Figure 2. Exemplary low- and mid-level motion stimuli. (A) Gratings. First-order, luminance modulated grating and second-order, contrast modulated grating. For illustration gratings are shown at signal-to-noise levels of 100%, 75%, and 50%. The motion signal is elicited by moving the modulation either to the right or to the left. (B) Random dot kinematograms. Signal dots are here shown in gray and noise dots in white for clarification, but they are actually identical. Translational motion can be defined as horizontal coherent motion of the signal dots in a specific direction. Optic flow is elicited by signal dots expanding (or contracting) given a specific focus of expansion. The X gives the fixated reference.

can be reduced by behavioral training interventions, supporting the pivotal role of central mechanisms for functional effects (Ball & Sekuler, 1986; Bower & Andersen, 2012; Bower, Watanabe, & Andersen, 2013; Chang, Shibata, Andersen, Sasaki, & Watanabe, 2014).

Only few studies have explicitly tested for relationships between optical and age-related changes in motion perception. The impact of retinal illumination has been investigated in order to exclude a peripheral explanation for age-related differences in motion perception, but there is no evidence that it contributes to functional decline (Betts, Sekuler, & Bennett, 2012; Willis & Andersen, 2000). Variability of visual acuity most often is deliberately restricted in studies on visual perception by requiring normal or corrected-to-normal acuity in all observers. Some findings indicate that acuity limits performance in motion tasks that require the detection of small spatial displacements, e.g., in apparent motion tasks (Roudaia, Bennett, Sekuler, & Pilz, 2010). Congruently, it has been shown that visual blur, i.e., degraded high spatial frequency information, impairs motion discrimination (Burton et al., 2015). However, the detrimental effect seems only moderate in comparison with the massive threshold increase observed for form perception.

In contrast to the pronounced age effects on the optics of the eye, changes in photoreceptor functioning with increasing age are rather limited. Only a minor decline in the density of photoreceptors has been reported for the human retina, which primarily affects rods (Curcio, Millican, Allen, & Kalina, 1993; Gao & Hollyfield, 1992). Furthermore, studies in nonhuman primates have shown a stable number of retinal ganglion cells as well as preserved density, size, and functional properties of neurons in the LGN during aging (Ahmad & Spear, 1993; Kim, Pier, & Spear, 1997; Spear, Moore, Kim, Xue, & Tumosa, 1994; for a review, see Spear, 1993). Differential age-related vulnerabilities in magnocellular and parvocellular pathways have received little attention so far. However, neurophysiological evidence (Ahmad & Spear, 1993) as well as behavioral studies that tried to disentangle specific magnocellular and parvocellular functions (Elliott & Werner, 2010; Fiorentini, Porciatti, Morrone, & Burr, 1996), suggest that both pathways are subject to similar age-related changes. Thus, early neuronal processing of visual signals for motion perception appears remarkably robust during aging.

In summary, age-related changes in the early stages of visual processing shape the information that enters the system, but cannot account for changes in motion perception across the lifespan, which seem to be primarily related to changes in subsequent visual processing stages.

Age-related changes in low- and mid-level processing

The low- and mid-level processing stage refers to the basic analysis and computation of motion signals in striate and early extrastriate cortices. Age effects on this stage have been investigated using a variety of stimulus types and experimental designs. Although the principal finding that motion perception declines with increasing age dominates, the heterogeneity of results suggests that it describes effective functional changes only insufficiently (compare Billino et al., 2008). The following overview of findings summarizes the current knowledge on age-related changes and highlights modulators of age-related decline.

Studies on motion perception in healthy aging have usually focused either on local or global signal processing, using specific stimuli. Figure 2 illustrates the distinction between the most commonly used stimuli, gratings and random dot kinematograms (RDK). Gratings (Figure 2A) provide local motion

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information which can be either defined by luminance or by properties like local contrast, labelled as first- and second-order motion (Cavanagh & Mather, 1989). Whereas first-order motion is analyzed by linear filters of the visual system, second-order motion analysis requires more complex nonlinear processing steps (Lu & Sperling, 1995). In contrast, in RDKs (Figure 2B) individually moving dots elicit a global perception of pattern motion. A particularly important global motion pattern is optic flow that occurs when observers move through the environment. While local motion information in gratings is assumed to be comprehensively analyzed in early visual areas (Smith, Greenlee, Singh, Kraemer, & Hennig, 1998), global motion processing strongly relies on later extrastriate areas V5/MT and MST that facilitate integration of motion signals across space and contribute to noise reduction (Born & Bradley, 2005; but see also Furlan & Smith, 2016).

Table 1 provides a selective summary of core studies that investigated age-related changes in local and global motion processing. The compilation reflects different experimental approaches and, in particular, their heterogeneity with regard to stimuli, procedural details, and sample characteristics.

Local motion processing

Several studies used gratings to determine motion detection thresholds in healthy aging by varying either contrast (Betts, Taylor, Sekuler, & Bennett, 2005; Habak & Faubert, 2000; Tang & Zhou, 2009) or noise levels (Arena, Hutchinson, Shimozaki, & Long, 2013; Billino, Braun, Bremmer, & Gegenfurtner, 2011). Results consistently show elevated thresholds with increasing age. Only two studies investigated speed discrimination, and both found a decrease in age-related sensitivity (Raghuram, Lakshminarayanan, & Khanna, 2005; Snowden & Kavanagh, 2006). Neuronal correlates of these age effects have been primarily discussed based on electrophysiological studies in senescent nonhuman primates and cats. Myelinated fibers and synapses in V1 significantly degrade in older monkeys (Peters, Moss, & Sethares, 2001; Peters, Sethares, & Killiany, 2001) which has been linked to increased latencies and delayed transfer of information demonstrated in V1 neurons (Wang, Zhou, Ma, & Leventhal, 2005). Moreover, senescent neurons in striate and early extrastriate areas exhibit an increased level of neural noise, reduced selectivity and increased spontaneous excitability (Fu, Yu, Ma, Wang, & Zhou, 2013; Schmolesky, Wang, Pu, & Leventhal, 2000; Yang, Liang, Li, Wang, & Zhou, 2009; Yu, Wang, Li, Zhou, & Leventhal, 2006; Zhang et al., 2008). Based on the consistent behavioral results indicating compromised motion processing capacities, patterns of decline have been helpful in deriving insights into the mechanisms underlying functional aging.

Faubert (2002) put forward the processing complexity hypothesis for age effects on local motion perception. He suggested that age-related deficits are more pronounced the more processing steps are required for a perceptual task. The hypothesis is backed by evidence of larger and earlier age effects for second-order motion processing than for first-order motion processing (Habak & Faubert, 2000; Tang & Zhou, 2009). While first-order motion signals are already analyzed in V1, additional processing steps in further extrastriate areas are necessary to extract second-order motion information. Neuronal responses to second-order motion have been described as early as in area V1, but striate activity induced by this motion type is relatively weak and involves a small proportion of neurons (Baker, 1999; Mareschal & Baker, 1999). Functional brain imaging studies in humans support specialized processing in area V3 (Smith et al., 1998) as well as in higher cortical areas, e.g., the parietal lobe, and the superior temporal sulcus (Ashida, Lingnau, Wall, & Smith, 2007; Dumoulin, 2003; Noguchi, Kaneoke, Kakigi, Tanabe, & Sadato, 2005). However, increased vulnerability to age-related changes in second-order motion processing has not been found consistently. Several studies have indeed reported similar age effects on of first- and second-order motion perception, e.g., in motion detection tasks (Billino et al., 2011; for a critical discussion see Allard, Lagacé-Nadon, & Faubert, 2013) or in stereoscopic shape-from-motion tasks (Norman, Crabtree, Herrmann, et al., 2006). Thus, adverse effects of second-order motion information might critically depend on specific task characteristics.

The crucial role of inhibitory processes for age-related functional changes is supported by findings from a seminal study by Betts and colleagues (2005). Center-surround antagonisms that rely on inhibitory processes are well documented for direction selective neurons (Allman, Miezin, & McGuinness, 1985; Raiguel, Hulle, Xiao, Marcar, & Orban, 1995). They are believed to underlie behavioral evidence that direction discrimination thresholds strongly depend on contrast and size of motion stimuli (Tadin, Lappin, Gilroy, & Blake, 2003). Thresholds for high-contrast stimuli increase with size, indicating weakened responsiveness of neurons when the stimulus expands beyond the receptive field center and thus triggers suppression. However, for low-contrast stimuli increasing size reduces thresholds, indicating spatial summation. Aging affects this pattern differentially. Whereas behavioral evidence for spatial summation in motion perception is preserved across the adult lifespan, evidence for suppression is significantly attenuated. In older adults, the increase of motion thresholds with

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Study	Perceptual task	Measure	Duration	Speed	Direction	Age	Evidence
Local motion processing							
Habak & Faubert, 2000	motion detection in first- and second-order gratings	contrast threshold	750 ms	2-8 °/s	left/right	M=23 yr vs. M=69.7 yr	age effects, more pronounced for second-order motion
Raghuram et al., 2005	speed discrimination in gratings	Weber fraction	500 ms 1000 ms	standard speed 2 °/s and 8 °/s	left/right	M=24.6 yr vs. M=71.2 yr	age effect
Betts et al., 2005	motion detection in gratings varying in size and contrast	duration threshold	N/A	2 °/s	left/right	M=23.0 yr vs. M=67.9 yr	age effect, modulation by stimulus size and contrast
Snowden & Kavanagh, 2006	speed discrimination and motion detection in gratings	speed discrimination threshold absolute speed threshold	600 ms	standard speed 0.125-8 °/s	up/down	M=23.2 yr vs. M=61.5 yr	age effect
Tang & Zhou, 2009	motion detection in first- and second-order gratings	contrast threshold	300 ms	1-8 °/s	left/right	19-79 yr	age effects, earlier decline for second-order motion
Billino et al., 2011	motion detection in first- and second-order gratings	signal-to-noise threshold	500 ms	10.1 °/s	left/right	18-82 yr	age effects, similar for first- and second-order motion
Arena et al., 2013	motion detection in gratings	noise contrast thresholds	N/A	1 °/s	left/right	M=19.7 yr vs. M=69.8 yr	age effect
Global motion processing							
Ball & Sekuler, 1986	direction discrimination in RDKs	d’	500 ms	10 °/s	2–8° cw/ccw deviation from cardinal directions	M=21 yr vs. M=68 yr	age effect, modulation by motion direction
Wood & Bullimore, 1995	displacement detection in RDKs	displacement threshold	600 ms	N/A	cardinal directions	21-82 yr	age effect
Trick & Silverman, 1991	motion detection in RDKs	signal-to-noise threshold	4000 ms	5.8 °/s	cardinal directions	25-80 yr	age effect

Table 1. Overview of core findings on low- and mid-level motion perception during healthy aging. *Notes*: RDK, random dot kinematogram; cw, clockwise; ccw, counterclockwise; ISI, inter-stimulus interval; N/A, not applicable or available.

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Study	Perceptual task	Measure	Duration	Speed	Direction	Age	Evidence
Global motion processing –continued -							
Gilmore et al., 1992	motion detection in RDKs	signal-to-noise threshold	2750 ms	3.9 °/s	left/right	18-23 yr vs. 62-83 yr	age effect
Andersen & Atchley, 1995	motion detection in RDKs	d'	2000 ms	2.4 °/s	left/right t	M=20.7 yr vs. M=71.8 yr	age effect
Wojciechowski et al., 1995	motion detection in RDKs	signal-to-noise threshold	298 ms	28 °/s	cardinal directions	M=22.8 yr vs. M=66.6 yr	age effect, modulation by stimulus location in the visual field
Atchley & Andersen, 1998	motion detection in RDKs	adjustment threshold	until response	4.8 °/s or 22 °/s	left/right	M=22.5 yr vs. M=69.7 yr	age effect, modulation by eccentricity and speed
Tran et al., 1998	motion detection in RDKs	signal-to-noise threshold	10000ms	2.5 °/s	left/right	19-92 yr	age effect
Norman, Ross, Hawkes, & Long, 2003	moving strips of dots	speed discrimination threshold	until response	standard speed 1.22-24.34 °/s	left/right	M=21.8 yr vs. M=72.6 yr	age effect
Snowden & Kavanagh, 2006	motion detection in RDKs	signal-to-noise thresholds absolute speed threshold	360 ms 500 ms	0.5-4 °/s	up/down	M=23.2 yr vs. M=61.5 yr	age effect
Bennett et al., 2007	motion detection and direction identification in RDKs	confidence rating and sensitivity	75–470 ms	6°/s	random, span of 250 °	23-81 yr	age effect for >70 years of age
Billino et al., 2008	motion detection in RDKs	signal-to-noise threshold	400 ms	6.6 °/s	left/right	20-82 yr	age effect
Roudaia et al., 2010	apparent motion detection in RDK with varying ISIs and displacements	proportion correct	N/A	N/A	left/right	M=23.2 yr vs. M=68.1 yr	age effect, reduced spatial and temporal integration
Allen et al., 2010	motion detection in RDKs	signal-to-noise threshold	N/A	5.6 °/s	up/down expansion/ contraction cw/ccw rotation	M=21 yr vs. M=73 yr	age effect, modulation by dot contrast

Table 1. Continued.

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Study	Perceptual task	Measure	Duration	Speed	Direction	Age	Evidence
Global motion processing –continued -							
Arena et al., 2012	motion detection in RDKs varying in dot speed and displacement	signal-to-noise threshold	853 ms	0.625-10 °/s	up/down	20-79 yr	age effect for >70 years of age, modulation by speed and spatial displacement
Bocheva et al., 2013	direction discrimination in RDKs	signal-to noise threshold	830–1670 ms	6.72 °/s or 18.8 °/s	left/right from vertical	M=19.5 yr vs. M=73.9 yr	age effect, modulation by speed
Bogfjellmo et al., 2013	direction identification in RDKs	direction threshold	500 ms	1.6 °/s or 5.5 °/s	cw/ccw relative to up	20-89 yr	age effect, modulation by speed
Genova & Bocheva, 2013	speed discrimination in RDKs	Weber fraction	588 ms	standard speed 5.2 °/s or 10.4 °/s	up/down	M=20 yr vs. M=74 yr	age effect
Hutchinson et al., 2014	motion detection in RDKs with varying aperture size	signal-to-noise threshold	426.7 ms	5.7 °/s	up/down	M=21.7 yr vs. M=72.4 yr	age effect, modulation by aperture size
Pilz et al., 2017	motion detection and direction discrimination in RDKs	signal-to-noise threshold proportion correct	400 ms	6 °/s	cardinal directions cw from horizontal or vertical	M=22.5 yr vs. M=66.2 yr	no age effect, but strong anisotropy
Shain & Norman, 2018	judgment of motion direction behind apertures	judgment errors	2350 ms	2.4 °/s	0-360 °	M=21.9 yr vs. M=74.3 yr	age effect, modulation by motion direction
Optic flow							
Warren et al., 1989	heading detection in radial flow RDKs	detection accuracy	3700 ms	1-3.8 m/s	left/right	M=20 yr vs. M=69.4 yr	age effect
Atchley & Andersen, 1998	expansion detection in radial flow RDKs	adjustment threshold	until response	0.41-1.64 m/s	forward	M=22.5 yr vs. M=69.7 yr	no age effect
Billino et al., 2008	heading detection in radial flow RDKs	signal-to-noise threshold	400 ms	max. 18.6 °/s	left/right	20-82 yr	no age effect
Lich & Bremmer, 2014	heading identification in radial flow RDKs	recognition accuracy	200-2000 ms	1 m/s	left/right	M=26.2 yr vs. M=67.8 yr	age effect

Table 1. Continued.

increasing size of high-contrast stimuli is less pronounced in comparison to younger adults. The dissociation points to a specific inhibitory deficit that weakens the center-surround mechanism. These initial findings by Betts and colleagues (2005) have been complemented by several other studies that suggest an involvement of impaired inhibitory processes in age-related perceptual changes (Betts et al., 2012; Betts, Sekuler, & Bennett, 2009; but see also Karas & McKendrick, 2012). In line with this behavioral evidence, Leventhal, Wang, Pu, Zhou, and Ma (2003) found that response properties of V1 neurons of older monkeys are substantially affected by reduced levels of γ-aminobutyric acid (GABA), the main inhibitory neurotransmitter in the nervous system. The administration of GABA improved functions of visual neurons of older monkeys so that they displayed similar properties to those of younger monkeys. In addition, Hua, Kao, Sun, Li, and Zhou (2008) reported that even though the overall density of neurons in striate cortex does not differ between younger and older cats, the density of GABA-reactive neurons is significantly reduced with age. Although it is difficult to directly compare human behavioral results and neurophysiological results from monkeys, insights from both areas complement and support each other.

Age effects on local motion processing overall appear highly congruent. However, some limitations have to be considered. Age effects have been determined using a restricted range of stimulus characteristics. The so-far-used gratings show a bias towards slower speeds, with a maximum speed of 10°/s. Similarly, almost exclusively horizontal motion has been applied. Indeed, studies using RDKs that are described in the next section strongly suggest a modulation of age effects by speed and anisotropy, but corresponding results for gratings do not exist. Finally, findings about age-related changes are primarily based on age group comparisons, i.e., on the comparison between younger and older adults. The only two studies including continuous age samples when investigating local motion perception provide divergent patterns, i.e., uniform versus accelerated decline (Billino et al., 2011; Tang & Zhou, 2009). Thus, the time course of decline across the adult lifespan remains ambiguous.

Global motion processing

Studies that emphasize global motion processing, using RDKs as stimuli, provide the majority of findings on age-related changes in motion perception (compare also Hutchinson, Arena, Allen, & Ledgeway, 2012). The most consistent age differences have been found using RDKs with varying signal-to-noise ratios and determining coherence thresholds at which motion detection or discrimination can be accomplished. Stimuli typically involve coarse motion along the cardinal axes. The most consistent age-differences have been found using correlational designs across the adult age range (Billino et al., 2008; Bogfjellmo et al., 2013; Tran et al., 1998; Trick & Silverman, 1991). Estimated increases in coherence thresholds range from 1% per decade (Tran et al., 1998; Trick & Silverman, 1991) to 2.7% per decade (Billino et al., 2008) with larger increases coinciding with shorter stimulus durations.

Even though consistent changes have been observed using correlational designs, studies that compared performance across age ranges by decades have found most prominent changes in adults older than 70 years (Arena, Hutchinson, & Shimozaki, 2012; Bennett, Sekuler, & Sekuler, 2007; Bogfjellmo et al., 2013). Most studies indeed compared thresholds between just two age groups, i.e., between younger adults, typically aged between 18 and 30 years, and older adults, typically older than 60 years. Findings often show substantial age-related increase in coherence thresholds (Allen, Hutchinson, Ledgeway, & Gayle, 2010; Andersen & Atchley, 1995; Atchley & Andersen, 1998; Gilmore, Wenk, Naylor, & Stuve, 1992; Snowden & Kavanagh, 2006; Wojciechowski, Trick, & Steinman, 1995; but see also Porter et al., 2017). Moreover, speed discrimination (Genova & Bocheva, 2013; Norman, Ross, Hawkes, & Long, 2003) as well as motion direction discrimination (Ball & Sekuler, 1986; Bennett et al., 2007; Bocheva, Angelova, & Stefanova, 2013; Bogfjellmo et al., 2013) have been found to decline with increasing age. However, results seem to vary largely depending on stimulus parameters such motion direction (Ball & Sekuler, 1986; Pilz, Miller, & Agnew, 2017), stimulus size (Hutchinson, Ledgeway, & Allen, 2014), contrast (Allen et al., 2010), stimulus duration (Bennett et al., 2007; Conlon, Power, Hine, & Rahaley, 2017), or location (Wojciechowski et al., 1995). Indeed, the mechanisms that modulate age effects are often not well understood, but call for caution when trying to derive overall conclusions on functional changes. In the following, the most prominent parameters that modulate age effects on motion perception are considered.

A particular relevant stimulus parameter that modulates age effects is given by stimulus speed. Although only few studies have systematically varied speed (compare Table 1), there is increasing evidence that the perception of slower motion is more vulnerable to age than the perception of faster motion. This pattern has been reported for motion detection (Arena et al., 2012) as well as for motion direction discrimination (Bocheva et al., 2013; Bogfjellmo et al., 2013). The exact definition of slow and fast speeds differs between studies depending on the specific paradigms that overall have considered a speed range from < 1°/s to 18.8°/s. In general, a critical criterion of 5°/s has been assumed since coherent motion sensitivity peaks for

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speeds faster than this criterion (Chawla, Phillips, Buechel, Edwards, & Friston, 1998; Rodman & Albright, 1987). Whereas age-related changes in motion perception seem to be modulated by speed, changes in speed discrimination are comparable across a large range of standard speeds, i.e., 1.22°/s to 24.34°/s (Genova & Bocheva, 2013; Norman et al., 2003). Several studies investigating spatiotemporal properties of motion perception suggest that both spatial and temporal integration are affected by age, but whether they contribute differentially to speed-specific effects appears still ambiguous (Arena et al., 2012; Roudaia et al., 2010; Wood & Bullimore, 1995; see also Pilz, Kunchulia, Parkosadze, & Herzog, 2015). It should also be noted that quite heterogeneous stimulus durations have been used in different studies (compare Table 1) which might interact with spatiotemporal integration.

In line with a supposed weakened inhibition in areas related to motion processing (see Betts et al., 2005; Betts et al., 2009; Betts et al., 2012), evidence has been provided that age-related changes in global motion processing depend on stimulus size and contrast. Hutchinson and colleagues (2014) found that younger adults' motion detection thresholds are strongly affected by stimulus size, i.e., increase with decreasing size, whereas older adults' thresholds are stable. Consequently, age effects depend on the size of the RDK, which can even be in favor of older adults. Similarly, Allen and colleagues (2010) showed that the magnitude of age effects is more pronounced for low contrast signals than for high contrast signals. These findings further support the notion that age-related functional changes are subject to strong modulations depending on stimulus parameters.

Another recent interesting issue relates to anisotropies of age-related changes in motion perception. Age effects are well documented for perception of motion in cardinal directions, but barely specified for deviating directions (compare Table 1; but note Bennett et al., 2007). In addition, possible differences between different motion directions have been largely neglected. However, there is evidence that sizeable anisotropies exist (Ball & Sekuler, 1986; Pilz et al., 2017; Shain & Norman, 2018). Moreover, there seem to be substantial variations across the visual field, with age effects being more pronounced in central vision (Atchley & Andersen, 1998; Wojciechowski et al., 1995).

Processing of global motion predominantly relies on extrastriate motion areas, in particular area V5/MT (Maunsell & van Essen, 1983; Tootell et al., 1995). Neurophysiological studies on age-related changes in V5/MT are scarce; however, findings seem to mirror neuronal degradation found in striate cortex and provide a plausible correlate for human behavioral results. V5/MT neurons of older monkeys show not only increased noise and reduced directional selectivity (Liang et al., 2010; Yang, Liang et al., 2009), but also exhibit lower preferred speeds and broader speed tuning functions than those of younger monkeys (Yang, Zhang, et al., 2009). Similar to findings in early visual areas, these changes have been related to decreased intracortical GABAergic inhibition (Yang, Liang et al., 2009; Yu et al., 2006). Only a few studies have so far investigated the underlying neural mechanisms of age-related changes in global motion perception in humans. It has been suggested that a decrease in amplitudes and an increase in latencies of visually evoked potentials elicited by global motion stimuli relates to age-related neurophysiological changes in striate and extrastriate areas (Kavcic, Martin, & Zalar, 2013; Zanto, Sekuler, Dube, & Gazzaley, 2013). In addition, recent fNIRS (Ward, Morison, Simmers, & Shahani, 2018) and fMRI (Biehl, Andersen, Waiter, & Pilz, 2017) studies found increased activation in visual cortex and specifically area V5/MT, respectively, indicating compensatory recruitment of neural resources in older adults for processing global motion.

Overall, it can be concluded that age-related behavioral changes in global motion processing are well-documented. However, the variety of studies has not only provided robust evidence for compromised perceptual capacities, but has crucially revealed that the notion of a general decline is not appropriate. Future studies need to specifically elaborate on the modulation of age effects in order to clarify the conditions under which aging results in functional changes. Related to these open questions is the consideration of individual differences. Several studies describe that individual differences within the older adult groups are large and only a proportion of older adults shows reduced performance in motion tasks (e.g., Conlon et al., 2017; Pilz et al., 2015). Moreover, despite the number of available studies, it appears still controversial whether detrimental changes during healthy development uniformly across the adult lifespan (e.g., Billino et al., 2008; Tran et al., 1998; Trick & Silverman, 1991) or accelerate from a certain age on (e.g., Arena et al., 2012; Bennett et al., 2007; Bogfjellmo et al., 2013). More studies considering continuous age samples, and ultimately, longitudinal approaches are needed to derive reliable conclusions. It can be speculated that the diversity of results is rather underestimated due to given barriers for communicating null effects (but also see Enoch, Werner, Haegerstrom-Portnoy, Lakshminarayanan, & Rynders, 1999; Pilz et al., 2017). Finally, it is important to note that current knowledge does not allow for any precise conclusions on age-related changes in neural mechanisms underlying global motion perception. Most insights come from neurophysiological studies in monkeys and so far, conclusions on the neural correlates of human behavioral changes are merely speculative.

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Optic flow

Optic flow represents a specific type of global motion that occurs during locomotion. It is characterized by stimuli that spread a large portion of the visual field and contain complex speed gradients. The typical speed gradient is given by slower speeds in the central visual field and faster speeds in the periphery (Duffy & Wurtz, 1997; Koenderink, 1986). Since speed in optic flow pattern increases with viewing angle from fixation, higher velocities become more relevant than in common global motion stimuli (compare Table 1). Neurophysiological evidence shows that selectivity for optic flow emerges only in area MST which receives strong input from area V5/MT (Duffy & Wurtz, 1991a, 1991b). Moreover, imaging and lesion studies in humans suggest a rather large network of cortical areas involved in optic flow perception (Peuskens, Sunaert, Dupont, van Hecke, & Orban, 2001; Wunderlich et al., 2002).

Given the currently described age-related effects on motion processing and the additional signal complexity, substantial decline for the perception of optic flow might be expected. Indeed, few studies have addressed age-related changes in the perception of optic flow and only minor decline is documented. Atchley and Andersen (1998) as well as Billino and colleagues (2008) found heading detection to the left or right in radial flow pattern with varying noise unaffected by age. Warren, Blackwell, and Morris (1989) reported only a minimal increase in heading detection thresholds varying the deviation from a central focus of expansion, i.e., from 1.1° in young adults and 1.9° in older adults. In contrast, a more recent study by Lich and Bremmer (2014) found that older adults are less accurate in identifying heading direction using a reference ruler. Thus, more refined measurements might be needed to reveal effects of age in optic flow perception.

In summary, evidence so far suggests that effects of age on optic flow perception are relatively weak, and highlights that higher signal complexity does not necessarily trigger more pronounced functional decline during aging. It has consistently been shown that visual evoked potentials are subject to age-related delays for translational motion, but not for radial motion (Kuba et al., 2012). Increased stimulus complexity might allow for the involvement of a wider range of processes that support functional compensation and plasticity.

Age-related changes in high-level processing

The previous section assessed the effects of healthy aging on low- and mid-level motion processing. Given the documented age-related changes, the question arises as to which extent high-level motion perception is affected by functional constraints. High-level motion tasks can involve a complexity of additional cognitive processes and are often embedded in everyday interactions with our environment. Age-related changes in the processing of high-level motion have been particularly explored for two stimulus domains, i.e., 3D form and shape from motion and biological motion. Typical stimuli are illustrated in Figure 3. The following paragraphs summarize behavioral findings for both stimulus domains. Due to the heterogeneity of involved processing steps, the identification of putative neuronal correlates of age-related changes is rather complex. Essentially all cortical areas are subject to substantial volume decline during aging (Raz et al., 2004), but changes in connectivity and compromised neuromodulation might be most relevant for complex perceptual decline (Damoiseaux, 2017; Jacob & Nienborg, 2018).

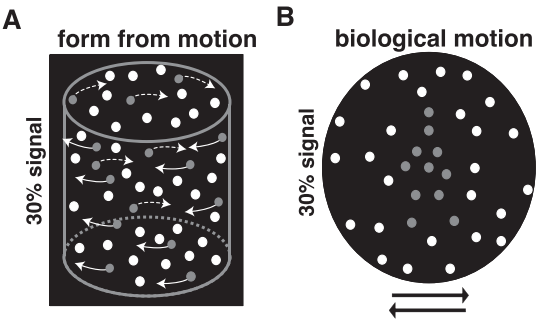

Figure 3. Exemplary high-level motion stimuli. Random dot kinematograms; signal dots are here shown in gray and noise dots in white for clarification, but they are actually identical. (A) 3D form from motion. Dots move as if attached to the surface of an object, here a transparent cylinder. The surface is perceived as a rotating cylinder. (B) Biological motion. A typical stimulus consists of a canonical point-light walker embedded in noise dots. It moves as if on a treadmill, walking or performing defined actions, facing either to the right or to the left.

3D form and shape from motion

Visual motion signals, among other cues such as binocular disparity, shading, or texture highlights, provide important information that can drive the perception of 3D object form or surface shape. The perception of shape or form from motion is usually assessed using moving dots that need to be integrated into a 3D percept. Given the decline in global motion perception as described in the previous section, age-related changes for this high-level ability are reasonable to assume.

Indeed, age-related decline has been observed for the perception of motion-defined surface shape (Andersen & Atchley, 1995; Norman et al., 2013; Norman et al., 2017; Norman, Clayton, Shular, & Thompson, 2004; Norman, Dawson, & Butler, 2000) as well as for object form (Mateus et al., 2013; Norman et al., 2017; Norman, Bartholomew, & Burton, 2008). In contrast,

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the ability to discriminate 3D shape from visual stimuli moving in depth seems to be preserved during aging (Norman, Crabtree, Norman, et al., 2006). The perception of 3D form and shape from other cues, e.g., binocular disparity, seems to be unaffected by age (Norman et al., 2008; Norman et al., 2012).

Notably, Andersen and Atchley (1995) showed that performance in a 2D motion task is not predictive for the perception of 3D surface from optic flow. Successful perception of 3D form and shape from motion appears to crucially rely on analyzing the temporal correspondence of visual cues. There is evidence that age-related decline for 3D form from motion substantially increases with decreasing dot lifetime (Norman et al., 2000; Norman et al., 2013) as well as with decreasing stimulus duration (Mateus et al., 2013). These findings imply that age specifically affects the integration of motion signals into meaningful 3D information. Only two studies considered continuous age samples, but results so far consistently suggest an accelerated decline of this capacity across the adult lifespan (Mateus et al., 2013; Norman et al., 2013).

Biological motion

An important and highly relevant aspect of high-level motion perception is the perception of biological motion such as, for example, facial or body motion. Biological motion is a highly familiar and socially relevant stimulus, which allows us to recognize and evaluate the actions, intentions, and emotions of other people. The processing of biological motion is often investigated using point-light walkers, a stimulus that consists of dots representing the major joints of a moving person (Johansson, 1973). Several studies have documented that perception of such point-light walkers is compromised with increasing age (Agnew, Phillips, & Pilz, 2016; Billino et al., 2008; Insch, Bull, Phillips, Allen, & Slessor, 2012; Legault, Troje, & Faubert, 2012; Norman, Payton, Long, & Hawkes, 2004; Pilz et al., 2010; Spencer, Sekuler, Bennett, Giese, & Pilz, 2016). The majority of studies compared different age groups and only two studies provide data for continuous age samples (Billino et al., 2008; Insch et al., 2012), both suggesting that biological motion perception declines linearly as a function of age.

Older adults have been found to require increased signal-to-noise ratios compared to younger adults for detecting point-light walkers in noise (Billino et al., 2008) and also increased stimulus durations to reach a comparable level of performance for discriminating their walking direction (Norman, Payton, et al., 2004; Pilz et al., 2010). The latter finding might suggest that older adults' perceptual processes are simply slower than those of younger adults (compare Salthouse, 1996). However, stimulus duration does not seem to be the only factor affecting biological motion processing in healthy aging; also, the familiarity of a stimulus plays an important role. Older adults, for example, show larger impairments for discriminating less familiar backward actions compared to forward actions (Norman, Payton, et al., 2004), and show consistent deficits at processing inverted compared to upright point-light walkers (Agnew et al., 2016; Pilz et al., 2010; Spencer et al., 2016).

Biological motion, as conveyed by point-light actions, contains three important kinds of information: the local motion of the single dots representing the joints, which is thought to be primarily processed in the dorsal stream; the global form of the action that is conveyed when the single dots are integrated into a global percept, thought to be primarily processed in the ventral stream; and the global motion information that can be attained by integrating the motion of the single dots or the global form of the point-light action over time. The integration of information from both dorsal and ventral pathways is thought to be achieved in higher-level areas such as the superior temporal sulcus (Giese & Poggio, 2003). This model of biological motion processing is based on behavioral studies, but also neuropsychological evidence showing that patients with brain lesions are able to process biological motion despite deficits in global motion perception (Vaina, Lemay, Bienfang, Choi, & Nakayama, 1990; Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001). Stimulus inversion affects the familiarity of the stimulus—we rarely see someone walking on the ceiling—but has also been suggested to affect the processing of the global form of the stimulus (Pavlova & Sokolov, 2000; Troje & Westhoff, 2006). Pilz and colleagues (2010) investigated the contribution of local motion, global form, and global motion for processing point-light walkers in healthy aging in more detail and found that older adults do not have difficulties processing the global form of the walkers but might be impaired at integrating local motion and global form information as efficiently as younger adults, at least for less familiar stimuli such as inverted walkers.

Based on these results, age-related differences in neural mechanisms related to biological motion processing are reasonable to assume, in particular mechanisms related to processing the local motion signals of point-light walkers, or integrating the information from both the dorsal and ventral pathway. However, a recent fMRI study which investigated potential neural differences in processing the local motion and global form information from point-light walkers in aging found no significant age-related differences (Biehl et al., 2017).

Interestingly, the ability to discriminate the walking direction of point-light walkers solely based on the local motion information seems to depend largely on

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the stimulus and task used. Whereas older and younger adults have difficulties discriminating the walking direction from computer-generated scrambled walkers (Pilz et al., 2010), both age groups are able to discriminate the walking direction or emotions from motion-captured scrambled walkers (Spencer et al., 2016), and also the matching of actions can be achieved based on local motion information alone (Agnew et al., 2016). However, it has to be noted, that performance for walkers that contain primarily local motion information is usually worse compared to walkers that contain both local motion and global form information, or global form information alone, which indicates that form information is most informative for discriminating point-light walkers.

Point-light walkers are important stimuli to assess biological motion perception in healthy aging, because they allow investigating the contribution of local motion and global form to biological motion perception. However, they are also rather minimalistic. In real life, we rarely encounter such stimuli, and we are more familiar with full body or facial motion. For younger adults, it has been shown that body and facial motion can facilitate the encoding and recognition of identity (O'Toole, Roark, & Abdi, 2002; Yovel & O'Toole, 2016). However, to what extent this information is beneficial in old age has been explored by only few studies so far. Maguinness and Newell (2014) assessed the effects of facial motion on identity matching and found that even though older adults' performance was worse than that of younger adults, performance improved when the target face was presented as a dynamic sequence as compared to a static one. Grainger, Henry, Phillips, Vanman, and Allen (2017) studied the recognition of affect from faces and also found age-related performance differences that were attenuated by dynamic information. These results indicate that motion information can be beneficial for older adults compared to static information. More research in this area is needed to fully assess the benefits or costs of facial and body motion information for the encoding and recognition of identity of more familiar and relevant stimuli in older adults. In addition, the neural mechanisms underlying age-related changes in processing dynamic information from more complex and socially relevant stimuli such as moving faces and bodies remain to be clarified.

Individual differences in aging of motion perception

Any functional ability is based on a number of complex and interlinked resources that can contribute to individual differences in age-related changes. We have already discussed the role of optical changes, concluding that they are unlikely to fully explain observed age effects on motion perception (e.g., Betts et al., 2005; Roudaia et al., 2010). Two further potential contributors to individual differences in motion perception related to healthy aging that have already been considered in more detail are gender differences and cognitive resources.

Gender differences

Gender-specific age differences in motion perception are reasonably well documented, but are often bound to specific stimulus parameters, e.g., eccentricity, stimulus duration, or stimulus density. Table 2 summarizes existing results on gender differences. Several studies have observed a significant interaction between gender and age effects on motion perception in that women were found to be more susceptible to functional decline than men.

An early study by Gilmore and colleagues (1992) estimated motion coherence thresholds for global motion detection and found that, on average, older women had a lower sensitivity to motion than older men. Results from later studies confirmed these results for similar tasks (Andersen & Atchley, 1995; Atchley & Andersen, 1998; Conlon et al., 2017), but also for discriminating the walking direction of point-light walkers in noise (Pilz et al., 2010). Gender differences in motion perception are not solely confined to the aging population, as some studies have shown that gender differences extend to all ages (Arena et al., 2012; Billino et al., 2008; Conlon, Brown, Power, & Bradbury, 2015; Snowden & Kavanagh, 2006). It is possible that differences in motion perception between men and women are present across ages, but are often too small to be observed in small samples of younger adults. This hypothesis is supported by a more recent study by Shaqiri and colleagues (2018) who assessed gender differences in a large sample of younger adults for a variety of perceptual tasks and found performance advantages for male participants in six out of fifteen tasks, including motion direction discrimination.

It has been suggested that stimulus duration affects gender differences in motion perception, as shorter stimulus durations enhance the effect (Pilz et al., 2010). Furthermore, tasks assessing gender differences in healthy aging often measure motion coherence thresholds for detecting global motion in random dot kinematograms, and it is likely that women are less efficient at extracting the signal from the noise, a hypothesis that has been supported by studies showing that gender differences are less pronounced without the presence of noise dots (Norman et al., 2003; Pilz et al., 2010). However, Conlon and colleagues (2017) mea-

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Study	Perceptual task	Measure	Evidence
Gilmore et al., 1992	motion detection in RDKs	signal-to-noise threshold	age x gender
Andersen & Atchley, 1995	motion detection in RDKs 3D shape detection from motion in RDKs	d'	age x gender no gender effect
Atchley & Andersen, 1998	motion detection in RDKs expansion detection in radial flow RDKs	adjustment threshold	age x gender x eccentricity no gender effect
Tran et al., 1998	motion detection in RDKs	signal-to-noise threshold	no gender effect
Raghuram et al., 2005	speed discrimination in gratings	Weber fraction	gender effect
Snowden & Kavanagh, 2006	speed detection in gratings and RDKs motion detection in RDKs speed discrimination in gratings	absolute speed threshold speed detection signal-to-noise threshold speed discrimination threshold	no gender effect gender effect gender effect
Billino et al., 2008	motion detection in RDKs heading detection in radial flow RDKs PLW direction discrimination	signal-to-noise threshold	gender effect gender effect gender effect
Pilz et al., 2010	PLW direction discrimination under varying display conditions	recognition accuracy without noise recognition accuracy with noise	no gender effect age x gender x duration
Roudaia et al., 2010	apparent motion detection in RDK with varying ISIs and displacements	proportion correct	no gender effect
Arena et al., 2012	motion detection in RDKs varying in dot speed and displacement	signal-to-noise threshold	gender effect
Conlon et al., 2015	motion detection in RDKs	signal-to-noise threshold	gender effect
Conlon et al., 2017	motion detection in RDKs	signal-to-noise threshold	gender x age x dot number

Table 2. Gender differences in motion perception. *Notes*: RDK, random dot kinematograms; PLW, point-light walker.

sured motion detection in noise and found that the addition of noise did not solely explain performance differences between men and women. They rather observed that the number of dots present within the display was crucial to elevate gender differences and therefore suggested that gender differences occur due to difficulties integrating motion signals across space and time and not due to a lower sensitivity to motion per se. These results are supported by an earlier study by Schieber, Hiris, White, Williams, and Brannan (1990, as cited in Schieber, 2006) who found an overall effect of age for motion detection for oscillating dot kinematograms, whereas only older women showed a reduction in motion detection for RDKs. Findings suggest that the deficits are related to the spatial pooling of motion signals, as a reduced sensitivity to motion should have affected performance for both oscillating-dot and random-dot kinematograms.

In conclusion, there is only weak evidence that age-related changes in motion processing are modulated by gender. Most likely gender differences extend to all age ranges, but are difficult to detect in relatively small groups of younger adults. Documented gender effects on perceptual abilities clearly warrant further investigation, and their particular role for age-related functional changes remains to be clarified.

Cognitive modulation

The decline of cognitive resources with age has been prominently documented. In addition, it has been shown that the deterioration of optical functions is

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linked to changes in cognitive abilities during aging (Baltes & Lindenberger, 1997; Li & Lindenberger, 2002; Lindenberger, Scherer, & Baltes, 2001). However, the impact of cognitive abilities on age-related changes in perceptual functions has not been extensively explored yet. For high-level perceptual tasks in particular, cognitive resources might be critical. Previous research on age-related changes in motion perception has provided some impetus that we feel is important to develop and pursue.

In several studies on high-level motion perception it has become evident that familiarity of stimulus characteristics modulates age effects. The more prevalent and familiar a stimulus is within our visual environment the less pronounced age effects seem to be. This has been shown with regards to different types of point-light walkers (Pilz et al., 2010) as well as for 3D shape perception from different motion cues (Norman et al., 2012; Norman, Crabtree, Norman, et al., 2006). Therefore, it is likely that processes related to long-term memory are involved in age-related decline in high-level motion perception, a relationship that certainly requires focused investigation.

Another important cognitive function that is potentially related to perceptual changes in motion perception is attention. The role of attention has been repeatedly described for biological motion perception. In younger adults, this perceptual ability crucially relies on attentional processes (Battelli, Cavanagh, & Thornton, 2003; Cavanagh, Labianca, & Thornton, 2001; Pavlova, Birbaumer, & Sokolov, 2006; Safford, Hussey, Parasuraman, & Thompson, 2010; Thornton, Rensink, & Shiffrar, 2002). It has been also shown that biological motion discrimination is related to performance in the Stroop task, a well-known measure of selective attention (Chandrasekaran, Turner, Bülthoff, & Thornton, 2010). Given that attentional control is compromised with increasing age (e.g., Lincourt, Folk, & Hoyer, 1997; for review see Park & Reuter-Lorenz, 2009), it seems reasonable to assume that age-related changes in biological motion perception are mediated by attentional abilities. Evidence, however, is still scarce. Agnew, Phillips, and Pilz (2018) assessed the relationship between different attentional tasks and biological motion perception. Similar to previous studies, they found that attention is necessary to process biological motion. However, a direct link between attentional abilities and age-related changes in biological motion processing was not established.

It is important to note that recent studies on age-related changes in perceptual abilities have repeatedly highlighted large individual differences, particularly within the group of older adults (Agnew et al, 2018; Conlon et al., 2017; Pilz et al., 2015; Shaqiri et al., 2015). Some older adults perform as well as younger adults; some show large deficits. The contribution of cognitive resources to these differences is still largely unexplored. Interestingly, there is some evidence from clinical studies that deficits scale across a continuum of age-related cognitive changes observed in healthy aging, mild cognitive impairment, and dementia (Porter et al., 2017). More research is needed in order to clarify to which extent cognitive resources can explain changes in motion perception during aging. We suggest that multiple factors underlie age-related perceptual changes (compare also Herzog, Pilz, Clarke, Kunchulia, & Shaqiri, 2016) and a stronger emphasis on individual differences in contrast to group analyses might reveal how cognitive and perceptual abilities are interlinked during aging.

Optimizing motion perception

An extensive volume of literature documents that visual performance improves with practice (for recent reviews see Dosher & Lu, 2017; Watanabe & Sasaki, 2015). Noise reduction at early processing levels is considered as a principal mechanism that optimizes visual processing during perceptual learning (Dosher & Lu, 1998). However, this mechanism interacts with complex high-level contributions that shape plasticity, e.g., attention, memory, or decision rules (Amitay, Zhang, Jones, & Moore, 2014). Thus, perceptual learning is supposed to functionally involve rather widespread neural networks. Regarding perceptual learning within the context of age-related changes in motion perception, the question arises whether the documented changes can be compensated by visual perceptual learning.

Several studies have shown learning effects for motion perception (Ball & Sekuler, 1982; Lu, Chu, & Dosher, 2006; Watanabe et al., 2002), but optimization seems to be challenged at multiple levels during aging. Firstly, behavioral (Arena et al., 2013; Bennett et al., 2007; Bogfjellmo et al., 2013) as well as neurophysiological findings (Leventhal, Wang, Pu, Zhou, & Ma, 2003; Liang et al., 2010; Schmolesky et al., 2000) indicate that internal noise levels increase with age. At the same time, tolerance to external noise decreases (Bennett et al., 2007; Pilz et al., 2010). Finally, cognitive plasticity has been found to decrease with increasing age (Jones et al., 2006; Lustig, Shah, Seidler, & Reuter-Lorenz, 2009). These issues might plausibly constrain perceptual learning; however, empirical findings have provided congruent evidence for remarkably robust learning effects in motion perception tasks across the adult lifespan.

Early evidence for efficient learning of motion discrimination in older adults was provided by Ball and Sekuler (1986). They used random dot stimuli and

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measured direction discrimination performance in younger and older adults. Older adults showed lower discrimination performance than younger adults, but their performance improved equivalently across seven training sessions. Bower and Andersen (2012) measured direction discrimination thresholds by manipulating contrast levels of noise embedded sine wave gratings and random dot kinematograms. Younger and older adults were trained across six sessions and consistently showed a decrease in thresholds for both stimulus types. Learning rates were found to be similar across both age groups. A model-based analysis indicated that overall high thresholds in older adults can be attributed to higher internal noise levels and a lower tolerance to external noise. Perceptual learning decreased noise levels and increased tolerance to external noise. Further evidence for the efficiency of perceptual learning in motion direction discrimination came from a study by Bower and colleagues (2013). Using drifting Gabor patches of different contrast levels and sizes, they confirmed substantial improvement of motion discrimination performance in younger and older adults. Their training procedure spread over five days, and results again suggested that perceptual learning is effective for optimizing noise levels. Age-related differences in spatial suppression remained unchanged across the training procedure. Whereas the so far described studies corroborate robust perceptual learning across the adult lifespan using low-level motion stimuli, data for high-level motion stimuli is still sparse. Legault and colleagues trained older adults with a multiple object tracking task for five weeks (Legault, Allard, & Faubert, 2011; Legault & Faubert, 2012). They observed that improvement in the trained task, i.e., attentional control based on motion information, transferred to biological motion perception. This finding provides preliminary support that perceptual learning provides a critical resource also for complex motion tasks during aging.

In summary, perceptual learning studies indicate a high degree of plasticity for motion perception that can counteract age-related decline. The efficiency of this putatively compensational resource, however, is still insufficiently understood. Although equivalent perceptual learning rates have been observed in older and younger adults, optimization seems to be limited by task difficulty and external noise levels (DeLoss, Watanabe, & Andersen, 2014). In addition, efficient learning in more complex scenarios requires a balance of plasticity and stability. A decrease in stability might sweep off the benefit of robust plasticity in perceptual learning (see Chang et al., 2014; Yotsumoto et al., 2014).

Motion perception for action

Action control crucially relies on visual information and dorsal stream processing (Goodale, 2011; Goodale & Westwood, 2004; for a review, see also Kravitz et al., 2011). In this framework, motion information in particular contributes to the smooth and efficient guidance of our actions. The link between age-related changes in motion perception and action control has been extensively explored for two action domains in which motion information provides a fundamental input: pursuit eye movements and locomotion. Although it is highly plausible that age-related problems in action control are substantially triggered by a decline in motion perception, specific contributions ultimately need further clarification. Since the link between motion perception and action is inherently modulated by the capacities of the motor system and the dynamics of sensorimotor integration, the contribution of perceptual aging to declined action control might be limited.

Pursuit eye movements

Smooth tracking of moving objects with our eyes requires a continuous calibration of visual motion signals and motor commands. It is generally accepted that motion perception and smooth pursuit eye movements are tightly coupled (for a review, see Schütz, Braun, & Gegenfurtner, 2011; but also compare Spering & Carrasco, 2015). Numerous studies have documented that smooth pursuit is compromised across the adult lifespan.

Congruent with general slowing older adults show increased latencies of pursuit initiation (Knox, Davidson, & Anderson, 2005; Morrow & Sharpe, 1993; Sharpe & Sylvester, 1978). Furthermore, accuracy and precision during steady-state pursuit are substantially reduced (Bozhkova, Surovicheva, Nikolaev, Nikolaev, & Bolshakov, 2015; Mateus et al., 2013; Morrow & Sharpe, 1993). It is tempting to associate these age-related differences with an underlying decline in motion perception. However, motion perception represents only one possible source of vulnerability in the process of sensorimotor transformation that drives pursuit eye movements.

Indeed, observed age-related effects on pursuit have usually been interpreted very broadly as a sign of deterioration in the visuo-motor pathways, without specifying contributions of different systems (e.g., Moschner & Baloh, 1994; Paige, 1994). Only one study so far has tried to disentangle potential vulnerabilities. Sprenger and colleagues (2011) systemically dissociated predictive contributions to

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smooth pursuit and found remarkable stability across an age range from 20 to 75 years. They concluded that age-related deficits primarily emerge from noisy motion signals, while predictive processes in the sensorimotor transformation are robust across the lifespan and putatively compensate for perceptual decline. However, it remains ambiguous as to which extent increasing noise in the motor system or deteriorated coordination within the sensorimotor cycle affect pursuit performance during aging.

Locomotion

When navigating through our environment, motion signals provide an essential source of information for efficiently controlling our track. The timely and precise detection of moving objects allows us to identify and avoid hazardous situations. Determining heading direction and speed of locomotion substantially relies on optic flow information. Several studies have explored the potential relationship between age-related changes in motion perception and locomotion, in particular when walking and driving a vehicle.

When walking, optic flow contributes to adapting gait and postural control. As a starting point of safe navigation, Agathos, Bernardin, Baranton, Assaiante, and Isableu (2017) investigated how optic flow affects postural control in younger, middle-aged, and older adults. They found that the center of pressure was less influenced by optic flow information in older compared to younger adults, potentially compromising postural stability during locomotion. It has been found that older adults adapt their walking speed as well as their walking direction less efficiently to changes in the optic flow field than younger adults (Berard, Fung, McFadyen, & Lamontagne, 2009; Lalonde-Parsi & Lamontagne, 2015). Incongruent with these finding, Chou and colleagues (2009) provided evidence that older and younger adults make comparable use of optic flow information during walking, suggesting additional factors that contribute to age-related differences in locomotion control.

During driving, age-related impairments in motion perception have been suggested to contribute to critical traffic situations. Older adults have been shown to be less sensitive to changes in vehicle velocities (Scialfa, Guzy, Leibowitz, Garvey, & Tyrrell, 1991) and to have difficulties judging vehicle trajectories (DeLucia & Mather, 2006). In addition, they often fail to identify moving hazards in driving scenes (Lacherez, Turner, Lester, Burns, & Wood, 2014) and miss upcoming collision events (Andersen, Cisneros, Saidpour, & Atchley, 2000; Andersen & Enriquez, 2006; Bian, Guindon, & Andersen, 2013). There is correlational evidence that reduced motion sensitivity might contribute to these difficulties (Conlon et al., 2015; Conlon & Herkes, 2008; Wilkins et al., 2013). Moreover, the significance of motion perception for detecting driving-relevant hazards seems to be independent of other visual functions that are subject to age-related decline, e.g., acuity, contrast sensitivity, and attentional resources (Henderson, Gagnon, Bélanger, Tabone, & Collin, 2010; Lacherez, Au, & Wood, 2014). However, it is unclear whether this link is based on specific deficits analyzing motion information or more general difficulties extracting signal from noise in cluttered visual scenes (see Conlon et al., 2015). In addition, it is still an open question as to how the described findings affect driving performance in real-life traffic situations. Although statistical analyses of road accidents show a slightly increased risk for older drivers to be involved in an accident, consideration of individual yearly driving exposure indicates that reduced yearly driving distance rather than age per se might explain the difference between younger and older adults (Hakamies-Blomqvist, Raitanen, & O'Neill, 2002). It can be assumed that safe driving relies on the interplay of a diversity of perceptual and cognitive abilities that are subject to large individual differences, not only shaped by age. Thus, the predictive power of age-related differences in motion perception for driving skills might be limited.

Concluding remarks

This review has elaborated on age-related changes in motion perception as a prominent example of perceptual development across the adult lifespan. Motion perception is a crucial visual ability and there is no doubt that it changes with age, as summarized and discussed throughout our review. However, in order to capture the functional mechanisms underlying these changes and also the scope of behavioral consequences, we have to go beyond the descriptive nature of findings from isolated tasks.

The heterogeneity of studies on age-related changes in motion perception overall has provided evidence that the notion of general perceptual decline falls short of the complex functional dynamics that fuel actual abilities. Depending on detailed task characteristics, abilities can be well preserved across the adult lifespan. The vulnerability of specific abilities can often not be explained by a hierarchy of task complexity, but seems to depend on abilities in other functional domains, e.g., cognition and motor control. It should be also noted that the fact that we see age differences in controlled experimental settings does not lead to the direct conclusion that those changes also affect older adults'

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everyday life, e.g., during driving. In addition, large individual differences suggest that a diversity of factors modulates age-related perceptual changes and that there is not one common underlying factor that drives functional decline. Finally, the longitudinal development of perceptual abilities across adulthood is barely understood. Cross-sectional results tend to support continuous changes starting in young adulthood, in contrast to a sudden functional drop at a certain age.

In conclusion, we propose that motion perception can be used as a conceptual model for studying perceptual aging. The exceptional knowledge-base on age effects in this domain provides a robust framework that can guide future research on age-related perceptual changes. It reveals critical issues that have to be considered when aiming to understand the functional changes across the adult lifespan. Age-related changes in motion perception highlight the complexity of changes that are rarely confined to specific functions, but are embedded in sensory, perceptual, cognitive, as well as motor processes. The whole picture of functional limits and resources during healthy aging might be only grasped by a comprehensive consideration of this complex interplay that is inherently linked to motion perception, but putatively also shapes other perceptual capacities across the lifespan.

Keywords: motion perception, perceptual aging, healthy aging, visual decline, individual differences

Acknowledgements

This work was supported by the German Research Foundation (Deutsche Forschungsgemeinschaft, DFG), Collaborative Research Centre SFB/TRR 135: Cardinal Mechanisms of Perception, project number 222641018.

Commercial relationships: none.
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