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# Differential aging of motion processing mechanisms: Evidence against general perceptual decline

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ABSTRACT

While the percentage of older people in our society is steadily increasing, knowledge about perceptual changes during healthy aging is still limited. We investigated age effects on visual motion perception in order to differentiate between general decline and specific vulnerabilities. A total of 119 subjects ranging in age from 20 to 82 years participated in our study. Perceptual thresholds for different types of motion information, including translational motion, expanding radial flow, and biological motion, were determined. Results revealed a substantial increase of thresholds for translational motion with age. Biological motion perception was only moderately affected by age. For both motion types, threshold elevation seemed to develop gradually with age. In contrast, we found stable radial flow analysis across lifespan. There was no evidence that age effects were dependent on gender. Results demonstrate that visual capabilities are not equally prone to age-related decline. Surprisingly, higher motion complexity might not be necessarily associated with more pronounced perceptual constraints. We suggest that differential age effects on the perception of specific motion types might indicate that specialized neuronal processing mechanisms differ in their vulnerability to physiological changes during aging.



## 1. Introduction

Demographic changes have attracted notice to the identification of capabilities and deficits in an aging population. However, studies on age effects have been dominated by the interest in cognitive changes across lifespan. Accordingly, research has provided elaborate theories of cognitive aging and has identified neural correlates of age-related changes (Hedden & Gabrieli, 2005; Raz et al., 2005). In contrast, we face a lack of information concerning how different perceptual capabilities are affected by normal aging. Although vision represents the best studied perceptual system, knowledge about visual changes during aging is limited. While it is well documented that many aspects of visual function can deteriorate during the normal aging process (Faubert, 2002; Spear, 1993; Weale, 1986), there remains insufficient differentiation between general decline and specific vulnerabilities.

Anatomical and physiological studies have provided evidence that age-related deterioration of visual functions might be prevalently due to neuronal changes in central areas. There is consensus that senescent optics of the eye cannot sufficiently explain the reported functional declines (Ball & Sekuler, 1986; Bennett, Sekuler, & Ozin, 1999; Weale, 1987). Furthermore, the retino-geniculostriate pathway appears to be relatively unaffected by age. Curcio, Millican, Allen, and Kalina (1993) have found only minor loss of photoreceptors in the human retina. Studies in monkeys have shown a stable number of retinal ganglion cells as well as preserved density, size, and receptive field properties of neurons in the lateral geniculate nucleus during aging (Ahmad & Spear, 1993; Kim, Tom, & Spear, 1996; Spear, Moore, Kim, Xue, & Tumosa, 1994). Thus, the interest has turned to aging in the cortical visual pathways. Volumetric studies in monkeys (Peters, Nigro, & McNally, 1997) and in humans (Giedd et al., 1999; Raz et al., 2004) support that striate cortex is subject to only moderate volume loss. However, it has been pointed out that functional declines during normal aging are probably due to more subtle neurophysiological changes, such as loss of myelin, degradation of synapses, decrease in neurotransmitters, or dysfunction of receptors (Wickelgren, 1996). In fact, myelinated fibres and synapses in V1 degrade in old monkeys (Peters, 2002; Peters, Moss, & Sethares, 2001; Peters & Sethares, 2002; Peters, Sethares, & Killiany, 2001). These changes are supposed to account for increased latencies and delayed transfer of information demonstrated in V1 neurons (Wang, Zhou, Ma, & Leventhal, 2005). Findings in humans which show that visually evoked potentials typically decrease in amplitude and increase in latency with aging might also be attributed to loss of synapses in striate cortex (Fiorentini, Porciatti, Morrone, & Burr, 1996). Neurophysiological studies in cats and monkeys moreover indicate that senescent V1 neurons exhibit decreased selectivity and increased spontaneous activity (Hua et al., 2006; Schmolesky, Wang, Pu, &

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Leventhal, 2000). There is strong evidence that these degraded response characteristics result from reduced GABA-mediated inhibition (Leventhal, Wang, Pu, Zhou, & Ma, 2003). Functional degradation of extrastriate cortex has been rarely addressed so far. Single unit recordings in V2 have mirrored findings in striate cortex (Wang et al., 2005; Yu, Wang, Li, Zhou, & Leventhal, 2006).

In the light of neurophysiological results the investigation of visual motion perception represents a particularly interesting behavioral approach to a better understanding of aging processes in the visual system. Motion perception is generally considered to rely on cortical areas. Directional selectivity in the visual pathways is not found before V1 and complex motion analysis relies on a variety of extrastriate areas (see for review Culham, He, Dukelow, & Verstraten, 2001; Maunsell & Newsome, 1987). Sophisticated knowledge about motion processing mechanisms has been developed and offers an excellent prerequisite for studying age-related changes. Different processing mechanisms can be distinguished dependent on the type of motion information provided. The impact of age on the perception of particular motion types can be expected to depend on the underlying neural substrates and pathways whose specific neurophysiological characteristics might make them more or less vulnerable to age-related changes. However, psychophysical studies concerned with age effects on motion perception have yielded fragmentary results because of insufficient distinction between different motion processing mechanisms. They predominantly investigated a single motion type at a time, primarily pure translation in space.

Translational motion is supposed to be processed early in the visual pathways. The first analysis and computation of translational motion occurs in V1, but extrastriate area V5/MT facilitates integration of motion signals over space and noise reduction (see for review Born & Bradley, 2005). Brain imaging and lesion studies in humans have confirmed area V5/MT as critical functional region (Dumoulin et al., 2000; Schenk & Zihl, 1997; Sunaert, Van Hecke, Marchal, & Orban, 1999; Vaina, Cowey, Eskew, LeMay, & Kemper, 2001). Translational motion is most often defined by luminance (first-order). Processing of motion signals defined by contrast, texture, or depth (second-order) seems to involve additional extrastriate areas, such as V3 and VP (Smith, Greenlee, Singh, Kraemer, & Hennig, 1998). Previous studies interested in translational motion perception as a function of age differed with regard to experimental design and stimulus characteristics so that results are not directly comparable. However, there is consensus about sensitivity decline starting in the twenties. Porciatti, Fiorentini, Morrone, and Burr (1999) have described an increase in response time to motion onset which can partially be attributed to a sensory origin. Several studies using gratings and random dot kinematograms have shown age-related elevation of motion detection thresholds (Gilmore, Wenk, Naylor, & Stuve, 1992; Habak & Faubert, 2000; Snowden & Kavanagh, 2006; Tran, Silverman, Zimmerman, & Feldon, 1998; Trick & Silverman, 1991; Wojciechowski, Trick, & Steinman, 1995). Habak and Faubert (2000) have specified that threshold elevation is more pronounced for second-order motion compared to first-order motion. They have argued that vulnerability might be increased due to more complex processing networks which make degradation more evident. Only the studies of Tran et al. (1998) and Trick and Silverman (1991) considered samples with an age range allowing for calculation of correlations between age and detection thresholds. They reported coefficients of $r(46) = 0.37$ and $r(95) = 0.46$, respectively. There is also some evidence that speed discrimination performance deteriorates with age (Norman, Ross, Hawkes, & Long, 2003; Snowden & Kavanagh, 2006). A possible dependency of motion sensitivity decline on gender is under debate. Gilmore et al. (1992) found women's performance more strongly affected by age. In contrast, Snowden and Kavanagh (2006) did not confirm gender-specific age effects. However, their female observers showed overall 50% higher thresholds than their male observers. Recent psychophysical studies aimed not only to determine age-related decline, but also to explore underlying neurophysiological mechanisms. Betts, Taylor, Sekuler, and Bennett (2005) have demonstrated that direction discrimination improves with age when motion information is extracted from large, high-contrast pattern. They have argued that this result might be linked to a degradation of GABA-mediated inhibition which weakens the center-surround antagonism found also in motion areas (Born, 2000; Pack, Hunter, & Born, 2005; Tadin, Lappin, Gilroy, & Blake, 2003). Bennett, Sekuler, and Sekuler (2007) have considered motion detection as well as direction identification during aging and fitted results with a multichannel model of motion. The derived model mirrors well neurophysiological findings of decreased selectivity and increased spontaneous activity in senescent V1 neurons.

Motion information beyond translation has rarely been considered in aging studies so far. Particularly radial flow and biological motion represent two other motion types which have high ecological relevance.

Radial flow occurs for example when an observer moves through the environment. Expanding radial flow generated by forward motion is important for heading and navigation in space. The anatomical basis of radial flow analysis and heading perception remains elusive. Selectivity for expanding radial flow emerges at the level of area MST which receives strong input from area V5/MT (Duffy & Wurtz, 1991a; Duffy & Wurtz, 1991b; Saito et al., 1986). In comparison to V5/MT neurons, MST neurons exhibit stronger spatial summation while antagonistic surrounds are less frequent (Lagae, Maes, Raiguel, Xiao, & Orban, 1994). Imaging and lesion studies in humans agree on the significant contribution of areas V5/MT and MST to flow analysis, but selective responses have been described for various distributed areas (Beardsley & Vaina, 2005; de Jong, Shipp, Skidmore, Frackowiak, & Zeki, 1994; Field, Wilkie, & Wann, 2007; Greenlee, 2000; Morrone et al., 2000; Peuskens, Sunaert, Dupont, Van Hecke, & Orban, 2001; Royden & Vaina, 2004; Vaina & Soloviev, 2004; Wunderlich et al., 2002). Findings support the view that heading perception engages a network of neural regions including V5/MT, parietal and frontal regions. The behavioral relevance of radial flow analysis and its development across lifespan is not reflected by research interest. There have been only two suitable aging studies. Atchley and Andersen (1998) found radial flow detection to be unaffected by age. With regard to heading detection, Warren, Blackwell, and Morris (1989) reported that the minimal focus of expansion shift from a central fixation point needed to detect heading increases from 1.1° in young adults to 1.9° in senior adults.

Even less is known about the influence of age on biological motion perception. Biological motion is elicited by the moving form of a human figure and contributes to social interaction. Understanding of specific processing mechanisms has rapidly developed over the last years. Although some involvement of area V5/MT in biological motion analysis has been demonstrated, lesion and brain imaging studies in humans have assigned crucial functional significance to other brain areas, in particular the posterior superior temporal sulcus and premotor areas (Battelli, Cavanagh, & Thornton, 2003; Grossman, Battelli, & Pascual-Leone, 2005; Grossman et al., 2000; Saygin, 2007; Saygin, Wilson, Hagler, Bates, & Sereno, 2004; Vaina & Gross, 2004; Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001). Neurophysiological changes during aging in these critical areas are unexplored. The only psychophysical study concerned with aging of biological motion perception found well preserved abilities to discriminate different activities (Norman, Payton, Long, & Hawkes, 2004).

In summary, knowledge about aging of motion perception is sparse and obviously requires further investigation. The view of a

general age-related decline in sensitivity to all motion types might be an oversimplification. Processing of different motion types involves specific neural subsystems which might be differentially prone to deterioration.

In our present study, we were interested in the effect of aging on the perception of different types of motion information, namely translational motion, expanding radial flow, and biological motion. We intended to collect data from a large representative sample covering a wide age range because small samples sizes could obscure changes due to interindividual variability in trajectories of aging effects. We expected to win insight into specific perceptual vulnerabilities by measurement of performance in different tasks. Stimuli were chosen according to attentional capacity of senior participants so that sensitivity determination could be accomplished conveniently at all age levels. Although we aimed to design our stimuli and procedures as comparable as possible, we did not intend to match motion stimuli exactly according to certain parameters, such as speed, size or density of motion signals. Specific motion types differ inherently in these parameters, for example the velocity distribution of expanding radial flow is dominated by high velocities whereas natural biological motion is composed of slow motion signals. Therefore, we considered these differences as inevitable and set our primary focus to the specificity of the different motion types. Furthermore, careful review and comparison of previous psychophysical studies on motion perception did not yield conclusive reason to predict a modification of age effects by various parameters. Despite substantial differences in used stimuli, most studies agree in their description of age-related threshold elevation (Gilmore et al., 1992; Tran et al., 1998; Trick & Silverman, 1991; Wojciechowski et al., 1995). However, a recent study of Snowden and Kavanagh (2006) has varied stimulus speed systematically and provided some evidence that threshold increase might be limited to slow speeds. Although the study draws attention to a possible modification of age effects by stimulus parameters, there remains definitely the need for further investigation how this inconsistent result relates to the majority of previous findings.

## 2. Method

### 2.1. Participants

A total of 119 subjects (62 females) ranging in age from 20 to 82 years participated in the main study. In addition, 8 young and 6 senior participants were recruited for a subsidiary experiment. Visual acuity was measured binocularly by using a Landolt C chart constructed for near space. All subjects had normal or corrected-to-normal vision. Subjects were free from ocular diseases and were not taking medications known to interfere with visual functioning. None had a history of neurological disorders. Informed consent was obtained from all participants. Methods and procedures were approved by the local ethics committee.

### 2.2. Apparatus

Stimuli were generated by a Dell Latitude 600 at a frame rate of 35 Hz and displayed on a 21 inch Iiyama Vision Master Pro 513 CRT monitor driven by a NVIDIA Quadro NVS 285 graphics card. The monitor resolution was set to 1154 × 864 pixels. White and black pixels had a luminance of 97.5 and 0.3 cd/m$^2$, respectively, resulting in a maximum Michelson contrast of 99%. A gamma correction ensured linearity of gray levels. Subjects were seated in a darkened room at a distance of 60 cm in front of the monitor. Viewing was binocular and subjects' head was stabilized by a chinrest.

### 2.3. Stimuli

Random dot kinematograms were used to present translational motion, radial flow, and biological motion. They were composed of white dots with a diameter of 0.1° on a black background. Fig. 1 illustrates the stimuli.

The translational motion stimulus was presented within a circular aperture with a diameter of 9.4° containing 60 dots. A certain percentage of dots moved in the same horizontal direction, either to the right or to the left, at a speed of 6.6°/s, resulting in coherent motion. The other dots moved in random direction. Dots moving out of the aperture reappeared at a new random position within the aperture. Dots had a limited lifetime of four frames. Signal intensity was defined by percentage of coherently moving dots. For a subsidiary experiment, we modified the translational motion stimulus so that it consisted of 100 dots moving within a rectangular aperture (37.5° × 28.5°). A certain percentage of dots moved in the same horizontal direction, either to the right or to the left, at a speed of 18.6°/s. The rest of the dots moved in random direction. All other parameters remained identical to the original stimulus. The original task was well suited to determine sensitivity for translational motion and could be considered as representative with regard to studies on motion perception using random dot stimuli (e.g., Britten, Shadlen, Newsome, & Movshon, 1992; Newsome & Pare, 1988). However, we realized that results from previous aging studies on translational motion perception provide only fragmentary or inconsistent knowledge of how age effects might be modified by specific stimulus parameters (Gilmore et al., 1992; Habak & Faubert, 2000; Snowden & Kavanagh, 2006; Tran et al., 1998; Trick & Silverman, 1991; Wojciechowski et al., 1995). Thus, we intended to check for a possible dependency of observed effects on parameters which could be easily manipulated without changing the main characteristics of the motion type. In addition, the chosen size, speed, and dot density of the modified translational motion stimulus enhanced direct comparability with the radial flow stimulus described in the following paragraph.

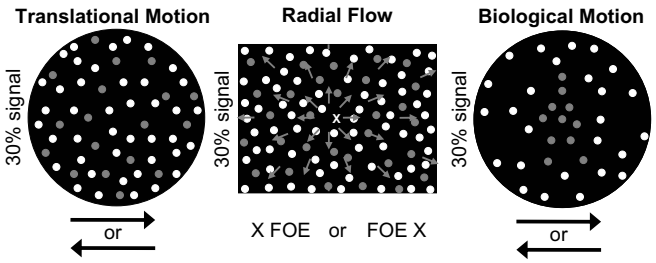


**Fig. 1.** Static representation of motion stimuli. Signal dots are shown in gray and noise dots in white for clarification. In the actual stimuli, all dots were white. Translational motion was defined as horizontal coherent motion of the signal dots either to the right or to the left. In the radial flow stimulus, signal dots expanded with the focus of expansion (FOE) either right or left of the fixation dot. The latter is replaced here by *X* to demarcate the fixation sign from the dots. Small gray arrows indicate the motion direction of the signal dots but were not present in the actual stimulus. The biological motion stimulus consisted of a canonical point-light walker embedded in noise dots. It moved as if on a treadmill, facing either to the right or to the left.

The radial flow stimulus consisted of 100 dots expanding within a rectangular aperture (37.5° × 28.5°) simulating forward motion on a straight path. A certain percentage of dots expanded coherently whereas the rest moved in random direction. The focus of expansion was shifted horizontally 5.6° either to the right or to the left of the center of the field. Since we aimed to determine sensitivity by manipulating the signal-to-level in the stimulus, we chose a heading angle which lay well beyond the perceptual thresholds of 1.9° reported by Warren et al. (1989) for senior adults. Speed of expansion increased linearly from the focus of expansion to a maximum speed of 18.6°/s in the periphery. Again, dots had a limited lifetime of four frames and dots moving out of the aperture reappeared at random position within the aperture. Signal intensity was defined by percentage of coherently expanding dots.

A point-light walker represented the biological motion stimulus. The walker consisted of eleven dots and was defined by the point-light walker algorithm described by Cutting (1978). It subtended a visual angle of 5.3° in height and 2.0° in width. The walker was shown in a sagittal view and moved in place as if on a treadmill with either left- or rightward gait. Duration of a stride cycle was set to 1 s which falls in the range for normal human walking as reported by Inman, Ralston, and Todd (1981). The walker appeared in a circular aperture with a diameter of 9.4° and was masked by a varying number of noise dots. Noise dots moved in random direction, had a limited lifetime of four frames and reappeared at random position when moving out of the aperture. Signal intensity was defined by percentage of walker dots relative to the total number of dots.

### 2.4. Procedure

Stimuli were presented in spatial 2-alternative-forced-choice-paradigms. Subjects were instructed to fixate at the center of the screen that was set to minimum luminance. A red fixation dot with a diameter of 0.7° was provided 500 ms before stimulus onset. Stimuli were displayed for 400 ms.

In the translational motion task, two apertures appeared simultaneously right and left of the fixation dot. Their centers were shifted horizontally to an eccentricity of 7.5°. One aperture contained coherent motion whereas in the other one all dots moved randomly. Subjects had to indicate on which side they had seen coherent motion. In the modified translational motion task, subjects were presented with wide field motion and had to detect the direction of translation. In the radial flow

task, subjects had to detect the direction of heading, i.e., they had to indicate whether the focus of expansion was shifted to the right or to the left of the fixation dot. In the biological motion task, again two apertures appeared simultaneously right and left of the fixation dot with their centers shifted horizontally to an eccentricity of 7.5°. In one aperture, a canonical point-light walker occurred masked by noise dots. In the other one, a scrambled walker and the same amount of noise dots were presented. The scrambled walker consisted also of eleven dots whose motion matched the motion of the dots in the canonical walker. However, dots' spatial position was randomized within the aperture so that the canonical structure was lost. Subjects had to indicate at which side they had seen the canonical walker.

In all motion tasks, responses were entered without temporal constraints directly on the keyboard after stimulus presentation. No feedback was given. Subjects started each new trial by pressing the space bar. Before obtaining threshold data, sufficient practice trials were given so that subjects got used to the task and could effortlessly handle the keyboard.

We used the method of constant stimuli to measure perception thresholds. Signal intensity was varied by five different noise levels. Each signal-to-noise level was presented in 32 trials, resulting in a total of 160 trials. The number of correct responses at each noise level was recorded. Due to technical reasons and time constraints during testing, some subjects could not complete all of the motion tasks. We were able to test detection of (i) translational motion in 117 subjects, (ii) radial flow in 117 subjects, and (iii) biological motion in 112 subjects.

### 2.5. Psychophysical data analysis

Thresholds were obtained by fitting the percentage of correct responses with a Weibull function for a performance level of 75%. We used the psignifit toolbox in Matlab (Wichmann & Hill, 2001a, 2001b) and assessed the goodness of fit of the psychometric function. Summary statistics yielded a good fit between the model and the data. Threshold data was subject to correlational analysis. For each motion type, we determined the correlation between individual thresholds and age by Pearson's coefficient $r$. We then transformed each correlation coefficient by using Fisher's normalizing and variance-stabilizing $Z$ transformation (compare Fisher, 1990). $Z$ coefficients facilitate comparison between coefficients and allow for testing via a $z$ statistic if coefficients differ significantly. In addition, perceptual thresholds for each motion type were regressed on age using least-squares linear regression. Regression equations and standard errors of the estimate were derived. All analyses were performed on the complete data set as well as on gender-specific data subsets. Age-specific thresholds obtained from the subsidiary experiment as well as overall gender-specific thresholds were compared via $t$ tests for independent samples.

## 3. Results

Fig. 2A demonstrates the effect of age on motion perception by performance of single observers. For each motion task, psychometric functions of a typical young and a typical senior observer are shown together. Observers showed representative detection thresholds according to their specific age (see Fig. 2B). Psychometric functions differed most clearly for translational motion indicating decreased sensitivity in the senior subject. Age-related sensitivity decline appeared less pronounced for biological motion and almost absent for radial flow.

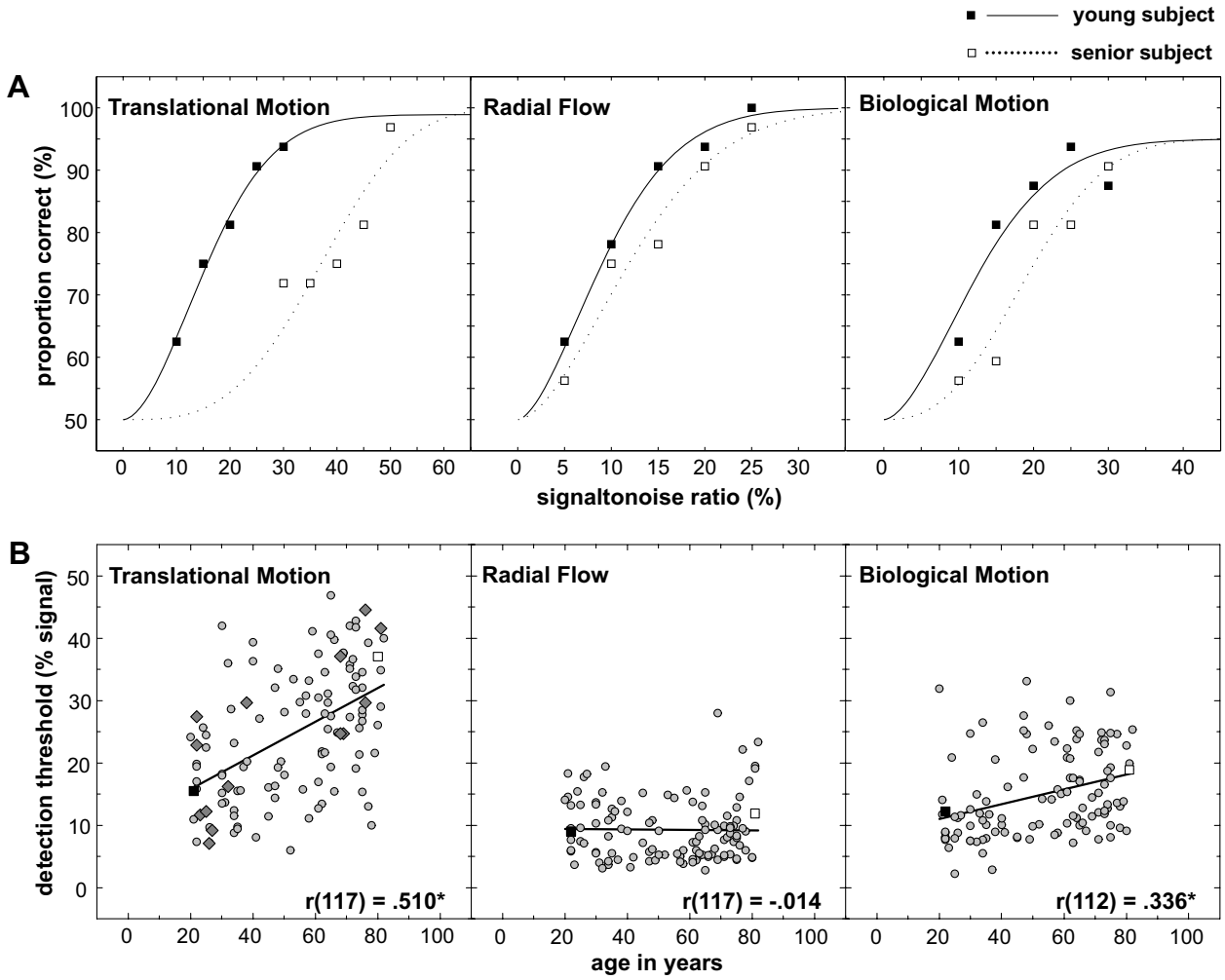


**Fig. 2.** Detection thresholds for different motion types. (A) Psychometric functions. Detection accuracy is plotted as function of signal intensity. For each motion type, performance of a typical young subject (solid lines, solid squares) and a typical senior subject (dotted lines, open squares) with representative thresholds referring to their age group (see B) is shown. Note that scaling of the $x$-axis varies with stimulus type. (B) Detection thresholds plotted as a function of age. Solid squares and open squares correspond to the young and senior subjects whose psychometric functions are shown in (A). For each motion type, the regression line and Pearson's $r$ coefficient are given, $^{*}p < .05$. In the translational motion plot, data of subjects who participated in the subsidiary experiment with wide field translational motion is added by dark gray diamonds.

**Table 1**
General and gender-specific relation between age and detection thresholds for different motion types

| Motion type | Correlation with age | | Regression on age | |
|---|---|---|---|---|
| | *r* | *Z* | Regression equation | $s_e$ |
| *Translational motion* | | | | |
| All subjects | | | | |
| *n* = 117 | .510* | .563 | *Y′* = 10.414 + .270*X* | 8.941 |
| *Males* | | | | |
| *n* = 57 | .452* | .487 | *Y′* = 9.134 + .245*X* | 9.200 |
| *Females* | | | | |
| *n* = 60 | .602* | .693 | *Y′* = 11.538 + .295*X* | 8.054 |
| *Radial flow* | | | | |
| All subjects | | | | |
| *n* = 117 | −.014 | −.014 | *Y′* = 9.491 −.004*X* | 4.913 |
| *Males* | | | | |
| *n* = 57 | −.181 | −.183 | *Y′* = 9.551 −.035*X* | 3.626 |
| *Females* | | | | |
| *n* = 60 | .094 | .094 | *Y′* = 9.531 + .025*X* | 5.446 |
| *Biological motion* | | | | |
| All subjects | | | | |
| *n* = 112 | .336* | .350 | *Y′* = 8.649 + .119*X* | 6.549 |
| *Males* | | | | |
| *n* = 53 | .335* | .348 | *Y′* = 7.526 + .101*X* | 5.435 |
| *Females* | | | | |
| *n* = 59 | .374* | .393 | *Y′* = 9.538 + .138*X* | 6.962 |

*Note.* *r*, Pearson's *r* coefficient; *$p < .05$; *Z*, Fisher's *Z*-transformed correlation coefficient; $s_e$, standard error of the estimate.

Differences of exemplary psychometric functions were corroborated by analysis of threshold data for the complete sample. Correlations of detection thresholds in different motion tasks with age are illustrated in Fig. 2B. Table 1 gives correlation coefficients and regression data.

Significant correlations were found in the translational motion task and the biological motion task, but not in the radial flow task. Observed threshold increase appeared to emerge gradually during aging. Fishers *Z*-transformation of correlation coefficients allowed direct comparison.

Perception of translational motion showed the strongest correlation with age. Thresholds increased by 2.7% signal per decade. Data predicts a relative threshold increase of approximately 68% from age of 20 to age of 60. Thresholds in the radial flow task were not affected by age. Finally, a medium correlation between perception of biological motion and age was found. The increase of thresholds per decade added up to 1.2% signal. This corresponds to a relative threshold increase of about 43% from age of 20 to age of 60.

Comparison of the observed correlations between specific thresholds and age confirmed that the coefficient for radial flow differed significantly from those for translational motion, $z = 4.35$, $p < .01$, and biological motion, $z = 2.71$, $p < .01$. The difference between the coefficients for translational motion and biological motion did not reach significance, $z = 1.6$ $p = .11$.

To summarize results, perception thresholds for the three motion types were affected differentially by age. In terms of effect sizes, increase of thresholds for translational motion could be considered as medium whereas increase of thresholds for biological motion turned out to be rather small. Finally, radial flow strikingly differed from both other motion types in that perceptual thresholds were not affected by age.

### 3.1. Subsidiary experiment: Wide field translational motion

In a subsidiary experiment, we manipulated speed, size, and dot density of the original translational motion task. We aimed to explore a possible dependency of the described age effects on these parameters. Modifications also enhanced comparability with the radial flow task. Additionally recruited young and senior subjects showed representative thresholds for translational motion in the original task. Data is added to Fig. 2B by dark gray diamonds. Thresholds in the wide field translation task exhibited a significant age effect, $t(12) = -6.37$, $p < .01$. Young subjects showed significantly lower thresholds ($M = 2.8$, $SD = 1.4$) than senior subjects ($M = 7.3$, $SD = 1.2$). This result corroborated our original finding. Thus, it appears that manipulation of speed, size, or dot density does not change the age effect on perception of translational motion. Furthermore, the absent effect on radial flow perception is unlikely to be explained by mere differences in the considered parameters since comparability was given in the subsidiary experiment.

### 3.2. Sensitivity to different motion types: Intercorrelations

Fig. 3 depicts intercorrelations between thresholds for different motion types.

Translational motion thresholds significantly correlated with radial flow and biological motion thresholds, $Z = 0.293$ and $Z = 0.383$, respectively. Correlations of medium size might point to shared underlying processing mechanisms. In contrast, the correlation between thresholds for biological motion and radial flow turned out to be not significant, $Z = 0.105$. This might indicate that processing of both motion types relies on less shared resources.

### 3.3. Dependence of age effects on gender

Thresholds for motion perception were further analyzed with regard to a possible dependency on gender. Table 1 includes gender-specific correlation coefficients and regression data for

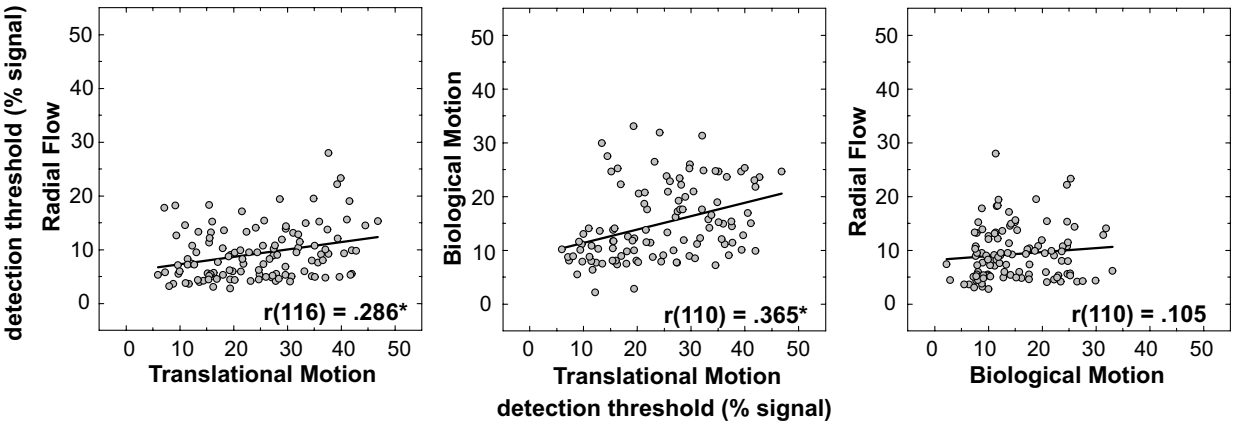


**Fig. 3.** Intercorrelations between detection thresholds for different motion types. Pearson's *r* coefficient is given for each intercorrelation, *$p < .05$.

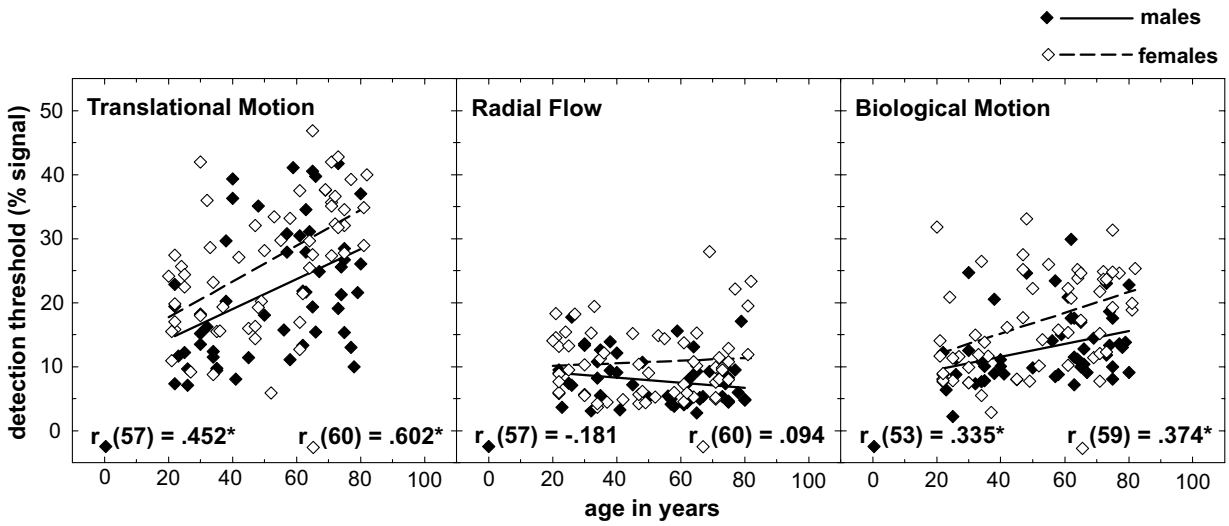


**Fig. 4.** Gender-specific detection thresholds. Detection thresholds separately plotted for male and female subjects as a function of age. Solid and open diamonds represent data for male and female subjects, respectively. For each motion type, gender-specific regression lines and Pearson's $r$ coefficients are given, $^{*}p < .05$.

the different motion types. In Fig. 4, performance in different motion tasks as a function of age is plotted separately for male and female subjects.

Female subjects showed higher thresholds for translational motion, $t(115) = -2.58$, $p = .01$, for radial flow, $t(110) = -3.03$, $p < .01$, as well as for biological motion, $t(115) = -3.68$, $p < .01$. However, the absolute differences between gender-specific mean thresholds could be considered as rather small. Respective thresholds (with standard deviations in parentheses) for male and female subjects were 22.2 (10.2) and 27.0 (10.0) for translational motion, 12.9 (5.7) and 16.7 (7.4) for radial flow, and 7.7 (3.7) and 10.8 (5.4) for biological motion. We found no evidence for a gender-specific threshold increase with age. Comparison of correlation coefficients yielded nonsignificant results for translational motion, $z = 1.10$, $p = .27$, for radial flow, $z = 1.46$, $p = .14$, and for biological motion, $z = 0.23$, $p = .82$. Thus, age effects on motion perception appear comparable in male and female subjects.

## 4. Discussion

Although the percentage of older adults in our society is steadily increasing, knowledge about changes in perceptual capabilities during healthy aging still appears limited. We aimed to investigate age effects on visual motion perception in order to differentiate between general decline and specific vulnerabilities. Whereas most previous aging studies on motion perception have investigated only one type of motion, we decided to collect data for three different motion types. Furthermore, our sample comprised more observers and covered a broader age range than in any aging study on motion perception before. Our results point to differential age effects on the perception of specific motion types. This might indicate that specialized neuronal processing mechanisms differ in their vulnerability to physiological changes during aging.

We showed a clear increase of thresholds for translational motion from an average signal-to-noise ratio of 18% in young adulthood to a ratio of approximately 30% in old age. Observed correlation between age and thresholds, $r(117) = 0.51$, sufficiently agrees with previous reports by Tran et al. (1998) and Trick and Silverman (1991), $r(46) = 0.37$ and $r(95) = 0.46$, respectively. Snowden and Kavanagh (2006) recently found evidence that age-related deterioration of translational motion perception is restricted to slow speeds less than 2°/s. In the present as well as in previous aging studies stimuli at higher speeds were used and significant age effects were confirmed. Hence, a possible dependency of age effects on speed remains puzzling and needs further clarification. In contrast to translational motion, changes in perception of other motion types during aging have been neglected so far. We additionally considered analysis of radial flow and biological motion. Heading determination from wide field radial flow was not affected by age. Observers required an average signal-to-noise ratio of about 10% independent of their age. This result corroborates previous findings showing that detection of radial flow is robust to aging (Atchley & Andersen, 1998), but moreover shows that heading detection is preserved during aging. Warren et al. (1989) reported small decrements in heading detection with age. However, they varied FOE shift and the fixed FOE shift we used (5.6°) lay well beyond described thresholds (1.9°). For detection of biological motion, we only found a small age effect. The average threshold signal-to-noise ratio increased from 11% in early adulthood to 17% in old age. Relatively robust biological motion detection complements the study of Norman et al. (2004) in which discrimination of different activities defined by biological motion proved to be comparable in young and senior adults. Our data did not confirm a dependence of aging effects on motion perception by gender (Gilmore et al., 1992). In line with Snowden and Kavanagh (2006) female observers showed higher thresholds than male observers for all applied motion types, but there was no differential increase in thresholds with age. It should also be noted that we observed gradually increasing thresholds across age levels. In the study of Bennett et al. (2007) age-related changes became only apparent in subjects older than 70 years. However, analysis was based on group data and sample size per age group was rather small. Thus, changes at earlier age levels might have been obscured.

We are aware of some methodological factors that might complicate the interpretation of our results and deserve careful consideration. Since we were primarily interested in different motion types, we accepted differences in stimulus parameters, such as size, speed, or dot density, as inherent to the specific motion characteristics. For the benefit of measurement of thresholds for three different motion types in the same sample, including senior participants with limited general resilience, we refrained from extensively varying motion parameters. Reviewing previous aging

studies on motion perception, we considered this procedure as appropriate. For example, age effects on translational motion perception in random dot kinematograms have been described for stimulus speeds ranging between 1.2 °/s (Norman et al., 2003) and 28°/s (Wojciechowski et al., 1995) as well as for stimulus sizes ranging between a circular aperture of 10° (Gilmore et al., 1992) and a square of 60° by 60° (Trick & Silverman, 1991). Similarly, age effects on radial flow perception have not been found to be modified by such parameters as dot density (Warren et al., 1989) or stimulus eccentricity (Atchley & Andersen, 1998). Finally, our own subsidiary experiment pointed to invariance of results for translational motion despite manipulation of speed, size, or dot density. We cannot completely exclude that observed differential age effects might be elicited to some degree by differences in motion parameters. Indeed, Snowden and Kavanagh (2006) found aging affects only for slow speeds. However, for the range of speeds relevant to our stimuli all previous studies reported a significant age dependency. We therefore consider it as rather unlikely that differences in motion parameters significantly contribute to the explanation of differential effects. Bearing in mind the conceptual constraints of our study, we therefore propose the following conclusions from our results.

Selective age effects on visual perception of different motion types put into question general perceptual decline during aging. In contrast to most previous aging studies on motion perception (but see Habak & Faubert, 2000), the present study investigated different motion types at the same time. Hence, unspecific factors like motivation or concentration are unlikely to account for the observed differential effects. Perception of different motion types seems to be carried out by networks that differ in their vulnerability to neurophysiological changes during aging. Correspondingly, performance in specific motion tasks has been shown to mature differentially in infants (Banton & Bertenthal, 1997).

Faubert (2002) has argued that magnitude of age-related deterioration depends on complexity of neural networks involved in a specific perceptual process. Deficits have been thought to become more obvious the more resources are required. In line with this argument, it has been shown that perception of second-order motion declines more with age than perception of first-order motion (Habak & Faubert, 2000). With regard to our data, one might speculate that motion types with high ecological relevance, e.g., radial flow or biological motion, are processed especially efficiently and are therefore less affected by age-related decline. Indeed, a multiplicity of functional pathways which bypass primary visual cortex and directly connect vast cortical regions involved in motion processing has been reported (Schoenfeld, Heinze, & Woldorff, 2002). Recent studies have furthermore distinguished between low-level motion extraction and specialized mechanisms of velocity analysis and life detection for heading determination and biological motion perception, respectively (Li, Sweet, & Stone, 2006; Troje & Westhoff, 2006). However, an additional argument might be derived from our results. Vulnerability to age-related decline might not only be determined by the number of required processing steps, but also by the specific brain regions that are functionally involved. We considered motion types which share some processing pathways, but which also activate quite distinct brain regions. Though highly interconnected, motion areas differ in their neuronal characteristics, in particular in their response properties which ultimately rely on specific neurotransmitters. Neurophysiological studies have so far focused on senescent neurons in V1 and V2 (Leventhal et al., 2003; Schmolesky et al., 2000; Wang et al., 2005; Yu et al., 2006). Changes in higher areas in the visual pathways and their implications for motion perception remain to be explored. In this context, a study of Carter et al. (2004) appears relevant. Their results indicate that enhanced serotonin activity impairs motion perception in random dot kinematograms, believed to rely on area V5/MT, but not motion perception in gratings, believed to be accomplished already by area V1. Thus, there is some evidence that global neurophysiological changes might have quite different effects on perception of specific motion stimuli.

In conclusion, our findings support the hypothesis that perceptual capabilities are not equally prone to age-related deterioration. We found differential aging of motion processing mechanisms. During healthy aging, heading perception from radial flow and biological motion perception seem to be well preserved. Robustness might be attributed to especially efficient processing mechanisms as well as to specific neurophysiological characteristics of functionally involved brain regions.

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