

# Differential aging effects in motion perception tasks for central and peripheral vision

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The perception of motion is considered critical for performing everyday tasks, such as locomotion and driving, and relies on different levels of visual processing. However, it is unclear whether healthy aging differentially affects motion processing at specific levels of processing, or whether performance at central and peripheral spatial eccentricities is altered to the same extent. The aim of this study was to explore the effects of aging on hierarchically different components of motion processing: the minimum displacement of dots to perceive motion ( $D_{min}$ ), the minimum contrast and speed to determine the direction of motion, spatial surround suppression of motion, global motion coherence (translational and radial), and biological motion. We measured motion perception in both central vision and at 15° eccentricity, comparing performance in 20 older (60–79 years) and 20 younger (19–34 years) adults. Older adults had significantly elevated thresholds, relative to younger adults, for motion contrast, speed,  $D_{min}$ , and biological motion. The differences between younger and older participants were of similar magnitude in central and peripheral vision, except for surround suppression of motion, which was weaker in central vision for the older group, but stronger in the periphery. Our findings demonstrate that the effects of aging are not uniform across all motion tasks. Whereas the performance of some tasks in the periphery can be predicted from the results in central vision, the effects of age on surround suppression of motion shows markedly different characteristics between central and peripheral vision.

## Introduction

The perception of motion is critical for everyday tasks, such as locomotion, social interaction, and driving. This ability relies on different levels of processing, ranging from the detection of spatial changes of objects over time (Nakayama & Tyler, 1981) and the perception of contrast at early stages of the visual pathway (Boynton, Demb, Glover, & Heeger, 1999), to more complex levels of processing that require broad integration of spatial and temporal motion signals (e.g., optic flow: Duffy & Wurtz, 1991) or integration between motion and form (e.g., biological motion: Grossman et al., 2000).

In humans, it is possible to study specific components of motion processing using different psychophysical stimuli. For example, sine wave gratings, which are commonly used to test low levels of visual processing, such as contrast sensitivity, have been used to explore perceptual motion receptive fields (Watson & Turano, 1995). Sine wave gratings are also used to study surround suppression of motion. Neuronally, surround suppression refers to the decrease in the neural response to a suprathreshold stimuli when surrounded by a

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pattern of similar visual characteristics, or when a large stimulus extends outside the classical receptive field (Cavanaugh, Bair, & Movshon, 2002). Neurons exhibiting surround suppression properties are present at all levels of motion processing (Eifuku & Wurtz, 1998; Huang, Albright, & Stoner, 2008; Jones, Grieve, Wang, & Sillito, 2001). Another type of stimulus widely used to explore motion perception is the random-dot kinematograms (RDKs). The use of this type of stimulus has helped identify different brain regions utilized in the perception of more complex motion patterns, such as translational global motion in the middle temporal area/V5 (Albright, 1984; Newsome & Pare, 1988; Zeki, 1980), and optic flow in the medial superior temporal (MST) area (Britten & van Wezel, 1998; Duffy & Wurtz, 1991; Graziano, Andersen, & Snowden, 1994). RDKs can also be used to test low levels of processing, such as the minimum displacement of motion or  $D_{\min}$  (Bullimore, Wood, & Swenson, 1993; Turano & Wang, 1992). As mentioned earlier, a more complex motion pattern corresponds to the perception of biological motion. To explore this type of motion, a specific dot pattern called the point light walker is used (Johansson, 1973). Human behavioral studies have related the perception of this type of motion to the superior temporal sulcus area (Grossman & Blake, 2002; Grossman et al., 2000; Puce & Perrett, 2003).

It is well established that physiological aging affects many aspects of visual performance, but not all aspects of visual processing are affected in the same way or to the same extent (for reviews see: Allard, Renaud, Molinatti, & Faubert, 2013; McKendrick, Chan, & Nguyen, 2018; Owsley, 2011; and Spear, 1993). With regard to motion perception, a recent review by Billino & Pilz (2019) provided evidence that the effects of healthy aging in motion perception are still unclear, and the results of different motion tasks are highly dependent on experimental design or individual performance. There is evidence that older adults, when compared with younger adults, have elevated thresholds for tasks processed at early stages of the motion pathway, such as the minimum displacement of dots required to perceive motion:  $D_{\min}$  (Wood & Bullimore, 1995). Additionally, Snowden and Kavanagh (2006) reported that older adults have elevated thresholds for perceiving differences in the speed of moving gratings. More complex stages of motion processing are also affected by aging. Numerous authors have reported an elevation of coherence thresholds for translational global motion in older adults (Arena, Hutchinson, & Shimozaki, 2012; Billino, Bremmer, & Gegenfurtner, 2008; Genova & Bocheva, 2013; Gilmore, Wenk, Naylor, & Stuve, 1992; Roudaia, Bennett, Sekuler, & Pilz, 2010; Snowden & Kavanagh, 2006; Tran, Silverman, Zimmerman, & Feldon, 1998). However, the results for the perception of optic flow are more ambiguous. Although

Billino et al. (2008) did not find an aging effect on the ability to perceive this type of motion, Bennett, Sekuler, and Sekuler (2007) reported that older adults have problems discriminating radial motion signals from random noise. Biological motion is an even more complex motion percept, with previous studies showing that in central vision older adults experience difficulties in the recognition of the direction of point light walkers embedded in noise (Billino et al., 2008; Norman, Payton, Long, & Hawkes, 2004; Pilz, Bennett, & Sekuler, 2010).

Regarding age-related changes in surround suppression of motion, Betts, Taylor, Sekuler, and Bennett (2005) reported that older adults required shorter presentation times to discriminate the direction of motion of larger gratings of higher contrast compared with younger adults, which suggests a decrease in the magnitude of surround suppression produced by these large stimuli in older adults.

Despite these reports of differences in motion perception between younger and older adults, there is limited evidence regarding the relative impact on different components of motion processing in the same cohort of participants (Billino et al., 2008; Snowden & Kavanagh, 2006). In particular, the methodologies in previous studies differ in terms of the stimuli used, the experimental set-ups and participant characteristics. As suggested by Billino and Pilz (2019) in their review, applying a battery of tests with a common experimental procedure to a single cohort, would enable clarification of whether previous differences in aging effects reported both within and between studies are due to specific deficits in the visual system rather than other factors, such as differences in the cognitive demands of the tasks. Another important point to highlight is that previous studies have largely focused on motion perception in central vision, yet it is known that the effects of aging on central and peripheral visual function may be different, as previously shown by Atchley and Andersen (1998) and Nguyen and McKendrick (2016). From an applied point of view, exploring peripheral motion perception may also be informative to determine whether age-related changes in motion perception can explain the difficulties that older adults experience in everyday tasks (such as peripheral object recognition, hazard avoidance, and driving).

Hence the main aim of this study was to systematically explore whether there are age-related changes in motion perception at different levels of processing in central and peripheral vision. In this study, we designed a battery of seven motion tasks with different complexities to hierarchically explore specific components of the motion pathway and used the same cohort of participants for all the tasks.

## Methods

### Participants

Participants were 20 healthy younger adults (mean age 25 years, range, 19–34) and 20 healthy older adults (mean age 72 years, range, 60–79). Participants were recruited through advertisements placed around the university, local newspapers, university online portals, and from a database of participants previously tested in our laboratory. Ethics approval was obtained from The University of Melbourne Human Research Ethics Committee (HREC 1749806), and all procedures complied with the tenets of the Declaration of Helsinki. A \$20 (AUD) gift voucher per session was provided to participants to help offset any expenses incurred in attending.

Each participant underwent a screening ophthalmic examination to verify their vision was normal. This screening consisted of assessment of refractive error, slit lamp examination, direct ophthalmoscopy, measurement of visual acuity, and automated visual field screening of each eye (O600 screening test using the Octopus 600 perimeter, Haag-Streit AG, Köniz, Switzerland; [Turpin, Myers, & McKendrick, 2016](#)). Inclusion criteria consisted of best corrected visual acuity better than 6/12, spherical equivalent refraction within the range of  $\pm 6$  diopters (D), and no ophthalmic or systemic disease that could affect vision (such as glaucoma, diabetic retinopathy, advanced lens opacities, or age-related macular degeneration). Uncomplicated cataract surgery was not grounds for exclusion. All participants had best corrected binocular visual acuity better than 6/9.5. The spherical equivalent refractive error of the participants ranged from  $-4.25$  to  $+4.75$  D. Additionally, a cognitive function screening was performed using the Mini-Mental State Examination ([Folstein, Folstein, & McHugh, 1975](#)), with normal cognition indicated by a score of 23 or higher. All participants had scores higher than 28.

### Apparatus

Experiments were developed in Python (Python Software Foundation, Scotts Valley, CA) using the coder module of Psychopy v1.85.2 details are provided in the citation ([Peirce, 2007](#)). Stimuli were displayed on a calibrated 32-in. Display++ monitor (Cambridge Research Systems, Ltd., Rochester, UK), with a refresh rate of 120 Hz, a spatial resolution of 1920 x 1080 pixels, and a pixel size of 0.36 mm. For each experiment, the viewing distance was 100 cm, unless noted otherwise. Older participants wore a refractive correction for the 100-cm working distance, mounted in a trial frame. Testing was performed in a dark room

with no ambient illumination other than that from the computer monitor.

### Testing procedure

In this study motion perception was measured systematically at different levels of processing using two types of psychophysical stimuli: gratings and dots. All testing was performed binocularly, with the center of the stimulus located either foveally ( $0^\circ$  eccentricity) or peripherally ( $15^\circ$  to the right and  $5^\circ$  up from foveal center, to avoid the physiological blind spot). The testing procedure was common for all the tasks, using a three-down one-up staircase with six reversals to determine thresholds for the parameter of interest for each task, with participants indicating their responses via a keypress on a keyboard. The duration of each task was between 2 to 3 minutes, and auditory feedback (a tone) was given for incorrect answers. To minimize the effects of fatigue or learning, we grouped the tasks into four possible combinations (dots vs. gratings, and central vs. peripheral), which were presented in a counterbalanced order, with similar numbers of participants performing each combination. Participants were required to complete three to four complete runs of each task. However, for data analyses, only the last four reversals of the final two staircases were included.

### Motion perception tasks

The seven tasks are outlined as follows:

1. *Minimum dot displacement* ( $D_{\min}$ ). This task determines the smallest displacement of dots required to perceive the direction of motion, and is based on previous work by [Bullimore et al. \(1993\)](#), [Turano and Wang \(1992\)](#), and [Wood and Bullimore \(1995\)](#). A circular RDK containing 1 x 1 pixel dots (individual dot luminance of  $200 \text{ cd m}^{-2}$ ) and a dot density of 0.1% was presented against a black background (luminance of  $1.74 \text{ cd m}^{-2}$ ). The RDK window was 800 pixels wide, with the intensity of the dots in an outermost annulus of 100 pixels width progressively reduced to the background intensity via a raised cosine envelope, to avoid participants guessing the direction of motion from the manner in which dots either appeared or disappeared. A longer viewing distance of 6 m (obtained by viewing using a mirror) was adopted to avoid floor effects, as was seen in younger participants in our pilot work with shorter distances, and as reported previously ([Kuo, Atchison, & Schmid, 2018](#)). At 6 m, one pixel subtends a visual angle of 0.2 min of arc, providing a stimulus size of  $3^\circ$  of diameter, similar to that used previously by one of our research groups ([Lacherez,](#)

Au, & Wood, 2014; Lacherez, Turner, Lester, Burns, & Wood, 2014). Participants wore their optimum refraction for the 6-m working distance, using large aperture trial lenses in a trial frame. The testing procedure involved the participant viewing the pattern directly (central condition) or peripherally while viewing a fixation dot located on the plain white wall at  $15^\circ$  from the center of the pattern (eccentric condition). Two consecutive RDK images of 24 frames were presented (200 msec each) giving a total stimulus duration of 400 msec.

Participants were required to indicate the direction of the motion (left or right), with the staircase procedure modifying the displacement of dots between the two images. After the initial image presentation, the second image was displaced horizontally either to the left or to the right in step sizes of 5 pixels for the first reversal, 2 pixels for the second, and 1 pixel for the final four reversals in central vision, and in steps of 50 pixels, 20 pixels, and 10 pixels for the first, second, and final four reversals, respectively, in peripheral vision. The initial value of the staircase was set at 15 pixels for central and 100 pixels for peripheral testing.

2. *Contrast task.* This task measured the lowest level of contrast required to determine the direction of motion of a vertically oriented Gabor patch ( $\sigma = 1.35^\circ$ ) presented on a uniform gray background (luminance  $94 \text{ cd m}^{-2}$ ). For all the tasks involving Gabors, the size was truncated at  $\pm 3\sigma$ . The spatial frequency was  $3 \text{ c}^\circ$ , with a duration of 250 msec and a drift rate of  $2^\circ/\text{s}$ . This stimulus was similar to that used previously (Watson & Turano, 1995). The stimulus drifted rightward or leftward, with participants required to indicate the direction of motion. The staircase modified the contrast of the pattern in a log scale from a starting value of 22% Michelson contrast. The step size of the staircase was set as 0.2 log units for the first two reversals, and 0.1 log units subsequently.
3. *Speed task.* This task measured the slowest speed required to determine the direction of motion of a Gabor. The pattern had similar characteristics to the previous task, except for the contrast level, which was set at 92% Michelson contrast. Participants were required to judge the direction of motion (right or left). The staircase modified the speed of the pattern in step sizes of 0.2 log units for the first reversal, 0.1 for the second, and 0.05 for the final four reversals. The initial speed of the pattern was  $4^\circ/\text{s}$ .
4. *Surround suppression of motion.* Based on the work of Tadin, Lappin, Gilroy, and Blake (2003), this task explored whether the size of a drifting Gabor affected the stimulus duration required to correctly identify the direction of motion. We used a Gabor

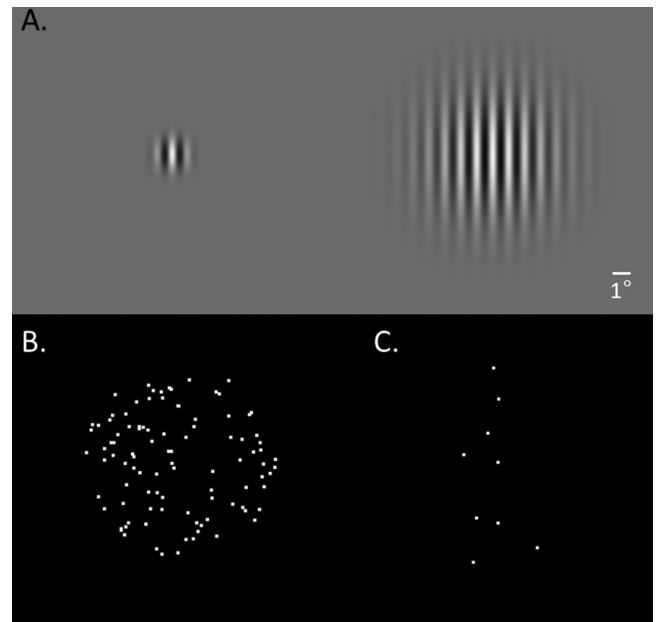


Figure 1. Illustration of a selection of the stimuli used in the experiment. (A) Illustrates two Gabor patches of different sizes used for the surround suppression of motion task. A similar pattern was used to explore the percentage of contrast required to determine direction of motion and to determine the minimum speed. (B) Shows a single frame of the circular RDK pattern used to test  $D_{\min}$  and global motion coherence task (translational and radial). (C) Shows a single frame of the point light walker moving in a leftward direction used for the biomotion task.

with a spatial frequency of  $1 \text{ c}^\circ$ , a drift rate of  $2^\circ/\text{s}$ , a Michelson contrast of 92%, and one of two sizes: either smaller ( $\sigma = 1.35^\circ$ ) or larger ( $\sigma = 5^\circ$ ) (Figure 1A). Observers were required to judge the direction of motion of the Gabor sine wave carrier (right or left). The staircase modified the stimulus presentation time from the initial value of 250 msec (= 30 frames). The step sizes of the staircase were set to four frames for the first two reversals and two frames subsequently.

5. *Translational global motion coherence.* This task determined the lowest percentage of signal dots required to detect translational motion. A circular pattern of  $10^\circ$  diameter, containing 100 white dots (individual dot luminance:  $200 \text{ cd m}^{-2}$ ), moving coherently rightward or leftward, was presented over a black background (Figure 1B). Each dot was  $5 \times 5$  pixels, with a speed of  $2^\circ/\text{s}$ . Stimulus duration was 420 msec. Participants were required to judge whether the direction of motion of the pattern was to the left or right. The initial value of the staircase was set to 80% coherence, and the staircase modified the number of noise dots in step sizes of 20 dots for the first reversal, 10 dots for the second, and 5 dots for final four.

6. *Radial global motion coherence.* This task determined the lowest percentage of signal dots required to detect expansion or contraction of a pattern embedded in noise dots. The stimulus parameters and the experimental procedure was similar to the translational global motion task, with an expansion/contraction speed of the dots of 2°/s from the center of the stimulus. The staircase modified the number of noise dots in step sizes of 8 dots for the first reversal, 4 dots for the second, and 2 dots for the final four. The initial value of the staircase was set to 100% signal dots.
7. *Biological motion.* This task determined the maximum number of noise dots that allowed detection of an embedded biological motion stimulus. We used a point light walker, adapted from Shipley and Brumberg (2004), which consisted of 13 animated dots of 5 x 5 pixels and a dot luminance of 200 cd m<sup>-2</sup>, configured in a rectangular array approximately 4° wide and 7.4° high, eliciting the perception of a human walking rightward or leftward but with no overall translation (Figure 1C). The speed of the walker was set to complete a full stride in 900 msec, similar to a previous study (Billino et al., 2008). The task started with presentation of a point light walker without noise dots. Subsequently, the staircase added scrambled noise dots in step sizes of 50 dots for the first reversal, 20 dots for the second, and 10 dots for the final four in central vision, and 10 dots for the first reversal, 5 dots for the second, and 1 dot for the final four in peripheral vision. These noise dots adopted a pattern of motion representative of the joints of the point light walker, but at random locations, similar to a previous study (Ikeda, Blake, & Watanabe, 2005).

## Statistical analysis

Statistical analysis was performed using R Studio Version 1.1.456 (RStudio Team, 2016). For the majority of the data analyses, the level of significance was set to  $p < 0.05$ , unless otherwise specified. A repeated measures two-way analysis of variance (ANOVA) was used, performing a between-samples comparison between age groups (younger-older) and a within-subjects comparison for eccentricity. To use parametric statistical tests, we transformed raw values into log values.

To evaluate whether age-related differences were greater for some motion tasks relative to others, we calculated z-scores for the central and peripheral log threshold values. We normalized each value for the older adults using the following formula:

$$Z\text{-score} = \frac{\text{Threshold} - \text{Younger mean}}{\text{Younger SD}}$$

where “threshold” is the older adult value for the task at the specific eccentricity (central or peripheral), and “younger mean” and “younger SD” are the mean and standard deviation of the younger group for the same task at the same eccentricity.

Additionally, we wanted to assess potential statistical relationships between each of the motion tasks. For this purpose, we calculated Pearson correlations between the various motion tasks, adjusting for multiple comparisons using a Bonferroni correction. As we performed 25 comparisons, the  $p$  value for significance was set to  $<0.002$ . To evaluate the strength of the evidence supporting the presence or absence of correlations between tasks, we reported Bayes Factors (Ly, Verhagen, & Wagenmakers, 2016). These Bayes Factors provide an estimate of the likelihood of support for the alternate, rather than the null hypothesis (i.e., that there is a relationship between the tests), and were calculated using the R package “BayesFactor” (Morey & Rouder, 2018).

The data used for analyses are provided as Supplementary Material (Tables S1 and S2).

## Results

Figure 2 shows thresholds for the motion tasks, excluding the surround suppression of motion, which was analyzed separately because this task cannot be defined in terms of “better” or “poorer” performance. For the centrally presented stimuli, we found significantly higher thresholds in older adults compared with younger adults for the following tasks: motion contrast,  $F(1,38) = 14.80$ ,  $p < 0.001$ ; speed,  $F(1,38) = 10.05$ ,  $p = 0.003$ ;  $D_{\min}$ ,  $F(1,38) = 36.1$ ,  $p < 0.001$ ; and biological motion,  $F(1,38) = 10.58$ ,  $p < 0.01$ . For translational and radial global motion coherence, a main effect of age was not found,  $F(1,38) = 2.47$ ,  $p = 0.12$  and  $F(1,38) = 2.48$ ,  $p = 0.12$ , respectively. Regardless of age group, thresholds were significantly higher in peripheral vision compared with central vision [motion contrast,  $F(1,38) = 80.46$ ,  $p < 0.001$ ; speed,  $F(1,38) = 9.10$ ,  $p = 0.004$ ;  $D_{\min}$ ,  $F(1,38) = 659.54$ ,  $p < 0.001$ ; translational global motion coherence,  $F(1,38) = 5.46$ ,  $p = 0.02$ ; radial global motion coherence,  $F(1,38) = 4.21$ ,  $p = 0.047$ ; and biological motion,  $F(1,38) = 131.16$ ,  $p < 0.001$ ]. There was no interaction between age and eccentricity for any of the tasks [motion contrast,  $F(1,38) = 3.23$ ,  $p = 0.08$ ; speed,  $F(1,38) = 0.01$ ,  $p = 0.91$ ;  $D_{\min}$ ,  $F(1,38) = 0.43$ ,  $p = 0.51$ ; translational,  $F(1,38) = 0.22$ ,  $p = 0.64$ ; and radial,  $F(1,38) = 3.06$ ,  $p = 0.09$ ; global motion coherence and biological motion,  $F(1,38) = 0.03$ ,  $p = 0.86$ ], demonstrating that peripheral viewing did not exacerbate the effects of age.

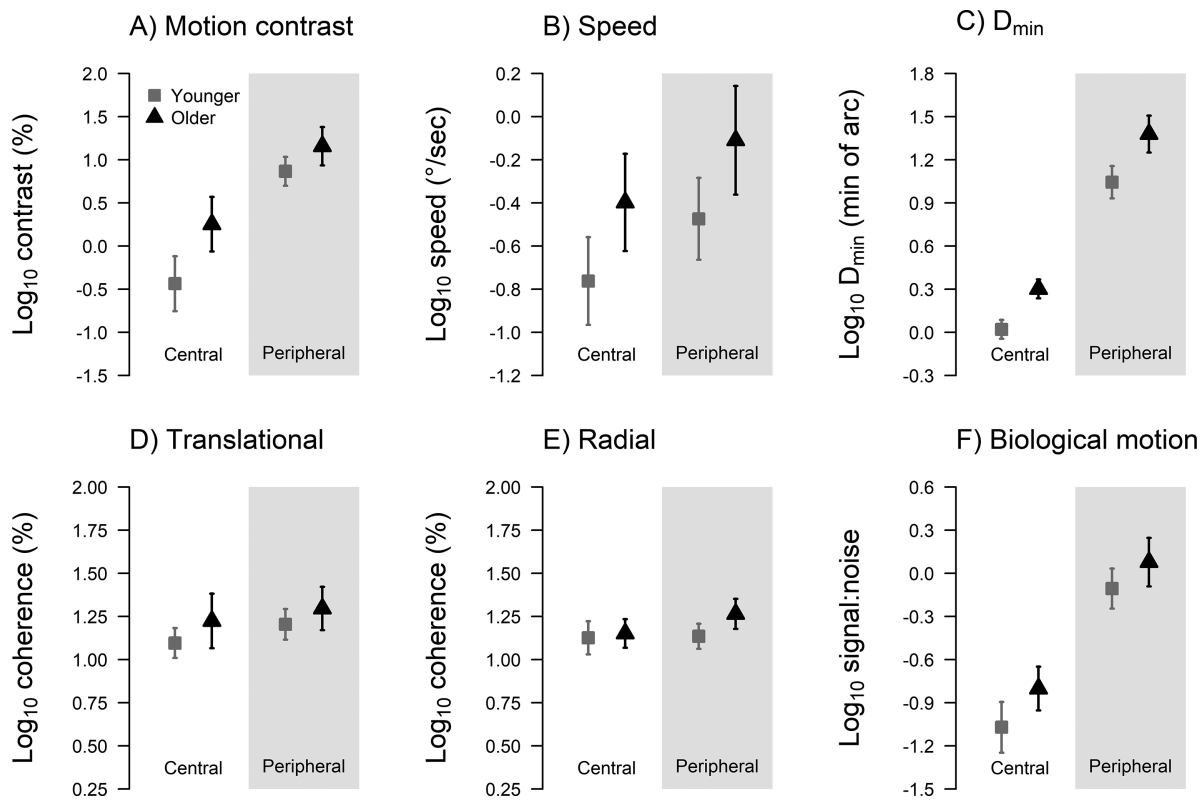


Figure 2. (A–F) Motion perception thresholds for all tasks, excluding the surround suppression task, in central (white panels) and peripheral vision (gray panels). Mean values are represented by squares for younger adults and triangles for older adults. Error bars represent the 95% confidence interval of the mean.

### Magnitude of between-group differences in task performance: motion tasks Z-scores

One of our aims was to assess whether age-related differences are greater for some motion tasks relative to others. Figure 3 shows the Z-scores for central and peripheral vision, in which a higher value represents poorer performance of older adults relative to younger adults.

For central vision, a pairwise comparison using multiple *t*-tests with Bonferroni correction ( $p = 0.008$ , for comparison between six tasks) showed  $D_{\min}$  to be different from speed, radial global motion, and biological motion, illustrating that the greatest difference between the older and younger group was for this task. In peripheral vision (Figure 3B), none of the tasks were significantly different from each other.

### Relationships between performance on each task

In Figures 2 and 3, we demonstrated that younger and older adults exhibited similar magnitudes of between-group differences for many motion tasks. To assess whether performance on the various motion

tasks was related, we calculated Pearson correlations between tasks, which are shown in Table 1 for the age groups combined. Correlations for each age group separately are provided as Supplementary Material (Table S3).

The highest correlations were between the tasks that share similar stimulus characteristics: that is, motion contrast and speed, using Gabor patches. These higher correlation values are present for both central and peripheral vision. Despite  $D_{\min}$  being significantly correlated with motion contrast and speed in central vision, there were no significant correlations between these measures in peripheral vision once strict Bonferroni correction was applied. Inspection of the Bayes Factors, however, demonstrates that the magnitude of the observed correlations between  $D_{\min}$  and motion contrast, and  $D_{\min}$  and speed in the periphery, provide moderate evidence in support of the alternate hypothesis (that there is a relationship between the tasks).

### Surround suppression of motion

Figure 4 shows the results for the surround suppression of motion task. In central vision

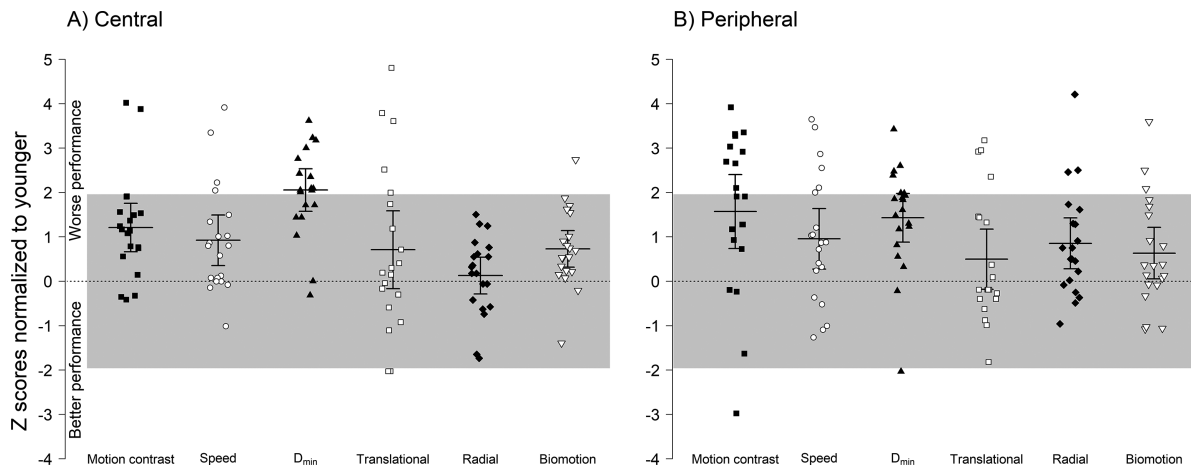


Figure 3. Z-scores of older adults in central (A) and peripheral vision (B) relative to group performance for the younger adults. A value of zero (dashed line) represents no difference between older adult performance compared with younger. Gray areas represent the  $\pm 1.96$  standard deviation of the mean. A value higher than zero represents worse performance of older adults and vice-versa. Horizontal lines represent the mean, and the error bars the 95% confidence intervals of the mean.

**Central**

Task	Biological motion	Radial	Translational	D <sub>min</sub>	Speed
Motion contrast	0.31 <i>p</i> = 0.05 BF = 1.93	0.07 <i>p</i> = 0.67 BF = 0.38	0.22 <i>p</i> = 0.18 BF = 0.78	<b>0.54</b> <i>p</i> < <b>0.001</b> BF = <b>95.61</b>	<b>0.65</b> <i>p</i> < <b>0.001</b> BF = <b>3517.28</b>
Speed	0.36 <i>p</i> = 0.02 BF = 3.63	0.24 <i>p</i> = 0.14 BF = 0.91	0.26 <i>p</i> = 0.10 BF = 1.13	<b>0.49</b> <i>p</i> = <b>0.001</b> BF = <b>31.67</b>	
D <sub>min</sub>	0.40 <i>p</i> = 0.01 BF = 6.38	0.18 <i>p</i> = 0.27 BF = 0.60	<b>0.50</b> <i>p</i> = <b>0.001</b> BF = <b>37.42</b>		
Translational	0.13 <i>p</i> = 0.41 BF = 0.48	0.28 <i>p</i> = 0.08 BF = 1.38			
Radial	0.33 <i>p</i> = 0.04 BF = 2.41				
<b>Peripheral</b>					
Motion contrast	0.06 <i>p</i> = 0.71 BF = 0.38	0.17 <i>p</i> = 0.30 BF = 0.57	-0.14 <i>p</i> = 0.40 BF = 0.48	0.42 <i>p</i> = 0.007 BF = 8.62	<b>0.80</b> <i>p</i> < <b>0.001</b> BF = <b>4850807</b>
Speed	0.10 <i>p</i> = 0.54 BF = 0.42	0.41 <i>p</i> = 0.01 BF = 6.92	0.15 <i>p</i> = 0.37 BF = 0.50	0.46 <i>p</i> = 0.003 BF = 17.32	
D <sub>min</sub>	0.27 <i>p</i> = 0.09 BF = 1.25	0.28 <i>p</i> = 0.08 BF = 1.35	0.08 <i>p</i> = 0.62 BF = 0.39		
Translational	-0.25 <i>p</i> = 0.12 BF = 1.00	<b>0.52</b> <i>p</i> < <b>0.001</b> BF = <b>70.90</b>			
Radial	-0.11 <i>p</i> = 0.50 BF = 0.43				

Table 1. Pearson correlation between tasks, adjusted for multiple comparisons. Bold values represent statistically significant results (*p* < 0.002). Note: BF = Bayes factor.

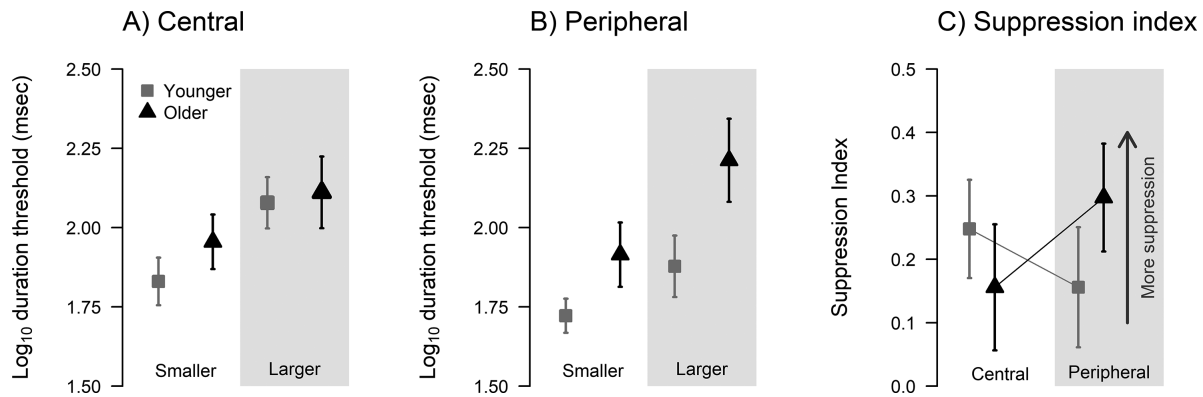


Figure 4. Surround suppression of motion task. (A–B) Show duration thresholds in younger and older adults for the smaller and larger stimuli in central and peripheral vision. (C) Shows the SI (calculated as the log value of the larger minus the log value of the smaller). In this context, positive values correspond to more suppression.

(Figure 4A), younger adults had lower duration thresholds for both the smaller and larger stimuli when compared with older adults. Additionally, our findings showed that the difference in duration thresholds of older and younger adults was greater for the smaller stimuli. This trend is similar to the findings of [Betts et al. \(2005\)](#), who reported that older adults required shorter presentation times for larger and higher contrast patterns compared with younger adults in central vision. They did not explore these effects in peripheral vision, however.

In peripheral vision (Figure 4B), we found that older adults had higher duration thresholds than younger adults for both smaller and larger stimuli. A multifactorial ANOVA showed a main effect of target size,  $F(1,38) = 94.53$ ,  $p < 0.001$ ; age,  $F(1,38) = 11.9$ ,  $p < 0.001$ ; and eccentricity,  $F(1,38) = 5.18$ ,  $p = 0.029$ . There was a significant interaction between age and location,  $F(1,38) = 11.50$ ,  $p = 0.002$ ; as well as between group, size, and location,  $F(1,38) = 7.91$ ,  $p = 0.008$ . In central vision, younger adults required less time to determine the direction of motion for the smaller stimuli, but older and younger adults required similar presentation times for the larger stimulus. In peripheral vision, the younger observers had lower duration thresholds than the older participants for both sizes. There was no significant interaction between age and size,  $F(1,38) = 0.31$ ,  $p = 0.58$ ; nor size and location,  $F(1,38) = 0.36$ ,  $p = 0.55$ .

We calculated a suppression index (SI) by subtracting the log threshold of the larger stimulus from the log threshold of the smaller stimulus ([Betts et al., 2005](#); Figure 4C). A positive SI indicates suppression, and a negative SI indicates summation. Consistent with [Betts et al. \(2005\)](#), our results showed that, in central vision, younger adults have more suppression than older adults. However, in peripheral vision we found the opposite effect, in which older adults had more suppression than younger. This finding

was supported by a significant age-location interaction,  $F(1,38) = 7.91$ ,  $p = 0.008$  (Figure 4C).

## Discussion

In this study, we explored the question of whether motion perception is different in older compared with younger adults. Our study was novel in that we considered different levels of motion processing using similar stimulus characteristics and we also tested motion perception at different eccentricities. We found that older adults had poorer performance on most of the tasks, regardless of eccentricity. This is consistent with previous research showing age-related declines in motion perception on a variety of tasks:  $D_{\min}$  ([Wood & Bullimore, 1995](#)), speed perception of gratings ([Snowden & Kavanagh, 2006](#)), and biological motion ([Billino et al., 2008](#); [Norman et al., 2004](#); [Pilz et al., 2010](#)). Additionally, we did not find age-related changes in the perception of radial global motion coherence, in agreement with the work of [Billino et al. \(2008\)](#). In contrast to previous reports ([Arena et al., 2012](#); [Billino et al., 2008](#); [Genova & Bocheva, 2013](#); [Gilmore et al., 1992](#); [Roudaia et al., 2010](#); [Tran et al., 1998](#)), we found no evidence of an age effect on translational global motion coherence, although in a recent study, [Pilz, Miller, and Agnew \(2017\)](#) also did not report age differences for this task. It is not immediately clear why the results for this task are so variable, however, it is worth noting that we used a motion speed ( $2^\circ/s$ ), which was slower than that used by previous authors ([Billino et al., 2008](#); [Genova & Bocheva, 2013](#); [Gilmore et al., 1992](#); [Tran et al., 1998](#)). As reported by [Edwards, Badcock, and Smith \(1998\)](#), global motion detectors differentially process RDK patterns according to their speed. In this experiment, we decided to use a speed of  $2^\circ/s$  to be consistent with the speed used in



the other tasks within our series of experiments (i.e., motion contrast and surround suppression of motion). Further experiments would be required to establish whether between-group differences are revealed at faster rather than slower speeds for motion coherence stimuli.

A key novel finding from our experiments is that surround suppression of motion was the only task affected by age and eccentricity differently. In central vision, we found a higher suppression index for younger compared with older adults, consistent with previous reports (Betts et al., 2005; Karas & McKendrick, 2012). Conversely, in peripheral vision, we obtained the novel finding that older adults demonstrated higher suppression. The differences in suppression index according to the eccentricities are explained by the fact that older adults exhibited higher duration thresholds for the larger stimulus. Our results illustrate that age-related changes in motion-based surround suppression differ between central and peripheral vision, as was reported previously for a static suprathreshold contrast surround suppression task (Nguyen & McKendrick, 2016).

Betts, Sekuler, and Bennett (2009) hypothesized that the reduced suppression reported in older adults may be related to reduced levels of neurotransmitters in the aging visual cortex, particularly the inhibitory neurotransmitter gamma aminobutyric acid (GABA). Subsequent experimental investigation of this hypothesis by Pitchaimuthu et al. (2017) showed that magnetic resonance spectroscopy estimates of GABA are actually elevated in visual cortex in older adults. Furthermore, these elevated GABA levels were positively correlated with a reduction in surround suppression of motion observed centrally in older adults, in contrast to Betts et al. (2009) hypothesis. Notably, our current finding of enhanced motion suppression outside of the fovea is consistent with this previously observed elevated GABA-ergic inhibition, albeit in an independent group of participants. It is worth noting that neurophysiological studies of surround suppression at a cellular level are typically performed in the parafovea (e.g., Jones et al., [2001] tested cells between 2° and 6° of spatial eccentricity), hence the precise neural circuitry of the foveal representation is less well understood. Relating mid-peripheral behavioral performance—as measured in the current study—to neurophysiology may yield closer interspecies comparison between human behavior (Nguyen & McKendrick, 2016) and primate cellular physiology (Shushruth et al., 2013), than comparisons with foveal human performance alone.

Although there has been substantive previous research investigating motion perception in older adults, our study has two major novel contributions to highlight. First, to our knowledge, this is the first time that a large battery of motion tasks has been used to

systematically explore different components of motion perception according to complexity in the same group of participants and with the same methodological approach (two alternative forced choice, with stimuli presented on identical instrumentation). Furthermore, we maintained similar stimulus characteristics between different tasks, where possible: i.e., including the spatial frequency of the Gabor, and speed or stimulus duration. Hence our experimental procedure allowed us to control for a range of factors, such as learning effects, task requirements, stimulus characteristics, and selection criteria for participants, which made quantitative comparisons of performance on the various tasks difficult across previous studies.

Second, our work explored the effects of healthy aging on motion perception in peripheral vision, whereas the majority of previous studies have tested central visual performance only. In our study, we tested peripheral vision (15° eccentricity), finding that both age groups had increased thresholds in peripheral vision when compared with central. Our findings are consistent with previous studies that reported poorer performance for many motion tasks in peripheral vision in younger adults:  $D_{\min}$  (Kuo et al., 2018), motion contrast (To, Regan, Wood, & Mollon, 2011), and biological motion (Ikeda et al., 2005; Thompson, Hansen, Hess, & Troje, 2007).

Overall, our findings illustrate that physiological aging predominantly affects those tasks that are processed at the lower levels of the motion pathway, including  $D_{\min}$ , contrast, and speed. This is also supported by the higher correlational values obtained between these tasks. The initial stages of motion processing rely on detecting changes in the position of objects over time (Adelson & Bergen, 1985), which is also related to the perception of speed. The changes at these low levels of processing might be explained by aging changes in older adults, such as changes in optical quality and/or neural declines at either a retinal level or in cortical area V1. Despite the observed changes to the processing of the initial inputs to motion perception, we did not find an age effect on two tasks that require the integration of local motion signals: the perception of translational and radial global motion. Similar to newer evidence by Shaqiri et al. (2019), our correlational analysis did not show statistically significant relationships between the three more complex motion tasks (translational and radial global motion coherence, and biological motion), implying that mechanistically, the perception of these complex patterns does not rely directly on lower levels of processing. For example, small deficits in the perception of individual components of the RDK stimuli may not impact on the determination of overall global motion coherence. Motion coherence thresholds have also been shown to be quite robust to blur (Zwicker, Hoag, Edwards, Boden, & Giaschi,

2006). An additional explanation for the preserved global motion perception in older adults relates to the existence of higher-level mechanisms that have the potential to compensate for local deficits. For instance, in a recent study using imaging techniques, Biehl, Andersen, Waiter, and Pilz (2017) reported that older adults have additional activation of frontal areas when perceiving global motion patterns (particularly radial). Aside from motion, there is evidence from neurophysiological and imaging studies of additional activation of frontal regions in older adults to compensate some features of visual function, such as visual attention and object recognition (Cabeza et al., 2004; Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008), as well as audio-visual integration (Chan, Pianta, Bode, & McKendrick, 2017). Overall, our findings indicate that integrative processes presumed to operate in global motion tasks are intact in older adults, at least for the speeds of dot motion used in our experiments.

With regard to a more complex task, we found a decline in biological motion perception with age. Previous reports have demonstrated that the ability to perceive biological motion is well preserved in older adults in the absence of noise dots (Norman et al., 2004). However, the deficits experienced by older adults to recognize the point light walker embedded in noise may relate to difficulties in separating signal from noise, similar to that reported by Thompson et al. (2007) in younger adults. In our study, we did not find deficits in the other tasks that required separating signal from noise (i.e., translational and radial global motion coherence), which was also supported by the absence of statistically significant correlations between these tasks. Our findings are in line with a previous study by Miller, Agnew, and Pilz (2018), which reported that the mechanisms for processing global motion and biological motion in noise are different. Finally, our data provides indirect support for the notion of Pilz et al. (2010) that the deficits exhibited by older adults for biomotion extends from problems in integrating local motion and global form.

## Conclusions

Our findings demonstrate that physiological aging affects motion processing stages differently, with changes predominantly occurring for tasks with lower levels of complexity. The perception of biological motion was the only more complex task that showed a decline with aging that could not be related to changes at lower levels of processing. Additionally, we showed that aging effects on surround suppression of motion are in the opposite direction in peripheral vision to those found foveally (weakened spatial suppression foveally, stronger spatial suppression in the periphery).

Stronger suppression in the periphery suggests that older adults will have more difficulty segregating objects moving in the periphery from their backgrounds. Therefore aging effects cannot be assumed to be uniform across visual space or type of motion task. Because of this, it is important to study performance at different eccentricities, so that age-related changes in performance can be more completely appreciated, along with their likely impact on daily tasks in natural visual environments.

*Keywords:* aging, biological motion, motion coherence, motion perception, surround suppression

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