Different effects of aging and gender on the temporal resolution in attentional tracking

Eugenie Roudaia École d'optométrie, Université de Montréal, Montreal, QC, Canada

Jocelyn Faubert École d'optométrie, Université de Montréal, Montreal, QC, Canada

The current study examined the role of temporal resolution of attention in the decline in multiple object tracking abilities with healthy aging. The temporal resolution of attention is known to limit attentional tracking of one and multiple targets (Holcombe & Chen, 2013). Here, we examined whether aging is associated with a lower temporal resolution of attention when tracking one target, the efficiency of splitting attention across multiple targets, or both. Stimuli comprised three concentric rings containing five or 10 equally spaced dots. While maintaining central fixation, younger and older participants tracked a target dot on one, two, or three rings while the rings rotated around fixation in random directions for 5 s. Rotational speed was varied to estimate speed or temporal frequency thresholds in six conditions. Results showed that younger and older participants had similar temporal frequency thresholds for tracking one target, but the addition of one and two more targets reduced thresholds more in the older group compared to the younger group. Gender also affected performance, with men having higher temporal frequency thresholds than women, independently of the number of targets. These findings indicate that the temporal resolution of attention for a single target depends on gender but is not affected by aging, whereas aging specifically affects the efficiency of dividing attention across multiple targets.

Introduction

Many situations in everyday life require us to attend to multiple locations or objects at the same time, such as when we are watching team sports or crossing a busy street. The ability to track several moving items simultaneously has been studied using the multiple object tracking (MOT) task, in which participants track a subset of identical moving objects over a period of time (Pylyshyn & Storm, 1988). Studies have shown that tracking performance strongly depends on the number of targets and their speed: Observers can track up to eight targets at very slow speeds or only one target at very fast speeds (Alvarez & Franconeri, 2007; Cavanagh & Alvarez, 2005; Holcombe & Chen, 2012). Other factors that influence performance include the number and spatial proximity of distracters (Drew, Horowitz, & Vogel, 2013; Pylyshyn, Haladjian, King, & Reilly, 2008; Scholl, 2009) and the spatial distribution of targets across the visual field (Alvarez & Cavanagh, 2005, 2015; Carlson, Alvarez, & Cavanagh, 2007). MOT ability shows large variability across individuals, with higher capacity in athletes (Faubert, 2013; Trick, Hollinsworth, & Brodeur, 2008) and action video game players (Boot, Blakely, & Simons, 2011; Green & Bavelier, 2006; Sekuler, McLaughlin, & Yotsumoto, 2008; Trick et al., 2008).

Tracking capacity also varies across the lifespan, gradually increasing from childhood to adolescence (Trick et al., 2008) and steadily declining with age starting in the third decade (Kennedy, Tripathy, & Barrett, 2009; Sekuler et al., 2008; Trick, Perl, & Sethi, 2005). The causes of age-related decline in tracking capacity are unknown. Given the complexity of the MOT task, differences in performance may be due to changes in one or several processes, from object motion processing, attentional modulation of targets and distracters, or higher order functions such as visuo-spatial working memory, sustained attention, and eye movement strategies. Here we briefly summarize what factors have been shown to influence age differences in MOT. Trick et al. (2005) tested tracking of one to four targets among 10 objects moving at one speed level for 10 s. They found worse performance in the older group with three and four targets only, although performance with one and two targets was near ceiling for both groups. Sekuler et al. (2008) tested tracking of one to five targets among 10 objects moving at two speed levels for 5 and 10 s. They found that increases in target

Citation: Roudaia, E., & Faubert, J. (2017). Different effects of aging and gender on the temporal resolution in attentional tracking. *Journal of Vision*, *17*(11):1, 1–16, doi:10.1167/17.11.1.

doi: 10.1167/17.11.1 Received January 16, 2017; published September 1, 2017 ISSN 1534-7362 Copyright 2017 The Authors

This work is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License.

Downloaded From: http://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/936469/ on 09/05/2017

number, speed, and tracking duration all had a greater detrimental effect on performance in the older group compared to the younger group. Consistent with those findings, Legault, Allard, and Faubert (2013) found that older participants had lower maximum tracking speeds than younger participants for tracking three or four spheres among eight moving in a virtual three-dimensional (3-D) cube. Aging did not affect memory for locations of stationary targets, ruling out the possibility that declines in visual short-term memory can account for aging effects in MOT (Sekuler et al., 2008; Trick et al., 2005). Störmer, Li, Heekeren, and Lindenberger (2011) examined whether tracking performance was affected by irrelevant objects that were of the same or a different color than the targets and that were moving in an unattended region of the visual field. They found that same-color distracters affected younger and high-performing older adults more than different-color distracters, while low-performing older adults had equally poor performance for both types of distracters. Using an electroencephalogram study, Störmer, Li, Heekeren, and Lindenberger (2013) showed that the time point at which neural response amplitudes differed between targets and nontargets was delayed in older adults, indicating that aging may specifically affect the early visual processing of targets during MOT. The above studies showed that aging impairs tracking of multiple targets at higher speeds and that this impairment may be due to attentional or perceptual processing delays.

Given that changes in target number and speed in the classical MOT task are confounded with the number of collisions, changes of direction of the targets, and proximity of nontarget objects, it is unclear whether performance in the older group suffers due to difficulty with dealing with collisions, greater spatial interference between objects, or whether it is due to poorer efficiency in dividing attention across multiple targets. It is also not known whether aging affects attentional tracking capacity for a single item, as studies that assessed performance with one target did not measure the limits of performance. Previous studies that examined the limits of tracking performance in displays where the spatial proximity of targets and distracters was kept constant have demonstrated that attentional tracking fails when the target speed increases beyond a certain speed limit or when the rate at which objects pass a certain location reaches a certain temporal frequency limit (Holcombe & Chen, 2013; Verstraten, Cavanagh, & Labianca, 2000). In displays where objects are widely separated, such as when one target and one distracter are rotating around the same circular trajectory, tracking performance fails at the point where attention cannot keep up with the target (Holcombe & Chen, 2012, 2013; Verstraten et al., 2000). In displays that contain many objects circulating on the same trajectory, tracking fails at much lower speeds as the temporal frequency of the stimulus reaches the temporal resolution of attention, which determines the maximum rate at which attention can individuate objects in time. Verstraten et al. (2000) found that the maximum rotational speed for tracking one object among multiple equally spaced objects sharing the same trajectory asymptoted at speeds corresponding to temporal frequency rates between four to seven objects per second. Holcombe and Chen (2013) also found a temporal frequency rate limit of approximately seven objects/second when a single target moved on the same trajectory as six to 12 distracters. Interestingly, when participants had to track two or three targets moving on separate trajectories, the temporal frequency limit dropped to $\sim$4 and $\sim$2.6 Hz, respectively (Holcombe & Chen, 2013). These results indicated that temporal frequency thresholds for tracking one target reflected the temporal resolution of attention, while the change in the temporal frequency thresholds with the addition of the second and third target reflected the efficiency of dividing attention across multiple targets.

As mentioned previously, there were no age group differences in MOT performance for tracking one or two targets, and the age effect increased with increasing target number (Sekuler et al., 2008; Trick et al., 2005). This pattern of results is consistent with the possibility that aging leads to small reductions in the temporal resolution of attention that are insufficient to affect tracking performance for one or two targets or at low speeds. Alternatively, it is also consistent with the possibility that aging does not affect the temporal resolution of attention, but that older adults are less efficient at dividing their attention across targets, explaining the increasing age difference in performance with increasing target number. Thus, the goal of the current study was to examine whether aging affects the temporal resolution of attention when tracking one target, the efficiency of dividing attention across targets, or both. To do this, we adopted the paradigm of Holcombe and Chen (2013) and measured rotational speed thresholds for tracking one, two, and three targets rotating around fixation on a trajectory containing five or 10 objects per ring. Examining performance at two distracter density levels allowed us to test whether temporal frequency alone is the limiting factor, or whether distracter density per se also plays a role in aging effects. This study also allowed to us to examine the effect of speed and target number on tracking without confounding changes in spatial interference, collisions, and occlusions that accompany these variables in the classical MOT paradigm. We also controlled for age differences in eye movement strategies by requiring participants to maintain central fixation during tracking.

Downloaded From: http://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/936469/ on 09/05/2017

Participant group	N	Age, years *M* (*SD*)	Acuity, log MAR *M* (*SD*)	MOCA *M* (*SD*)	Action video games, hr *M* (range)
Younger	9 F	22.8 (1.8)	0.00 (0.06)		0.26 (0–2)
	9 M	23.5 (2.9)	−0.01 (0.07)		2.89 (0–14)
Older	9 F	69.4 (5.6)	0.05 (0.08)	28.4 (1.3)	0 (0)
	9 M	72.7 (6.2)	0.07 (0.07)	27.1 (2.2)	0 (0)

Table 1. Means and standard deviations of participant age, visual acuity (log MAR), Montreal Cognitive Assessment scores (MOCA, max = 30), and hours of action video game played per month in each group.

Lastly, we were also interested in examining the effect of gender on tracking performance. Although gender differences in MOT have not been previously reported, gender accounted for significant variability in MOT performance in a recent study in our lab (Roudaia, Lacoste, & Faubert, 2016). Although there is strong evidence for gender differences in spatial cognition across the lifespan (Geiser, Lehmann, & Eid, 2008; Jansen & Heil, 2010; Voyer et al., 1995), gender differences in visuospatial attention remain little investigated. One study reported better performance in males than females in a visual spatial attention task (Feng, Spence, & Pratt, 2007). Some studies have also reported greater age-related declines in global motion perception in women compared to men (Hutchinson, Arena, Allen, & Ledgeway, 2012). Anticipating that there may be gender differences in tracking performance, we recruited a gender-balanced sample and examined potential effects of gender on MOT performance in our task.

Methods

Participants

Eighteen younger (nine females, aged 20–29 years) and 18 older (nine females, aged 60–83 years) participants completed this study. Younger participants were university students recruited at the Université de Montréal, and older participants were independently living residents of Montreal recruited through advertisements in community centers and local newspapers. All participants gave written informed consent to participate in the study and received financial compensation for their participation. The research protocol was approved by the health research ethics committee of the Université de Montréal and adhered to the tenets of the Declaration of Helsinki.

All participants completed a general health questionnaire and none reported previous history of neurological disorders, nor any ongoing visual abnormalities such as cataracts, glaucoma, macular degeneration, etc. To screen for cognitive impairment, we administered the Montreal Cognitive Assessment (Nasreddine et al., 2005) to older participants, who all scored above the cutoff score of 23/30 for mild cognitive impairment (Luis, Keegan, & Mullan, 2009). Participants' visual acuity was measured with the Trifocal chart on the Nearpoint Rotochart (Reichert Technologies, Depew, NY) for intermediate distances. Participants were tested at a viewing distance of 80 cm, which corresponded to the distance used during the experiment, while wearing their habitual optical correction. Participants also completed a questionnaire on their computer or video game habits in the last 6 months, from which we extracted the number of hours per month spent playing action video games, as these kinds of games have been previously linked to improved performance in MOT (Green & Bavelier, 2006; Sekuler et al., 2008). Participants who engaged in more than 20 hours of action video games per month in the last 6 months were not recruited for the study. Table 1 summarizes the demographic measures for all participants.

Apparatus

The experiment was programmed in MATLAB (R2012a, The MathWorks Inc., Natick, MA) using software from the Psychophysics and Video Toolboxes (v3; Brainard, 1997; Pelli, 1997) as well as the Eyelink Toolbox (Cornelissen, Peters, & Palmer, 2002). Stimulus generation and presentation were controlled by a Lenovo ThinkCentre computer (Lenovo, Beijing, China) equipped with a NVIDIA Quadro K6000 graphics card. The stimuli were presented on a VIEWPixx display measuring 52 × 29.5 cm with a resolution of 1920 × 1080 and refresh rate of 120 Hz. The full display subtended 36° × 21° at a viewing distance of 80 cm. Mean luminance of the display was 16 cd/m^2. Participants' eye gaze was monitored by recording the pupil position using a video-based eye tracker (Eyelink 1000 Plus, SR Research Ltd., Kanata, ON, Canada) set up in remote/head free mode, having a sampling rate of 500 Hz and a spatial precision of < 0.05°. Participants were seated in an office chair and were asked to find a comfortable position from which they would not move. The monitor placement was then adjusted to maintain

Downloaded From: http://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/936469/ on 09/05/2017

a distance of 80 cm from the participants' eyes and the eye-tracker camera was placed at the appropriate distance between the monitor and the participant. The experimenter ensured that the viewing distance remained constant throughout the experiment by monitoring this information in the eye tracker software. Participants made responses using a standard PC mouse.

Stimuli and procedure

The experimental task involved four stages (see Figure 1B). First, a pattern of black dots appeared on the screen. Second, a subset of the dots was colored white for 1 s to designate them as targets. Third, all the dots moved around on the screen while participants covertly tracked the target dots. Fourth, a response screen prompted the participants to indicate the location of one of the target dots.

Each trial began with a brief sound tone and a flickering blue fixation point ($r = 0.18°$) in the middle of the screen. Following a brief pause (0.3 s), a pattern of 15 or 30 black dots appeared on the screen for 1 s. The dots were positioned at equally spaced intervals on three invisible concentric rings centered on fixation. All the dots had a diameter of 0.8° and the imaginary rings had diameters of 6°, 12°, and 18°. The absolute position of the dots along their respective rings was randomized across trials. The stimuli with 15 dots contained five dots on each ring (spaced at 3.53°, 7.05°, and 10.58° for the inner, middle, and outer rings, respectively) and the stimuli with 30 dots contained 10 dots on each ring (spaced at 1.85°, 3.71°, and 5.56°). All the dots were black (0.13 cd/m^2) and were presented against a uniform gray background (16 cd/m^2).

Across trials, either one, two, or three dots turned white (90 cd/m^2) for 1 s to designate them as targets (see Figure 1B). When there was one target, it was always located on the outer ring. In the case of two targets, one target was on the inner ring and the other target was on the outer ring. When there were three targets, there was one target on each ring. Participants were told to attend to all dots that turned white and to keep track of their positions as they moved during the motion phase. During the motion phase, all dots returned to black and began to move in a circular motion, gradually accelerating over the first 0.3 s to reach a constant and equal angular rate of rotation on all three rings. The starting direction of rotation was randomized across trials but was always the same for the inner and outer rings and opposite for the middle ring. Each ring then independently reversed its rotation direction at random time intervals ranging 0.5–2.5 s. To reduce perceptual grouping of targets, the centers of the imaginary rings were also jittered using a two-

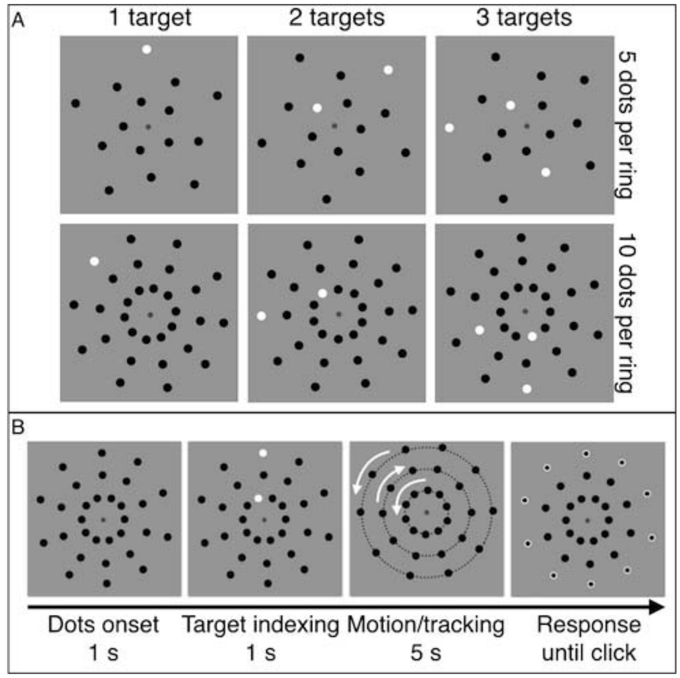

Figure 1. (A) Stimuli for each of the six conditions in the experiment. (B) Schematic of a typical trial sequence. The targets are highlighted in white.

dimensional random walk with a speed of 0.02°/s, limited within 0.1° of the center of the screen. The motion phase lasted 5 s. At the end of the motion phase, all the dots remained stationary at their last position. One of the target rings was cued by circling all the dots on that ring with thin white contours. Participants were asked to report the circled dot target by clicking on the dot with the mouse cursor. There was no time limit to complete the response and participants were allowed to move their eyes away from fixation during this phase. When the response was correct, the white contour became green and when the response was incorrect, the white contour became red, while the target dot was circled with a green contour. This feedback was displayed for 0.75 s, after which all the dots were erased. A new trial began 1.5 s later.

Prior to the experiment start, we performed a five-point calibration procedure for the eye tracker. Throughout the experiment, participants' eye gaze was recorded monocularly to ensure that participants maintained fixation in the middle of the screen during the motion phase. To begin a trial, participants had to fixate for more than 0.3 s within 1.5° radius of fixation. If the eye position moved more than 1.5° away from fixation for more than 0.5 s during the motion phase, the trial was aborted and rerun at a later stage. After every break, the experimenter performed a drift check to ensure that the eye tracker calibration remained accurate throughout the experiment.

Downloaded From: http://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/936469/ on 09/05/2017

The number of targets (one, two, or three) and the number of dots (five or 10 per ring) were fully crossed, resulting in a total of six conditions (Figure 1A). Each condition was presented at a range of angular rotation speeds to determine a threshold speed of rotation. Trials of different conditions were presented in a randomly intermixed order. To reduce fatigue, participants were given the opportunity to take a break every 10 min.

Due to the large variability in tracking ability across participants, a separate procedure was performed before the start of the main experiment to guide the selection of an appropriate range of speeds for each participant and each condition. Participants were told that they would perform a practice task before continuing to the main experiment to get them used to the task. The practice trials began with a set of black dots on the screen. Then, one, two or three dots turned white for 1 s and participants were asked to track those dots during the trial, while keeping their eyes fixated on the small dot in the middle of the screen. When the targets turned back to black, all the dots began rotating around the fixation point, with the speed of rotation gradually increasing in a linear fashion. Participants were asked to click on the right mouse button as soon as they felt that they had lost one of the targets. The mouse click aborted the trial and triggered the start of the next trial. Participants completed four trials at each of the six conditions in a randomly interleaved order. The maximum speed of rotation reached at the time of the mouse click was recorded for each trial. We then calculated the average maximum speed across the four trials in each condition and used this speed as a benchmark to guide speed selection. The speed ranges used for each participant were between ~0.4 and ~1.2 times the benchmark speed obtained with the above procedure. For the five dots/ring patterns, the median speed ranges were 0.3–1.2, 0.2–0.9, and 0.1–0.6 rps for one-, two-, and three-target conditions, respectively. For the 10 dots/ring patterns, the median speed ranges were 0.2–0.8, 0.1–0.6, and 0.05–0.4 for one-, two-, and three-target conditions, respectively. Each condition was tested at four speed levels equally spaced over the range of speeds indicated above, for a minimum of eight trials per speed. After these 32 trials, a Bayesian adaptive procedure (Vul, Bergsma, & MacLeod, 2010) took over control of the speed levels and continued presenting speeds chosen to reduce the uncertainty on the estimated speed threshold, taking into account previously accumulated data. The range of speeds allowed by the algorithm was much wider (0.01 to 2 rps) to account for the possibility that the manually chosen speed range was not appropriate. The algorithm continued sampling until the standard deviation on the estimated threshold was below 0.05, or until a maximum of 60 trials per condition. Testing was completed in two sessions lasting 70–90 min each.

Analysis

Data from the two sessions were combined and a logistic curve was fit separately for each subject and each condition using maximum likelihood estimation implemented in the Palamedes toolbox (Prins & Kingdom, 2009). The procedure estimated three parameters: the threshold, alpha; the slope, beta; and the lapse parameter, lambda. For the purposes of the analysis presented here, lambda was free to vary between 0–0.1. Speed threshold is defined as the speed yielding the success rate midway between chance and ceiling performance, which is determined by the lapse rate. For example, with an estimated lapse rate of 0.1, threshold speed corresponds to a success rate of 0.55 and 0.5 for the five dots/ring and 10 dots/ring conditions, respectively. The temporal frequency threshold was calculated by multiplying the speed threshold by the number of dots per ring to yield a temporal frequency threshold in dots per second (dps). Fitting logistic curves with speed expressed in temporal frequency units gave the same results. In nine cases, two older male participants and five older female participants showed poor performance at the slowest speeds and the fit of the logistic curve was inadequate, with the threshold estimated to be below zero. This occurred for two thresholds in the three targets and five dots/ring condition, one threshold from the two targets and 10 dots/ring condition, and six thresholds on the three targets and 10 dots/ring condition. These nine thresholds were coded as missing data in the linear mixed-effects model analyses and were not included in the summary statistics shown in the figures.

Statistical analyses were performed using the statistical computing environment R (R Core Team, 2015). Data were analyzed using linear mixed-effects models using the lme4, pbkrtest, and lmerTest packages (Baayen, Davidson, & Bates, 2008; Bates, Maechler, Bolker, & Walker, 2015; Kuznetsova, Brockhoff, & Christensen, 2016). Unlike repeated measures analysis of variance, linear mixed-effects analysis allows to analyze data sets containing missing data in repeated measures designs, allowing to keep all subjects' data. Model comparison and selection was performed by fitting reduced models without the terms of interest and comparing the two models using the F tests with the Kenward-Roger approximation for degrees of freedom (Halekoh & Hjsgaard, 2014) as implemented in the pbkrtest and lmerTest packages. Statistical significance of model coefficients was evaluated using bootstrapped confidence intervals and

Downloaded From: http://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/936469/ on 09/05/2017

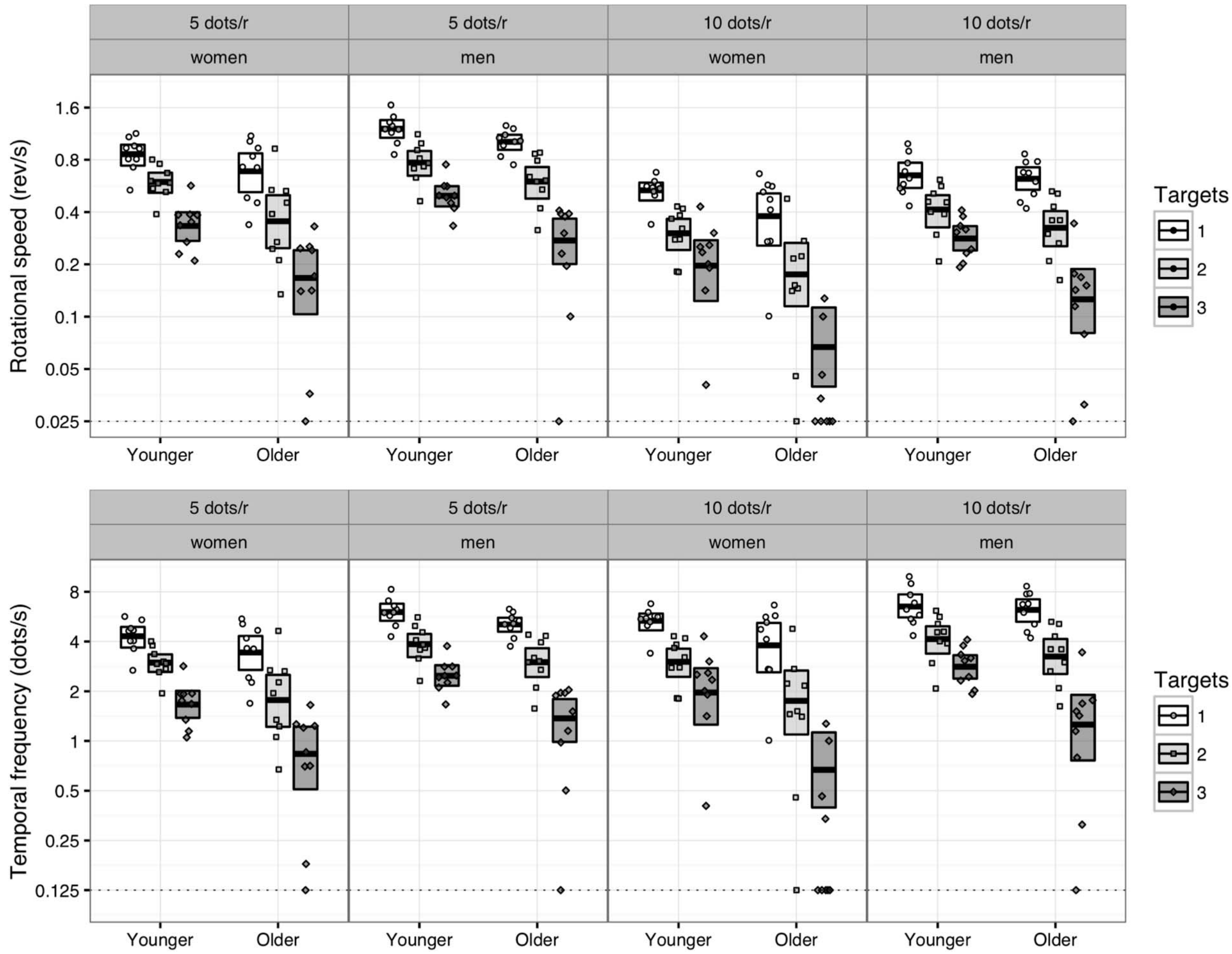

Figure 2. Rotational speed thresholds (top, revolutions/second) and temporal frequency thresholds (bottom, dots/second) for tracking one, two, and three targets in displays with five dots/ring and 10 dots/ring are shown separately for each group. Crossbars show the means and their 95% bootstrapped confidence intervals and small symbols show individual data. Note the log scale of the *y*-axis. The nine data points plotted on the dashed lines represent cases where performance did not reach threshold level. These points were not included in the summary statistics.

the Kenward-Roger approximation. Effect sizes for the fixed effects were evaluated using semi-partial R^2 (R^2_p), which represents the strength of association between the dependent variable and the fixed effect, controlling for the other effects in the model (Jaeger, 2016; Jaeger, Edwards, Das, & Sen, 2016; Johnson, 2014).

Results

Figure 2 shows the rotational speed thresholds (top) and temporal frequency thresholds (bottom) across all six conditions for participants separated by gender and age groups. As expected, thresholds decreased systematically with increasing number of targets. Rotational speed thresholds were lower for patterns with 10 dots/ring compared to five dots/ring, and this difference was virtually eliminated when thresholds were expressed in terms of temporal frequency (Holcombe & Chen, 2013). Comparing performance across age and gender groups revealed higher overall thresholds in men compared to women, and in younger participants compared to older participants. Importantly, the magnitude of the age group differences appeared to increase with the number of targets.

We analyzed the results using linear mixed-effects models both on raw and on log-transformed rotational speed and temporal frequency thresholds. Given that the pattern of results was similar for raw and log-transformed values, we report results for log-transformed analyses only. Note that effects observed on log-transformed values reflect differences in the ratios between groups and conditions as opposed to differences in means. The data were fit with the following linear mixed-effects model:

Downloaded From: http://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/936469/ on 09/05/2017

#T	Effect	β	95% CI	t	df	p value	R_p^2
1	Gender (male)	0.51	[0.23, 0.79]	3.5	33.0	0.001	0.24
	Age (young)	0.29	[−0.04, 0.57]	1.9	39.1	0.07	0.05
	DPR (10)	0.22	[0.09, 0.34]	3.5	34.0	0.001	0.03
	Age (years) × DPR (10)	−0.01	[−0.19, 0.17]	−0.1	34.0	0.94	0.00
2	Gender (male)	0.63	[0.25, 0.98]	3.27	33.0	0.003	0.22
	Age (young)	0.56	[0.17, 0.92]	2.79	37.4	0.008	0.10
	DPR (10)	0.03	[−0.12, 0.17]	0.37	33.2	0.71	0.00
	Age (years) × DPR (10)	0.03	[−0.18, 0.24]	0.32	33.1	0.75	0.00
3	Gender (male)	0.71	[0.30, 1.11]	3.22	31.9	0.003	0.18
	Age (young)	0.88	[0.34, 1.40]	3.42	51.3	0.001	0.16
	DPR (10)	−0.39	[−0.83, 0.09]	−1.66	32.8	0.11	0.03
	Age (year) × DPR (10)	0.60	[−0.02, 1.24]	1.99	30.5	0.06	0.04

Table 2. Results of separate linear mixed-effects sub-models fit to one, two, and three targets conditions examining effects of gender, age, dots/ring (DPR), and the Age × DPR interaction on log-transformed temporal frequency thresholds. *Notes*: The Table shows the fixed effect coefficient estimates (β) and its 95% bootstrapped confidence intervals (CIs), t values, Kenward-Roger approximation for error degrees of freedom (df) and associated p values, and the semi-partial R^2 values (R_p^2).

$$\begin{aligned}\log2(Y)_{ij} = {} & \beta_0 + \beta_g\text{gender} + \beta_a\text{age} + \beta_t\text{targets} \\ & + \beta_d\text{dpr} + \beta_{td}\text{targets:dpr} \\ & + \beta_{at}\text{age:targets} + \beta_{at}\text{age:dpr} \\ & + \beta_{atd}\text{age:targets:dpr} + b_{0i} + b_{ti} + b_{di} \\ & + b_{tdi} + \epsilon_{ij}\end{aligned}$$

where Y represents i-th subject's temporal frequency or the rotational speed threshold for j-th condition, β are the coefficients for the fixed effects terms, the b terms represent random effects for the by-subject intercept and slopes of the two within-subjects factors (targets and dots/ring), and ε_{ij} represents the normally-distributed residual errors. We specified the model's random effects terms with correlated intercepts and slopes for targets and dots/ring because this random-effects structure was a better fit than a model with uncorrelated slopes, $\chi^2_{(1)} = 17.0$, $p < 0.001$, and a model with random by-subject intercepts only, $\chi^2_{(8)} = 26.4$, $p < 0.001$. The fixed-effect terms included in the model were determined based on the effects of interest and a model comparison process. The terms for the age and gender interaction and higher order interactions containing age and gender effects were not included, due to the low power to detect these interactions with our sample size (the power to detect a two-way Age × Gender interaction was 0.28 and 0.09 for a medium and small effect size, respectively). The two- and three-way interactions between gender and the two within-subjects factors—target number and dots/ring—were also not included, because a comparison of the above model with a model containing these additional terms did not result in a significantly improved fit, $F(5, 56) = 0.84$, $p = 0.53$, which indicates that the effect of gender did not vary as a function of target number or dots/ring.

We examined the significance of the fixed-effects terms of the complete model using the Kenward-Roger degree of freedom approximation with type-III sums-of-squares. This analysis revealed significant main effects of gender, $F(1, 33) = 10.3$, $p = 0.003$; age group, $F(1, 33) = 15.2$, $p = 0.004$; and target number, $F(2, 33) = 198.9$, $p < 0.001$, for rotational speed and temporal frequency thresholds. The effect of dots/ring was significant for rotational speed thresholds only, $F(1, 34) = 317.0$, $p < 0.001$, and not for temporal frequency thresholds, $F(1, 34) = 0.05$, $p = 0.81$. Results of the main effects confirmed our earlier observations that men showed higher (better) thresholds than women, thresholds of older participants were generally lower (worse) than those of younger participants, thresholds decreased with increasing number of targets, and the number of dots/ring had no effect on temporal frequency thresholds. However, there were also significant two-way interactions between targets and dots/ring, $F(2, 65) = 9.51$, $p < 0.001$; age and target number, $F(2, 33) = 14.4$, $p < 0.001$; age and dots/ring, $F(1, 34) = 7.12$, $p = 0.01$; as well as a three-way interaction between age, target number, and dots/ring, $F(2, 66) = 11.8$, $p < 0.001$, for both measures. These interactions indicated that the effect of dots/ring varied with the number of targets and that the effect of aging depended on the number of targets and dots/ring.

To decompose the interactions, we fit separate mixed-effects submodels at each level of target number. The submodels contained terms for gender, age, dots/ring, and the interaction between age and dots/ring as fixed effects and by-subject random intercepts. Table 2 shows the estimated fixed-effects coefficients, their significance results, and the associated semi-partial R^2 for the models fits to log-transformed temporal frequency data. The effect of gender was large and statistically significant for all target number conditions (one target: $\beta = 0.51$, $p = 0.001$, $R^2{}_p = 0.24$; two targets: $\beta = 0.63$, $p = 0.003$, $R^2{}_p = 0.22$; three targets: $\beta = 0.71$, p

Downloaded From: http://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/936469/ on 09/05/2017

$= 0.003$, $R^2_p = 0.18$). In contrast, the effect of age was small and not statistically significant in the one target condition ($\beta = 0.29$, $p = 0.07$, $R^2_p = 0.05$) and increased as the number of targets increased. In the two targets condition, the age effect was statistically significant but smaller than the effect of gender ($\beta = 0.56$, $p = 0.008$, $R^2_p = 0.10$), whereas for the three targets condition, the effect of age was larger and of a similar magnitude as the gender effect ($\beta = 0.88$, $p = 0.001$, $R^2_p = 0.16$). Thus, while the gender difference in thresholds was large and constant across all target number conditions, the age difference in thresholds was not present with one target and progressively increased with additional targets.

With regards to the effect of dots/ring, temporal frequency thresholds were slightly higher in the 10 dots/ring condition for one target in both groups ($\beta = 0.22$, $p = 0.001$, $R^2_p = 0.03$). In the two targets condition, there was no main effect of dots/ring or any interaction between age and dots/ring. In the three targets condition, the main effect of dots/ring was not significant, but there was a trend for an Age × Dot/Ring interaction ($\beta = 0.60$, $p = 0.06$, $R^2_p = 0.04$). Whereas temporal frequency thresholds tended to be higher in the 10 dots/ring condition in the younger group ($\beta = 0.22$, $p = 0.17$, $R^2_p = 0.03$), the effect was reversed in the older group, ($\beta = -0.38$, $p = 0.23$, $R^2_p = 0.04$), although neither difference was statistically significant. Thus, when expressed in terms of objects/second, tracking thresholds were only slightly better in displays with 10 dots/ring when tracking one target compared to five dots/ring. With increasing number of targets, performance in the older group declined more for stimuli containing 10 dots/ring relative to five dots/ring. It is also important to remember that several older participants were unable to reliably track three targets even at slower speeds, resulting in two and six thresholds missing in the five and 10 dots/ring conditions, respectively. Results of the analysis of rotational speed thresholds were identical, except for the main effects of dots/ring, which was large and statistically significant for all target numbers (one target: $\beta = -0.78$, $p < 0.001$, $R^2_p = 0.24$; two targets: $\beta = -0.97$, $p < 0.001$, $R^2_p = 0.24$; three targets: $\beta = -1.39$, $p < 0.001$, $R^2_p = 0.27$), consistent with lower rotational speed thresholds for displays with greater number of dots/ring.

In sum, participants showed similar temporal frequency thresholds for both dots/ring conditions, which were highest when tracking one target and lowest when tracking three targets. Comparison of performance across age group and gender revealed that men had higher thresholds than women for all target number conditions, while the effect of age group was small and not statistically significant with one target and increased progressively with additional targets.

Discussion

The current study examined whether the decline in MOT with aging is associated with reductions in the temporal resolution of attention or changes in the efficiency of dividing attention across targets (Kennedy et al., 2009; Legault et al., 2013; Sekuler et al., 2008; Störmer et al., 2013; Trick et al., 2005). We measured the maximum speed at which participants could reliably track one, two, or three targets in displays with two levels of distracter density. The study revealed two main novel findings. First, results showed that attentional tracking of one target remains largely unchanged in older adults and that aging specifically affects the efficiency of splitting attention across multiple targets. Second, results showed significant gender differences in tracking performance in both age groups that, in contrast to the age effect, were present when tracking one target and did not vary with the number of targets.

Age and gender effect on attentional tracking of one target

The current study is the first to examine the limits of attentional tracking of one target in aging. Tracking one target may be qualitatively different from tracking multiple targets, as there is no need to divide attention across multiple spatial foci. Although Trick et al. (2005) had tested younger and older subjects' performance with one target, the speed used was too slow to assess the limits of performance. We found no evidence of an age-related decline in the temporal frequency limit for tracking a single target. To the extent that the temporal frequency limit for tracking one target is determined by the temporal resolution of attention, this result suggests that aging does not affect the temporal resolution of attention.

In contrast, we found that gender had an effect on temporal frequency thresholds, with men showing higher thresholds than women in both younger and older groups. On average, our results for younger men ($M = 6.4$ Hz, 95% CI [5.8, 7.2]) were similar to mean threshold reported by Holcombe and Chen (2013), who tested five men and one woman aged 29–37. Thresholds for younger women were much lower ($M = 4.9$, 95% CI [4.4, 5.3]). The gender gap was of the same magnitude in the older group (older men: $M = 5.7$, 95% CI [5.2, 6.3], older women: $M = 4.0$, 95% CI [3.3, 4.6]). We also observed large individual differences in thresholds in both groups. Considering that our participants were not practiced psychophysical observers or habitual video game players, our measures should provide fair estimates of performance in the general population.

Downloaded From: http://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/936469/ on 09/05/2017

The temporal resolution of attention is thought to limit performance across many different tasks, including the temporal frequency limit of the attentional motion system (Cavanagh, 1992; Lu & Sperling, 2001), the pairing of color and motion direction (Arnold, 2005), temporal individuation tasks (Verstraten et al., 2000; Wutz & Melcher, 2014), and others. It is distinct from the temporal resolution of vision that underlies our perception of flicker (critical flicker fusion) or the temporal frequency limit of luminance-defined motion, among others (for review, see Holcombe, 2009). The neural basis of the temporal resolution of attention appears to lie in the posterior parietal cortex (Battelli, Pascual-Leone, & Cavanagh, 2007; Howard, Bashir, Chechlacz, & Humphreys, 2016; Reddy, Rémy, Vayssière, & VanRullen, 2011).

Although there are many studies on the effects of aging on motion processing (Bennett, Sekuler, & Sekuler, 2007; Habak & Faubert, 2000; Hutchinson et al., 2012; Snowden & Kavanagh, 2006), only a couple of studies examined attention-mediated motion and its temporal limits in aging. One study measured contrast thresholds for perceiving the direction of motion of fractal rotation and found an age-related increase in contrast thresholds that was constant for all temporal frequencies that were tested (Allard, Lagacé-Nadon, & Faubert, 2013). These results indicated that although the neural efficiency for perceiving fractal rotation declines in aging, there was no evidence of reduced temporal resolution of attention with age. Aging is also known to affect translational motion perception for contrast-defined gratings (Habak & Faubert, 2000), which are thought to be mediated by the attentional-motion system (Allard & Faubert, 2013a, 2013b), but, again, the age deficit is not greater at higher temporal frequencies. Results of those studies are overall consistent with the current findings of preserved temporal limits of attention with aging when the attentional focus is not divided.

The current finding of preserved temporal resolution of attention in aging when tracking one target may seem at odds with other studies showing poorer temporal processing in older adults. For example, several studies have reported higher temporal order judgment thresholds in older adults with different types of stimuli and processing modalities (e.g., Busey, Craig, Clark, & Humes, 2010; Setti et al., 2011; Ulbrich, Churan, Fink, & Wittmann, 2009), as well as age-related increases in the duration and magnitude of the attentional blink (Georgiou-Karistianis et al., 2007; Lahar, Isaak, & McArthur, 2001). However, both the attentional blink and temporal order judgment tasks likely involve higher order cognitive factors other than spatial selective attention (Busey et al., 2010; Martens & Wyble, 2010; Ulbrich et al., 2009), which may account for the age-related slowing. That said, future studies should examine more closely the relationship between the temporal resolution of attention as measured in the current study and performance in temporal judgment and attentional blink tasks.

Performance with multiple targets and the efficiency of dividing attention

Dividing attention across multiple targets caused a greater decline in temporal frequency thresholds in older adults compared to younger adults. This finding is consistent with previous studies showing increasing age differences in MOT performance with greater number of targets and higher speeds (Legault et al., 2013; Sekuler et al., 2008; Trick et al., 2005). However, by removing the confounding factors of spatial interference between objects and number of collisions and occlusions that accompany speed and target number changes in the classical MOT paradigm, the current study showed that aging specifically impairs the efficiency of dividing attention across multiple targets in attentional tracking. The current results are also broadly consistent with results of a recent study that found an age-related decline in the rate of information processing for static visual targets, but only when the task contained two targets or a target among distracters, and not when the target was presented in isolation (Guest, Howard, Brown, & Gleeson, 2015). Thus, it appears that the process that allows concurrent sampling of information across multiple spatial locations is affected in aging.

Tracking multiple targets requires the ability to split attention across targets in some way. The manner in which this is achieved is still a matter of debate. Pylyshyn and Storm (1988) originally proposed that our attention system has a fixed number of pointers or indexes that attach to the targets and allow to track them in parallel, but do not allow access to the target features. The capacity-limited resource theory posits that attention can be split into multiple spatially separated foci in a flexible manner, such that some targets receive more or less attentional resource depending on the context (Alvarez & Franconeri, 2007; Cavanagh & Alvarez, 2005; Chen, Howe, & Holcombe, 2013; Iordanescu, Grabowecky, & Suzuki, 2009). Others proposed that the capacity limit of this resource arises primarily from the competition among targets for neural representation in the cortical maps (Franconeri, Alvarez, & Cavanagh, 2013; Franconeri, Alvarez, & Enns, 2007; Franconeri, Lin, Pylyshyn, Fisher, & Enns, 2008). Serial sampling theories propose that a unitary focus of attention samples targets in a serial fashion, rapidly switching from one to another (Holcombe & Chen, 2013; Jans, Peters, & De Weerd, 2010; Oksama

Downloaded From: http://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/936469/ on 09/05/2017

& Hyönä, 2004; VanRullen, Carlson, & Cavanagh, 2007).

If MOT is performed in a serial fashion, the efficiency of distributing attention across targets may be reduced by positing that older adults require more time to shift the focus of attention from one target to another. Previous studies have shown that shifting attentional focus across different targets requires some time (Hogendoorn, Carlson, & Verstraten, 2007). Although older adults are able to shift attention to specific locations as fast as younger adults when there are no distracters (Folk & Hoyer, 1992), there is some evidence of age-related delays in disengaging from processing one item before moving to another item. For example, older adults show delays in the onset of inhibition-of-return (Castel, Chasteen, Scialfa, & Pratt, 2003), their performance for detecting targets takes longer to recover after attentional capture by a distracter (Cashdollar et al., 2013) and older adults take longer to shift from a broad to a narrow focus of attention (Jefferies et al., 2013). If MOT involves shifting of attention from one target to another, a delay in the shifting process would cause greater impairment with increasing speed, as well as with increasing target numbers, both effects that we observe here.

The efficiency of tracking multiple targets may also be worse in older adults due to decreased or delayed suppression of distracters. For example, Störmer et al. (2013) found that whereas younger adults show higher ERP amplitudes to probes flashed on targets compared to distracters within 100 ms, this effect occurs 25 ms later in older adults and its magnitude is correlated with tracking performance in the older group. Studies have shown that attending to one target results in the enhancement of the signal associated with the target and suppression of responses to nontargets in its immediate surround (Hopf et al., 2006; Hopf, Boelmans, Schoenfeld, Heinze, & Luck, 2002; Mounts, 2000). When multiple objects are indexed for selection, similar top-down biasing signals may be directed to enhance the target signals and suppress surrounding nontargets, but the mechanism ultimately becomes less effective due to competition between target representations, overlap of suppressive zones around the targets (Cohen, Konkle, Rhee, Nakayama, & Alvarez, 2014; Franconeri et al., 2013; Scalf & Beck, 2010), or due to overall limits on suppression. Previous studies using static stimuli have shown that older adults show a greater decline in processing targets when the two targets are brought closer together (McCarley, Mounts, & Kramer, 2004) and that this effect is especially exacerbated in the context of clutter (McCarley, Yamani, Kramer, & Mounts, 2012). These results suggested that top-down biasing signals may be less efficient at resolving interitem competition in early visual areas in older adults. In the current experiment, increasing the density of distracters did not disproportionately affect older participants when they were tracking one or two targets. It is only when tracking three targets that the density of distracters was slightly more detrimental to older adults. Thus, it may be that older adults have somewhat less efficient suppression mechanisms, but it only becomes apparent when attention is distributed across multiple targets.

Tracking performance may also be limited by crowding or the spatial resolution of attention (Bex, Dakin, & Simmers, 2003; Franconeri, Jonathan, & Scimeca, 2010; Intriligator & Cavanagh, 2001). To what extent could age differences in crowding influence the pattern of results in the current experiment? The tangential spacing of dots on the concentric rings in the five and 10 dots/ring conditions was higher than the critical spacing at which crowding is typically observed. Furthermore, the fact that temporal frequency thresholds were similar for both dots/ring condition suggests that crowding did not limit performance in the more dense condition. It is possible that dots in the middle ring may have experienced some crowding from the dots on the outer ring in the radial direction, but this would have been constant across all conditions and likely affected both older and younger groups equally, as studies have shown that aging does not affect crowding strength or critical spacing thresholds (Astle, Blighe, Webb, & McGraw, 2014).

Although a wide network of brain areas in the frontal cortex, parietal cortex, as well as areas MT and MST, are active during attentive tracking compared to passive viewing (Culham et al., 1998), specific areas in the parietal cortex (intraparietal sulcus, superior parietal lobule, and posterior parietal cortex) show a dependence on the number of tracked targets (Culham, Cavanagh, & Kanwisher, 2001; Howe, Horowitz, Wolfe, & Livingstone, 2009; Jahn, Wendt, Lotze, Papenmeier, & Huff, 2012; Jovicich et al., 2001; Shim, Alvarez, Vickery, & Jiang, 2010). A recent functional magnetic resonance imaging investigation of MOT in aging found that older subjects show smaller load-dependent changes in BOLD activity than younger subject in the dorsal attention network when tracking one versus two targets (Drum et al., 2016). Older subjects also showed smaller reductions of activation in the default mode network during tracking. These findings indicate that older adults may be less able to modulate the recruitment of neural resources in the dorsal attention network, which may lead to reductions in the efficiency to track multiple targets as observed in the current experiment. The reduced ability of older adults to modulate neural resources with increasing target load may be mediated by the extent of age-related declines in gray and white matter in frontal and parietal areas (Crivello, Tzourio-Mazoyer, Tzourio, &

Downloaded From: http://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/936469/ on 09/05/2017

Mazoyer, 2014; Gunning-Dixon & Raz, 2000; Raz et al., 2005).

Gender effects

The current study revealed a significant gender difference in performance, with men showing higher tracking speed and temporal frequency thresholds for both age groups. To our knowledge, none of the previous published studies had examined gender effects in MOT or in the temporal resolution of attention. The fact that the gender effect is present when tracking one target and remains constant when tracking multiple targets suggests that the gender effect is not specific to the process of dividing attention across multiple items and may instead indicate a gender difference in the temporal resolution of attention.

Large studies examining performance on neurocognitive measures consistently find better performance in verbal memory and social cognition in females and better performance on spatial processing and motor speed in males (Gur & Gur, 2017; Jansen & Heil, 2010; Roivainen, 2011). In contrast to the wealth of data on cognitive measures, relatively few studies have examined or identified gender effects in perceptual or attentional tasks. One study reported that women had worse performance in a useful field of view task, which could be eliminated following training on a video game (Feng et al., 2007). Some studies have also noted gender differences in motion perception in younger and older adults (Billino, Bremmer, & Gegenfurtner, 2008) while other studies only find gender differences in older age (Atchley & Andersen, 1998; Gilmore, Wenk, Naylor, & Stuve, 1992), specifically in septuagenarians (Arena, Hutchinson, & Shimozaki, 2012). The current sample size was insufficient to answer the question of whether gender effects in performance remain constant or increase in older age. Future studies with significantly larger sample sizes are needed to answer this question.

What may be the etiology of the gender effects that we observe? First, there are gender differences in brain structural or functional connectivity, proportions of gray and white matter, and glucose metabolism in different regions (for a review, see Gur & Gur, 2017). Other studies have reported differences in the hemispheric asymmetry of the attentional blink depending on the stage of the menstrual cycle in women, highlighting a potential role of sex hormones in attentional tasks (Holländer, Hausmann, Hamm, & Corballis, 2005). In additional to potential biological differences, differences in the frequency with which participants engage in sports or video games throughout their life could also contribute to gender effects in our task (Faubert & Sidebottom, 2012; Green, Li, & Bavelier, 2010). More general sociocultural factors could also play a role. For example, a recent study reported a relationship between the level of a country's gender inequality and gender differences in sustained attention (Riley et al., 2016). The current finding of a gender effect in attentional tracking warrants further study of gender effects on the temporal resolution of attention and how it may relate to gender effects in motion perception, sustained attention, and higher order cognitive factors.

Conclusion

The current study demonstrated that the temporal limits of attentional tracking for a single target are not affected by aging. Instead, it is the ability to efficiently distribute attention across multiple targets that declines in older age. The current results also revealed a large effect of gender in MOT, highlighting the need to control for gender in studies comparing attentional tracking capacities in different participant groups.

Keywords: attentional tracking, *temporal resolution of attention*, *multiple object tracking*, *aging*, *gender*

Acknowledgments

This research was supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) discovery grant and the NSERC-Essilor Industrial Research Chair (JF). We thank Simon Lacoste for help with data collection, Dr. A. Z. Khan for the use of eye tracking equipment, and all participants for their time.

Commercial relationships: none
Corresponding author: Eugenie Roudaia.
Email: eroudaia@mcmaster.ca.
Address: Faubert Lab, Pavillion Jean-Brillant, Université de Montréal, Montréal, QC, Canada.

References

Allard, R., & Faubert, J. (2013a). No dedicated second-order motion system. *Journal of Vision*, *13*(11):2, 1–9, doi:10.1167/13.11.2. [PubMed] [Article]

Allard, R., & Faubert, J. (2013b). No second-order motion system sensitive to high temporal frequencies. *Journal of Vision*, *13*(5):4, 1–14, doi:10.1167/13.5.4. [PubMed] [Article]

Downloaded From: http://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/936469/ on 09/05/2017

Allard, R., Lagacé-Nadon, S., & Faubert, J. (2013). Feature tracking and aging. *Frontiers in Psychology*, *4*, 427, doi:10.3389/fpsyg.2013.00427.

Alvarez, G. A., & Cavanagh, P. (2005). Independent resources for attentional tracking in the left and right visual hemifields. *Psychological Science*, *16*(8), 637–643.

Alvarez, G. A., & Cavanagh, P. (2015). Anatomical constraints on attention: Hemifield independence is a signature of multifocal spatial selection, *12*(5):9, 1–20, doi:10.1167/12.5.9. [PubMed] [Article]

Alvarez, G. A., & Franconeri, S. L. (2007). How many objects can you track? Evidence for a resource-limited attentive tracking mechanism. *Journal of Vision*, *7*(4):14, 1–10, doi:10.1167/7.4.14. [PubMed] [Article]

Arena, A., Hutchinson, C. V., & Shimozaki, S. S. (2012). The effects of age on the spatial and temporal integration of global motion. *Vision Research*, *58*, 27–32, doi:10.1016/j.visres.2012.02.004.

Arnold, D. H. (2005). Perceptual pairing of colour and motion. *Vision Research*, *45*(24), 3015–3026, doi:10.1016/j.visres.2005.06.031.

Astle, A. T., Blighe, A. J., Webb, B. S., & McGraw, P. V. (2014). The effect of aging on crowded letter recognition in the peripheral visual field. *Investigative Ophthalmology and Visual Science*, *55*(8), 5039–5045. [PubMed] [Article]

Atchley, P., & Andersen, G. J. (1998). The effect of age, retinal eccentricity, and speed on the detection of optic flow components. *Psychology and Aging*, *13*(2), 297–308.

Baayen, R. H., Davidson, D. J., & Bates, D. M. (2008). Mixed-effects modeling with crossed random effects for subjects and items. *Journal of Memory and Language*, *59*(4), 390–412, doi:10.1016/j.jml.2007.12.005.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Package lme4. *Journal of Statistical Software*, *67*(1), 1–91. Retrieved from http://lme4.r-forge.r-project.org

Battelli, L., Pascual-Leone, A., & Cavanagh, P. (2007). The "when" pathway of the right parietal lobe. *Trends in Cognitive Sciences*, *11*(5), 204–210, doi:10.1016/j.tics.2007.03.001.

Bennett, P. J., Sekuler, R., & Sekuler, A. B. (2007). The effects of aging on motion detection and direction identification. *Vision Research*, *47*(6), 799–809, doi:10.1016/j.visres.2007.01.001.

Bex, P. J., Dakin, S. C., & Simmers, A. J. (2003). The shape and size of crowding for moving targets. *Vision Research*, *43*(27), 2895–2904, doi:10.1016/S0042-6989(03)00460-7.

Billino, J., Bremmer, F., & Gegenfurtner, K. R. (2008). Differential aging of motion processing mechanisms: evidence against general perceptual decline. *Vision Research*, *48*(10), 1254–1261, doi:10.1016/j.visres.2008.02.014.

Boot, W. R., Blakely, D. P., & Simons, D. J. (2011). Do action video games improve perception and cognition? *Frontiers in Psychology*, *2*, 1–6, doi:10.3389/fpsyg.2011.00226

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433–436, doi:10.1163/156856897X00357.

Busey, T., Craig, J., Clark, C., & Humes, L. (2010). Age-related changes in visual temporal order judgment performance: Relation to sensory and cognitive capacities. *Vision Research*, *50*(17), 1628–1640, doi:10.1016/j.visres.2010.05.003.

Carlson, T. A., Alvarez, G. A., & Cavanagh, P. (2007). Quadrantic deficit reveals anatomical constraints on selection. *Proceedings of the National Academy of Sciences, USA*, *104*(33), 13496–13500, doi:10.1073/pnas.0702685104.

Cashdollar, N., Fukuda, K., Bocklage, A., Aurtenetxe, S., Vogel, E. K., & Gazzaley, A. (2013). Prolonged disengagement from attentional capture in normal aging. *Psychology and Aging*, *28*(1), 77–86, doi:10.1037/a0029899.

Castel, A. D., Chasteen, A. L., Scialfa, C. T., & Pratt, J. (2003). Adult age differences in the time course of inhibition of return. *Journal of Gerontology, Series B: Psychological Sciences and Social* Sciences, *58*(5), 256–259.

Cavanagh, P. (1992). Attention-based motion perception. *Science*, *257*(5076), 1563–1565, doi:10.1126/science.1523411.

Cavanagh, P., & Alvarez, G. A. (2005). Tracking multiple targets with multifocal attention. *Trends in Cognitive Sciences*, *9*(7), 349–354, doi:10.1016/j.tics.2005.05.009.

Chen, W.-Y., Howe, P. D., & Holcombe, A. O. (2013). Resource demands of object tracking and differential allocation of the resource. *Attention, Perception & Psychophysics*, *75*(4), 710–725, doi:10.3758/s13414-013-0425-1.

Cohen, M. A., Konkle, T., Rhee, J. Y., Nakayama, K., & Alvarez, G. A. (2014). Processing multiple visual objects is limited by overlap in neural channels. *Proceedings of the National Academy of Sciences, USA*, *111*(24), 8955–8960, doi:10.1073/pnas.1317860111.

Downloaded From: http://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/936469/ on 09/05/2017

Cornelissen, F. W., Peters, E. M., & Palmer, J. (2002). The Eyelink Toolbox: Eye tracking with MATLAB and the Psychophysics Toolbox. *Behavior Research Methods, Instruments, & Computers*, *34*(4), 613–617, doi:10.3758/BF03195489.

Crivello, F., Tzourio-Mazoyer, N., Tzourio, C., & Mazoyer, B. (2014). Longitudinal assessment of global and regional rate of grey matter atrophy in 1,172 healthy older adults: Modulation by sex and age. *PLoS ONE*, *9*(12), 1–26, doi:10.1371/journal.pone.0114478.

Culham, J. C., Brandt, S. A., Cavanagh, P., Kanwisher, N. G., Dale, A. M., & Tootell, R. B. (1998). Cortical fMRI activation produced by attentive tracking of moving targets. *Journal of Neurophysiology*, *80*(5), 2657–2670.

Culham, J. C., Cavanagh, P., & Kanwisher, N. G. (2001). Attention response functions: Characterizing brain areas using fMRI activation during parametric variations of attentional load. *Neuron*, *32*(4), 737–745, doi:10.1016/S0896-6273(01)00499-8.

Drum, E. S., Alnæs, D., Kaufmann, T., Richard, G., Lund, M. J., Tnnesen, S., … Westlye, L. T. (2016). Age-related differences in brain network activation and co-activation during multiple object tracking. *Brain and Behavior*, *6*(11), 1–15. doi:10.1002/brb3.533.

Drew, T., Horowitz, T. S., & Vogel, E. K. (2013). Swapping or dropping? Electrophysiological measures of difficulty during multiple object tracking. *Cognition*, *126*(2), 213–223, doi:10.1016/j.cognition.2012.10.003.

Faubert, J. (2013). Professional athletes have extraordinary skills for rapidly learning complex and neutral dynamic visual scenes. *Scientific Reports*, *3*, 1154, doi:10.1038/srep01154.

Faubert, J., & Sidebottom, L. (2012). Perceptual-cognitive training of athletes. *Journal of Clinical Sport Psychology*, *6*, 85–102.

Feng, J., Spence, I., & Pratt, J. (2007). Playing an action video game reduces gender differences in spatial cognition. *Psychological Science*, *18*(10), 850–855, doi:10.1111/j.1467-9280.2007.01990.x.

Folk, C. L., & Hoyer, W. J. (1992). Aging and shifts of visual spatial attention. *Psychology and Aging*, *7*(3), 453–465, doi:10.1037/0882-7974.7.3.453.

Franconeri, S. L., Alvarez, G. A., & Cavanagh, P. (2013). Flexible cognitive resources: Competitive content maps for attention and memory. *Trends in Cognitive Sciences*, *17*(3), 134–141, doi:10.1016/j.tics.2013.01.010.

Franconeri, S. L., Alvarez, G. A., & Enns, J. T. (2007). How many locations can be selected at once? *Journal of Experimental Psychology: Human Perception and Performance*, *33*(5), 1003–1012, doi:10.1037/0096-1523.33.5.1003.

Franconeri, S. L., Jonathan, S. V., & Scimeca, J. M. (2010). Tracking multiple objects is limited only by object spacing, not by speed, time, or capacity. *Psychological Science*, *21*(7), 920–925, doi:10.1177/0956797610373935.

Franconeri, S. L., Lin, J. Y., Pylyshyn, Z. W., Fisher, B., & Enns, J. T. (2008). Evidence against a speed limit in multiple-object tracking. *Psychonomic Bulletin & Review*, *15*(4), 802–808, doi:10.3758/PBR.15.4.802.

Geiser, C., Lehmann, W., & Eid, M. (2008). A note on sex differences in mental rotation in different age groups. *Intelligence*, *36*(6), 556–563, doi:10.1016/j.intell.2007.12.003.

Georgiou-Karistianis, N., Tang, J., Vardy, Y., Sheppard, D., Evans, N., Wilson, M., … Bradshaw, J. (2007). Progressive age-related changes in the attentional blink paradigm. *Aging, Neuropsychology, and Cognition*, *14*(3), 213–226, doi:10.1080/13825580500320681.

Gilmore, G. C., Wenk, H. E., Naylor, L. A., & Stuve, T. A. (1992). Motion perception and aging. *Psychology and Aging*, *7*(4), 654.

Green, C. S., & Bavelier, D. (2006). Enumeration versus multiple object tracking: The case of action video game players. *Cognition*, *101*(1), 217–245, doi:10.1016/j.cognition.2005.10.004.

Green, C. S., Li, R., & Bavelier, D. (2010). Perceptual learning during action video game playing. *Topics in Cognitive Science*, *2*(2), 202–216, doi:10.1111/j.1756-8765.2009.01054.x.

Guest, D., Howard, C. J., Brown, L. A., & Gleeson, H. (2015). Aging and the rate of visual information processing. *Journal of Vision*, *15*(14):10, 1–25, doi:10.1167/15.14.10. [PubMed] [Article]

Gunning-Dixon, F. M., & Raz, N. (2000). The cognitive correlates of white matter abnormalities in normal aging: a quantitative review. *Neuropsychology*, *14*(2), 224–232.

Gur, R. C., & Gur, R. E. (2017). Complementarity of sex differences in brain and behavior: From laterality to multimodal neuroimaging. *Journal of Neuroscience Research*, *199*, 189–199, doi:10.1002/jnr.23830.

Habak, C., & Faubert, J. (2000). Larger effect of aging on the perception of higher-order stimuli. *Vision Research*, *40*(8), 943–950.

Halekoh, U., & Hjsgaard, S. (2014). A Kenward-Roger

Downloaded From: http://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/936469/ on 09/05/2017

approximation and parametric bootstrap methods for tests in linear mixed models—The R Package pbkrtest. *Journal of Statistical Software*, *59*(9), 1–32, doi:10.18637/jss.v059.i09.

Hogendoorn, H., Carlson, T. A., & Verstraten, F. A. J. (2007). The time course of attentive tracking. *Journal of Vision*, *7*(14):2, 1–10, doi:10.1167/7.14.2. [PubMed] [Article]

Holcombe, A. O. (2009). Seeing slow and seeing fast: Two limits on perception. *Trends in Cognitive Sciences*, *13*(5), 216–221, doi:10.1016/j.tics.2009.02.005.

Holcombe, A. O., & Chen, W. (2013). Splitting attention reduces temporal resolution from 7 Hz for tracking one object to 3 Hz when tracking three. *Journal of Vision*, *13*(1):12, 1–19, doi:10.1167/13.1.12. [PubMed] [Article]

Holcombe, A. O., & Chen, W.-Y. (2012). Exhausting attentional tracking resources with a single fast-moving object. *Cognition*, *123*(2), 218–228, doi:10.1016/j.cognition.2011.10.003.

Holländer, A., Hausmann, M., Hamm, J. P., & Corballis, M. C. (2005). Sex hormonal modulation of hemispheric asymmetries in the attentional blink. *Journal of the International Neuropsychological Society*, *11*, 263–272, doi:10.1017/S1355617705050319.

Hopf, J. M., Boehler, C. N., Luck, S. J., Tsotsos, J. K., Heinze, H.-J., & Schoenfeld, M. A. (2006). Direct neurophysiological evidence for spatial suppression surrounding the focus of attention in vision. *Proceedings of the National Academy of Sciences*, *103*(4), 1053–1058, doi:10.1073/pnas.0507746103.

Hopf, J. M., Boelmans, K., Schoenfeld, A. M., Heinze, H. J., & Luck, S. J. (2002). How does attention attenuate target-distractor interference in vision? Evidence from magnetoencephalographic recordings. *Cognitive Brain Research*, *15*, 17–29, doi:10.1016/S0926-6410(02)00213-6.

Howard, C. J., Bashir, N., Chechlacz, M., & Humphreys, G. W. (2016). Neural mechanisms of temporal resolution of attention. *Cerebral Cortex*, *26*(7), 2952–2969, doi:10.1093/cercor/bhv101.

Howe, P. D., Horowitz, T. S., Wolfe, J., & Livingstone, M. S. (2009). Using fMRI to distinguish components of the multiple object tracking task. *Journal of Vision*, *9*(4):10, 1–11, doi:10.1167/9.4.10. [PubMed] [Article]

Hutchinson, C. V., Arena, A., Allen, H. A., & Ledgeway, T. (2012). Psychophysical correlates of global motion processing in the aging visual system: A critical review. *Neuroscience and Biobehavioral Reviews*, *36*(4), 1266–1272, doi:10.1016/j.neubiorev.2012.02.009.

Intriligator, J., & Cavanagh, P. (2001). The spatial resolution of visual attention. *Cognitive Psychology*, *216*, 171–216, doi:10.1006/cogp.2001.0755.

Iordanescu, L., Grabowecky, M., & Suzuki, S. (2009). Demand-based dynamic distribution of attention and monitoring of velocities during multiple-object tracking. *Journal of Vision*, *9*(4):1, 1–12, doi:10.1167/9.4.1. [PubMed] [Article]

Jaeger, B. C. (2016). Package "r2glmm."Software package. Available at https://CRAN.R-project.org/package=r2glmm

Jaeger, B. C., Edwards, L. J., Das, K., & Sen, P. K. (2016). An R2 statistic for fixed effects in the linear mixed model. *Journal of Applied Statistics*, *27*(29), 1–20, doi:10.1080/02664763.2016.1193725.

Jahn, G., Wendt, J., Lotze, M., Papenmeier, F., & Huff, M. (2012). Brain activation during spatial updating and attentive tracking of moving targets. *Brain and Cognition*, *78*(2), 105–113, doi:10.1016/j.bandc.2011.12.001.

Jans, B., Peters, J. C., & De Weerd, P. (2010). Visual spatial attention to multiple locations at once: The jury is still out. *Psychological Review*, *117*(2), 637–684, doi.org/10.1037/a0019082.

Jansen, P., & Heil, M. (2010). Gender differences in mental rotation across adulthood. *Experimental Aging Research*, *36*(1), 94–104, doi:10.1080/03610730903422762.

Jefferies, L. N., Roggeveen, A. B., Enns, J. T., Bennett, P. J., Sekuler, A. B., & Di Lollo, V. (2013). On the time course of attentional focusing in older adults. *Psychological Research*, *79*(1), 1–14, doi:10.1007/s00426-013-0528-2.

Johnson, P. C. D. (2014). Extension of Nakagawa & Schielzeth's R2GLMM to random slopes models. *Methods in Ecology and Evolution*, *5*(9), 944–946, doi:10.1111/2041-210X.12225.

Jovicich, J., Peters, R. J., Koch, C., Braun, J., Chang, L., & Ernst, T. (2001). Brain areas specific for attentional load in a motion-tracking task. *Journal of Cognitive Neuroscience*, *13*(8), 1048–1058.

Kennedy, G. J., Tripathy, S. P., & Barrett, B. T. (2009). Early age-related decline in the effective number of trajectories tracked in adult human vision. *Journal of Vision*, *9*(2):21, 1–10, doi:10.1167/9.2.21. [PubMed] [Article]

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2016). lmerTest: Tests for random and fixed effects for linear mixed effect models. *R Package*

Downloaded From: http://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/936469/ on 09/05/2017

Version. Available at http://CRAN.R-project.org/package=lmerTest

Lahar, C. J., Isaak, M. I., & McArthur, A. D. (2001). Age differences in the magnitude of the attentional blink. *Aging, Neuropsychology, and Cognition*, *8*(2), 149–159, doi:10.1076/anec.8.2.149.842.

Legault, I., Allard, R., & Faubert, J. (2013). Healthy older observers show equivalent perceptual-cognitive training benefits to young adults for multiple object tracking. *Frontiers in Psychology*, *4*, 323, doi:10.3389/fpsyg.2013.00323.

Lu, Z.-L., & Sperling, G. (2001). Three-systems theory of human visual motion perception: Review and update. *Journal of the Optical Society of America, A: Optics, Image Science, and Vision*, *18*(9), 2331–2370, doi:10.1364/JOSAA.18.002331.

Luis, C. A., Keegan, A. P., & Mullan, M. (2009). Cross validation of the Montreal Cognitive Assessment in community dwelling older adults residing in the Southeastern US. *International Journal of Geriatric Psychiatry*, *24*(2), 197–201, doi.org/10.1002/gps.2101.

Martens, S., & Wyble, B. (2010). The attentional blink: Past, present, and future of a blind spot in perceptual awareness. *Neuroscience & Biobehavioral Reviews*, *34*(6), 947–957.

McCarley, J. S., Mounts, J. R. W., & Kramer, A. F. (2004). Age-related differences in localized attentional interference. *Psychology and Aging*, *19*(1), 203–210, doi:10.1037/0882-7974.19.1.203.

McCarley, J. S., Yamani, Y., Kramer, A. F., & Mounts, J. R. W. (2012). Age, clutter, and competitive selection. *Psychology and Aging*, *27*(3), 616–626, doi:10.1037/a0026705.

Mounts, J. R. (2000). Evidence for suppressive mechanisms in attentional selection: Feature singletons produce inhibitory surrounds. *Perception & Psychophysics*, *62*(5), 969–983, doi:10.3758/BF03212082.

Nasreddine, Z. S., Phillips, N. A., Bedirian, V., Charbonneau, S., Whitehead, V., Collin, I., … Chertkow, H. (2005). The Montreal Cognitive Assessment, MoCA: A brief screening. *Journal of the American Geriatrics Society*, *53*(4), 695–699, doi:10.1111/j.1532-5415.2005.53221.x.

Oksama, L., & Hyönä, J. (2004). Is multiple object tracking carried out automatically by an early vision mechanism independent of higher-order cognition? An individual difference approach. *Visual Cognition*, *11*(5), 631–671, doi:10.1080/13506280344000473.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*(4), 437–432, doi:10.1163/156856897X00366.

Prins, N., & Kingdom, F. A. A. (2009). Palamedes: Matlab routines for analyzing psychophysical data. Retrieved from http://www.palamedestoolbox.org

Pylyshyn, Z. W., Haladjian, H. H., King, C. E., & Reilly, J. E. (2008). Selective nontarget inhibition in multiple object tracking. *Visual Cognition*, *16*(8), 1011–1021, doi:10.1080/13506280802247486.

Pylyshyn, Z. W., & Storm, R. W. (1988). Tracking multiple independent targets: Evidence for a parallel tracking mechanism. *Spatial Vision*, *3*(3), 179–197, doi:10.1163/156856888X00122.

R Core Team. (2015). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Raz, N., Lindenberger, U., Rodrigue, K. M., Kennedy, K. M., Head, D., Williamson, A., … Acker, J. D. (2005). Regional brain changes in aging healthy adults: General trends, individual differences and modifiers. *Cerebral Cortex*, *15*(11), 1676–1689, doi:10.1093/cercor/bhi044.

Reddy, L., Rémy, F., Vayssière, N., & VanRullen, R. (2011). Neural correlates of the continuous wagon wheel illusion: A functional MRI study. *Human Brain Mapping*, *32*(2), 163–170, doi:10.1002/hbm.21007.

Riley, E., Okabe, H., Germine, L., Wilmer, J., Esterman, M., DeGutis, J., … Pollitt, E. (2016). Gender differences in sustained attentional control relate to gender inequality across countries. *PLoS ONE*, *11*(11), e0165100, doi:10.1371/journal.pone.0165100.

Roivainen, E. (2011). Gender differences in processing speed: A review of recent research. *Learning and Individual Differences*, *21*(2), 145–149, doi:10.1016/j.lindif.2010.11.021.

Roudaia, E., Lacoste, S., & Faubert, J. (2016). The hemifield independence in multiple object tracking is preserved in healthy aging. *Journal of Vision*, *16*(12):779, doi:10.1167/16.12.779. [Abstract]

Scalf, P. E., & Beck, D. M. (2010). Competition in visual cortex impedes attention to multiple items. *The Journal of Neuroscience*, *30*(1), 161–169, doi:10.1523/JNEUROSCI.4207-09.2010.

Scholl, B. (2009). What have we learned about attention from multiple-object tracking (and vice versa)? *Computation, Cognition, and Pylyshyn*, (2), 49–78.

Sekuler, R., McLaughlin, C., & Yotsumoto, Y. (2008). Age-related changes in attentional tracking of

Downloaded From: http://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/936469/ on 09/05/2017

multiple moving objects. *Perception*, *37*(6), 867–876, doi:10.1068/p5923.

Setti, A., Finnigan, S., Sobolewski, R., McLaren, L., Robertson, I. H., Reilly, R. B., … Newell, F. N. (2011). Audiovisual temporal discrimination is less efficient with aging: An event-related potential study. *Neuroreport*, *22*(11), 554–558, doi:10.1097/WNR.0b013e328348c731.

Shim, W. M., Alvarez, G. A., Vickery, T. J., & Jiang, Y. V. (2010). The number of attentional foci and their precision are dissociated in the posterior parietal cortex. *Cerebral Cortex*, *20*(6), 1341–1349, doi:10.1093/cercor/bhp197.

Snowden, R. J., & Kavanagh, E. (2006). Motion perception in the ageing visual system: Minimum motion, motion coherence, and speed discrimination thresholds. *Perception*, *35*(1), 9–24, doi:10.1068/p5399.

Störmer, V. S., Li, S.-C., Heekeren, H. R., & Lindenberger, U. (2011). Feature-based interference from unattended visual field during attentional tracking in younger and older adults. *Journal of Vision*, *11*(2):1, 1–12, doi:10.1167/11.2.1. [PubMed] [Article]

Störmer, V. S., Li, S., Heekeren, H. R., & Lindenberger, U. (2013). Normal aging delays and compromises early multifocal visual attention during object tracking. *Journal of Cognitive Neurosicence*, *25*(2), 188–202.

Trick, L. M., Hollinsworth, H., & Brodeur, D. A. (2008). Multiple-object tracking across the lifespan: Do different factors contribute to diminished performance in different age groups ? *Computation, Cognition, and Pylyshyn*, 79–100.

Trick, L. M., Perl, T., & Sethi, N. (2005). Age-related differences in multiple-object tracking. *The Journals of Gerontology Series B: Psychological Sciences and Social Sciences*, *60*(2), P102–P105, doi:10.1093/geronb/60.2.P102.

Ulbrich, P., Churan, J., Fink, M., & Wittmann, M. (2009). Perception of temporal order: The effects of age, sex, and cognitive factors. *Neuropsychology, Development, and Cognition. Section B, Aging, Neuropsychology and Cognition*, *16*(2), 183–202, doi:10.1080/13825580802411758.

VanRullen, R., Carlson, T., & Cavanagh, P. (2007). The blinking spotlight of attention. *Proceedings of the National Academy of Sciences, USA*, *104*(49), 19204–19209, doi:10.1073/pnas.0707316104.

Verstraten, F. A., Cavanagh, P., & Labianca, A. T. (2000). Limits of attentive tracking reveal temporal properties of attention. *Vision Research*, *40*(26), 3651–3664, doi:10.1016/S0042-6989(00)00213-3.

Voyer, D., Voyer, S., Bryden, M. P., Bigelow, A., Brooks, G. P., Bulman-Fleming, B., … Johnson, R. W. (1995). Magnitude of sex differences in spatial abilities: A meta-analysis and consideration of critical variables. *Psychological Bulletin*, *117*(2), 250–270, doi:10.1037/0033-2909.117.2.250.

Vul, E., Bergsma, J., & MacLeod, D. I. A. (2010). Functional adaptive sequential testing. *Seeing and perceiving*, *23*(5–6), 483–515, doi:10.1163/187847510X532694.

Wutz, A., & Melcher, D. (2014). The temporal window of individuation limits visual capacity. *Frontiers in Psychology*, *5*, 952, doi:10.3389/fpsyg.2014.00952.

Downloaded From: http://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/936469/ on 09/05/2017