# Impacts of older age on the temporal properties of collinear facilitation

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**Collinear facilitation is a visual phenomenon by which the contrast detection threshold of a central target is reduced (facilitation) when placed equidistant between two high-contrast flankers. The neural mechanisms underpinning this phenomenon originate from feed-forward lateral facilitation between cell layers in V1 (slower) and feedback facilitation from extrastriate visual areas to V1 (faster). The strength of these contributions has been explored in younger adults by presenting the central target and flankers at varying timing offsets. Here, we investigated the effects of older age on collinear facilitation with flankers presented in sync, before, and after target onset, to allow the inference of any characteristic effect of older age on feed-forward and feedback facilitatory mechanisms. Seventeen older and 19 younger observers participated. Our data confirms previous findings of an age-related reduction in facilitation when flankers and target occur at synchrony, but no age difference was found at other timings. Marked interindividual variability in facilitation for the different flanker onset timings was present, which was repeatable within individuals. Further research is required to ascertain the mechanistic underpinnings for different facilitation profiles between individuals. Longitudinal study across an individual's life span is needed to determine whether an individual's facilitation profile changes with age.**

## Introduction

Collinear facilitation is a visual phenomenon by which the contrast detection threshold of a central target is reduced (facilitation) when placed equidistant between two high-contrast flankers (Polat & Sagi, 1993). The magnitude of facilitation is modulated by changes to orientation, spatial frequency, phase, and flanker-to-target separation (Polat, 1999; Polat & Sagi, 1993; Solomon & Morgan, 2000; Woods, Nugent, & Peli, 2002). This perceptual task has been used to assess the integrity of low-level spatial vision and, by inference, the underlying neural mechanism in healthy older ageing (Chan, Battista, & McKendrick, 2012; McKendrick, Weymouth, & Battista, 2013) as well as in diseases and developmental disorders, such as schizophrenia (Must, Janka, Benedek, & Kéri, 2004; Schütze, Bongard, Marbach, Brand, & Herzog, 2007) and autism (Jachim, Warren, McLoughlin, & Gowen, 2015). The neural mechanisms underpinning the perceptual phenomenon of collinear facilitation are believed to originate from two types of neural connections: feed-forward facilitation between cell layers in V1 (Gilbert & Wiesel, 1983, 1989; Livingstone & Hubel, 1984; Polat & Sagi, 1993; Rockland & Lund, 1982) and feedback facilitation from extrastriate visual areas to V1 (Angelucci et al., 2002; Freeman, Driver, Sagi, & Zhaoping, 2003; Huang & Hess, 2008; Hupé et al., 1998). Current available work in the older human population can only point to a possible change in the spatial interactions underlying collinear facilitation (Chan et al., 2012; McKendrick et al., 2013) but are unable to differentially pinpoint if one or both types of neural connections are affected in the ageing process. This is what we aim to decipher in this study.

Several behavioral studies over the past decade have explored the strength of the two types of neural connections underlying collinear facilitation by presenting the central target and flankers at varying timing offsets (Cass & Alais, 2006; Huang & Hess, 2008; Jachim, Gowen, & Warren, 2017; Li, Polat, Scalzo, & Bavelier, 2010; Polat & Sagi, 2006; Polat, Sterkin, & Yehezkel, 2007; Sterkin, Yehezkel, Bonneh,

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Norcia, & Polat, 2009; Tanaka & Sagi, 1998).The underlying justification for this experimental approach is that feed-forward lateral facilitation between cell layers within V1 is slow (Sherman & Guillery, 1998), whereas feedback facilitation is relatively faster due to the intercortical connections being myelinated (Girard, Hupé, & Bullier, 2001). First, the target site in V1 can only be facilitated by lateral modulatory neural connections when the signals triggered by the flankers coincide with the signals triggered by the target stimulus in V1. The time taken for these lateral modulatory signals to arrive at the target site is dependent on the contrast-dependent onset latency of the flanker and the delay of the lateral signals as a result of the slow conduction rate of the unmyelinated lateral fibers. Such optimal facilitation can, therefore, occur if flankers (higher contrast, shorter latency) are presented after the target onset, which cancels out the target–flanker delay due to the contrast-dependent onset latency difference. Second, feedback facilitation from extrastriate areas (e.g., V2) to the target site in V1 is fast due to intercortical axons being myelinated. When the V2 integration site is synchronously activated by the target and flankers, feedback facilitation is optimally sent from V2 to the V1 target site. Lateral connections are unlikely to modulate target detection for flankers presented after the target (backward masking) because a briefly presented target has offset by the time information from the lateral connections arrive at the target site (Huang & Hess, 2008; Jachim et al., 2017). Therefore, it has been proposed that feedback connections mediate any facilitatory effects of flankers presented temporally later than the central target (Huang & Hess, 2008; Jachim et al., 2017).

In healthy, young human observers, Huang and Hess (2008) showed facilitation for central target contrast detection when flankers were presented up to 150 ms before and after target onset. However, Polat and Sagi (2006) reported facilitation for synchronous and for flankers presented 120 ms before target onset but no facilitation when flankers were presented 120 ms after target onset. In order to further investigate the influence of timing of flanker onset on the strength of collinear facilitation, Jachim et al. (2017) tested observers at a series of small timing offsets from −70 to 70 ms at 35-ms intervals. All observers showed facilitation when flankers were presented before target onset, but only about half of the observers showed facilitation when flankers appeared after target onset. To explain their results, Jachim et al. (2017) proposed a model that took into account the increase in processing latency with decreasing stimulus contrast (contrast-dependent onset latency, Reich, Mechler, & Victor, 2001) as well as the speed of feed-forward and feedback interactions. Despite large interindividual variability in the observed response to differences in flanker timing, Jachim's model reasonably fit individual observer's data. Although not explicitly discussed, visual inspection of the data presented by Huang and Hess (2008) also reveals interindividual variability for peak facilitation across flanker onset timings (see figure 3 in their paper).

In the context of studying the older human visual system, previous studies have concentrated on the spatial aspects of collinear facilitation (Chan et al., 2012; McKendrick et al., 2013), but none have reported on its temporal properties. When the flankers and target are presented synchronously, facilitation is reduced in older adults for key spatial separations that drive optimal facilitation in younger adults (Chan et al., 2012). For very closely spaced targets and flankers, masking of the target by the flankers is stronger in older adults than their younger counterparts (Chan et al., 2012). This age effect remained even after correcting for the age-related decline in contrast sensitivity (Chan et al., 2012) that occurs in the aging visual system (Derefeldt, Lennerstrand, & Lundh, 1979; Owsley, Sekuler, & Siemsen, 1983).

This study aimed to quantify the impact of healthy older age on the temporal properties of collinear facilitation. Specifically, we set out to investigate the effects of older age on collinear facilitation with flankers presented in sync, before, and after target onset. The intent was to use differential responses to flanker timing to infer any characteristic effect of older age on feed-forward and feedback facilitatory mechanisms. Consistent with previous work, we predicted reduced facilitation when the target and flankers were presented synchronously. If older observers show altered facilitative strength only when flankers are presented before target onset, the implied neuroanatomical mechanism is lateral facilitation within V1. Alternately, if facilitation strength is altered only when flankers are presented after target onset, the implied mechanism is age-related differences in the feedback connections from extrastriate visual cortices to V1. In addition to exploring for group differences, we also aimed to investigate the variability in individual facilitation profiles across flanker onset timings. Jachim et al. (2017) reported a bimodal distribution in their cohort in which only around half of the observers expressed facilitation when flankers were presented after target onset. The authors interpreted that data as possible evidence for significant interindividual variation in the strength of facilitation elicited by feedback connections to V1. Therefore, exploring the extent to which facilitation profiles might differ between older and younger individuals was a secondary aim of this study.

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# Methods

## Participants

Seventeen older (60–76 years, $M \pm SD$: 67.6 ± 4.7 years, six males) and 19 younger observers (18–34 years, 26.4 ± 5.1 years, nine males) participated in this study. Participants were recruited from an existing database of previous participants in research studies or from notices posted within The University of Melbourne Parkville campus. Participants underwent a brief optometric examination at the first test session to confirm eligibility. Included participants were required to have uncorrected or corrected visual acuity of no worse than 6/7.5 with a spectacle refraction of no more than ±5 diopters spherical and no more than 2 diopters of astigmatism. Participants with health conditions or medications known to affect vision were excluded. The study received human research ethics approval from the human research ethics committee of The University of Melbourne in accordance with the Declaration of Helsinki. Written informed consent was obtained from all participants prior to the commencement of any formal data collection, and participants were reimbursed a small amount to contribute to travel costs incurred in attending.

## Equipment

Stimuli were generated using a ViSaGe system (Cambridge Research Systems, Cambridge, UK) programmed by custom written software on MATLAB R2008a (MathWorks, Natick, MA) and presented on a CRT monitor (85 Hz, 1,024 × 768 pixels, max luminance = 100 cd/m$^2$; Sony Trinitron G520, Tokyo, Japan). The monitor was gamma corrected on a weekly basis using an OptiCal luminance meter (Cambridge Research Systems). Observers were instructed to position their head on a chin rest during all parts of the testing to fix binocular viewing distance at 80 cm. Refractive correction for the viewing distance was provided in a trial frame when required.

## Stimuli

Figure 1A illustrates the Gabor stimulus set used in this experiment, which was identical to previous work (Chan et al., 2012) except for reducing stimulus duration from 100 ms to 35 ms (three frames) to match that of Jachim et al. (2017). Flanker onset was fixed at 235 ms from interval onset. Target onset varied between test runs based on predefined flanker onset timing (FOT). The central Gabor and flankers were always vertically oriented and fixed at a spatial frequency of 3 c/°. The standard deviation of the Gaussian envelope was the inverse of the spatial frequency (0.33° visual angle). Flanker contrast was fixed at 60% (Michelson's contrast) of the mean background luminance of the monitor. Flankers were always positioned at 3.5λ (λ = inverse of spatial frequency) equidistant above and below from the central Gabor. Two horizontal white fixation lines were on the screen throughout every test run, positioned 2° visual angle away from the midline and subtending 0.86° visual angle in length (Figure 1B). Stimulus intervals were indicated by the presence of a big white square with edges subtending 8.8° visual angle away from central fixation (Figure 1B). This white square was absent between the task temporal intervals and while waiting for a button press. Contrast detection thresholds were measured for a centrally presented Gabor patch under seven flanker conditions in separate runs: no flanker (NF), synchronous flankers (FOT = 0 ms), flankers occurring prior to target onset (FOT = −35, −70 ms), and flankers appearing after target onset (FOT = 105, 70, 35 ms). The order of the runs was varied between individuals in a counterbalanced fashion to avoid order-dependent effects of fatigue or learning.

## Procedure

Individual contrast detection thresholds were acquired using a two-interval, forced-choice test paradigm incorporating two interleaved three-up-one-down staircases. Thresholds for each run were computed as the geometric mean of the last two of four reversals of each staircase. All observers completed two runs at each flanker timing condition. Staircases varied the contrast of the central target Gabor in steps of 20% of the contrast level presented in the preceding trial within the same staircase. Each of the two task temporal intervals was of equal duration (550 ms) (Figure 1C & D). The duration between each temporal interval was fixed at 800 ms. The target Gabor was presented randomly in either the first or second interval. At the end of the second presentation interval, participants indicated via a button press as to which of the two intervals contained the target Gabor. In trials in which observers were unable to distinguish the target Gabor in both intervals, they were instructed to balance their guesses between the two response buttons. The next interval onset commenced after a 500-ms post–button press delay.

## Analysis

Statistical analyses were performed on both the log contrast detection threshold as well as a computed

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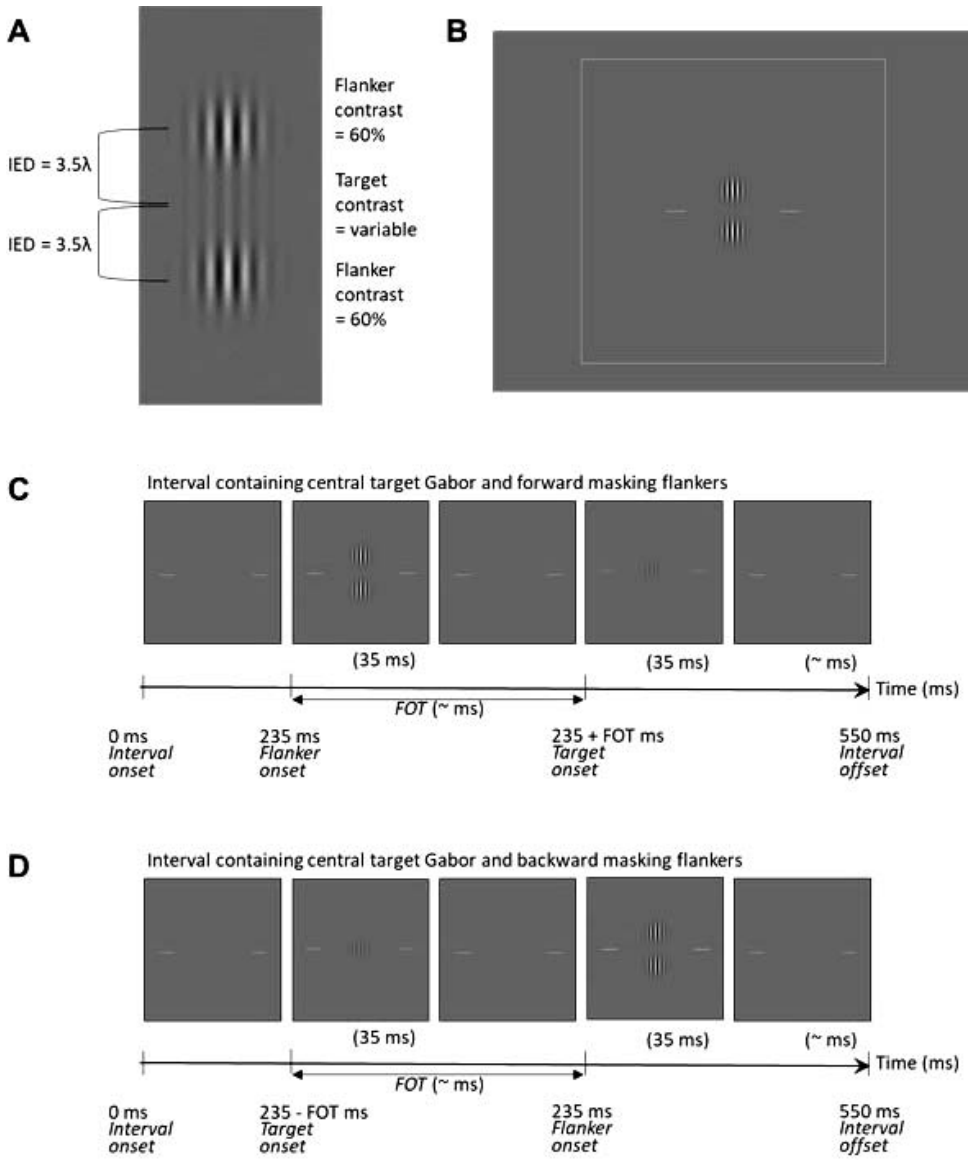


Figure 1. Schematic diagram illustrating the stimulus used in this experiment and the onset timing of target and flankers within stimulus intervals. (A) Flankers were fixed at an interelement-distance of 3.5λ and at 60% contrast. (B) Two horizontal white fixation lines were on the screen at all times to guide fixation, and a big white square was displayed on the screen throughout each stimulus interval. (C) Time course of a stimulus interval (550 ms total duration) containing target Gabor (35 ms stimulus duration) and forward masking flankers (35 ms duration) in which flanker onset was fixed at 235 ms from interval onset. Target onset varied depending on the predefined FOT for each test run. (D) Similar to panel C except this schematic represents the time course for backward masking instead of forward masking flankers.

facilitation index. Facilitation index was calculated in dB units as $-20 \times \log10$(contrast ratio), with which contrast ratio is the contrast detection threshold measured in the presence of flankers divided by that measured in the no-flanker condition. Facilitation index below zero was termed as a masking effect. Data were analyzed in a repeated-measures analysis of variance (RM-ANOVA) using IBM SPSS Statistics version 23 (IBM, New York) to assess effects of flanker onset timing and age.

## Results

### Reduced contrast detection thresholds in the presence of synchronous flankers

To assess if our findings were consistent with previous reports of facilitation by the presence of synchronous flankers, we ran an RM-ANOVA with

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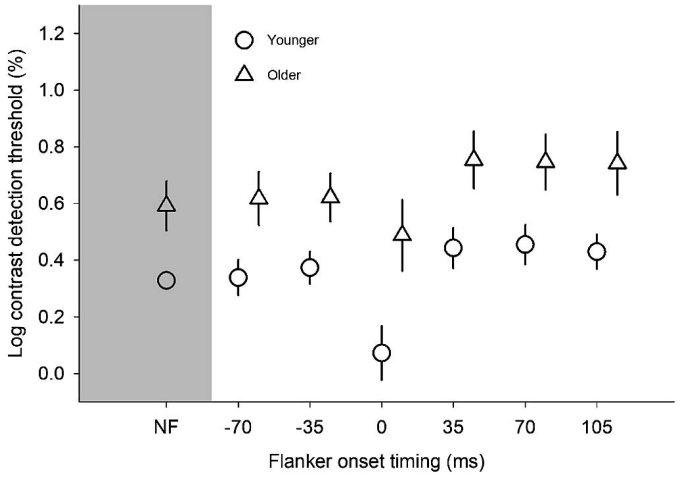


Figure 2. Log contrast detection thresholds in the older (triangles) and the younger (circles) cohorts plotted as a function of the seven flanker conditions. Symbols represent group means with error bars representing 95% confidence intervals of the mean.

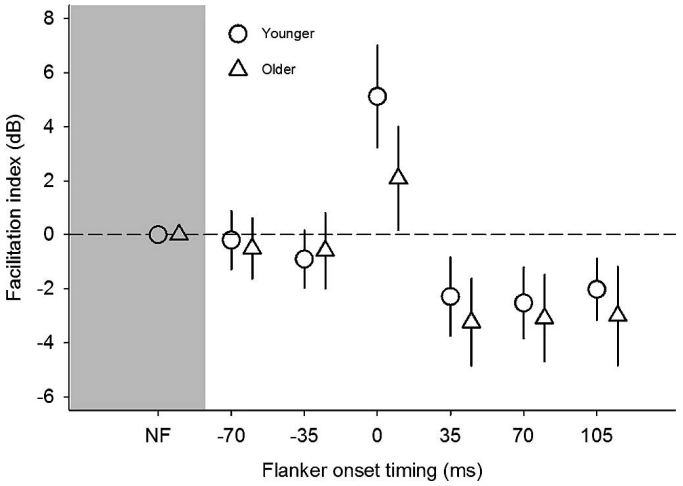


Figure 3. A significant age-related reduction in facilitation at synchrony. Group averaged facilitation index plotted as function of flanker onset timing. Symbols represent group means with error bars representing 95% confidence intervals of the mean.

presence or absence of flankers as a within-subject variable and age group as a between-subjects variable. Log contrast detection thresholds were significantly higher in the older group: main effect of group, $F(1, 34) = 44.18$, $p < 0.001$. Log contrast detection thresholds were reduced significantly by the presence of synchronous flankers as compared to the no-flanker condition in both age groups: main effect of flankers, $F(1, 34) = 31.79$, $p < 0.001$. This facilitative effect was of a greater magnitude in the younger than the older group: significant interaction between flanker condition and age group, $F(1, 34) = 5.65$, $p = 0.02$.

## Varying magnitudes of elevated contrast detection thresholds with older age across flanker onset timings

Next, we evaluated the effect of flanker onset timing on the log contrast detection thresholds by running a RM-ANOVA with the six flanker conditions (excluded the no-flanker condition) as the within-subject variable and age group as the between-subjects variable. Figure 2 shows the log contrast detection threshold estimates in the older and younger cohort at the seven flanker conditions. The log thresholds were elevated in the older group but to different extents across the various flanker onset timings: main effect of age group, $F(1, 34) = 36.14$, $p < 0.001$; significant interaction between flanker onset timing and age group, $F(1, 34) = 3.76$, $p < 0.01$. The largest elevation in contrast detection threshold in the older versus the younger group was when flankers were presented 105 ms after target onset (FOT = 105 ms, mean group threshold difference = 3.61%) and minimum threshold elevation when flankers were presented 35 ms before target onset (FOT = −35 ms, mean group threshold difference = 2.05%).

## Older observers had smaller magnitude of facilitation for synchronously presented flankers only

To quantify the effect of flankers on detection thresholds independent of individual differences in target detection at baseline, the facilitation index was calculated for each individual then averaged within the age groups. Figure 3 shows that facilitation was present for either group only when the stimuli were presented synchronously. Both groups showed masking of the target when the flankers were presented after the target. In an RM-ANOVA with the six flanker conditions as the within-subject variable and age group as the between-subjects variable, there was a main effect of flanker timing, $F(5, 170) = 70.27$, $p < 0.001$, that was dependent on age group: significant interaction between flanker timing and group, $F(5, 170) = 3.76$, $p < 0.01$. However, there was no main effect of age, $F(1, 34) = 1.24$, $p = 0.27$. To explore the interaction between timing and group, post hoc paired $t$ tests were performed. There was a significant reduction in facilitation in the older cohort when flankers were presented synchronously, FOT = 0 ms, $t(16) = 2.74$, $p = 0.01$, and presumably drove the significant interaction between timing and group (see Figure 3). Facilitation indices were similar between the two age groups at all other flanker timing conditions.

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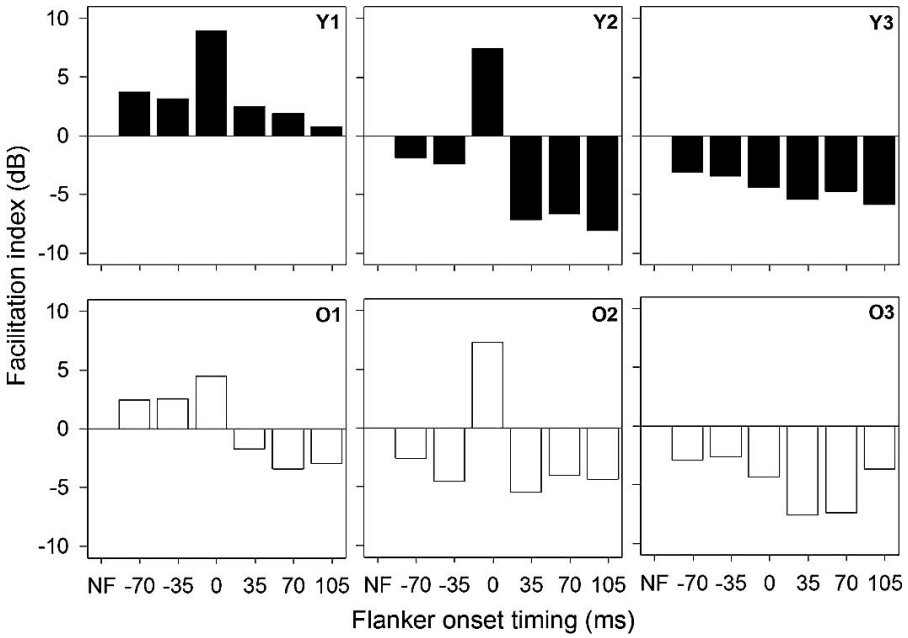


Figure 4. Large interindividual variability in facilitation profiles across flanker onset timings. Three younger observers are represented in the top row, and three older observers are shown in the bottom row. Bars above the zero asymptote indicate facilitation, and bars extending below the line indicate masking.

### Large interindividual variability in facilitation profiles across flanker onset timings

Previous literature has shown significant interindividual variability in the effect of flanker timing on collinear facilitation, particularly when flankers were presented after the target onset (Jachim et al., 2017). If present in our data, such differences in timing response profile between individuals could mask group differences or even create the situation in which the group mean profile does not actually reflect the response of any individual within the data set. Therefore, we looked at individual facilitation profiles across the younger and older cohorts. Figure 4 shows facilitation profiles from three representative younger and three older observers. Some observers showed facilitation at all flanker onset timings (e.g., Y1). Some observers showed facilitation only for forward masking and synchronous flankers (e.g., O1). A subset of observers showed facilitation only at synchrony (e.g., Y2, O2), and some others showed masking effects across all flanker onset timings (e.g., Y3, O3).

### Interindividual variability in facilitation profiles cannot be explained by test-retest variability

We subsequently retested a subset of four controls on a separate day to confirm if the variability in facilitation profiles between individuals reflects repeatable interindividual differences or is instead a reflection of test variability. Observers were retested using the identical test procedure as the main experiment. Figure 5 presents the test–retest results by comparing the facilitation profiles measured in the first (top row) to their respective second (bottom row) test sessions. The facilitation profile holds reasonably well between tests 1 and 2.

## Discussion

This study aimed to investigate whether the impacts of older age on collinear facilitation is different for flankers presented in sync, before, and after target onset. The motivation for exploring different flanker timings was to enable inference of any differential effect of older age on feed-forward and feedback facilitatory mechanisms. Consistent with previous reports (Chan et al., 2012; Huang & Hess, 2008; Jachim et al., 2017; McKendrick et al., 2013; Polat & Sagi, 1993), both the younger and older cohorts showed group averaged facilitation in the presence of synchronous flankers (Figure 2). The age-related reduction in facilitative strength at synchrony (Figure 3) was also consistent with previous work (Chan et al., 2012). However, older observers did not show a significant difference in facilitation strength for forward or backward masking flankers relative to younger observers (Figure 3), suggesting no consistent differential effect of older age on the contribution of feed-forward and feedback

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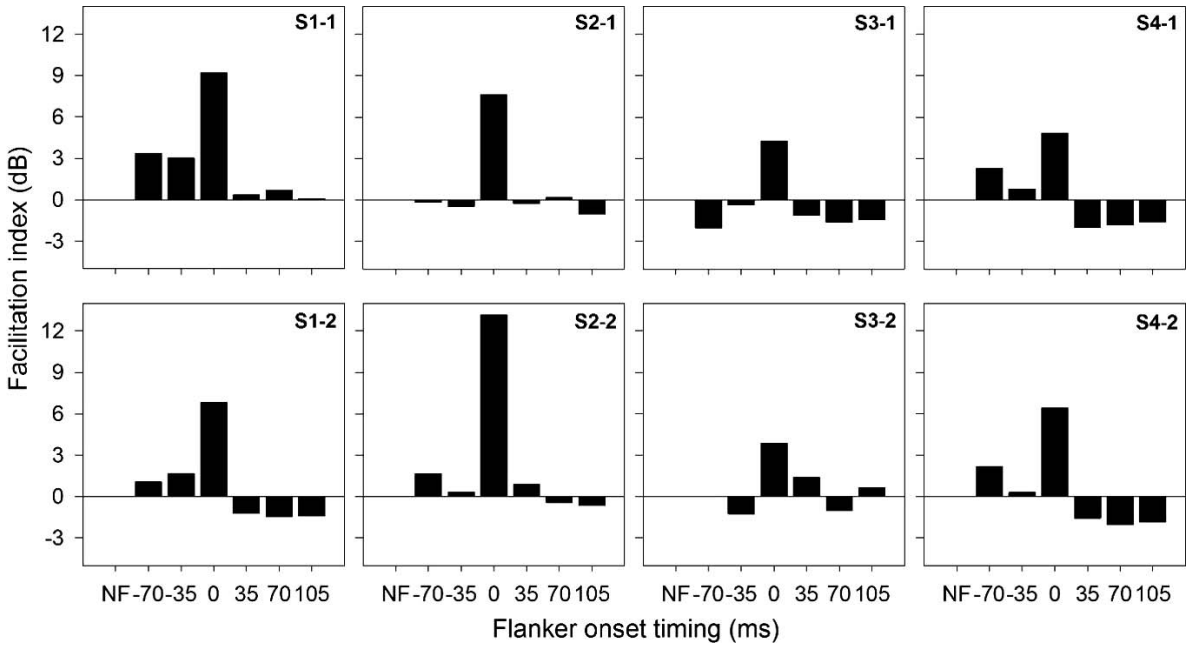


Figure 5. Test–retest variability assessed in four observers as represented by the four columns (S1–S4). Top row plots the individual facilitation profiles measured in their first test session, and the bottom row depicts their results from their second test session. Bars above the zero asymptote indicate facilitation, and bars extending below the line indicate masking.

facilitation to collinear facilitation. Inspection of individual facilitation profiles across flanker onset timings reveals large interindividual variability (Figure 4), which was also notable in Jachim et al.'s (2017) and Huang and Hess's (2008) reports on younger observers.

Besides collinear facilitation, other aspects of visual perception, such as center-surround contrast perception and contour integration, have also been proposed to be dependent on lateral feed-forward and extrastriate feedback interactions (Polat, 1999). The reduced magnitude of facilitation in the presence of synchronous flankers is in line with reports of elevated perceptual surround suppression for suprathreshold center-surround stimuli (Karas & McKendrick, 2009, 2011; Malavita, Vidyasagar, & McKendrick, 2017). Increased suppressive effects could also play a role in the age-related decline in contour integration (Del Viva & Agostini, 2007; Roudaia, Bennett, & Sekuler, 2008) as mediated by reduced facilitatory benefits from optimally aligned contour elements. However, neurophysiological evidence from animal models is suggestive of reduced cortical inhibition in the aging visual system (Dustman, Emmerson, & Shearer, 1996; Leventhal, Wang, Pu, Zhou, & Ma, 2003; Schmolesky, Wang, Pu, & Leventhal, 2000). It is worth noting however, that a recent human magnetic resonance spectroscopy study measured elevated levels of inhibitory GABA in the primary visual cortex of older people (>60 years old; Pitchaimuthu et al., 2017). Hence, the relationship between animal and human studies of inhibition within the aging visual pathways is far from clear.

The effects of forward and backward masking on spatial contextual stimuli have also been tested using other configurations, including center-surround contrast gratings (Kilpeläinen, Donner, & Laurinen, 2007). With increasing temporal offset between the surround (40% contrast) and center (20% contrast) grating onset, the effect of surround suppression decreased and reached close to no suppression at around ±75 ms. Peak suppression occurred between ±25 ms (Kilpeläinen et al., 2007). After equating for contrast-dependent processing latency differences due to surround and center size and contrast level, the suppressive effect was maximized when the surround was presented 5 ms before center grating onset. The authors concluded that this timing for optimal suppression is inconsistent with horizontal connections within V1 (slower; Kilpeläinen et al., 2007). Although both center-surround interactions and collinear facilitation at least in part share some neural contributions, it is important to note that, for near threshold detection, as measured in the current study, it is mechanistically different from suprathreshold stimulus processing, such as center-surround contrast discrimination. Perceptually, collinear facilitation is weak or absent in near-peripheral vision (Lev & Polat, 2011; Maniglia, Pavan, & Trotter, 2015; Shani & Sagi, 2005), whereas center-surround modulation has been shown to occur even at 16° visual angle away from the fovea (Xing & Heeger, 2000).

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Interindividual variability in human perceptual thresholds as reported here (Figure 4) has also been previously reported for other perceptual tasks, such as metacontrast visual masking (Albrecht & Mattler, 2016) and Vernier acuity tasks (Duncan & Boynton, 2003). In our participants, individual facilitative profiles were consistent between testing on different days (Figure 5), suggesting an underlying neuroanatomical difference between individuals. At present, there is no evidence for whether this difference derives from an anatomical structure difference or a neurochemical difference; however, both have been suggested to underlie performance differences on other tasks. For example, differences in the size of V1 have been related to visual search performance (Verghese, Kolbe, Anderson, Egan, & Vidyasagar, 2014) and Vernier acuity thresholds (Duncan & Boynton, 2003). Further, differences in the levels of cortical inhibitory neurotransmitter have also been correlated with perceptual measures of binocular rivalry (Pitchaimuthu et al., 2017; van Loon et al., 2013). Observers with higher inhibitory GABA levels in V1 were found to express longer rivalry percept durations and fewer perceptual switches (Pitchaimuthu et al., 2017). Other than cortical inhibitory and excitatory mechanisms, there is also the possibility for the involvement of motion processing pathways in this task due to the asynchronous presentation of the stimulus creating an apparent visual motion cue. It is unclear whether any visual motion cues generated by the relative presentation time difference between the central and flanking Gabors contribute to the measured perceptual thresholds here. Nevertheless, we cannot rule out differences in motion processing also contributing to observed interindividual differences. Further research is required to investigate potential differences in both wiring and perceptual performance, and how one might predict the state of the other. Outcome from such experiments may shed light on human visual development and neurophysiological changes through the lifetime.

## Conclusions

Our data confirms previous findings for an age-related reduction in facilitation when flankers and target occur at synchrony. We also show clear interindividual variability in facilitation profiles across flanker onset timings in both younger and older observers. A cross-sectional study of different age groups, therefore, cannot disentangle the individual shifts in relative effects of flanker onset timing with age. Longitudinal tracking of performance across individuals' life span will likely yield more informative outcomes on how individual facilitation profiles changes with older age.

*Keywords: collinear facilitation, aging, older adults, spatial vision, contrast sensitivity, inhibition*

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## References

Albrecht, T., & Mattler, U. (2016). Individually different weighting of multiple processes underlies effects of metacontrast masking. *Consciousness and Cognition*, *42*, 162–180.

Angelucci, A., Levitt, J. B., Walton, E. J., Hupe, J.-M., Bullier, J., & Lund, J. S. (2002). Circuits for local and global signal integration in primary visual cortex. *Journal of Neuroscience*, *22*(19), 8633–8646.

Cass, J., & Alais, D. (2006). The mechanisms of collinear integration. *Journal of Vision*, *6*(9):5, 915–922, https://doi.org/10.1167/6.9.5. [PubMed] [Article]

Chan, Y. M., Battista, J., & McKendrick, A. M. (2012). Aging effects on collinear facilitation. *Journal of Vision*, *12*(6):21, 1–10, https://doi.org/10.1167/12.6.21. [PubMed] [Article]

Del Viva, M. M., & Agostini, R. (2007). Visual spatial integration in the elderly. *Investigative Ophthalmology & Visual Science*, *48*(6), 2940–2946.

Derefeldt, G., Lennerstrand, G., & Lundh, B. (1979). Age variations in normal human contrast sensitivity. *Acta Ophthalmologica*, *57*(4), 679–690.

Duncan, R. O., & Boynton, G. M. (2003). Cortical magnification within human primary visual cortex correlates with acuity thresholds. *Neuron*, *38*(4), 659–671.

Dustman, R. E., Emmerson, R. Y., & Shearer, D. E. (1996). Life span changes in electrophysiological

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measures of inhibition. *Brain and Cognition*, *30*(1), 109–126.

Freeman, E., Driver, J., Sagi, D., & Zhaoping, L. (2003). Top-down modulation of lateral interactions in early vision: Does attention affect integration of the whole or just perception of the parts? *Current Biology*, *13*(11), 985–989.

Gilbert, C. D., & Wiesel, T. N. (1983). Clustered intrinsic connections in cat visual cortex. *Journal of Neuroscience*, *3*(5), 1116–1133.

Gilbert, C. D., & Wiesel, T. N. (1989). Columnar specificity of intrinsic horizontal and corticocortical connections in cat visual cortex. *Journal of Neuroscience*, *9*(7), 2432–2442.

Girard, P., Hupé, J., & Bullier, J. (2001). Feedforward and feedback connections between areas V1 and V2 of the monkey have similar rapid conduction velocities. *Journal of Neurophysiology*, *85*(3), 1328–1331.

Huang, P.-C., & Hess, R. F. (2008). The dynamics of collinear facilitation: Fast but sustained. *Vision Research*, *48*(27), 2715–2722.

Hupé, J., James, A., Payne, B., Lomber, S., Girard, P., & Bullier, J. (1998, August 20). Cortical feedback improves discrimination between figure and background by V1, V2 and V3 neurons. *Nature*, *394*(6695), 784–787.

Jachim, S., Gowen, E., & Warren, P. A. (2017). Individual differences in the dynamics of collinear facilitation? *Vision Research*, *133*, 61–72.

Jachim, S., Warren, P. A., McLoughlin, N., & Gowen, E. (2015). Collinear facilitation and contour integration in autism: Evidence for atypical visual integration. *Frontiers in Human Neuroscience*, *9*(115), 1–12.

Karas, R., & McKendrick, A. M. (2009). Aging alters surround modulation of perceived contrast. *Journal of Vision*, *9*(5):11, 1–9, https://doi.org/10.1167/9.5.11. [PubMed] [Article]

Karas, R., & McKendrick, A. M. (2011). Increased surround modulation of perceived contrast in the elderly. *Optometry and Vision Science*, *88*(11), 1298–1308.

Kilpeläinen, M., Donner, K., & Laurinen, P. (2007). Time course of suppression by surround gratings: Highly contrast-dependent, but consistently fast. *Vision Research*, *47*(26), 3298–3306.

Lev, M., & Polat, U. (2011). Collinear facilitation and suppression at the periphery. *Vision Research*, *51*(23–24), 2488–2498.

Leventhal, A. G., Wang, Y., Pu, M., Zhou, Y., & Ma, Y. (2003, May 2). GABA and its agonists improved visual cortical function in senescent monkeys. *Science*, *300*(5620), 812–815.

Li, R., Polat, U., Scalzo, F., & Bavelier, D. (2010). Reducing backward masking through action game training. *Journal of Vision*, *10*(14):33, 1–13, https://doi.org/10.1167/10.14.33. [PubMed] [Article]

Livingstone, M. S., & Hubel, D. H. (1984). Specificity of intrinsic connections in primate primary visual cortex. *Journal of Neuroscience*, *4*(11), 2830–2835.

Malavita, M. S., Vidyasagar, T. R., & McKendrick, A. M. (2017). The effect of aging and attention on visual crowding and surround suppression of perceived contrast threshold. *Investigative Ophthalmology & Visual Science*, *58*(2), 860–867.

Maniglia, M., Pavan, A., & Trotter, Y. (2015). The effect of spatial frequency on peripheral collinear facilitation. *Vision Research*, *107*, 146–154.

McKendrick, A. M., Weymouth, A. E., & Battista, J. (2013). Visual form perception from age 20 through 80 years. *Investigative Ophthalmology & Visual Science*, *54*(3), 1730–1739.

Must, A., Janka, Z., Benedek, G., & Kéri, S. (2004). Reduced facilitation effect of collinear flankers on contrast detection reveals impaired lateral connectivity in the visual cortex of schizophrenia patients. *Neuroscience Letters*, *357*(2), 131–134.

Owsley, C., Sekuler, R., & Siemsen, D. (1983). Contrast sensitivity throughout adulthood. *Vision Research*, *23*(7), 689–699.

Pitchaimuthu, K., Wu, Q.-Z., Carter, O., Nguyen, B. N., Ahn, S., Egan, G. F., & McKendrick, A. M. (2017). Occipital GABA levels in older adults and their relationship to visual perceptual suppression. *Scientific Reports*, *7*(1):14231.

Polat, U. (1999). Functional architecture of long-range perceptual interactions. *Spatial Vision*, *12*(2), 143–162.

Polat, U., & Sagi, D. (1993). Lateral interactions between spatial channels: Suppression and facilitation revealed by lateral masking experiments. *Vision Research*, *33*(7), 993–999.

Polat, U., & Sagi, D. (2006). Temporal asymmetry of collinear lateral interactions. *Vision Research*, *46*(6–7), 953–960.

Polat, U., Sterkin, A., & Yehezkel, O. (2007). Spatio-temporal low-level neural networks account for visual masking. *Advances in Cognitive Psychology*, *3*(1–2), 153–165.

Reich, D. S., Mechler, F., & Victor, J. D. (2001). Temporal coding of contrast in primary visual cortex: When, what, and why. *Journal of Neurophysiology*, *85*(3), 1039–1050.

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Rockland, K. S., & Lund, J. S. (1982, March 19). Widespread periodic intrinsic connections in the tree shrew visual cortex. *Science*, *215*(4539), 1532–1534.

Roudaia, E., Bennett, P. J., & Sekuler, A. B. (2008). The effect of aging on contour integration. *Vision Research*, *48*(28), 2767–2774.

Schmolesky, M. T., Wang, Y., Pu, M., & Leventhal, A. G. (2000). Degradation of stimulus selectivity of visual cortical cells in senescent rhesus monkeys. *Nature Neuroscience*, *3*(4), 384–390.

Schütze, C., Bongard, I., Marbach, S., Brand, A., & Herzog, M. H. (2007). Collinear contextual suppression in schizophrenic patients. *Psychiatry Research*, *150*(3), 237–243.

Shani, R., & Sagi, D. (2005). Eccentricity effects on lateral interactions. *Vision Research*, *45*(15), 2009–2024.

Sherman, S. M., & Guillery, R. (1998). On the actions that one nerve cell can have on another: Distinguishing "drivers" from "modulators." *Proceedings of the National Academy of Sciences, USA*, *95*(12), 7121–7126.

Solomon, J. A., & Morgan, M. J. (2000). Facilitation from collinear flanks is cancelled by non-collinear flanks. *Vision Research*, *40*(3), 279–286.

Sterkin, A., Yehezkel, O., Bonneh, Y. S., Norcia, A., & Polat, U. (2009). Backward masking suppresses collinear facilitation in the visual cortex. *Vision Research*, *49*(14), 1784–1794.

Tanaka, Y., & Sagi, D. (1998). Long-lasting, long-range detection facilitation. *Vision Research*, *38*(17), 2591–2599.

van Loon, A. M., Knapen, T., Scholte, H. S., John-Saaltink, E. S., Donner, T. H., & Lamme, V. A. (2013). GABA shapes the dynamics of bistable perception. *Current Biology*, *23*(9), 823–827.

Verghese, A., Kolbe, S. C., Anderson, A. J., Egan, G. F., & Vidyasagar, T. R. (2014). Functional size of human visual area V1: A neural correlate of top-down attention. *NeuroImage*, *93*, 47–52.

Woods, R. L., Nugent, A. K., & Peli, E. (2002). Lateral interactions: Size does matter. *Vision Research*, *42*(6), 733–745.

Xing, J., & Heeger, D. J. (2000). Center-surround interactions in foveal and peripheral vision. *Vision Research*, *40*(22), 3065–3072.

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