Perceptual learning of contour integration is not compromised in the elderly

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Older adults have decreased ability to extract visual contours from noisy backgrounds. The neural mechanisms underpinning the integration of local features into global shapes are key to human visual object perception. Our study demonstrates that older adults maintain plasticity in these mechanisms. We tested 15 younger (20-34 years) and 17 older (62-78 years) adults on six occasions. The first five sessions were conducted over several weeks, with 3-7 days between visits. The final session was 3 months after the fifth session. Contour processing was measured using closed contours (circles or ellipses) constructed of Gabor elements, embedded in noise (identical Gabors of random orientation). At visits one, five, and six, Glass pattern coherence thresholds were also measured to determine whether learning transferred to an alternate task requiring the extraction of shape signal from noise. Older adults improved in their ability to perform the contour tasks in a similar fashion to younger adults. Improvement was specific to the trained task and performance improvements were maintained over a 3-month period. Our results indicate that plasticity of the aging human visual system is maintained for contour integration.

Introduction

The ability to identify shapes and borders in the visual environment requires the integration of information across space, so that individual elements comprising contours are linked (Field, Hayes, & Hess, 1993; Kovàcs & Julesz, 1993; Loffler, 2008). Whether elements are grouped into elongated contours depends on local feature proximity and orientation (Field et al., 1993). These grouping processes change with normal aging. A closer spacing of local elements is required to identify contours from noise in older adults (Del Viva & Agostini, 2007; McKendrick, Weymouth, & Battista, 2010); however, the contour integration ability of older and younger adults shows a similar dependence upon local orientation (McKendrick et al., 2010; Roudaia, Farber, Bennett, & Sekuler, 2011). These findings are consistent with age-related differences in integrating contour elements, rather than from errors in encoding the lower level features. The purpose of our study was to determine whether older adults can improve their ability to integrate local elements into contours with training.

The neural mechanisms underlying contour integration are thought to commence with long-range cortical connections within V1 that link cells with similar orientation preferences but nonoverlapping receptive fields (Gilbert, 1992; Kapadia, Ito, Gilbert, & Westheimer, 1995). V1 responses are facilitated by collinear line segments, consistent with the proposed involvement of V1 in contour integration (Li & Gilbert, 2002; Polat, Mizobe, Pettet, Kasmatsu, & Norcia, 1998). The response of V1 neurons can also closely correlate with the perceptual saliency of contours (Li, Piëch, & Gilbert, 2006). Human fMRI data shows stronger responses to collinear than random elements in both early retinotopic areas (V1, V2), as well as in areas involved in later stages of object perception (lateral occipital complex; Altmann, Bulthoff, & Kourtzi, 2003), suggesting multistage processing of these features.

Previous studies show that performance on contour integration tasks can improve with training in younger adults (e.g., Kovàcs, Kozma, Feher, & Benedek, 1999; Li & Gilbert, 2002). One feature of training-induced improvement is an increase in the spatial range of local interactions (Li & Gilbert, 2002). Awake-behaving primate research has demonstrated that the mechanisms involved in the perceptual learning of contour tasks are retinotopic, indicating functional modification of circuitry early in visual processing (Li, Piëch, & Gilbert,

2008). However, top-down influences are also important in primates (Li et al., 2008). During a contour detection task in awake-behaving primate, V1 neuronal responses showed strong retinotopic contour-related effects (Li et al., 2008). When recording from the same, but anaesthetized, animals, the contour specific responses in V1 largely disappeared (Li et al., 2008), suggesting that training invokes top-down influences that create dynamic alterations to specific, retinotopic, neural circuits earlier in the visual pathways.

Numerous studies have shown that practice improves simple detection tasks in the elderly, such as letter discrimination, orientation and motion discrimination (for review see Kausler, 1994). Previous perceptual learning studies have also looked at trade-offs between speed and accuracy (Ratcliff, Thapar, & McKoon, 2006), and whether learning improves performance for visual search tasks in older adults (Rogers, Fisk, & Hertzog, 1994). These studies have been motivated, at least partially, by the proposal that reduced processing speed underlies many cognitive performance differences with aging (Cerella, 1985; Salthouse, 1996). Masking paradigms have been used to show that the minimum stimulus time required to obtain a useful stimulus percept can be decreased with training, with control experiments showing that improvements were not simply due to improved ability to divide attention across space (Andersen, Ni, Bower, & Watanabe, 2010).

In this study, we were interested in whether improvements in threshold performance are achievable with training in older adults for contour integration and contour shape discrimination tasks. Global contour tasks are considered a building block for closed object shape recognition and discrimination (e.g., faces/head shape). Older adults require an increased number of contour elements to discriminate the shape of a closed contour embedded in noise elements (McKendrick et al., 2010). For contours comprised of a suprathreshold number of elements, older adults require larger differences in shape to discriminate a circular global contour from an elliptical one (McKendrick et al., 2010). We specifically chose contour integration as the neural mechanisms underpinning contour integration are reasonably understood, training has been shown to increase the spatial range of interactions in both younger humans and primates (Li et al., 2008; Li & Gilbert, 2002), and the neural mechanisms that are specifically modified by training have also been studied in awake-behaving primate (Li et al., 2008). Contours were placed in the parafoveal region (4° radius), as the capacity to train the linking and extraction of contours parafoveally might have implications for improving performance on some object perception tasks in people with central vision loss.

Participants were tested at five visits approximately 1 week apart (3-7 days), and then returned for a retention visit after 3 months. We deliberately chose to spread out the training visits to consolidate the training over a time period that is closer to that suitable for in-office clinical training of visual performance (e.g., to improve visual function in age-related macular degeneration, Chung, 2011; Seiple, Grant, & Szlyk, 2011). A key concern surrounding the interpretation of age-related changes to mechanisms involved in visual psychophysical task performance is the unknown level of impact of differences in nonvisual factors between groups. To explore this issue, we also included a control, untrained task that required the discrimination of shape from noise. Our results show that older adults have equivalent capacity as younger adults to improve their ability to detect and discriminate global contours in noise, and that such training is retained. The control task served to demonstrate that performance improvements were specific to the trained visual mechanisms, and did not reflect nonvisually-related improvements in the capacity to perform forced choice psychophysical experiments.

Methods

Participants

Fifteen younger (aged 20–34, mean age = 28 years) and 17 older (aged 62–78, mean age = 69 years) adults participated. Participants underwent an optometric assessment to ensure normal vision and ocular health for age, and also a Mini-Mental State Examination (Psychological Assessment Resources, Inc., Lutz, FL, USA) to ensure cognitive performance fell within age norms. Visual acuity was required to be 6/7.5 or better, with distance refractive correction no greater than 5 diopters spherical or 2 diopters astigmatism. Participants were interviewed about their medical history and current systemic health and were excluded if they had any conditions known to affect vision or cognitive performance. None of the participants had prior experience on the computerized visual tasks or tasks of a similar nature.

The project had human research ethics approval from The University of Melbourne, and prior to participation, all volunteers provided written informed consent in accordance with the Declaration of Helsinki. Participants received a small reimbursement to partially offset travel expenses incurred in attending.

Test sessions

All participants attended the laboratory on six occasions. The first five sessions were scheduled with
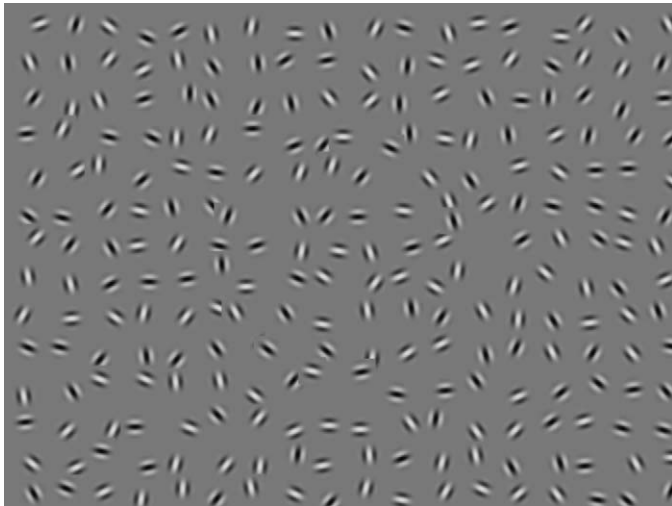
Figure 1. Example of the global contour stimulus used to explore training-related improvements in performance in older and younger adults. This example shows a circular contour comprised of 15 elements.

no fewer than 3 days and no more than 7 days between sequential sessions. The sixth session was scheduled for approximately 3 months after the fifth visit. Thus there were 32 participants, each attending for six sessions for a total of 192 test sessions in the study. The first, fifth and sixth sessions were approximately 50 minutes in duration, and the intervening sessions approximately 40 minutes. At each session, participants performed computer-based visual perceptual testing.

Equipment

Stimuli were presented on a gamma corrected 21-inch monitor (G520 Trinitron, Sony, Tokyo, Japan; maximum luminance: 100 cd/m^2; frame rate: 70 Hz; resolution: 1408 × 1056 pixels) using a ViSaGe system (Cambridge Research Systems, Kent, UK). Software was custom written in Matlab 7.0 (Mathworks, Natick, MA, USA). The viewing distance was 1 m, secured via a chinrest. The screen was viewed binocularly, and all volunteers were refractively corrected for this distance. For all tasks, a central fixation marker (0.25° black square) was present during interstimulus intervals and prior to test commencement.

The training tasks–global contour shape discrimination

The global contour tasks were a subset of those we have used previously (McKendrick et al., 2010). Figure 1 shows a representative example of the stimulus comprised of Gabor patches (Gaussian windowed sinusoidal gratings) aligned to form circles (radius of 4 degrees of visual angle) or ellipses. The spatial frequency of individual Gabors was 1.5 c/deg, with an envelope standard deviation of 0.33°. The contours were centered on the screen, and were formed by a variable number of elements. The positioning of the elements was such that all contours had approximately the same geometrical area. Alternate contour elements were of opposite spatial phase (0° or 180°), and were surrounded by random noise elements (Gabors of the same characteristics except random orientation). Contours constructed of elements of constant spatial phase can be detected by simple linear filters so do not necessarily invoke contour integration processes (Hess & Field, 1999). The full monitor area was divided into a grid of 18 × 14 (approximately 1.25° of visual angle), with one Gabor being allowed within each grid in order to avoid density cues to the position of the contour. Within each grid, the centre of the Gabor was jittered within ±0.5 grid square. Contour and noise elements were randomly computed for each presentation.

Two measures of global contour processing were made at every session:

1. The threshold aspect ratio for discriminating between an elliptical and a circular contour embedded in noise, where the contour comprised 15 elements;
2. The threshold number of elements required to discriminate an elliptical from a circular contour, for a fixed, suprathreshold aspect ratio. For each individual, this was computed as three times the threshold aspect ratio measured on the same day for a 15-element contour.

While not particularly sensitive to the contrast of the individual elements comprising the contours and noise, contour integration performance shows some decline at low contrast (McIlhagga & Mullen, 1996). Because it is well established that older adults have reduced contrast sensitivity (Elliot, Whitaker, & MacVeigh, 1990; Owsley, Sekuler, & Siemsen, 1983), contrast detection thresholds for the presence of the contour elements were measured at each session, and the subsequent experiments were conducted using stimuli that were five times the individual's contrast detection threshold as measured on that day. The choice of five times contrast threshold was based on previous similar methods that were used to study global contour integration in amblyopia (Levi, Yu, Kuai, & Rislove, 2007). Depending on the differences between individuals in the slope of the psychometric function for contrast detection, the five times multiplier may not result in balanced suprathreshold contrast conditions across observers. However, for spatially discrete stimuli, such as the individual Gabor elements in our stimuli, age-related effects on suprathreshold contrast processing such as
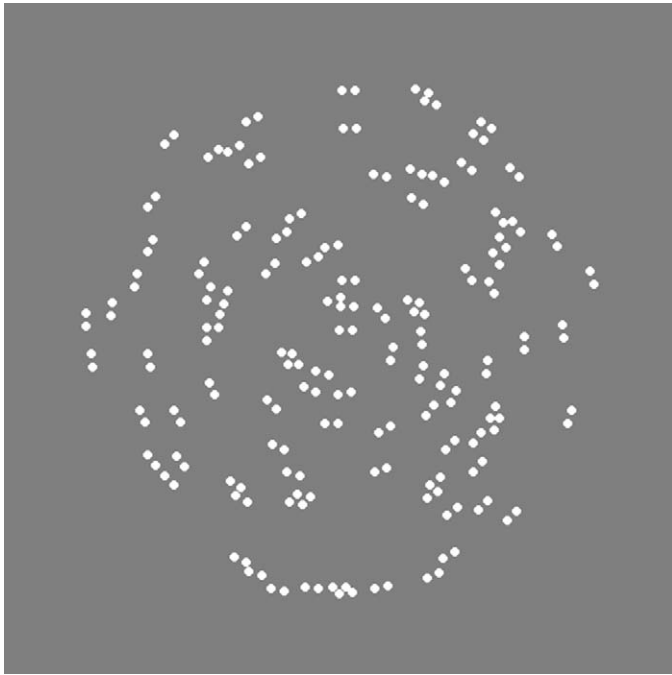
Figure 2. An example of a 100% coherence concentric Glass pattern.

contrast discrimination have been shown to be largely predictable by contrast sensitivity decline (Beard, Yager, & Neufeld, 1994).

The control task–Glass pattern shape discrimination

At the first, fifth and sixth (retention) visit, an additional task was included–Glass pattern shape discrimination. Glass patterns are comprised of pairs of dots (dipoles), arranged according to a global rule to generate a global shape percept (see Figure 2 for an example of a concentric Glass pattern). Within an individual Glass pattern (Glass, 1969), many orientations are represented: it is the global integration of these oriented dipoles that allows the discrimination of the global shape. Training-related improvements for contour tasks are generally thought to involve alterations to the mechanisms involved in making the spatial linkages between elements (Li & Gilbert, 2002), and it is not expected that such changes should impact on Glass pattern performance. Instead, our inclusion of the Glass pattern task was to investigate the possibility of training enhancements resulting from nonvisual factors such as the capacity to: understand the requirements of a computer based test of shape discrimination; perform two-interval forced choice judgments; and attend to and process briefly-presented visual stimuli.

The Glass patterns were comprised of white dots (100 cd/m^2), 6 min arc, with dots within a pair being separated by 9 min arc. One hundred dot pairs were presented within a 5° diameter circular window, on a gray background of mean luminance (50 cd/m^2). A proportion of the dot pairs were arranged according to the concentric rule (the signal dots), with the remainder being positioned as random noise dots. Participants were required to discriminate a concentric pattern from a noise pattern. The noise pattern had the same number of signal dipoles and noise dots; however, the signal dipoles were positioned with random orientations rather than according to the global rule. This results in test stimuli and noise stimuli having similar local density cues. Coherence thresholds were measured (see Methods): a measure of the minimum number of signal pairs to distinguish the coherent pattern from noise.

Generalized thresholding procedures and requirements for all tasks

For all tasks, thresholds were measured using a two-interval forced choice paradigm, where each interval was 200 ms duration with a 500 ms interstimulus interval between the two presentations. For the contour tasks, participants were required to indicate, via a button press, whether the ellipse appeared in the first or second interval (circular contour shown in the other interval). For the Glass pattern task, participants identified the interval with the concentric coherent pattern (noise pattern shown in the other interval). After each pair of presentations, participants were allowed as long as they needed to respond, and received auditory feedback in the form of a high-pitched beep for a correct answer, and a lower pitched tone for an incorrect answer. An adaptive staircase methodology was used, with three sequential correct responses resulting in increasing task difficulty and every incorrect response decreasing the task difficulty. The staircase step-sizes for the relevant experiments were: 20% change in contour aspect ratio; reducing/increasing the number of contour elements by one; or a 10% change in number of stimulus dots within the Glass pattern. Each run consisted of two interleaved staircases of six reversals, with the final threshold estimate of each staircase being computed as the average of the last four reversals. Measures were repeated twice at each visit, hence the final estimate of threshold was the mean of four staircase runs.

The three-down, one-up staircase methodology converges on approximately the 79% correct level (Wetherill & Levitt, 1965). We chose to use a staircase method as a considerable proportion of presentations are close to threshold for all observers. As base thresholds were expected to differ between groups, we

wanted to ensure that all participants were trained on a significant number of trials where the correct decision wasn't obvious. This may not occur if the procedure is terminated after a fixed number of trials, unless that number is large which can be impractical for elderly observers. The mean ($\pm$ standard deviation) number of presentations per session for each task and group were: younger $= 156 \pm 23$, older $= 162 \pm 27$ (global contour aspect ratio); younger $= 130 \pm 23$, older $= 127 \pm 27$ (global contour element number); younger $= 161 \pm 31$, older $= 152 \pm 30$ (Glass pattern coherence). These figures are the average pooled across all sessions because repeated-measures ANOVA confirmed that there was no significant difference in the number of presentations for a given task between sessions for either group [main effect of session: aspect ratio: $F(5, 150) = 0.49$, $p = 0.78$; global contour element number: $F(5, 150) = 0.37$, $p = 0.87$; glass pattern coherence: $F(2, 60) = 0.15$, $p = 0.86$]. The number of presentations did not differ between groups for any of the tasks (no significant main effect of group nor group by session interaction for any task): [no main effect of group: aspect ratio: $F(1, 30) = 0.40$, $p = 0.53$; global contour element number: $F(1,30) = 0.12$, $p = 0.73$; glass pattern coherence: $F(1,30) = 0.72$, $p = 0.40$; no group by session interaction: aspect ratio: $F(5, 150) = 0.33$, $p = 0.89$; global contour element number, $F(5, 150) = 0.36$, $p = 0.87$; glass pattern coherence: $F(1,30) = 0.72$, $p = 0.40$]. Note that perceptual learning has been demonstrated with many fewer trials than used here albeit for different types of perceptual tasks (face and texture identification; Hussain, Sekuler, & Bennett, 2009).

To ensure familiarity with the task requirements, all observers had some initial training prior to formal data collection. For this initial training, the stimuli were presented for 1 sec rather than the 200 ms used in the main experiments. The pretraining ensured that all participants understood the requirements of the task, both in terms of the perceptual judgments and practical issues such as where to fixate and which button to press. Approximately 5 minutes of training was performed, until both the experimenter (author JB) and the participant were satisfied that the task requirements were well understood.

Results

The trained contour tasks

Group mean thresholds at each visit are shown in Figure 3. For both of the global contour tasks, the older observers had significantly elevated thresholds relative to younger observers [repeated-measures AN-OVA, between factor of group, within factors of
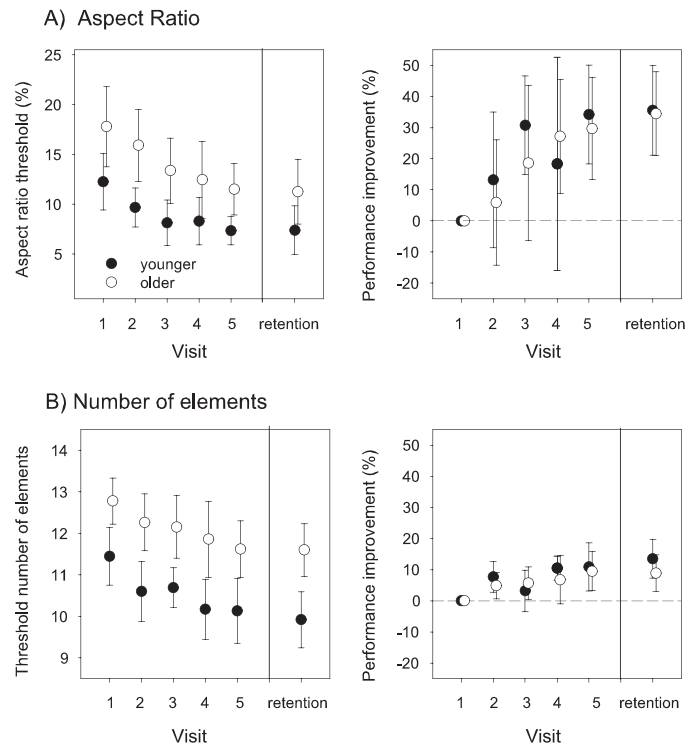

Figure 3. Mean thresholds (left-hand side) for older (unfilled circles) and younger (filled circles) adults for the (A) Aspect Ratio measurement and (B) Number of ellipses required to discriminate a circular contour from an elliptical contour. Error bars are 95% confidence intervals of the mean. The right-hand panels show the mean ($\pm$95% confidence interval of the mean) percentage improvement from baseline at each visit.

session: aspect ratio, $F(1, 30) = 10.24$, $p = 0.003$; number of elements, $F(1, 30) = 19.27$, $p < 0.001$]. Both age groups showed improved performance with training [main effect of session: aspect ratio, $F(5, 150) = 9.64$, $p < 0.001$; number of elements, $F(5,150) = 7.70$, $p < 0.001$]. The average benefit of training did not differ between age groups for either task [no significant interaction between group and session: aspect ratio, $F(5, 150) = 0.43$, $p = 0.62$; number of elements, $F(5, 150) = 0.40$, $p = 0.85$].

After five visits, the average performance improvement relative to baseline for the aspect ratio judgment was 34% for the younger observers and 30% for the older group (see Figure 3, right-hand side). Despite the similar average effect of training on the two groups, Figure 3A demonstrates large differences in the percentage improvement between individuals in both age groups. A 95% confidence limit for the difference in percentage improvement between the group mean older and group mean younger data was determined using a resampling procedure (Efron & Tibshirani, 1993), with 10,000 bootstrap samples and ranged from −16% to 24% for the aspect ratio thresholds.
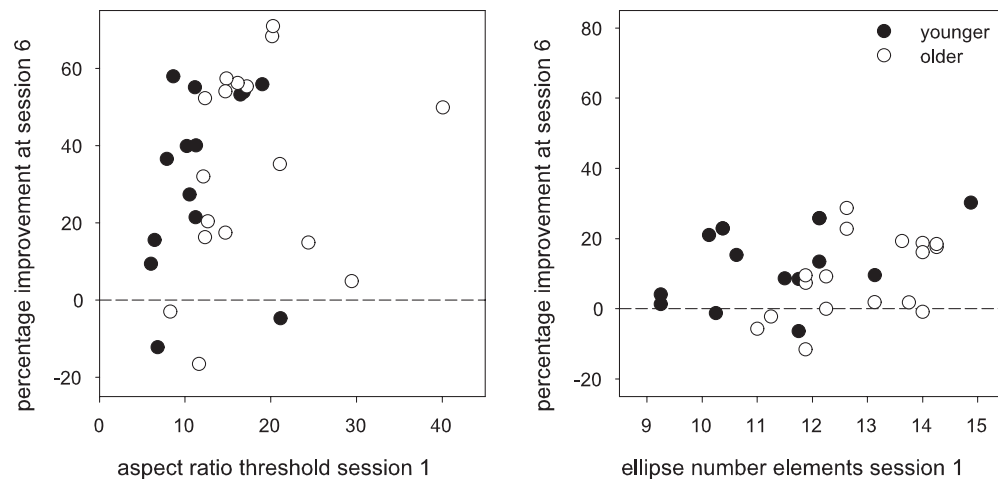
Figure 4. Percentage improvement at the final session relative to initial threshold for the aspect ratio task (left-hand panel) and threshold number of ellipse elements to discriminate contour shape (right-hand panel). Data are shown for each individual participant. Points above the reference line at zero showed improvement in performance.

The average number of elements required to discriminate the circular from elliptical contour also decreased with training over the first five visits (Figure 3B, right-hand panel) by on-average 13% for younger and 10% for older adults (95% confidence interval for the difference between older and younger adult group means was −7% to 10%). There was no significant difference between thresholds at visit five and visit six for either test or group implying that training-related performance improvements had been maintained during that 3-month period, paired *t*-tests; aspect ratio: young, $t(14) = -0.05$, $p = 0.96$; older, $t(16) = 0.20$, $p = 0.84$; number elements: young, $t(14) = 0.75$, $p = 0.47$; older, $t(16) = -0.28$, $p = 0.78$.

Figure 3 shows considerable variability in training outcomes, particularly for the threshold aspect ratio task. Participants received significant initial training on the procedural aspects of the task; however, it is worth considering whether the data supports the idea that variability was enhanced due to the baseline thresholds being contaminated for some individuals due to incomplete familiarity with the task. If this were the case, those individuals with higher initial thresholds might be expected to show the most learning improvement. Figure 4 plots the percentage improvement at the final session (relative to the first session) against the initial threshold for both tasks. There was no significant correlation between percentage improvement in threshold and initial threshold for either task, assessed for both groups independently and all participants pooled (Spearman Rank-Order correlation, all $p > 0.05$).

The control task

Glass pattern coherence thresholds are shown in Figure 5. The older observers required larger numbers of signal dipoles relative to younger observers at all test visits, main effect of group: $F(1, 30) = 19.55$, $p < 0.001$. Neither group showed any improvement or deterioration in performance relative to baseline at visit five, or at the retention visit approximately 3 months later, no main effect of session: $F(2, 30) = 1.26$, $p = 0.30$; and no significant interaction between session and group, $F(2, 60) = 0.47$, $p = 0.63$.

Contrast thresholds

Figure 6 shows that the contrast thresholds also improved with increasing session number, $F(5, 150) = 3.14$, $p = 0.01$. The amount of improvement at the final session was not significantly different between groups [average 13% improvement for younger observers, 11% for older observers (95% CI for the difference in the percentage improvement at visit five between the older and younger adult group means = −14% to 9%): no session × group interaction, $F(5, 150) = 0.37$, $p = 0.87$].

Discussion

Consistent with previous studies (Casco, Robol, Barollo, & Cansino, 2011; Del Viva & Agostini, 2007; McKendrick et al., 2010; Roudaia, Bennett, & Sekuler, 2008), our results show that healthy normal aging results in a decreased ability to discriminate global shapes constructed from local elements embedded in noise. Our novel finding is that the neural mechanisms involved in such tasks maintain plasticity in older adults, and can retain the benefits of training for at least 3 months. Thresholds for the older group
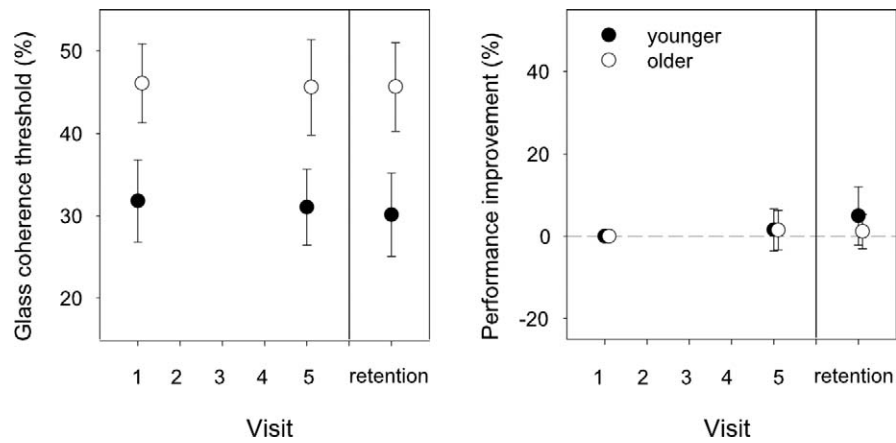
Figure 5. Glass pattern coherence thresholds for the older (open symbols) and younger (filled symbols) adults at each test session (left-hand panel), and percentage improvement relative to baseline (right-hand panel). In all panels, data are shown as means ± 95% confidence intervals of the mean.

posttraining were similar to those of younger adults pretraining.

The Glass pattern discrimination task had exactly the same stimulus timing, and procedural requirements (two-interval forced choice comparison) as the global contour tasks, yet neither older nor younger adults showed any performance improvement for Glass pattern discrimination in the absence of repeated training. This control experiment shows that learning of the procedural aspects of the task cannot explain the improvements on the contour discrimination tasks for either age group. Similarly, if global contour discrimination improvement resulted from training enhancements in managing the memory requirements of the temporal two-interval forced choice comparison, or from improvements in the ability to process short duration stimuli (200 ms), such nonvisual learning

should also transfer to the Glass pattern task. Our data show no evidence for these effects.

Consistent with previous reports, our older group demonstrated elevated contrast thresholds (Elliot et al., 1990; Owsley et al., 1983). Contrast thresholds also improved with training in both groups. To guard against the learning benefits shown for the global contour tasks being influenced by improving contrast detectability of the stimulus, we approximately matched the contrast of the stimuli on an individual participant basis at each visit. Contour integration is not highly dependent on contrast; however, the ability to detect contours in noise deteriorates at low contrast (McIlhagga & Mullen, 1996).

Our stimuli were presented for 200 ms to minimize the possibility of participants making eye movements to search for the contours. Despite being brief, the stimulus duration is unlikely to have critically limited
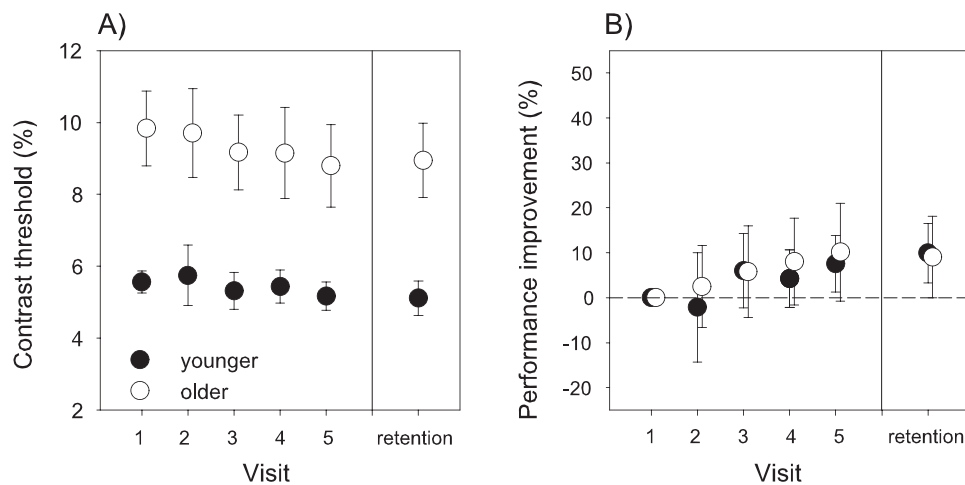

Figure 6. Contrast thresholds for the older (open symbols) and younger (filled symbols) groups at each test session (left-hand panel), and percentage improvement relative to baseline (right-hand panel). In all panels, data are shown as means ±95% confidence intervals of the mean.

performance. There is some evidence that older adults require longer duration stimuli than younger adults to reach a given level of contour discrimination performance, however that average threshold duration is less than 200 ms (Roudaia et al., 2011). Two hundred milliseconds is also substantially longer than the threshold stimulus duration for global shape discrimination of radial frequency patterns measured for older observers (Habak, Wilkinson, & Wilson, 2009). Our tasks were somewhat different than those described in these previous works; however, required the detection of contours and the discrimination of their global shape. Given that our stimuli were suprathreshold contrast it seems unlikely that stimulus duration limited performance in our older adult observers.

Glass pattern discrimination performance was significantly impaired in our older adult group and did not improve. Glass pattern discrimination is not expected to entirely share the same mechanisms as contour integration (for mechanisms likely to underpin Glass pattern discrimination, see: Ostwald, Lam, Li, & Kourtzi, 2008; Smith, Bair, & Movshon, 2002), however, glass pattern discrimination is also a visual form task that requires the extraction and discrimination of concentric shapes. The purpose of including this task was to determine whether older adults improved in their ability to generally make judgments about concentric shapes within a 2IFC psychophysical experiment. Perceptual learning studies often explore for retinotopic transfer or for transfer of learning across stimulus attributes (e.g., spatial frequency or orientation). Previous studies of perceptual learning of contour integration tasks have shown the learning effects to be retinotopic (Li et al., 2008), to show interocular transfer (Kovàcs et al., 1999), and to be enhanced by sleep (Gervan & Kovacs, 2010). Given that our results show no difference in the magnitude or time-course of learning effects between older and younger adult groups, it is simplest to assume that the underlying mechanisms for learning are the same. A more complicated explanation is that the same amount and approximate rate of learning is achieved via different mechanisms in the older group. This possibility cannot be ruled out by our experiments; however, in the absence of a clear prediction, the simpler explanation seems more parsimonious.

Age-related increases in Glass pattern coherence thresholds have recently been reported (Weymouth & McKendrick, 2012). Despite being comprised of small dots, it is important to note that the ability to perform Glass pattern tasks is quite robust to optical change. In younger adults, glass pattern coherence thresholds do not deteriorate unless the contrast of the stimulus is reduced to approximately two times threshold, and are also not reduced by up to 2D of spherical blur (Weymouth & McKendrick, 2012), as these manipula-

tions still enable accurate encoding of the centroid of the dot elements, hence accurate encoding of the dipole pairings. Our Glass pattern stimuli were high contrast hence it seems unlikely that our inability to find an improvement in Glass pattern discrimination performance in either participant group represents some floor effect whereby the effects of optical deterioration mask the ability to detect neural performance improvement.

The neural mechanisms underlying contour integration are relatively well studied, rendering it a particularly useful task for exploring plasticity within the human visual system (Altmann et al., 2003; Li et al., 2006, 2008; Li & Gilbert, 2002). Our results show that the minimum number of elements required to discriminate between a circular and elliptical contour reduces with training implying an increase in the distance over which local spatial interactions occur. The discrimination of global shapes presumably requires later processing than simple contour extraction, with convergent evidence from neurophysiology and functional imaging indicating that area V4 plays a key role in global shape encoding (Gallant, Braun, & Van Essen, 1993; Gallant, Shoup, & Mazer, 2000; Wilkinson, James, Wilson, Gati, Menon, & Goodale, 2000). While improved performance may result from functional alterations to neural networks early in the cortical visual system, primate experiments suggest that a key role is played by top-down feedback connections because training-induced modifications to neural behavior disappear when the animal is anaesthetized (Li et al., 2008). Nevertheless, explicit attention to the contours is not mandatory for learning in humans, as contour integration performance can also improve when contours are presented subliminally (Rosenthal & Humphreys, 2010). A key difference between human and primate studies is the inability to explicitly instruct primates on the specific task requirements. It is possible that learning to perform the task initially by trial and error for reward utilizes different mechanisms to those employed by people who have the benefit of explicit verbal instructions and task demonstration.

This study shows that training can improve contour integration task performance in older adults, and adds to a growing body of research that shows considerable plasticity of visual neural systems in the older brain (Andersen, Ni, Bower, & Watanabe, 2010; Bower & Andersen, 2011). Our experiments do not determine whether with prolonged training asymptotic performance in older adults can reach that of their younger counterparts, as it is unclear what level of training is required to reach asymptotic performance and this may vary between groups. The data hints at a hardwired improvement limit because learning appears to begin to plateau at a similar rate in both groups, with older adults still being poorer performers. For the training duration conducted here, the asymptotic limit of older

adults was similar to untrained performance in younger adults. Relatively few trials can improve performance in both groups, which suggests positive outcomes for applications of perceptual training in older adults beyond the laboratory.

Acknowledgments

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