Age-related deficits in attentional control of perceptual rivalry

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A B S T R A C T

Some aspects of attentional processing are known to decline with normal aging. To understand how age affects the attentional control of perceptual stability, we investigated age-related changes in voluntarily controlled perceptual rivalry. Durations of the dominant percept, produced by an ambiguous Rubin vase-faces figure, were measured in conditions that required passive viewing and attentional control: holding and switching the dominant percept. During passive viewing, mean dominance duration in the older group was significantly longer (63%) than the dominance duration found in the young group. This age-related deficit could be due to a decline in the apparent strength of the alternating percepts as a result of higher contrast gain of visual cortical activity and a reduction in the amount of attentional resources allocated to the ambiguous stimulus in older people compared to young adults. In comparison to passive viewing, holding the dominant percept did not significantly alter the dominance durations in the older group, while the dominance durations in the young group were increased (~100%). The dominance durations for both age groups in switch conditions were reduced compared to their passive viewing durations (~40%). The inability of older people to voluntarily prolong the duration of the dominant percept suggests that they may have abnormal attentional mechanisms, which are inefficient at enhancing the effective strength of the dominant percept. Results suggest that older adults have difficulty holding attended visual objects in focus, a problem that could affect their ability to carry out everyday tasks.

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1. Introduction

Our ability to select relevant sensory information among unrelated sensory messages is vital for efficient performance in various cognitive tasks. Some aspects of this attentional processing are known to decline with normal aging. Impairments due to aging are usually found in tasks that require flexible control of attention, for example dividing or switching attention among multiple inputs or tasks (McDowd & Craik, 1988). However, selective attention, which involves searching for a target item that is surrounded by other non-target items, is relatively preserved in older adults. Despite responding to a target slower than younger adults, the older adults performed similarly to the younger group as a function of distractor number (Verhaeghen & Cerella, 2002). Older adults exhibit normal performance in tasks that require sustained attention to maintain focus on specific stimuli for longer periods of time (Posner & Petersen, 1990), for example in easy vigilance tasks requiring detection of rare events (Parasuraman, Nestor, & Greenwood, 1989). However, vigilance tasks, involving higher event rate and spatial uncertainty, revealed an age-related decrement in detection performance (Mouloua & Parasuraman, 1995).

Attention, however, is a complex process that involves a range of neuronal mechanisms at various processing stages (for a review see Carrasco, 2011). As a result our current knowledge of age-related changes in attentional processing and their underlying neuronal mechanisms remains limited. It is therefore important that new behavioral approaches be used to provide information about the age-related decline in the neuronal mechanisms involved in attentional control.

The paradigm of perceptual rivalry is a useful tool for exploring mechanisms of perceptual organization, which is characterized with spontaneous alternations between mutually exclusive interpretations of the same sensory input (Blake & Logothetis, 2002). Age-related deficits in the dynamics of perceptual rivalry, however, have seldom been addressed. A few studies have found that the spontaneous rate of binocular rivalry, produced by simultaneously presented different images to each eye, diminished with age (Jalavisto, 1964; Ukai, Ando, & Kuze, 2003). These findings cannot be accounted for by the aging of visual functions, such as presbyopia, reduced contrast sensitivity, light scattering of the lens, or pupil size reduction (Ukai, Ando, & Kuze, 2003). Motivated by these findings, Norman et al. (2007) found that older people had lower sensitivity than younger people to a probe spot when presented to the suppressed eye during binocular rivalry. Using a binocular matching circuitry model, Lehky and Blake (1991) suggested that

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the increased binocular rivalry suppression results from an age-related reduction of inhibition in the visual cortex.

The contribution of voluntary attentional control on the rate of binocular rivalry was suggested over hundred years ago (von Helmholtz, 1866). Lack (1978) presented data confirming this suggestion by showing that eye movements, blinking, accommodation, and pupillary activity could not explain the attentional effects. Meng and Tong (2004) found that selective attentional control of one of the rivalry percepts, produced by an ambiguous Necker cube, increased the dominance duration of the desired percept and decreased the duration of the non-desired percept, compared to passive viewing. Binocular rivalry, produced by face and house images, showed stronger effects on the reduction of the dominance duration of the non-desired percept than that of the desired percept. The attentional modulation was stronger (37%) for the Necker cube and weaker (10%) for binocular rivalry. The authors concluded that binocular rivalry may involve a more automatic, stimulus-driven form of perceptual bistability which is less biased by selective attention. Similar results were reported by van Ee, van Dam, and Brouwer (2005), comparing binocular rivalry, the Necker cube and a bistable stereo-slant stimulus. This study also showed that a task to speed up the perceptual alternations resulted in an increase in rivalry rate.

As older people experience attentional deficits, we wondered how attentional control would affect the dynamics of their perceptual rivalry. To examine this we have employed an ambiguous Rubin figure (Rubin, 1921) that produces spontaneous alternations of two different percepts, a vase and faces. We used this ambiguous image instead of binocular bistable stimulation because it easily evokes perceptual rivalry of two distinct percepts in naïve observers without mixed and patchy percepts and return transitions, which could be experienced during binocular rivalry (Mueller & Blake, 1989) especially in elderly people (Jalavisto, 1964). Additionally, perceptual rivalry produced by the Rubin figure does not require two functioning eyes; it is less dependent on refractive errors and as noted before, it is more strongly modulated by selective attention than binocular rivalry.

We recorded the duration of the dominant percept under passive viewing and attentional control of perceptual rivalry involving holding and switching of the dominant percept. Attentional control was achieved by instructing the subjects to hold the dominant percept as long as possible or to switch it as fast as possible. Such an endogenous attentional control, however, could be inefficient in the elderly due to working memory deficiencies (Gazzaley et al., 2005). Therefore, exogenous stimulus-driven aids were also used. In older people, long-lasting perceptual alternations may induce fatigue reducing the rivalry rate across experimental trials. On the other hand, the perception of rivalry percepts may be accompanied by training effects that, in turn, could increase the rivalry rate over a longer period of time. To test whether such effects characterize perceptual rivalry in young and older subjects, we measured the drift of alternation rate across experimental trials.

Eye movements while fixating on bistable stimuli could modulate the dynamics of perceptual rivalry to some extent. Studies employing methods that compensate for eye movements (Pritchard, 1958; Scotto, Oliva, & Tuccio, 1990) or using after-images (Blake, Fox, & McIntyre, 1971; Lack, 1971) have shown that perceptual alternations of binocular rivalry stimuli may occur without eye movements. Other studies, however, have found correlation between eye movements and perceptual alternations (Einhauser, Martin, & Konig, 2004; Ito et al., 2003; van Dam & van Ee, 2005). These contradictory findings are further complicated by the fact that attentional control of perceptual rivalry could be responsible for altering the dynamics of eye movements. Glen (1940) showed that a task requiring subjects to slow down the rate of perceptual alternations produced by a Necker cube reduced the frequency of eye movements, while voluntary speeding up of rivalry rate increased the frequency of eye movements compared to that in passive viewing. We recorded eye movements in order to test their potential influences on the dynamics of perceptual rivalry in both age groups.

In this study, as in most studies investigating the dynamics of perceptual rivalry, the estimation of perceptual switches is based on subjective reports using button presses indicating the dominance percept. Recent studies have shown that pupil dilation could be used as an objective measure of rivalry (Einhauser et al., 2008; Hupe, Lamirel, & Lorenceau, 2009; Naber, Frassle, & Einhauser, 2011). We used this approach to test whether older and young subjects reported their percept accurately.

2. Methods

2.1. Subjects

We recruited 18 young (mean age = 24.4, SD = 4.12 years) and 16 older adults (mean age = 69.2, SD = 6.90 years). All subjects had normal or corrected-to-normal vision at a viewing distance of 1 m. Each participant passed the Mini-Mental-State-Examination (Folstein, Folstein, & McHugh, 1975), which minimized the possibility of subjects having dementia and other cognitive impairments. Ethical approval was obtained from the Glasgow Caledonian University ethics board, and all tests were conducted in accordance with the tenets of the Declaration of Helsinki.

2.2. Apparatus

The stimuli were presented on an RGB monitor (Vision Master Pro 450, Iiyama) at a screen resolution of 1024×768 pixels and a frame rate of 75 Hz. Custom software was used to carry out the experiment.
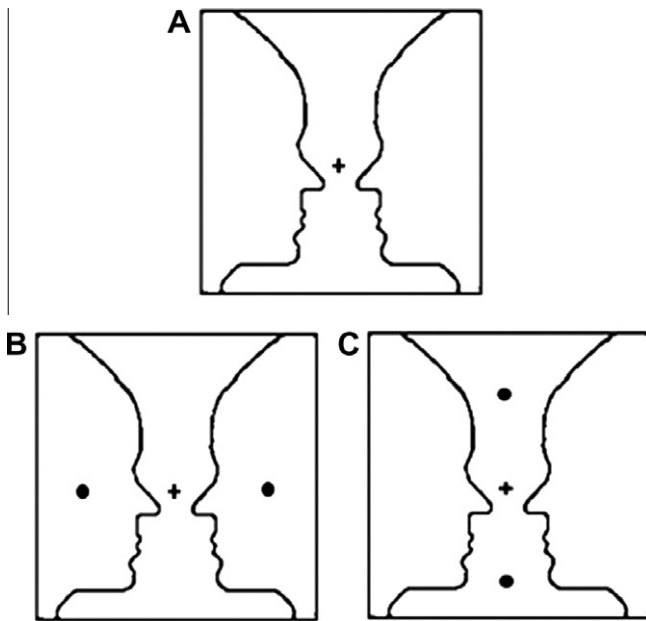
2.3. Stimuli

The stimuli contained a Rubin vase-faces figure. The image had a size of 9.0×8.8 deg and was viewed binocularly at 1 m. The luminance of the screen was 35 cd/m² and the luminance of the image contours (width of 0.01 deg) was 7 cd/m². A fixation cross was shown in the central area of the ambiguous image (see Fig. 1). In conditions with exogenous marks, two dark disks (diameter of 0.23 deg; luminance of 7 cd/m²) were presented within the areas forming the faces at 3 deg to the left and right from the fixation cross (Fig. 1B) and within the region of the vase at 3 deg above and below the fixation cross (Fig. 1C). The disks were introduced abruptly (with a delay of one screen frame 16 ms) when the subjects pressed a mouse button, indicating a change in the dominant percept, and remained on the screen until the next button press.

2.4. Procedure

Subjects were instructed to focus on the fixation cross and when, for example, the dominant percept was the vase, to press and hold the left mouse button. When the faces became the dominant percept, they pressed and held the right button and released the left one. Dominance durations were measured as the time interval between two button presses in five experimental conditions:

(1) Passive viewing: Subjects were instructed to fixate on the fixation cross (Fig. 1A) without attempting to control the alternating rate.

Fig. 1. Stimuli used in this study. Subjects were instructed to keep their gaze on the fixation cross of the ambiguous Rubin vase/faces figure throughout each experiment trial. During passive viewing, subjects reported the dominant percept, produced by the Rubin figure (A), without attempting to control the rivalry rate. During endogenous control of perceptual rivalry (A), subjects were instructed to hold voluntarily the dominant percept as long as possible or switch voluntarily attention to the non-dominant percept as fast as possible. In the exogenously driven holding and switching conditions, subjects were asked to follow two disks which were presented synchronously with the dominant percept [faces (B) and vase (C)] or asynchronously with the dominant percept [faces (C) and vase (B)], respectively.

(2) Holding the dominant percept under endogenous control: Subjects were asked to fixate on the fixation cross (Fig. 1A) and voluntarily hold the reported dominant percept as long as possible.

(3) Holding the dominant percept with the aid of exogenous marks: Subjects were asked to hold as long as possible the current dominant percept which was marked by disks presented synchronously with the reported dominant percept. For example, when subjects reported that the faces were the dominant percept, the disks were presented within the area corresponding to the faces (Fig. 1B). When the vase became the dominant percept, the disks were shown within the area corresponding to the vase (Fig. 1C).

(4) Switching the dominant percept under endogenous control: Subjects were instructed to switch attention voluntarily from the dominant to the non-dominant percept as fast as possible (Fig. 1A).

(5) Switching the dominant percept with the aid of exogenous marks: Disks were presented asynchronously with the reported dominant percept. For instance, when subjects reported that the vase was the dominant percept, the disks were presented within the area corresponding to the faces (Fig. 1B). If the dominant percept was the faces, the disks were displayed within the area corresponding to the vase (Fig. 1C). Subjects were instructed to follow the marks, switching the dominant percept as fast as possible.

In our study, subjects were asked to attend each dominant percept in hold conditions and attend the non-dominant percept in switch conditions. In contrast to previous studies of perceptual rivalry (Meng & Tong, 2004; van Ee, van Dam, & Brouwer, 2005) we did not instruct subjects to attend only one of the percepts as preliminary tests showed that older people experienced difficulties performing such a task.

The conditions were presented in random order. Each condition was repeated 7 times. The duration of trials was 30 s in the passive condition, 40 s in hold conditions and 20 s in switch conditions. We used a longer duration for hold conditions and a shorter duration for switch conditions. This allowed us to collect similar numbers of perceptual alternations in all conditions due to the slower reversal rate in hold conditions and faster reversal rate in switch conditions. The first trial in each session was used as a training trial and the data from this trial were not analyzed. As the initial reports may contain subject biases, the first two reports in each trial were not included in the data analysis.

2.5. Eye-movement recording and analysis

In a control experiment, eye position and pupil diameter were recorded at 250 Hz with an infrared eye tracker (Eyelink I; SMI, Teltow, Germany) in 7 young and 7 older adults who had taken part in the main experiment. Calibration was carried out at the beginning of each experimental condition session and drift correction was performed before each trial. Data for the right eye were analyzed offline using software written in Matlab (Mathworks, Natick, MA). Dominance durations that contained eye blinks were not used in the analysis. An eye blink was identified when the pupil signal was below 60% of the median of the pupil signals for at least 50 ms.

For each subject and dominance duration, the bivariate contour ellipse area (BCEA), including 68% of the fixation points, was calculated using the following equation:

$$2.28\pi\sigma_h\sigma_v(1 - \rho^2)^{0.5},$$

where σ_h and σ_v are the SD of eye position in the horizontal and vertical meridian and ρ is the product-moment correlation between the two position components (Steinman, 1965).

The eye positions in a polar coordinate system with an origin at the fixation cross were calculated as the distance from the origin:

$$(x^2 + y^2)^{0.5},$$

where x and y represent horizontal and vertical eye positions. For each subject and each experimental condition, mean and standard deviation of eye position were computed across the observation period, excluding dominance durations with eye blinks. In order to collapse eye position data across subjects, they were converted into z scores by normalizing to zero mean and unit standard deviation. The normalized eye positions were averaged for dominance durations longer than 1.5 s in the interval 1 s before and after button presses, indicating perceptual switches. A similar analysis was performed to calculate the z scores of the pupil diameter data.

2.6. Statistical analysis

Statistical analysis of the reported data was performed using PASW Statistics 18 (SPSS, Inc.). Statistical significant effects of the experimental factors on the data were tested by means of repeated-measures ANOVA.

For both eye position and pupil diameter data, the probability of each data point being different from zero was estimated. To correct for multiple comparisons, we employed an adaptive procedure for controlling the false discovery rate, that is the proportion of false positives (incorrect rejections of the null hypothesis) among those tests for which the null hypothesis is rejected (Benjamini, Krieger, & Yekutieli, 2006). To this end, we used a Matlab function written by David Groppe (http://www.mathworks.com/matlabcentral/fileexchange/27423-two-stage-benjaminikrieger-yekutieli-fdr-procedure). This procedure is a less conservative and more powerful method than the Bonferroni

procedure for correcting for multiple comparisons, which is widely used in fMRI data analysis (Genovese, Lazar, & Nichols, 2002).
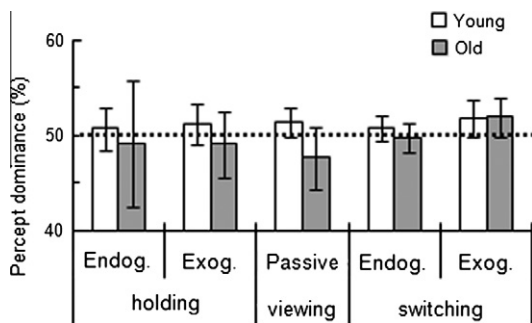
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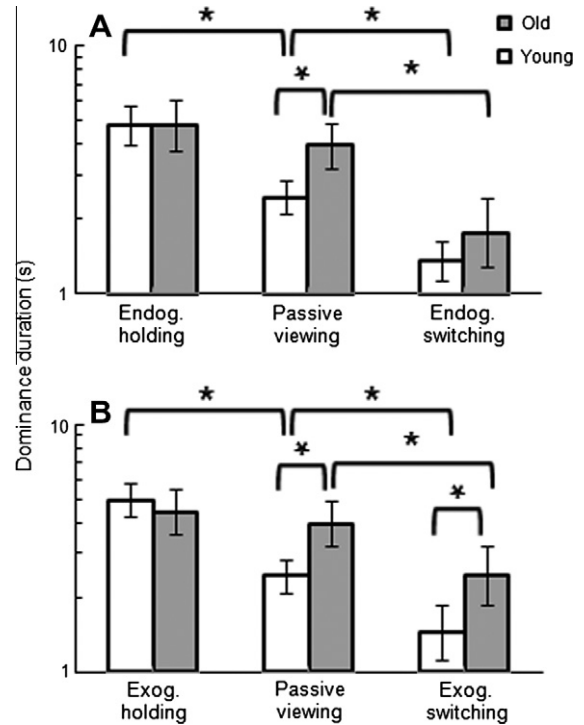
3.1. Dominant durations

The majority of the distributions of dominance durations for all subjects, collected in the five experimental conditions (110 out of 170), were not normal (Shapiro–Wilk test, $p < 0.05$). Therefore, we analyzed the log-transformed dominance durations (Lehky, 1995), most of which (86%) had a normal distribution. Those (14%) that did not follow a normal distribution, had skewness within the range ± 2SE implying that they could be regarded as approximately normal.

Data for percentage percept dominance (expressed as $100 * D_f/(D_f + D_v)$, where D_f and D_v represent the mean dominance durations for the percepts faces and vase, respectively) for each condition averaged across each subject group are shown in Fig. 2. The mean values of all percept dominances did not differ significantly from 50% (one-sample t-test, t values were in the range between −1.608 and 1.951, $p > 0.07$). These results show that mean durations of each subject group for both percepts, vase and faces, were not significantly different. Therefore, for each subject we analyzed the combined dominance durations for both percepts.

A repeated-measures ANOVA [between-subjects factor, age (2); within-subjects factor, attentional conditions (5)] found a significant main effect of the factor attentional condition [$F(4, 128) = 106.6$, $p < 0.001$]. The interaction between both factors was significant [$F(4, 128) = 8.167$, $p < 0.001$] indicating that age has a significant effect on the dominance durations at different attentional conditions. Post hoc multiple comparisons ($p < 0.05$, Tukey HSD test) showed that the dominance durations for younger adults during exogenous and endogenous holding were significantly longer compared to the passive viewing durations (Fig. 3, empty bars). The 40-s observations interval in holding conditions did not have a ceiling effect because the subjects reported perceptual alternations in all trials excluding the first two reports which were not used in the data analysis. The average number of reported perceptual alternations per trial was 7.4 (range of 2.5–12.5) for older people and 6.6 (range of 2.4–16.2) for young subjects. During both types of switching the dominant percept, the dominance durations of younger adults were significantly shorter than those in passive viewing. Compared to passive viewing, older adults showed a significant
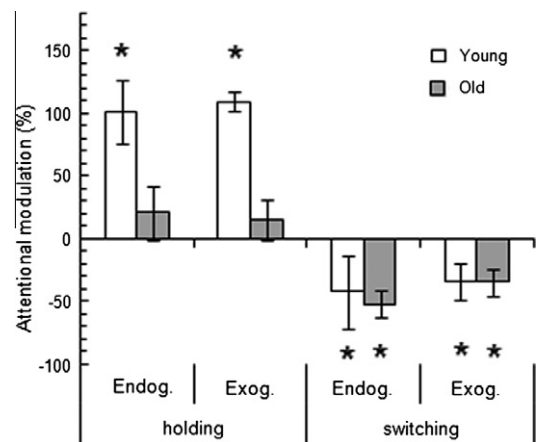
Fig. 3. Dominance duration for young (empty bars) and older (filled bars) adults in conditions with passive viewing (A and B), endogenous (A) and exogenous (B) attentional control. *Illustrate significant ($p < 0.05$) differences between the mean dominance found by post hoc multiple comparisons (Tukey HSD test). Error bars denote 95% confidence intervals.

reduction of the dominance duration in switch conditions, but not in hold conditions (Fig. 3, filled bars). Older adults were significantly slower than young adults in the task requiring passive viewing and exogenous switching (Fig. 3B).

3.2. Attentional modulation

The effect of attentional control on the dynamics of perceptual rivalry is illustrated in Fig. 4. To this end, for each subject we calculated attentional modulation as $100 * (D_a - D_p)/D_p$, where D_a is the mean dominance duration in a condition involving attentional

Fig. 2. Percentage percept dominance representing the relative dominance durations for the percept faces normalized by the sum of the dominance durations for both percept. Data for young (empty bars) and older (filled bars) adults in conditions with passive viewing, holding and switching the dominant percept under endogenous and exogenous attentional control are shown. The dotted line illustrates equal percept dominance (50%). Values above (below) 50% indicate that the percept "faces" has been perceived longer (shorter) than the percept "vase". Error bars denote 95% confidence intervals.

Fig. 4. Attentional modulation of the dominance durations for young (empty bars) and older (filled bars) subjects in hold and switch conditions under endogenous and exogenous attentional control. *Illustrate significant ($p < 0.001$, one-sample t-tests with Bonferroni correction for multiple comparisons) difference of the mean attentional modulations from zero. Error bars illustrate 95% confidence intervals.

control (holding or switching) on the dominant percept and D_p is the mean dominance duration during passive viewing. Exogenously and endogenously driven attentional control of perceptual rivalry in hold conditions significantly prolonged the dominance interval by 100% in young people (Fig. 4 open bars), compared to that in the passive viewing condition (one-sample t-tests, $p < 0.001$; one-sample t-tests with Bonferroni correction for multiple comparisons). Young subjects significantly reduced the dominant duration in switch conditions for exogenous and endogenous attentional control by about 40% (one-sample t-tests, $p < 0.001$). The attentional modulation in older people (Fig. 4 filled bars), however, was not significantly different from zero in hold conditions with both types of attentional control (about 17%, one-sample t-tests, $p > 0.06$). In switch conditions, they showed significant amplitude modulations of about 40% (one-sample t-tests, $p < 0.001$).
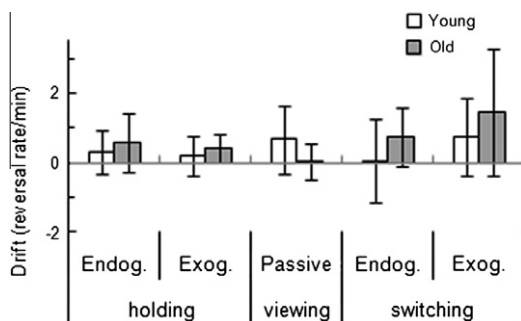
3.3. Drift of reversal rate

Reversal rate drift across successive experimental repetitions ($n = 6$) was calculated for each subject and experimental condition. The mean drift values (Fig. 5) were close to and above zero. The increase of the reversal rate as a function of experimental trial was stronger for older people, mainly in switch conditions (by 1.4 reversals per minute). However, these effects were not significantly different from zero (one-sample t-tests, $p > 0.10$).
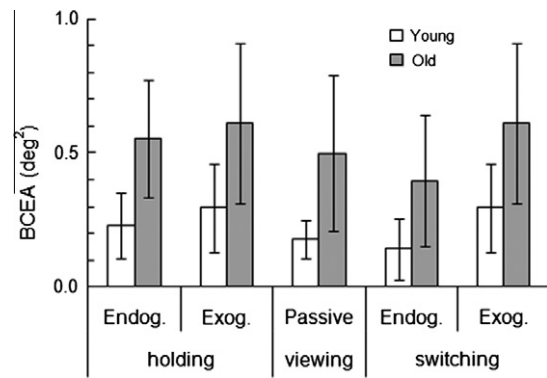
3.4. Eye movement and pupil-diameter recordings

To assess possible influences of eye movements on the findings of the present study, the bivariate contour ellipse area (BCEA) was calculated using eye-movement recordings during the dominance durations for both percepts, vase and faces, since there was no significant difference between the two (Fig. 6). A repeated-measures ANOVA found significant main effects of the factors attentional condition [$F(4, 48) = 6.8$, $p < 0.001$] and age [$F(1, 12) = 7.1$, $p < 0.05$]. The interaction between the two factors was not significant. Post hoc multiple comparisons did not show significant differences for each subject group between the mean BCEAs in conditions with attentional control and passive viewing ($p > 0.16$, Games–Howell test, Levene test: $p < 0.005$). For each experimental condition, the differences between the mean BCEAs for both age groups were also not significant. The comparison of the average BCEA data across attentional conditions showed that the BCEA for older adults (0.51 ± 0.10 deg^2) was significantly ($p < 0.001$, t-test) larger than that for young adults (0.19 ± 0.04 deg^2).

The average eye-position data, expressed as z scores of the distance from the fixation cross in the interval 1 s before and after
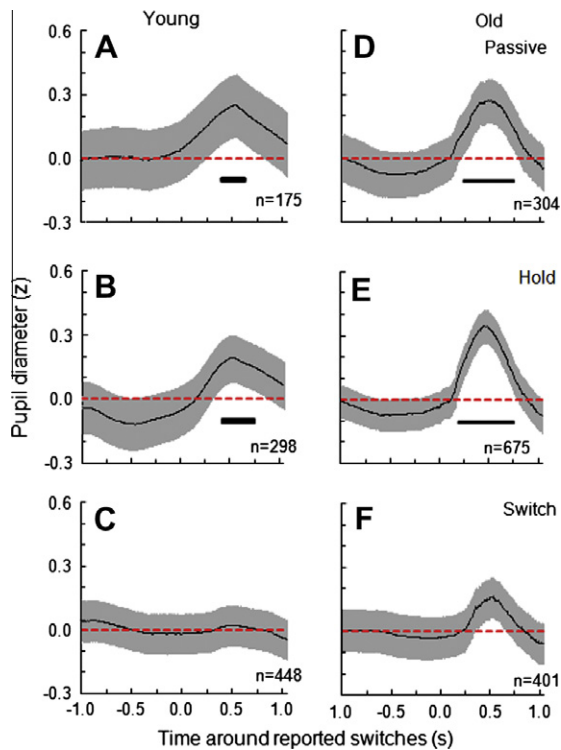

Fig. 6. Bivariate contour ellipse area during perceptual rivalry in conditions with passive viewing, holding and switching the dominant percept for young (empty bars) and older (filled bars) adults. Error bars illustrate 95% confidence intervals.
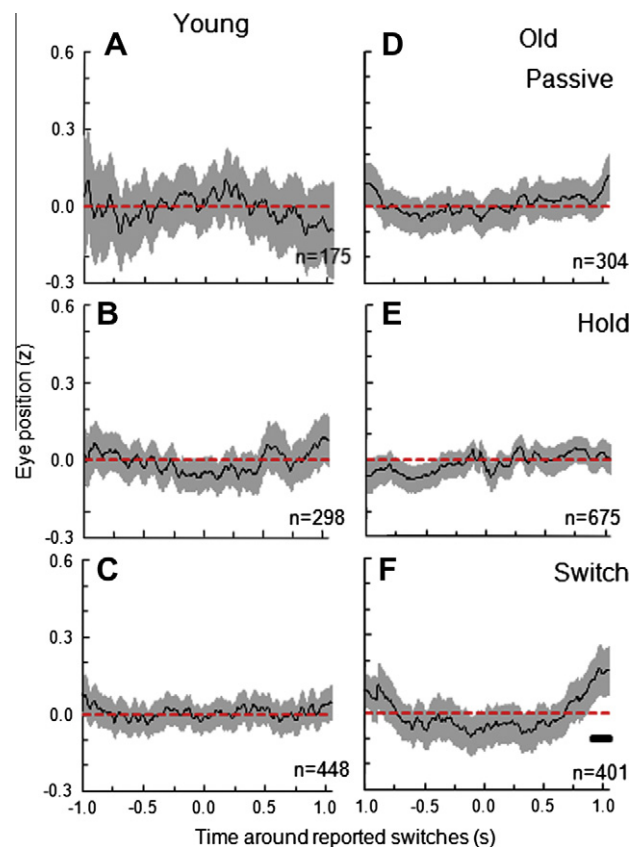
Fig. 7. Eye position (thin lines) during perceptual rivalry in conditions with passive viewing (A and D), attentional holding (B and E) and switching (C and F) the dominant percept in young (left panels) and older adults (right panels). Data are normalized to zero mean and unit standard deviation (z scores) and shown 1 s before and after perceptual switches indicated by button presses. Tick horizontal lines denote periods significantly different from zero at an expected false discovery rate of 0.05. Gray areas illustrates 95% confidence intervals.

button presses indicating perceptual switches are presented in Fig. 7. The results did not show significant departures from the mean eye positions, excluding a short period at about 0.9 s after the perceptual switch for older adults in switch conditions (Fig. 7F solid line, $p < 0.05$, corrected by false discovery rate).

For both age groups, the pupil dilated significantly from the mean pupil diameter value mainly after the button presses, indicating perceptual switches, in passive and hold conditions (Fig. 8A, B, D, and E). The peak latencies of the pupil diameter did

Fig. 5. Drift of reversal rate across experimental trials for young (empty bars) and older (filled bars) subjects. Positive and negative values correspond to an increase and decrease of reversal rate in concessive trials, respectively. Error bars show 95% confidence intervals.

Fig. 8. Pupil diameter (thin line) during perceptual rivalry in conditions with passive viewing (A and D), attentional holding (B and E) and switching (C and F) the dominant percept in young (left panels) and older adults (right panels). Pupil responses are normalized to zero mean and unit standard deviation (z score) within an interval of 1 s before and after perceptual switches indicated by button presses. Tick horizontal lines denote intervals significantly different from zero at an expected false discovery rate of 0.05. Gray areas show 95% confidence intervals.

not differ significantly (t-tests, $p > 0.23$) for older and young subjects in the passive viewing condition (542 ± 121 ms for young subjects; 464 ± 112 ms for older subjects) and hold conditions (583 ± 116 ms for young subjects; 501 ± 107 ms for older subjects). Neither age groups showed significant changes in pupil diameter for switch conditions.

4. Discussion

4.1. Age-related changes in the dynamics of perceptual rivalry during passive viewing

During passive viewing, older adults experienced slower perceptual rivalry (mean dominance duration ± 95%CI: 4.33 ± 1.12 s) compared to young adults (2.54 ± 0.38 s). This finding is in a close agreement with a previous binocular rivalry study in elderly (4.29 ± 0.78 s; $n = 24$, range 50–72 years) and young (2.73 ± 0.45 s, $n = 19$, range 20–34 years) individuals (Ukai, Ando, & Kuze, 2003).

These results suggest that similar mechanisms could be responsible for the age-related effects in both rivalry paradigms during passive viewing. Binocular rivalry is related to dissimilar percepts associated with two monocular stimuli. It has been proposed that binocular rivalry is resolved at early stages of the visual cortex, resulting from mutual inhibition between V1 neuronal populations associated with each percept (Blake, 1989). Indeed, fMRI studies have found that neural activity in monocular regions of V1 changed in time with subjective perception during binocular rivalry (Haynes, Deichmann, & Rees, 2005; Lee, Blake, & Heeger, 2005, 2007; Meng, Remus, & Tong, 2005; Polonsky et al., 2000; Tong & Engel, 2001). Other studies have shown that rivalry may reflect

competition between incompatible patterns in higher processing stages, rather than competition between the eyes (Leopold & Logothetis, 1996; Logothetis, Leopold, & Sheinberg, 1996). These different views have converged into a hybrid model which assumes that binocular rivalry involves the basic reciprocal inhibition framework operating at multiple stages (Dayan, 1998; Freeman, 2005; Ooi & He, 2003; Wilson, 2003).

Unlike binocular rivalry, the ambiguous Rubin figure produces pictorial representations of the same input that are formed by figure–ground segregation processes with respect to border ownership involving neurons in higher levels (V2 and V4) (Zhou, Friedman, & von der Heydt, 2000). Studies found that the ambiguous Rubin image evoked enhanced fMRI activation in face-related regions during the dominance of the percept "faces" compared to the percept "vase" suggesting that the object-selective activation in human face-related regions is associated with global grouping processes, rather than local processing of stimulus features (Hasson et al., 2001). The event-related hemodynamic activity during perceptual reversals of classical ambiguous images, including the Rubin figure, was also strong in the fusiform and intraparietal extrastriate areas (Kleinschmidt et al., 1998). However, the posterior thalamus and striate cortex were deactivated during perceptual rivalry suggesting a crucial functional contribution of the primary visual cortex to perceptual stability. Percept-related modulations of activity in early visual cortical areas, including the primary visual cortex, were also found in a study using MEG signals evoked by dynamic luminance noise whose temporal frequencies in the regions of a Rubin image, corresponding to the vase and faces, were different (Parkkonen et al., 2008).

Thus, current knowledge of the neuronal architecture underlying rivalry phenomena suggests that perceptual rivalry produced by both ambiguous images and binocular stimulation with distinct images may involve multiple, early, and higher-level processing stages. A common characteristic of these perceptual phenomena is their similar temporal dynamics, which conform closely to the gamma or log–normal distributions (Brascamp et al., 2005; Lehky, 1995; Levelt, 1968), suggesting a similar neural basis.

Studies of binocular rivalry have shown that the contrast of rivaling stimuli affects the dynamics of perceptual alternations: decreasing the contrast of bistable stimuli increases dominance durations [Levelt's fourth proposition, Levelt (1968)]. Contrast discrimination functions for above-threshold stimuli are characterized by compressive nonlinearities (Campbell & Kulikowski, 1966; Legge, 1981) and aged people have manifested a shallower slope of contrast-discrimination functions than young people (Elliott & Werner, 2010). This produces a shift in the contrast gain (the contrast at which the response amplitude is half of the maximal response) to higher contrast levels for older than for younger adults. Similar age-related effects were found in studies using single-cell recordings, where the responses of V1 and MT cells in aged monkeys, compared to young monkeys had increased half-saturation constant, shallower slope of the contrast-response functions, and higher maximum levels (Yang et al., 2008). The age-related increase in contrast gain predicts that a stimulus would produce responses (relative to the maximal response levels) of lower strength for older people than for young adults. This could be associated with age-related reduction in the effective strength of the bistable percepts, which according to the Levelt's fourth proposition would result in longer dominance durations during passive viewing of bistable stimuli for older people than for young adults, as the present study and Ukai, Ando, and Kuze (2003) found.

Attention could also play an important role in the dynamics of rivalry alternations in passive viewing conditions. Paffen, Alais, and Verstraten (2006) showed that diverting attention from binocular bistable stimuli to a secondary motion-detection task increased the dominance durations compared to those during

passive viewing. Moreover, the increase of dominance durations was inversely proportional to the amount of attentional resources determined by the difficulty of the motion-detection task. Another study has shown that this effect on the dynamics of binocular rivalry can also be observed when attention is distributed within a single task. Using a single task in which subjects reported perceptual alternations from a display with various numbers of rivaling elements, Paffen and Hooge (2011) showed an increase in dominance duration for a single rivaling element in the presence of multiple elements, suggesting that the distributed spatial attention was the main factor influencing the dynamics of binocular rivalry. Paffen, Alais, and Verstraten (2006) demonstrated that the effects of diverting subject's attention on the dominance durations were similar to the effects produced by reducing the contrast of the bistable stimulation. The relationship between stimulus contrast and dominance duration suggests that the influence of attention on binocular rivalry can be represented as a change in effective contrast. This suggestion is in line with data showing that engagement of attention resulted in amplification of neuronal responses associated with the attended percept, while disengagement of attention diminished neuronal responses (Hillyard, Vogel, & Luck, 1998; Kastner et al., 1999; Murray & Wojciulik, 2004; Treue & Trujillo, 1999). It is possible that older people have reduced attentional resources allocated to the bistable stimulus, which could be an additional factor underlying the age-related slowing of perceptual rivalry.

It is worth noting that other factors underlying the dynamics of perceptual rivalry might potentially contribute to the observed age-related effects during passive viewing. "Oscillatory models" for binocular rivalry assume that the perceptual switches are determined by slow adaptation of firing rate, reducing the dominant population activity to a level where perceptual alternations occur (Lago-Fernandez & Deco, 2002; Laing & Chow, 2002; Lehky, 1988; Moreno-Bote, Rinzel, & Rubin, 2007; Noest et al., 2007; Shpiro et al., 2007; Wilson, 2003, 2007). Slow spike-frequency adaptation is often associated with effects produced by slow neuronal after-hyperpolarizing currents (McCormick & Williamson, 1989). An age-related increase in dominance duration could be due to a reduction of slow after-hyperpolarization. However, some other studies have found opposing age-related effects; the amplitude of slow after-hyperpolarization was enhanced and fire rate was reduced in aged rodent hippocampal CA1 pyramidal cells (Faber & Sah, 2003). Further studies are needed to understand the effect of age on the slow after-hyperpolarization and firing-rate adaptation in visual cortical neurons.

"Noise-driven attractor models" assume that perceptual alternations are mainly due to neuronal noise (Brascamp et al., 2006; Freeman, 2005; Kim, Grabowecky, & Suzuki, 2006; Moreno-Bote, Rinzel, & Rubin, 2007; Riani & Simonotto, 1994). The increase in dominance duration with age could result from lower levels of neuronal noise in older subjects. However, spontaneous activity in the absence of external stimulation (Leventhal et al., 2003; Yang et al., 2008) and the variability of visually evoked responses in macaque V1 and MT cells (Yang et al., 2009) are enhanced in old monkeys compared to young monkeys. Therefore, if we delineate the variable component of electrophysiological activity as internal noise (Shadlen & Newsome, 1998), age-related enhancement of neuronal noise would decrease dominant durations in older people, a prediction that is not supported by the data found by Ukai, Ando, and Kuze (2003) and the present study.

4.2. Age-related changes in the dynamics of perceptual rivalry under attentional control

Our results showed that dominance durations for young adults in hold conditions increased by a factor of 2, while attentional switching halved the dominance duration compared to passive viewing (Fig. 3A and B, empty bars). These results are in line with previous studies showing that attention increases the dominance duration of the attended percept and decreases the duration of the non-attended percept produced by a Necker cube (Meng & Tong, 2004; van Ee, van Dam, & Brouwer, 2005). A task to speed up the perceptual alternations (similar to our switch task) also decreased the dominance duration (van Ee, van Dam, & Brouwer, 2005). These findings could be attributed to attentional modulation of visual cortical activity: amplification of neuronal responses associated with the attended percept when attention is engaged and reduction of neuronal responses when attention is disengaged (Hillyard, Vogel, & Luck, 1998; Kastner et al., 1999; Murray & Wojciulik, 2004; Treue & Trujillo, 1999). Single-cell recordings from visual MT area have found that sustained attention shifted the contrast response function leftwards for neurons selective to the target stimulus corresponding to an increase in effective contrast of the actual stimulus (Martinez-Trujillo & Treue, 2002; Reynolds, Pasternak, & Desimone, 2000). Psychophysical studies of attentional control on contrast sensitivity have also shown that sustained attention operates via contrast gain (Ling & Carrasco, 2006).

Thus, the observed increase of dominant durations in hold conditions for young adults could be explained by an attention-driven increase in the effective strength of the dominant percept (for recent review papers see Dieter & Tadin, 2011; Paffen & Alais, 2011). This suggestion is in line with findings of prolonged perceptual dominance during binocular rivalry when attention is engaged to track changes in the rivaling images (Chong, Tadin, & Blake, 2005). Such an attentional effect was simulated by increasing the physical contrast of the attended stimulus, only when it was dominant. These results seem to contradict Levelt's second proposition (Levelt, 1968) which states that increasing the contrast of one rival stimulus decreases the duration of the stimulus with lower contrast but does not increase the dominance duration of the stimulus with higher contrast. This discrepancy, however, is due to the fact that attention enhances effective contrast only when that stimulus is dominant (attention cannot operate when a stimulus is invisible), while Levelt's second proposition refers to conditions in which contrast values are maintained constant during perceptual rivalry and a physical increase in contrast can affect suppression durations (Chong, Tadin, & Blake, 2005).

We found that older adults did not significantly prolong the dominant durations in hold conditions, compared to passive viewing (Fig. 3A and B, filled bars). This might results from the inability of older people to enhance the effective strength of the dominant percept when sustained attention is engaged to hold the dominant percept. This age-related deficit suggests that older people have inefficient attentional mechanisms.

Sustained attention, that is the ability to maintain focus endogenously on a target (Posner & Petersen, 1990) has traditionally been tested by vigilance tasks, which involve measuring reaction times and error rates for detecting rarely occurring signals (Mackworth, 1948). Studies found that older adults had normal performance in easy vigilance tasks (Parasuraman, Nestor, & Greenwood, 1989), but age-related decrement was observed in vigilance tasks with a higher event rate and spatial uncertainty (Mouloua & Parasuraman, 1995). The quality of performance when attention is continuously engaged is an important aspect of sustained attention; however, its basic characteristic is the ability to maintain stable percepts. Our results showed that the durations for holding the dominant percept in the older group were as long as those in the young group (Fig. 3). This finding suggests that both age groups have a similar ability to maintain a stable percept; this may correlate with the normal performance of older people in easy vigilance tasks. However, the inability of older adults to voluntarily

hold the dominant percept longer than in passive viewing, which shows inefficient attentional mechanisms, may play a role in the age-related performance impairment in complex vigilance tasks.

In switch conditions, attention is disengaged from the dominant percept and is directed towards the non-dominant percept. The reduced dominance durations could be related to weakened responses to the dominant percept and strengthened response to the non-dominant percept. These attentional effects were similar for both age groups suggesting the attentional ability of older people to switch voluntarily between the two rivaling percepts remains intact. Usually, the performance of older adults is impaired when attention must be switched from one task to another, requiring a change of mental set number (Verhaeghen & Cerella, 2002). However, perceptual rivalry in switch conditions is unlikely to involve a high amount of attentional resource, potentially explaining the lack of an age-related deficit in this task.

4.3. Control tests

We found no evidence to suggest that eye movements during fixation could influence the dynamics of perceptual rivalry. The bivariate contour ellipse areas were relatively small for both age groups. Older adults had a wider area of fixation (0.51 ± 0.10 deg^2) than young adults (0.19 ± 0.04 deg^2), but these differences were not dependent on the presence or absence of attentional control on perceptual rivalry (Fig. 6). These findings differ from those of other studies which found no significant differences in fixation stability were found between young and old observers when fixating a target presented on a uniform background (Crossland et al., 2008; Kosnik, Fikre, & Sekuler, 1986). In our study, observers experienced perceptual rivalry and reported the dominant percept. It could be possible that the eye-movement control in older people is less stable during perceptual rivalry than during a simple fixation task. The analysis of eye position around button presses, indicating perceptual switches, did not show significant departures from the mean eye position which could be correlated with perceptual alternations (Fig. 7). The significant increase of the mean eye position in switch conditions for older adults (Fig. 7F), which occurred about 0.9 s after the perceptual switch, could be regarded as a consequence rather than a causal factor for perceptual alternations. Therefore, eye movements are unlikely to trigger perceptual alternations in the conditions of the present study.

Additionally, we found that both young and old people reported their percept accurately. Both age groups showed a significant increase of pupil diameter, which peaked around 500 ms after perceptual switches indicated by button presses (Fig. 8A, B, D, and E). This effect was observed in passive and hold conditions. These results are similar to data reported in recent studies (Einhauser et al., 2008; Hupe, Lamirel, & Lorenceau, 2009; Naber, Frassle, & Einhauser, 2011) which suggest that pupil dilation can be used as an objective measure of rivalry. We found no significant pupil dilation in switch conditions, but this may be due to the fact that the pupil response spans nearly 2 s, which is comparable with the shorter dominance durations in these conditions.

The attentional effects on the dynamics of perceptual rivalry were similar when using exogenous and endogenous attentional control. These findings do not show age-related inefficiencies in using the working memory to control attention in perceptual rivalry. The significantly longer dominance durations in older people in exogenous switching conditions compared to those in young adults (Fig. 3B) could be due to age-related slower processing of the exogenous marks. The results also found no significant drift in reversal rate, implying that tiredness and training effects within the experimental conditions were not significant factors in this study (Fig. 5). Therefore, this ambiguous image seems to be a reliable tool for investigating age-related deficits in perceptual stability.

5. Conclusions

Older people had longer dominance durations during passive viewing of the Rubin figure than young adults. This age-related deficit could be related to a reduction in the apparent strength of the rivaling percepts due to higher contrast gain of visual cortical activity in older compared to young adults. Weakened apparent strength of the switching percepts in older people could also be due to a smaller amount of attentional resource being allocated to the ambiguous stimulus.

Older people were not able to voluntarily increase the dominance duration in the same manner as young people did. This finding suggests that older people have abnormal attentional mechanisms that are inefficient at enhancing the effective strength of the dominant percept. Both age groups showed similar abilities to voluntarily switch the dominant percept as fast as possible.

The observed age-related attentional deficit suggests that older adults may have difficulty holding their attention on attended visual objects when carrying out various everyday activities such as driving, reading, shopping and searching in the Internet.

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