Published in final edited form as:

Neuropsychol Dev Cogn B Aging Neuropsychol Cogn. 2017 March ; 24(2): 115–134. doi: 10.1080/13825585.2016.1173646.

Bistable Perception in Normal Aging: Perceptual Reversibility and its Relation to Cognition

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Abstract

The effects of age on the ability to resolve perceptual ambiguity are unknown, though it depends on fronto-parietal attentional networks known to change with age. We presented the bistable Necker cube to 24 middle-aged and older adults (OA; 56–78 years) and 20 younger adults (YA; 18–24 years) under passive-viewing and volitional control conditions: *Hold* one cube percept and *Switch* between cube percepts. During passive viewing, OA had longer dominance durations (time spent on each percept) than YA. In the *Hold* condition, OA were less able than YA to increase dominance durations. In the *Switch* condition, OA and YA did not differ in performance. Dominance durations in either condition correlated with performance on tests of executive function mediated by the frontal lobes. Eye movements (fixation deviations) did not differ between groups. These results suggest that OA's reduced ability to hold a percept may arise from reduced selective attention. The lack of correlation of performance between *Hold* and executive-function measures suggests at least a partial segregation of underlying mechanisms.

Keywords

aging; perceptual ambiguity; Necker cube; attention; cognition

Aging leads to structural and functional changes in the brain, even in the absence of pathology. Structural changes include atrophy, most prominent in frontal (especially prefrontal) and parietal cortices (DeCarli et al., 2005; Hedden and Gabrieli, 2004; Goh, Beason-Held, An, Kraut, & Resnick, 2013; Nyberg et al., 2010; Pfefferbaum, Adalsteinsson & Sullivan, 2005; Raz et al., 2005; Raz, Ghisletta, Rodrigue, Kennedy, & Lindenberger, 2010; Walhovd et al., 2011; Yuan & Raz, 2014). These frontal and parietal brain regions are

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There were no financial interests or benefits arising from the direct applications of the current research.

implicated in attention, visuospatial perception, and executive control (Beauchamp, Petit, Ellmore, Ingelholm, & Haxby, 2001; Rees and Lavie, 2001; Tamber-Rosenau, Esterman, Chiu, & Yantis, 2011; Verhaeghen & Cerella, 2002). Neuroimaging studies have shown that greater frontal-lobe activation differentiates older and younger adults during performance of attentional control tasks (Ansado, Monchi, Ennabil, Faure, & Joannette, 2012; Grady, 2000; Madden et al., 2007). It is as yet unknown how these fronto-parietal structural and functional changes in the aging brain, and their attendant compromise of perception, attention, and executive control, may affect the resolution of perceptual ambiguity, a process hypothesized to be subserved by attentional networks (for review see Koch & Tsuchiya, 2007).

Perception can be considered ambiguous in that the brain creates the best possible interpretation from complex visual input. Bistable figures have two equally plausible interpretations, and while the stimulus remains unchanged, the individual's perception of the image alternates. The ambiguity of bistable figures makes them useful tools to examine visual perception because they offer insight into how humans derive one percept from competing visual inputs (Blake and Logothetis, 2002; Leopold & Logothetis, 1999; Long and Toppino, 2004). Neuroimaging studies with younger adults have demonstrated the role of top-down processes in bistable perception, showing activation in frontal and parietal cortices during perceptual reversal (Britz, Landis, & Michel, 2009; Knapen, Brascamp, Pearson, van Ee, Blake, 2011; Rees and Lavie, 2001; Slotnick and Yantis, 2004; Sterzer and Kleinschmidt, 2007; Tong, Wong, Meng, and McKeef, 2002; Weinhhammer, Ludwig, Hesselmann, Sterzer, 2013). These higher-order brain regions have been associated with the attentional network, suggesting that this system may be involved in selection among competing visual perceptions; that is, disambiguating visual information in the environment (Leopold and Logothetis, 1999; Long and Toppino, 2004; Tekin and Cummings, 2002; Windmann, Wehrmann, Calabrese, and Gunturkun, 2006). Aging affects frontal regions, including the dorsolateral prefrontal circuit, and parietal regions (see references at the beginning of this section), but it is unknown whether these age-related structural and functional changes affect bistable perception and if so, whether these perceptual deficits occur prior to or concurrently with cognitive attentional-control impairments.

Few studies have investigated the role of aging in bistable perception under contrasting experimental conditions, including passively (spontaneously) viewing the image, as opposed to conditions in which observers show their ability to *hold* one percept (increase the time of perceiving a single percept), or *switch* between the two percepts (decrease the time of perceiving a single percept). The first of these studies used the bistable Necker cube and found that only six elderly adults out of 31 eligible participants (ages 65–90) were able to understand the task and report reversals (Heath and Orbach, 1963). The investigators noted that the reversal rate for four out of the six participants (1, 2, 4, and 8 reversals while viewing the cube *passively* for two minutes) was comparable to that of younger patients (ages 23–51) with frontal-lobe damage (8 reversals, Yacorzynski and Davis, 1945). Holt and Matson (1976) also reported a significantly lower number of reversals in older adults (>65 years old) than in groups ranging in age from 10 to 55, with the highest number of reversals attained by the participants aged 25–45. More recent studies have reported aging effects in bistable perception by using binocular rivalry under passive viewing conditions (Norman, Norman, Pattison, Taylor and Goforth, 2007; Ukai, Ando, and Kuze, 2003). Binocular

rivalry occurs when two dissimilar images are presented simultaneously, one to each eye. Rather than perceiving a fusion of the two, one image at a time dominates conscious awareness while the other image is suppressed (Blake and Logothetis, 2002). Norman and colleagues (2007) presented two different sinusoidal gratings, one to each eye, and asked younger and older participants to report when they perceived a probe, which was present in either the dominant or suppressed view. They found that the magnitude of binocular rivalry suppression was significantly larger for older than younger individuals, meaning that one percept dominated for a longer period of time. In another binocular rivalry study, Ukai and colleagues (2003) found significant differences in mean binocular rivalry alternation time between younger (20's), middle-aged (40's) and older adults (60's) asked to passively observe the stimuli. The alternation time for the younger adults (2.7 seconds) was significantly faster (that is, shorter dominance duration) than that of the other groups (3.6 seconds for middle-aged adults and 4.29 seconds for older adults). These studies, taken together, document the effect of aging on perception while viewing bistable images or dichoptic presentation passively.

A more recent study investigated the effect of aging on volitional control over bistable figures, that is, the ability to *hold* one percept (increase the time of perceiving a single percept), and *switch* between the two percepts (decrease the time of perceiving a single percept). Aydin, Strang and Manahilov (2013) used the ambiguous Rubin vase-faces figure and found that compared to younger adults, older adults had more difficulty holding one percept while showing intact ability to expedite the switch between the two percepts. These findings suggest that age-related structural and functional brain changes may selectively compromise specific attentional networks used for the stabilization of ambiguous perception, but leave unaffected other networks supporting voluntary reversibility.

Prior to the study by Aydin and colleagues, volitional control of bistable perception was described only in healthy young adults and in clinical populations, such as those with frontal-lobe dysfunction (Windmann et al., 2006) and schizophrenia (McBain, Norton, Kim, and Chen, 2011). In Windmann and colleagues' (2006) study, individuals with prefrontal damage (mean age = 61.4, age range 33–80) were less able than a healthy matched control group to intentionally switch between the two possible views of bistable images (including the Necker cube), but were equally successful at holding one percept of the figure. The investigators concluded that the frontal lobes might support the voluntary reversibility of bistable images. McBain and colleagues (2011) used the Necker cube to study the volitional control capacities of individuals with schizophrenia (age 40.7 ± 16 years) and found that when instructed to keep one percept dominant, they were able to do so only 58% of the time, whereas the age-matched control group was successful 73% of the time. The interpretation of the results was that schizophrenia, with its associated impairments in prefrontal and posterior parietal cortices, compromises the stabilization of bistable perception.

These behavioral studies together suggest that bistable perception is mediated by brain areas associated with the fronto-parietal attentional network, which is affected by normal aging (Aydin, Strang, & Manahilov, 2013; Heath and Orbach, 1963; Holt & Matson, 1976; McBain, Norton, Kim, and Chen, 2011; Norman, Norman, Pattison, Taylor and Goforth, 2007; Ukai, Ando, and Kuze, 2003; Yacorzynski and Davis, 1945; Windmann et al., 2006).

Research has shown that structural and functional changes in these brain regions associated with normal aging also lead to cognitive deficits on tests of executive function including working memory (Gunning-Dixon, and Raz, 2003), processing speed and reasoning (Stebbins et al., 2001). It is as yet unknown whether, in regard to the resolution of perceptual ambiguity, there may be aging effects that map onto these well-known cognitive changes in the aging brain.

In the present study, performance of older and younger adults was compared under conditions of passive viewing and volitional control (*Hold* and *Switch*) of an ambiguous Necker cube stimulus. The first aim was to examine whether the perception of older adults would differ from that of younger adults in spontaneous viewing and in their ability to manipulate their attention to exert volitional control over the bistable image. This examination would extend the findings of Aydin and colleagues with the Rubin vase-faces by inclusion of a different and well-studied bistable figure, the Necker cube. We hypothesized that compared to younger adults, older adults would have a reduced ability to hold one percept of the bistable image. The second novel aim, which was exploratory, was to establish whether group differences in perceptual attentional control, if they existed, would be related to group differences in frontally-mediated cognitive performance.

Methods

Participants

Participant characteristics are displayed in Table 1. There were 24 healthy older adults (OA: mean age: 65.9, SD: 5.6 years, range: 56–78) and 20 younger adults (YA: mean age: 19.4, SD: 1.5 years, range: 18–24). OA were volunteers from the community and YA were recruited from Boston University introductory psychology classes. We note that the YA group, which had fewer years of education than OA, was composed of current undergraduates who are expected to have a higher terminal than current education level. OA scored similarly to YA on baseline intellectual functioning, as measured by the Wechsler Test of Adult Reading.

All participants were interviewed about their medical history to rule out confounding diagnoses such as stroke, head injury, and serious medical illness including psychological disorders (e.g., substance abuse disorder, depressive disorders, anxiety disorders). No participant had undergone surgery affecting any brain regions. OA were non-demented, as indexed by scores on the modified Mini-Mental State Examination (mMMSE with score conversion to standard MMSE, mean 28.8; SD = 1.0; no score below 27; Stern, Sano, Paulson, & Mayeux, 1987).

To evaluate mood, we administered the Beck Anxiety Inventory (BAI; Beck, Epstein, Brown, & Steer, 1988] and the Beck Depression Inventory-II (BDI-II; Beck, Steer, Ball, & Ranieri, 1996]. There were no group differences in depression, as measured by the BDI, or anxiety, as measured by the BAI. Participants also answered questions regarding ophthalmologic health to ensure that they did not have ocular or optical abnormalities that would have influenced performance on the visual measures. OA had undergone a detailed neuro-ophthalmological examination within a year of the study and were determined not to

have any ocular disease (e.g., cataracts, glaucoma, macular degeneration) or other abnormalities.

Materials and Procedure

The Necker cube was used as the ambiguous stimulus for all experimental conditions because of the extensive history of empirical investigations with this stimulus in examining bistable perception in younger adults, as well as in clinical populations including frontal-lobe dysfunction (Heath and Orbach, 1965; Ricci and Blundo, 1999; Windmann et al., 2006) and schizophrenia (McBain et al., 2011). A right-face forward-down Necker cube was presented on a white background in the center of a 21-inch LCD monitor (Figure 1; width = 8 ° of visual angle). A fixation cross was presented in the center of the cube, while head movements were stabilized with a chin rest at a viewing distance of 62cm. Observers were instructed to maintain fixation throughout each 60-s trial and to avoid eye movements. Eye movements were tracked in each condition and recorded with an Applied Science Laboratories (ASL) eye tracking system. The camera had a sampling rate of 60 Hz, and the system used an ASL EYE-TRAC 6 Control unit (system accuracy is 0.5° of visual angle, and resolution is 0.25°). We were unable to collect reliable eye tracking data from all participants for various reasons including bumpy sclera or small pupils or eyes. Reliable data were collected from 15 OA and 12 YA participants.

Participants with eye-tracking data did not significantly differ in demographic characteristics from those participants who did not have (reliable) eye-tracking data. They also did not differ in performance on the Necker cube experiments (dominance durations); both those with and without eye tracking showed an effect of condition, but there was no main effect of group, nor a group by condition interaction (OA: [1] Condition: $F [1.89, 34.07] = 27.27$, $p < .001$; [2] Group: $F [1, 18] = 1.04$, $p = .32$; [3] Interaction: $F [1.89, 34.07] = .17$, $p = .84$; YA: [1] Condition: $F [1.19, 19.11] = 26.11$, $p < .001$; [2] Group: $F [1, 16] = 1.67$, $p = .21$; [3] Interaction: $F [1.19, 19.11] = .53$, $p = .51$). Our interpretation of the similar findings by condition, and the lack of group effects, is that the groups are probably behaving similarly in regard to eye movements, and accordingly it is legitimate to collapse across the groups for further analyses of the data, retaining the power of the combined group size.

After providing informed consent, participants received a comprehensive interview to collect historical and demographic information and screening in regard to inclusion and exclusion criteria. Eligible participants completed mood assessments (BDI-II, BAI) and then the perceptual experiments. The perceptual tasks were conducted across several short testing sessions alternating with the neuropsychological assessments in order to minimize visual fatigue (discussed below).

Participants were initially presented with two 3-D models of a cube and asked if they had seen these types of cubes before. The experimenter then explained that the same cube could have different interpretations depending on the viewing angle if the person were to rotate it. After viewing the 3-D models, participants were presented with a 2-D graphic of an ambiguous Necker cube on an 11" x 8 1/2" piece of paper and asked whether they could perceive the two possible cube interpretations. Once the participant reported both percepts,

the experimenter showed another 2-D graphic with three cubes: (1) an ambiguous Necker cube in the middle, (2) an unambiguous Necker cube denoting the right cube interpretation on the right (that is, right face perceived as in front), and (3) an unambiguous Necker cube denoting the left cube interpretation on the left (that is, left face perceived as in front). Participants were instructed, with the help of these drawings, to report aloud “right” every time the cube in the middle resembled the unambiguous cube on the right, and to say “left” every time the cube in the middle resembled the unambiguous cube on the left, all while maintaining fixation on a cross placed in the middle of the ambiguous Necker cube (Figure 1). Participants were instructed to verbalize their perception of the cube and its reversals throughout the conditions. The use of verbal response (rather than button press, for example) was required because the present aging study was conducted as part of the larger research project that included participants with Parkinson’s disease (Díaz-Santos, Cao, Yazdanbakhsh, Norton, Neargarder & Cronin-Golomb, 2015), in order to circumvent the potential effects of motor rigidity, tremor and slowness of movement on motor response. For this reason, throughout the present experiment, participants provided verbal responses, and the examiner pressed the response keys on the computer.

The perceptual experiments were conducted with the lights off in a windowless room after dark adaptation. There were five 60-second learning trials to ensure reliable reporting of perceptual alternations. For the first two practice trials, one graphic demonstrating the right cube interpretation and one graphic representing the left cube interpretation were placed on either side of the computer monitor to ensure reliable reporting of reversals. The graphics were then removed for the last three practice trials. Data were collected during all five practice trials for eye movements and behavioral responses of reversals to ensure that the participant was able to do the task; these data were not included in analyses.

Following the practice trials, participants were introduced to the Passive condition. Here, they were instructed to “just look at the cube passively without trying to force any of the percepts.” The order of the two volitional conditions was counterbalanced across participants. In the Hold condition, participants were instructed to “attempt to hold the lower right cube in front as long as possible” for three 60s trials, and “attempt to hold the upper left cube in front as long as possible” for the last three 60s trials, all while reporting switches. These two Hold conditions (lower right, upper left) were counterbalanced. “Right cube” referred to the right face being perceived in front; “left cube” to the left face being perceived in front. In the Switch condition, they were to “attempt to speed up between the two cube percepts as fast as possible” (Figure 1). Participants continuously monitored their perceptual state and reported perceptual reversals aloud (e.g., “right” for lower right cube or “left” for upper left cube) and the examiner pressed the respective key of the computer to record the response. Each Passive and Switch condition was presented for five 60-second trials and the Hold condition was presented for six trials (three “hold right” and three “hold left”) of the same duration.

Neuropsychological assessment

Participants were administered several neuropsychological tests in order to examine whether perceptual reversibility (as measured by dominance durations; discussed below) among

older and younger adults was associated with executive functioning including inhibition and attentional control (Stroop Color Word Test; Stroop, 1935), verbal flexibility (D-KEFS Verbal Fluency; Delis et al., 2001; Delis et al., 2004), nonverbal fluency and mental flexibility (Ruff Figural Fluency Test; Ruff et al., 1987), attention, working memory, and cognitive flexibility (Trail Making Tests A and B; Tombaugh, 2004), set-shifting and perseveration (Wisconsin Card Sorting Test – 64 Computer Version; WCST-64; Kongs et al., 2000).

Data analysis

Dominance durations (mean time in seconds spent perceiving either the left or right cube) were analyzed for each participant. Outlier trials were identified across participants in each group. Dominance durations above or below two standard deviations from the group mean in each condition (Passive, Hold and Switch) were eliminated from the analysis. For OA, 6.7% of the data were eliminated (5 out of 75 dominance durations; each mean consisting of 5–6 trials). For YA, 5.0% of the data were eliminated (3 out of 60 dominance durations). These absolute dominance durations in all three conditions did not follow a normal distribution (Shapiro Wilk Test < 0.05). Accordingly, for each group, the absolute dominance durations were then normalized to the passive condition by dividing the mean dominance duration of the Hold and Switch conditions by the mean dominance duration of the Passive condition. By normalizing the data to Passive, it is possible to compare how participants increased or decreased their dominance durations in the Hold and Switch conditions relative to their performance in the Passive condition. For OA, 4.0% of the normalized dominance durations were eliminated (2 out of 50). For YA, 5.0% of the normalized dominance durations were eliminated (2 out of 40).

Mixed-model ANOVAs with group as the between subject factor and condition (dominance durations) as the within subjects factors were used to determine significant group differences between OA and YA. Huynh-Feldt correction was applied as appropriate. Post-hoc planned independent groups t tests were performed to compare the effect of group (OA, YA) on dominance durations to further explore group differences. Post-hoc planned dependent group t -tests were conducted to determine whether each group was able to increase (Hold) or decrease (Switch) their dominance durations compared to their performance during Passive viewing.

Our main hypothesis was that relative to YA, OA would show a reduced ability to increase the time perceiving the instructed cube in the Hold condition relative to their performance during Passive viewing (that is, normalized dominance durations). Accordingly, we applied one-tailed tests for the overall mixed design model ANOVA and on the individual planned comparisons in the Hold condition, but two-tailed for the Passive and Switch conditions.

Pearson correlations were used to examine correlations between performance on neuropsychological tests and dominance durations (absolute and normalized) for each condition.

Results

Necker cube: Absolute dominance durations

Passive viewing—Compared to YA, OA had a significantly longer mean dominance duration in the Passive condition ($t[28.73] = 3.18$, $p < .003$, partial $\eta^2 = .19$, 95% CI [.60, 3.02]). OA saw each percept for a mean of 5.4 (2.4) seconds (s), whereas YA had mean dominance duration of 3.6s (1.0s).

Hold and Switch viewing—In the Hold condition, OA increased their dominance duration to a mean of 8.6s (4.5s) seconds, and YA increased their dominance duration to a mean of 8.3s (4.5s). In the Switch condition, OA decreased their time perceiving a particular cube to a mean of 3.4s (1.6s), and YA to a mean of 2.5s (1.0s). A mixed design ANOVA with two levels of group (OA, YA) and two levels of conditions (Hold and Switch) revealed a significant main effect of condition ($F[1, 36] = 75.7$, $p < .001$), no main effect of group [$F(1,36) = .57$, $p = .45$] and no interaction [$F(1,36) = .29$, $p = .59$].

Planned dependent groups t-tests revealed that the changes relative to performance under Passive viewing were significant for both groups (OA - Hold: $t[20] = 5.07$, $p < .001$, partial $\eta^2 = .58$, 95% CI [-5.16, -2.15]; Switch: $t[20] = 3.79$, $p < .001$, partial $\eta^2 = .44$, 95% CI [0.90, 3.09]; YA - Hold: $t[18] = 5.32$, $p < .001$, partial $\eta^2 = .61$, 95% CI [-6.46, -2.80]; Switch: $t[17] = 4.66$, $p < .001$, partial $\eta^2 = .56$, 95% CI [.64, 1.70]). Each group was able to increase (Hold) or decrease (Switch) their dominance durations compared to their performance during Passive viewing.

Normalized dominance durations—For each participant, data were normalized to the Passive condition. Volitional modulation was calculated as $(D_X - D_P)/D_P \times 100$, where D_X is the normalized mean dominance duration of one of the volitional control conditions (Hold or Switch) and D_P is the mean dominance duration of the Passive condition. Values in parentheses are the standard deviations. Relative to Passive, OA increased their dominance duration by 62% (58%) in the Hold condition, and YA increased their dominance duration by 111% (65%). Relative to Passive, OA reduced their dominance duration by 34% (28%) and YA by 33% (27%) in the Switch condition. A mixed design ANOVA with two levels of group (OA, YA) and two levels of conditions (Hold and Switch) revealed a significant main effect of condition ($F[1, 37] = 142.12$, $p < .001$, partial $\eta^2 = .79$) and a significant main effect of group ($F[1,37] = 4.65$, $p < .04$, partial $\eta^2 = .11$). There was a significant interaction between group and condition ($F[1, 37] = 5.92$, $p < .02$, partial $\eta^2 = .14$). OA were significantly less able than YA to increase the time spent seeing the face of the designated cube in the Hold condition ($t[40] = 2.20$, $p < .015$, partial $\eta^2 = .08$, 95% CI [.03, .82], one-tailed test for Hold planned comparison, as per directional hypothesis). The groups did not differ in their ability to decrease their dominance durations in the Switch condition ($t[39] = .19$, $p = .85$, two-tailed test). The results are shown in Figure 4.

Because the OA group included individuals with a wide age range (56–78 years; mean 65.9), we examined the correlation of age and performance within this group. There was no correlation between OA age and absolute dominance durations on passive viewing ($r = .05$, $p = .81$), or on either normalized condition (Hold: $r = -.25$, $p = .25$; Switch: $r = .01$, $p = .96$).

Comparing the performance of the younger OA (10 individuals aged 56–64 years) with the older OA (14 individuals aged 65–78 years) revealed no group differences in either experimental condition (Passive: $t(20) = 1.4$, $p = .18$; Normalized Hold: $t(12.53) = 1.36$, $p = .20$; Normalized Switch: $t(20) = .54$, $p = .60$)

Necker cube: Switch rate

During Passive viewing, OA switched an average of 10.3 times per minute ($SD = 4.5$), while YA switched an average of 16.5 times (4.4). During the Hold condition, both groups reduced their switch rate (OA mean = 8.2 [4.2]; YA mean = 11.4 [4.7]) and during the Switch condition, both groups increased their switch rate (OA mean = 16.9 [7.9]; YA mean = 25.7 [10.6]). A repeated measures ANOVA revealed significant effects of group ($F [1, 37] = 16.1$, $p < .001$, $\eta^2 = .30$) and condition ($F [1.3, 46.9] = 46.8$, $p < .001$, $\eta^2 = .56$), with no group by condition interaction ($F [1.3, 46.9] = 2.64$, $p = .10$). These results indicate that the OA and YA groups were both able to modulate their perceptual alternations. The lack of interaction was also found when switch rate for the Hold and Switch conditions was normalized to the Passive switch rate (Hold: OA mean switch rate reduction = 21% [$SD = 27\%$]; YA mean switch rate reduction = 33% [20%]; Switch: OA mean switch rate increment = 65% [83%]; YA mean switch rate increment = 94% [102%]). A repeated measures ANOVA revealed a significant main effect for condition ($F [1, 39] = 22.6$, $P < .001$, $\eta^2 = 0.37$), no main effect of group ($F [1, 39] = .12$, $p = .73$) and no interaction of group by condition ($F [1, 39] = .82$, $p = .37$).

Taken together, these results indicate that both OA and YA, as groups, tended to alternate between the two percepts an equal number of times per minute, whereas the length of time between the switches, that is, the dominance durations, was significantly different for the groups under the Passive viewing and Hold conditions. This relation between switch rate and dominance duration reflects the fact that some individuals tend to be faster or slower at switching, and may hold one percept longer than the other (see Borsellino A., De Marco A., Allazetta A., Rinesi S., & Bartolini B. [1972]).

Eye movements: Deviation from fixation point and association with Necker cube performance

To assess the possible influence of eye movements on performance for those participants who provided reliable data (14 OA and 12 YA), we calculated the ability to maintain fixation as the mean deviation from fixation (degrees of visual angle) for each experimental condition. Each participant had three mean deviation scores for horizontal eye positions and three mean deviations scores for vertical eye positions, with the three scores corresponding to the Passive, Hold and Switch conditions. For horizontal eye positions, on average OA moved their eyes .63° (.45°) left of center during the Passive condition, and YA moved their eyes .43° (.42°) left of center. In the Hold condition, on average OA moved their eyes .53° (.53°) left of center and YA .35° (.40°) left of center. In the Switch condition, on average OA moved their eyes left of center by .69° (.79°) and YA by .39° (.71°). For vertical eye positions, OA moved their eyes an average of .01° (1.27°) above the center during the Passive condition, and YA moved their eyes .48° (1.47°) above the center. In the Hold condition, on average OA moved their eyes above the center by .70° (.63°) and YA by 1.0° (1.35°). In the

Switch condition, OA moved their eyes above the center by an average of $.98^\circ$ ($.80^\circ$) and YA by $.66^\circ$ (1.60°).

A mixed design ANOVA, with group (YA and OA) and fixation deviation in conditions (Passive, Hold and Switch) as factors, found no main effects of group, condition or their interaction for either horizontal (all F-values < 1.17) or vertical (all F-values < 1.70) eye movements. We further evaluated whether eye movements, specifically the deviation away from the fixation cross, impacted performance during the Passive, Hold and Switch conditions. We found no significant correlations between horizontal eye movements and performance by OA (Passive: $= -.49$, $p = .09$; Hold: $= -.37$, $p = .21$; Switch: $= -.33$, $p = .26$), or YA (Passive: $= -.22$, $p = .48$; Hold: $= .52$, $p = .13$; Switch: $= -.19$, $p = .60$). There were also no significant correlations between vertical eye movements and performance for either group [OA (Passive: $= -.28$, $p = .38$; Hold: $= .19$, $p = .56$; Switch: $= .06$, $p = .87$); YA (Passive: $= -.31$, $p = .33$; Hold: $= -.11$, $p = .75$; Switch: $= -.57$, $p = .07$)]. That is, eye movements away from the fixation cross did not predict performance under the passive-viewing or volitional-control conditions.

Neuropsychological assessment: Association between Necker cube performance and cognitive flexibility

YA outperformed OA on the following tests: Ruff Unique Designs – Total (non-verbal fluency); three conditions of the Stroop Test: Word, Color, and Color-Word; Trail Making Test A & B; WCST Total Score, Perseverative Responses, and Perseverative Errors. Groups were not significantly different on Letter Fluency – Total (FAS); Category Fluency Total (Animals); Category Switching (D-KEFS Verbal Fluency); or Trails B-A (scores on B corrected by scores on A).

We examined whether there was an association between cognitive function and performance under the three Necker cube conditions (Passive, Hold and Switch; absolute and normalized). Because we administered several cognitive tests and conducted a corresponding number of correlations, a conservative alpha of .01 was used to assess significance. Reaction time to complete Trails B (cognitive set-shifting measure) correlated significantly with absolute dominance durations ($r = .74$, $p < .001$) during the Switch condition for the OA group. Correlations were not significant for Trails B after correcting for the processing speed component associated with the task (Trails B minus Trails A), however. No other correlations were significant for the OA group. There were no significant correlations between performance on the Necker cube and any neurocognitive test for the YA group.

Discussion

The present study examined the role of aging in bistable perception. The older and younger age groups differed on bistable perception in the Passive and Hold conditions, but not in the Switch condition. Relative to YA, OA saw a dominant percept for a significantly longer period of time during Passive viewing. Both groups were able to increase and decrease the time spent observing one particular cube percept in each volitional control condition. OA were significantly less successful than YA at increasing their dominance duration in the

Hold condition, relative to their dominance duration in the Passive condition, however. OA and YA showed a similar decrease in dominance durations in the Switch condition relative to their performance in the Passive condition, and they did not differ in switch rate under any condition. Eye movements (specifically, deviation from fixation) did not drive the group differences. There was no association between bistable perception and cognitive functioning as assessed by empirically-based neuropsychological tests of executive-function known to measure abilities subserved by the frontal lobes, such as inhibition (e.g., Stroop Color-Word Test), cognitive flexibility, and resistance to perseveration (Trail Making Test, Wisconsin Card Sorting Test, verbal fluency).

Age-related changes in bistable perception during passive viewing

During Passive viewing, OA showed longer mean dominance durations (mean 5.4s [2.4s]) than YA (mean 3.6 [1.0s]), a finding consistent with the results of a study by Aydin and colleagues (2013), which initially explored the mechanisms of bistable perceptual organization with the use of another well-known stimulus (i.e., Rubin face-vase). Brain lesions studies (i.e., frontal-lobe craniotomy versus parietal craniotomy/healthy adults; Ricci and Blundo, 1990; Meenan and Miller, 1994; Yacorzynski and Davis, 1945) as well as imaging studies have implicated fronto-parietal networks in bistable perception (Britz, Landis, & Michel, 2009; Knapen, Brascamp, Pearson, van Ee, Blake, 2011; Rees and Lavie, 2001; Slotnick and Yantis, 2004; Sterzer and Kleinschmidt, 2007; Tong, Wong, Meng, and McKeef, 2002; Weilhhammer, Ludwig, Hesselmann, Sterzer, 2013), suggesting that attention-related brain areas support spontaneous perceptual alternations by sending top-down signals to guide activity in visual cortex towards one perceptual representation or the other (see Blake & Logothetis, 2002, Knapen, Brascamp, Pearson, van Ee, Blake, 2011; Leopold & Logothetis, 1999).

Recent studies have identified potential further differentiation of the neuronal substrates for spontaneous vs. controlled viewing of bistable stimuli, suggesting that frontal activity is not critical to passive viewing (de Graaf, de Jon, van Ee & Sack, 2011; Frässle, Sommer, Jansen, Naber, & Einhäuser, 2014). De Graaf and colleagues used repetitive transcranial magnetic stimulation (rTMS) to cause virtual lesions in frontal and parietal regions during the passive viewing of a bistable structure-from-motion stimulus. They found that rTMS to dorsolateral prefrontal cortex impacted the Switch condition, but rTMS to either the frontal or parietal regions had no effect on passive viewing (note, there was no Hold condition in this experiment). Frässle and colleagues (2014) used a combination of fMRI and measures of optokinetic nystagmus and pupil size to objectively and continuously map perceptual alternations during binocular rivalry (with both static and dynamic gratings) in order to assess neural activity while controlling for the confounding effects of verbal responses. They found that activation in frontal areas (middle frontal gyrus bilaterally) was absent when young adult observers passively viewed bistable stimuli without reporting perceptual alternations, whereas occipital and parietal areas remained active. These investigators suggested that the frontal activation typically seen during binocular rivalry experiments might be associated with introspection and verbally reporting a particular percept when passively viewing bistable stimuli rather than serving as the neuroanatomical foci underlying spontaneous perceptual organization. These studies together support the hybrid model of

bistable perception, suggesting that rivalry occur at multiple stages in the visual system (for review see Kornmeier & Bach, 2012; Ooi and He, 2003).

Regarding the healthy aging brain, imaging studies have revealed thinning in widespread cortical areas, including sensory-motor primary and association cortex (i.e., primary motor cortex and calcarine cortex [V1]; Salat et al., 2004). Other or additional neuronal substrates could underlie this perceptual slowness in healthy older adults, including, for example, slow adaptation of firing neuronal rate (oscillatory models; Pettigrew, 2001) or neuronal noise (noise-driven attractor model, reviewed in Braun & Mattia, 2010). These possibilities underscore the need for further studies exploring the neuronal mechanisms underlying perceptual organization in older as well as in younger and middle-aged adults

Age-related changes in bistable perception during volitional control

We found that OA were able to both increase (Hold condition) and decrease (Switch condition) the time spent perceiving one particular percept. Nonetheless, OA in the Hold condition showed a smaller increase in dominance duration (mean 62% [58%] than YA (mean 111% [65%]) relative to their performance during the Passive condition. The groups did not differ in their ability to decrease dominance durations in the Switch condition relative to the Passive condition (OA 34% [28%] and YA 33% [27%]). These results indicate that OA have a selective vulnerability in their ability to hold one percept of a bistable figure, with their ability to switch between two percepts being conserved.

Aging effects on the brain may underlie reductions in the ability to implement selective attentional control in holding one percept while suppressing the other, rather than switching attention between the two competing perceptual interpretations. Supporting this hypothesis are imaging and neuropsychological studies that have indicated aging effects specifically in selective attention (i.e., ability to filter out relevant stimuli to focus on goal-relevant information), but not switching attention (i.e., ability to flexibly alternate between two competing environmental demands) (Gazzaley & D'Esposito, 2007; for review see McDowd and Shaw, 2000; Knight, McMahon, & Skeaff, 2010). For example, Knight, McMahon, and Skeaff (2010) found that the speed of visual search for digit targets (2 and 7) under same-category (other digits) and different-category (letter) distracter conditions declined with increasing age, using the Ruff 2 and 7 Selective Attention Test (Ruff, Niemann, Allen, Farrow, & Wylie, 1992). An fMRI study investigated brain activity of YA (mean age 23.3) and OA (mean age 67.8) performing a selective attention letter-name matching task with two levels of attentional load (Ansado et al., 2012). With increasing attentional load, OA displayed an increased recruitment of bilateral frontal regions, whereas YA used more occipital regions. These findings highlight potentially different functional networks in younger and older adults subserving the ability to voluntarily disambiguate perceptual interpretation and maintain it, which may accord with our finding of OA being less able than YA to hold one percept of the Necker cube.

On tasks that measure switching attention, speed and accuracy of performance by OA has been found to be comparable to that of YA, including switching between spatial locations (Folk and Hoyer, 1992; Yamaguchi, Tsuchiya, and Kobayashi, 1995) and switching between tasks (Kramer, Hahn, and Gopher, 1999; Wasylyshyn, Verhaeghen, and Sliwinski, 2011). In

the Switch condition of our study, participants needed to repeatedly deactivate the percept that was initially relevant and activate the currently relevant percept. fMRI studies with YA found activation of the dorsal anterior cingulate cortex and inferior temporal cortex during attentional switching (Kim, Johnson, and Gold, 2012) and of the superior parietal cortex during perceptual switching (Ravissa and Carter, 2008). These brain areas are distinct from those suggested to be involved in selective attention and holding one percept of the Necker cube, which is in agreement with our findings of differential performance under Hold and Switch conditions. As discussed above, de Graaf and colleagues found that rTMS in the dorsolateral prefrontal cortex impacted the ability of healthy young adults to decrease their dominance durations of a bistable stimulus during the Switch condition compared to occipital activation during passive viewing. Even though the investigators did not assess the Hold condition in their study, their results highlight the need to disentangle the neuronal and functional mechanisms subserving holding one perceptual representation vs. expediting the switch between possible perceptual interpretations in response to environmental demands.

Age-related changes in bistable perception and association with cognition

Our results showed no association between executive functioning and perceptual reversibility. As previously noted, frontal (including the dorsolateral prefrontal cortex) and parietal areas have been found to support perceptual reversals. Though non-overlapping brain areas may explain the lack of correlation between resolution of perceptual ambiguity and executive function, another reason for the lack of correlation may be the cognitive functions assessed in this study, which included inhibition, processing speed, verbal fluency and set-shifting. Data from these measures were collected as part of a larger study assessing perceptual rigidity in Parkinson's disease (Díaz-Santos, Cao, Yazdanbakhsh et al., 2015). Another approach may be to employ neuropsychological tests that measure working memory or different facets of attention (i.e. selective, switching, divided, sustained) to help elucidate the neurocognitive mechanisms subserving bistable perception in older adults.

Limitations of the study

This study was subject to a number of limitations. First, having the examiner record the participants' verbal reports of perceptual state is a source of variability in the reaction time data. This aspect of the study design was dictated by the need to accommodate the motoric limitations of individuals with Parkinson's disease in the larger concurrent study (Díaz-Santos, Cao, Yazdanbakhsh et al., 2015). Future investigations should consider participant recording of perceptual state. As noted above, this study was also restricted to certain neuropsychological tests of attention and cognition, which were used because they were part of the larger concurrent study; those tests are standard for neuropsychological assessments. In the future, it would potentially be valuable to evaluate multiple aspects of attention and working memory, in order to probe for correlations between these type of functions and deficits in the volitional control of bistable perception in the aging population, adding to the literature of healthy young adults (Intaitè, Koivisto, & Castelo-Branco, 2014a, 2014b). It would also be of interest to examine individual differences in the perception of ambiguous figures, as there was substantial variability in performance within groups (e.g., fast switchers vs. slow switchers). Finally, the age range of our OA participants was broader than the age

range for the YA participants, which is a study limitation even though differences in age ranges are common in studies comparing performance of older and younger adults.

Conclusions

The results of this study indicate that OA had longer dominance durations than YA during passive viewing of a Necker cube, and were significantly less able to increase their dominance duration in the Hold condition relative to their performance in the Passive condition. By contrast, their performance in the Switch condition was comparable to the performance of YA. There were no group differences in eye movements or cognitive performance that would account for these findings, suggesting that differences in the integrity of brain areas recruited for selective attention may have driven the group effects. The importance of the topic is underscored by potential real-world implications. Our population is aging and increasingly will encounter challenges while navigating the perceptually ambiguous world. Better understanding of the perceptual changes occurring in the aging brain may lead to evidence-based interventions aimed at maintaining the ability of older adults to carry out their usual activities of daily living, as has been a focus of work with older adults with neurodegenerative conditions (e.g., Dunne, Nearing, Cipolloni, & Cronin-Golomb, 2004; Díaz-Santos, Cao, Mauro, Yazdanbakhsh, Nearing & Cronin-Golomb, 2015; Laudate et al., 2012).

Acknowledgments

This work was supported in part by grants from the National Institute of Neurological Disorders and Stroke, including a Ruth L. Kirschstein National Research Service Award (F31 NS074892) to MDS, and RO1 NS067128 to ACG, the Clara Mayo Foundation Fellowship from the Department of Psychological and Brain Sciences at Boston University (MDS), the National Science Foundation (NSF SBE-0354378 to AY and BC) and Office of Naval Research (ONR N00014-11-1-0535 to YA and BC). These funding agencies did not have any involvement in the study design, data collection, analysis and interpretation, in writing the manuscript, or in the decision to submit the article for publication.

We would like to thank all the individuals who participated in this study. Our recruitment efforts were supported, with our gratitude, by Marie Saint-Hilaire, M.D., and Cathi Thomas, R.N., M.S.N. of Boston Medical Center Neurology Associates, Boston area Parkinson's disease support groups, and the Fox Trial Finder. We thank Laura Pistorino for her assistance in screening and scheduling participants. We also thank Lindsay Clark and Michael Horgan for aspects of tests administration and technical assistance.

References

- Ansado J, Monchi O, Ennabil N, Faure S, Joannette Y. Load-dependent posterior-anterior shift in aging in complex visual selective attention situations. *Brain Research*. 2012; 1454:14–22. [PubMed: 22483790]
- Aydin S, Strang NC, Manahilov V. Age-related deficits in attentional control of perceptual rivalry. *Vision Research*. 2013; 77:32–40. [PubMed: 23206550]
- Beauchamp MS, Petit L, Ellmore TM, Ingelholm J, Haxby JV. A parametric fMRI study of overt and covert shifts of visuospatial attention. *NeuroImage*. 2001; 14:310–321. [PubMed: 11467905]
- Beck AT, Epstein N, Brown G, Steer RA. An inventory for measuring clinical anxiety: psychometric properties. *Journal of Consulting and Clinical Psychology*. 1988; 56(6):893–897. [PubMed: 3204199]
- Beck AT, Steer RA, Ball R, Ranieri W. Comparison of Beck Depression Inventories -IA and -II in psychiatric outpatients. *Journal of Personality Assessment*. 1996; 67(3):588–597. [PubMed: 8991972]

- Blake R, Logothetis NK. Visual competition. *Nature Reviews Neuroscience*. 2002; 3:13–21. [PubMed: 11823801]
- Borsellino A, De Marco A, Allazetta A, Rinesi S, Bartolini B. Reversal time distribution in the perception of visual ambiguous stimuli. *Kybernetik*. 1972; 10:139–14410. [PubMed: 5021011]
- Braun J, Mattia M. Attractor and noise: Twin drivers of decisions and multistability. *NeuroImage*. 2010; 52:740–751. [PubMed: 20083212]
- Britz J, Landis T, Michel CM. Right parietal brain activity precedes perceptual alternation of bistable stimuli. *Cerebral Cortex*. 2009; 19:55–65. [PubMed: 18424780]
- DeCarli C, Massaro J, Harvey D, Hald J, Tullberg M, Au R, Beiser A, D'Agostino R. Measures of brain morphology and infarction in the Framingham heart study: establishing what is normal. *Neurobiology of Aging*. 2005; 26:491–510. [PubMed: 15653178]
- Delis DC., Kaplan, E., Kramer, JH. Delis-Kaplan Executive System (D-KEFS). San Antonio, T., editor. The Psychological Corporation; 2001.
- Delis DC, Kramer JH, Kaplan E, Holdnack J. Reliability and validity of the Delis-Kaplan Executive Function System: An update. *Journal of the International Neuropsychological Society*. 2004; 10:301–303. [PubMed: 15012851]
- de Graaf TA, van Ee R, Goebel R, de Jong MC, Sack AT. On the functional relevance of frontal cortex for passive and voluntarily controlled bistable vision. *Cerebral Cortex*. 2011; 10:2322–2331.
- Díaz-Santos M, Cao B, Mauro SA, Yazdanbakhsh A, Neargarder S, Cronin-Golomb A. The effect of visual cues on the resolution of perceptual ambiguity in Parkinson's disease. *Journal of International Neuropsychological Society*. 2015; 21:146–155.
- Díaz-Santos M, Cao B, Yazdanbakhsh A, Norton DJ, Neargarder S, Cronin-Golomb A. Perceptual, cognitive, and personality rigidity in Parkinson's disease. *Neuropsychologia*. 2015; 69:183–193. [PubMed: 25640973]
- Dunne TE, Neargarder SA, Cipolloni PB, Cronin-Golomb A. Visual contrast enhances food and liquid intake in advanced Alzheimer's disease. *Clinical Nutrition*. 2004; 23(4):533–538. [PubMed: 15297089]
- Folk CL, Hoyer WJ. Aging and shifts of visual spatial attention. *Psychology and Aging*. 1992; 7:453–465. [PubMed: 1388867]
- Frässle S, Sommer J, Jansen A, Naber M, Einhäuser W. Binocular rivalry: Frontal activity relates to introspection and action but not to perception. *Journal of Neuroscience*. 2014; 34:1738–1747. [PubMed: 24478356]
- Gazzaley A, D'Esposito M. Top3down modulation and normal aging. *Annals of the New York Academy of Sciences*. 2007; 1097:67–83. [PubMed: 17413013]
- Grady CL. Functional brain imaging and age-related changes in cognition. *Biological Psychology*. 2000; 54:259–281. [PubMed: 11035226]
- Grady C. The cognitive neuroscience of ageing. *Nature Reviews Neuroscience*. 2012; 13:491–505. [PubMed: 22714020]
- Goh JO, Beason-Held LL, An Y, Kraut MA, Resnick SM. Frontal function and executive processing in older adults: Process and region specific age-related longitudinal functional changes. *NeuroImage*. 2013; 69:43–50. [PubMed: 23266746]
- Gunning-Dixon FM, Raz N. Neuroanatomical correlates of selected executive functions in middle-aged and older adults: A prospective MRI study. *Neuropsychologia*. 2003; 41:1929–1941. [PubMed: 14572526]
- Heath HA, Orbach J. Reversibility of the Necker cube: IV. Responses of elderly people. *Perceptual and Motor Skills*. 1963; 17:625–626. [PubMed: 14057288]
- Hedden T, Gabrieli JDE. Insights into the ageing mind: A view from cognitive neuroscience. *Nature Reviews Neuroscience*. 2004; 5:87–96. [PubMed: 14735112]
- Holt GL, Matson JL. The effects of age on perceptual changes using two new perspectives of the Necker cube. *Bulletin of the Psychonomic Society*. 1976; 8:4–6.
- Intaitè M, Koivisto M, Castelo-Branco M. Event-related potential responses to perceptual reversals are modulated by working memory load. *Neuropsychologia*. 2014a; 56:428–428. [PubMed: 24565733]

- Intaitè M, Koivisto M, Castelo-Branco M. The linear impact of concurrent working memory load on dynamics of Necker cube perceptual reversals. *Journal of Vision*. 2014b; 14:1–9.
- Kim C, Johnson NF, Gold BT. Common and distinct neural mechanisms of attentional switching and response conflict. *Brain Research*. 2012; 1469:92–102. [PubMed: 22750124]
- Knapen T, Brascamp J, Pearson J, van Ee R, Blake R. The role of frontal and parietal brain areas in bistable perception. *The Journal of Neuroscience*. 2011; 31:10293–10301. [PubMed: 21753006]
- Knight RG, McMahon J, Skeaff CM, Green TJ. Reliable change indices for The Ruff 2 and 7 Selective Attention Test in older adults. *Applied Neuropsychology*. 2010; 17(4):239–245. [PubMed: 21154036]
- Koch C, Tsuchiya N. Attention and consciousness: Two distinct brain processes. *Trends in Cognitive Science*. 2007; 11:16–22.
- Kongs, SK., Thompson, LL., Iverson, GL., Heaton, RK. Wisconsin Card Sorting Test-64 Card Version (WCST-64). Odessa, FL: Psychological Assessment Resources; 2000.
- Kornmeier J, Bach M. Ambiguous figures – what happens in the brain when perception changes but not the stimulus. *Frontiers in Human Neuroscience*. 2012; 6:1–23. [PubMed: 22279433]
- Kramer AF, Hahn S, Gopher D. Task coordination and aging: Explorations of executive control processes in the task switching paradigm. *Acta Psychologica*. 1999; 101:339–378. [PubMed: 10344190]
- Laudate TM, Nearing S, Dunne TE, Sullivan KD, Joshi P, Gilmore GC, Tatiana Riedel TM, Cronin-Golomb A. Bingo! Externally-supported performance intervention for deficient visual search in normal aging, Parkinson's disease and Alzheimer's disease. *Aging, Neuropsychology, and Cognition*. 2012; 19:102–121.
- Leopold, NK Logothetis. Multistable phenomena: Changing views in perception. *Trends in Cognitive Sciences*. 1999; 3:254–264. [PubMed: 10377540]
- Long GM, Toppino TC. Enduring interest in perceptual ambiguity: Alternating views of reversible figures. *Psychological Bulletin*. 2004; 130:748–768. [PubMed: 15367079]
- Madden DJ, Spaniol J, Whiting WL, Bucur B, Provenzale JM, Cabeza R, White LE, Huettel SA. Adults age differences in the functional neuroanatomy of visual attention: A combined fMRI and DTI study. *Neurobiology of Aging*. 2007; 28:459–476. [PubMed: 16500004]
- Madden DJ. Aging and visual attention. *Current Directions in Psychological Science*. 2007; 16:70–74. [PubMed: 18080001]
- McBain R, Norton DJ, Kim J, Chen Y. Reduced cognitive control of a visually bistable image in Schizophrenia. *Journal of the International Neuropsychological Society*. 2011; 17:551. [PubMed: 21385517]
- McDowd, JM., Shaw, RJ. Attention and aging: A functional perspective. In: Craik, F., Salthouse, T., editors. *The handbook of aging and cognition*. 2. Mahwah, New Jersey: Lawrence Erlbaum Associates, Inc; 2000. p. 221–292.
- Meenan JP, Miller LA. Perceptual flexibility after frontal or temporal lobectomy. *Neuropsychologia*. 1994; 32:1145–1149. [PubMed: 7991080]
- Meng M, Tong F. Can attention selectively bias bistable perception? Differences between binocular rivalry and ambiguous figures. *Journal of Vision*. 2004; 4:539–551. [PubMed: 15330700]
- Nyberg L, Salami A, Andersson M, Eriksson J, Kalpouzos G, Kaupia K, ... Nilsson LG. Longitudinal evidence for diminished frontal cortex function in aging. *Proceedings of the National Academy of Science of the United States of America*. 2010; 107:22682–22686.
- Norman JF, Norman HF, Pattison K, Taylor MJ, Goforth KE. Aging and the depth of binocular rivalry suppression. *Psychology and Aging*. 2007; 22:625. [PubMed: 17874959]
- Ooi Z, He J. A distributed interocular processing of binocular rivalry: Psychophysical evidence. *Perception*. 2003; 32:155–166. [PubMed: 12696662]
- Pettigrew JD. Searching for the switch: Neural bases for perceptual rivalry alternations. *Brain & Mind*. 2001; 2:85–118.
- Pfefferbaum A, Adalsteinsson E, Sullivan EV. Frontal circuitry degradation marks healthy adult aging: Evidence from diffusion tensor imaging. *NeuroImage*. 2005; 26:891–899. [PubMed: 15955499]

- Ravizza SM, Carter CS. Shifting set about task switching: Behavioral and neural evidence for distinct forms of cognitive flexibility. *Neuropsychologia*. 2008; 46(12):2924–2935. [PubMed: 18601941]
- Raz N, Ghisletta P, Rodrigue KM, Kennedy KM, Lindenberger U. Trajectories of brain aging in middle-aged and older adults: Regional and individual differences. *NeuroImage*. 2010; 51:501–511. [PubMed: 20298790]
- Raz N, Lindenberger U, Rodrigue K, Kennedy K, Head D, Williamson A, Dahle C, Gerstorf D. Regional brain changes in healthy aging adults: General trends, individual differences and modifiers. *Cerebral Cortex*. 2005; 15:1676–1689. [PubMed: 15703252]
- Rees G, Lavie N. What can functional imaging reveal about the role of attention in visual awareness? *Neuropsychologia*. 2001; 39:1343–1353. [PubMed: 11566316]
- Ricci C, Blundo C. Perception of ambiguous figures after focal brain lesions. *Neuropsychologia*. 1990; 28:1163–1173. [PubMed: 2290491]
- Ruff R, Light R, Evans R. The Ruff Figural Fluency Test: A normative study with adults. *Developmental Neuropsychology*. 1987; 3:37–52.
- Ruff RM, Niemann H, Allen CC, Farrow CE, Wyllie T. The Ruff 2 and 7 Selective Attention Test: A neuropsychological application. *Perceptual Motor Skills*. 1992; 75:1311–1319. [PubMed: 1484803]
- Salat DH, Buckner RL, Snyder AZ, Greve DN, Desikan RS, Busa E, Morris JC, Dale AM, Fischl B. Thinning of the cerebral cortex in aging. *Cerebral Cortex*. 2004; 14:721–730. [PubMed: 15054051]
- Slotnick SD, Yantis S. Common neural substrates for the control and effects of visual attention and perceptual bistability. *Cognitive Brain Research*. 2004; 24:97–108.
- Stern Y, Sano M, Paulson J, Mayeux R. Modified Mini-Mental State Examination: Validity and reliability [abstract]. *Neurology*. 1987; 37(Suppl 1):179. [PubMed: 3808297]
- Sterzer P, Kleinschmidt A. A neural basis for inference in perceptual ambiguity. *Proceedings of the National Academy of Sciences (PNAS)*. 2007; 104:323–328.
- Stroop J. Studies of interference in serial verbal reactions. *Journal of Experimental Psychology*. 1935; 18:643–662.
- Tamber-Rosenau BJ, Esterman M, Chiu YC, Yantis S. Cortical mechanisms of cognitive control for shifting attention in vision and working memory. *Journal of Cognitive Neuroscience*. 2011; 23:2905–2919. [PubMed: 21291314]
- Tekin S, Cummings JL. Frontal-subcortical neuronal circuits and clinical neuropsychiatry: An update. *Journal of Psychosomatic Research*. 2002; 53:647. [PubMed: 12169339]
- Tombaugh TN. Trail making test A and B: Normative data stratified by age and education. *Archives of Clinical Neuropsychology*. 2004; 19:203–214. [PubMed: 15010086]
- Tong F, Wong A, Ming M, McKeeff TJ. Brain areas involved in attentional control and perception of ambiguous figures. *Journal of Vision*. 2002; 2:677a.
- Ukai K, Ando H, Kuze J. Binocular rivalry alternation rate declines with age. *Perceptual and Motor Skills*. 2003; 97:393–397. [PubMed: 14620224]
- Wallhovd KB, Westlye LT, Amlie I, Espeseth T, Reinvang I, Raz N, ... Fjell AM. Consistent neuroanatomical age-related volume differences across multiple samples. *Neurobiology of Aging*. 2011; 32:916–932. [PubMed: 19570593]
- Wasylyshyn C, Verhaeghen P, Sliwinski MJ. Aging and task switching: A meta-analysis. *Psychology and Aging*. 2011; 26:15–20. [PubMed: 21261411]
- Windmann S, Wehrmann M, Calabrese P, Gunturkun O. Role of the prefrontal cortex in attentional control over bistable vision. *Journal of Cognitive Neuroscience*. 2006; 18:456–471. [PubMed: 16513009]
- Weilhammer VA, Ludwig K, Hesselmann G, Sterzer P. Frontoparietal cortex mediates perceptual transitions in bistable perception. *The Journal of Neuroscience*. 2013; 33:16009–16015. [PubMed: 24089505]
- Verhaeghen P, Cerella J. Aging, executive control, and attention : A review of meta-analyses. *Neuroscience and Biobehavioral Reviews*. 2002; 26:849–857. [PubMed: 12470697]

- Yacorzynski GK, Davis L. An experimental study of the functions of the frontal lobes in man. *Psychosomatic Medicine*. 1945; 7:97–107.
- Yamaguchi S, Tsuchuya H, Kobayashi S. Electrophysiologic correlates of age effects on visuospatial attention shift. *Cognitive Brain Research*. 1995; 3:41–49. [PubMed: 8719021]

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Experimental Conditions			
	Passive	Hold (for “hold lower right” instructions)	Switch (for “speed up” instructions)
Stimulus Presented	(1)	(2)	(3)
Participants’ Perception	or		↔

Figure 1. Necker cube stimulus with cube interpretations (lower right cube and upper left cube) and outline of experimental conditions: (1) Passive viewing (report reversals without any manipulation; (2) Hold condition (hold either the lower right view or upper left view while reporting any reversals); (3) Switch condition (alternate between the two views as quickly as possible while reporting reversals). “Lower right cube” refers to the lower right face being perceived in front (as shown by shading). “Upper left cube” refers to the upper left face being perceived in front (as shown by shading).

Figure 2.

Normalized mean dominance durations of younger (YA) and older (OA) adults in the Hold and Switch conditions. (*) = $p < .05$. In the Hold condition, OA were significantly less able to increase the dominance duration of a particular cube percept, relative to their performance during the Passive condition. There were no group differences in the Switch condition. Error bars indicate the standard error of the mean.

Table 1

Participant characteristics

	OA n = 2414F, 10M	YA n = 209F, 11M	t-test	p-value	partial η^2	95% CI lower upper
Education (years)	17.1 (2.3)	12.6 (1.1)	t(34.2) = 8.5	.000	.60	3.41 5.56
WTAR (Raw Score)	44.1 (5.31)	41.7 (4.8)	t(42) = 1.58	.12		
BDI-II	2.3 (3.0)	2.8 (2.6)	t(40) = 0.61	.54		
BAI	1.5 (1.8)	2.7 (2.2)	t(38) = 1.93	.06		
MMSE	28.8 (1.0)	N/A				

All values are reported as means (standard deviations, SD). OA=older adults,

YA=younger adults. BDI=Beck Depression Inventory – 2nd Edition (total score range: 0–63 points), BAI=Beck Anxiety Inventory (total score range: 0–63 points), WTAR=Wechsler Test of Adult Reading (total score range: 0–50 points), MMSE=Mini-Mental State Examination (total score range: 0–30 points). There were group differences in years of education (see text). Degrees of freedom were adjusted for those t-tests that violated the homogeneity of variance assumption.

Table 2

Cognitive performance of older and younger adults

Test Name	OA (n)	YA (n)	OA Mean (SD)	YA Mean (SD)	t-test	p-value	partial η^2	95% CI lower upper
Ruff Unique Designs – Total Correct	18	19	80.0 (15.2)	109.2 (14.8)	t(35) = 5.9	.000	.50	19.26 39.28
Stroop Word – Total Correct	22	19	100.3 (12.5)	111.4 (12.2)	t(39) = 2.9	.007	.17	3.22 18.9
Stroop Color – Total Correct	23	19	71.1 (7.5)	81.4 (8.8)	t(40) = 4.1	.000	.30	5.23 15.35
Stroop Color-Word – Total Correct	23	19	42.6 (8.8)	51.2 (7.8)	t(40) = 3.4	.002	.22	3.40 13.81
Trails A time (sec)	23	19	25.8 (6.3)	19.9 (3.3)	t(34.5) = 3.9	.000	.26	2.87 8.99
Trails B time (sec)	21	18	55.7 (15.5)	42.8 (6.3)	t(27.3) = 3.5	.002	.23	5.29 20.47
Trails B minus A (sec)	20	19	25.9 (13.3)	23.5 (7.1)	t(29.3) = 0.70	.49		
Letter Fluency (FAS) – Total words	24	20	49.2 (13.6)	47.5 (10.1)	t(42) = 0.46	.65		
Semantic Fluency (Animals) – Total words	23	20	24.2 (4.9)	25.5 (4.5)	t(41) = 0.88	.39		
Category Switch Accuracy – Total Correct	22	19	14.2 (2.6)	13.3 (2.9)	t(39) = 1.1	.30		
WCST Total Correct Responses	23	18	52.1 (4.6)	55.1 (2.1)	t(32.5) = 2.7	.01	.14	.72 5.13
WCST Perseverative Responses	23	18	5.7 (2.2)	4.4 (.70)	t(27.4) = 2.7	.01	.13	.31 2.31
WCST Perseverative Errors	23	18	5.6 (2.2)	4.4 (.70)	t(27.7) = 2.6	.02	.12	.24 2.20

Letter, Category and Category Switch Fluency Subtests are from the D-KEFS (Delis-Kaplan Executive Function Scale); WCST – Wisconsin Card Sorting Test. All values represent raw, non-standardized values (Mean [SD]). Degrees of freedom were adjusted for those t-tests that violated the homogeneity of variance assumption.