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Age-related decline in global form suppression

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ABSTRACT

Visual selection of illusory 'Kanizsa' figures, an assembly of local elements that induce the percept of a whole object, is facilitated relative to configurations composed of the same local elements that do not induce a global form—an instance of 'global precedence' in visual processing. Selective attention, i.e., the ability to focus on relevant and ignore irrelevant information, declines with increasing age; however, how this deficit affects selection of global vs. local configurations remains unknown. On this background, the present study examined for age-related differences in a global-local task requiring selection of either a 'global' Kanizsa- or a 'local' non-Kanizsa configuration (in the presence of the respectively other configuration) by analyzing event-related lateralizations (ERLs). Behaviorally, older participants showed a more pronounced global-precedence effect. Electrophysiologically, this effect was accompanied by an early (150–225 ms) 'positivity posterior contralateral' (PPC), which was elicited for older, but not younger, participants, when the target was a non-Kanizsa configuration and the Kanizsa figure a distractor (rather than vice versa). In addition, timing differences in the subsequent (250–500 ms) posterior contralateral negativity (PCN) indicated that attentional resources were allocated faster to Kanizsa, as compared to non-Kanizsa, targets in both age groups, while the allocation of spatial attention seemed to be generally delayed in older relative to younger age. Our results suggest that the enhanced global-local asymmetry in the older age group originated from less effective suppression of global distracter forms on early processing stages—indicative of older observers having difficulties with disengaging from a global default selection mode and switching to the required local state of attentional resolution.

1. Introduction

Attentional selection of visual information becomes slower and more error-prone in older age (Madden, 2007). The degree of age-related decline, though, depends on the particular conditions and type of visual information, with older participants finding it especially hard to ignore task-irrelevant stimuli that provide strong attractors for visual attention (McDowd, 1997; Mevorach, Humphreys, & Shalev, 2006).

Illusory figures consist of fragments that are perceived as whole objects. For example, Kanizsa figures (Kanizsa, 1976) induce the percept of a global shape (e.g., a square; see Fig. 1, right) from local inward-facing 'pacman'-type inducer stimuli, whereas no coherent global form is perceived when the same local inducers face outwards (see Fig. 1, left). This type of global shape integration is generally thought to be an automatic process, originating from early processing stages (see Murray and Herrmann, 2013; for a recent review). Accordingly, there is a processing advantage for global relative to (in terms of the inducers elements: physically identical) local configurations, suggesting that visual scenes, by default, are interpreted initially on a global hierarchical level (Hochstein and Ahissar, 2002). As for Kanizsa-type configurations, global stimuli generate a strong bottom-up signal for visual selection, evidenced by the fact that they are detected equally efficiently irrespective of the number of non-Kanizsa-stimuli in the search display ("pop-out" effect; Davis and Driver, 1994). In turn, when the task requires attention to be directed towards local (rather than global) elements, participants' control settings need to be adjusted so that now task-irrelevant global signals can be suppressed (Rauschenberger and Yantis, 2001). Of theoretical importance, this search benefit for Kanizsa relative to non-Kanizsa targets has been demonstrated to derive primarily from the extraction of a closed region (i.e., a global surface), rather than specification of the bound-

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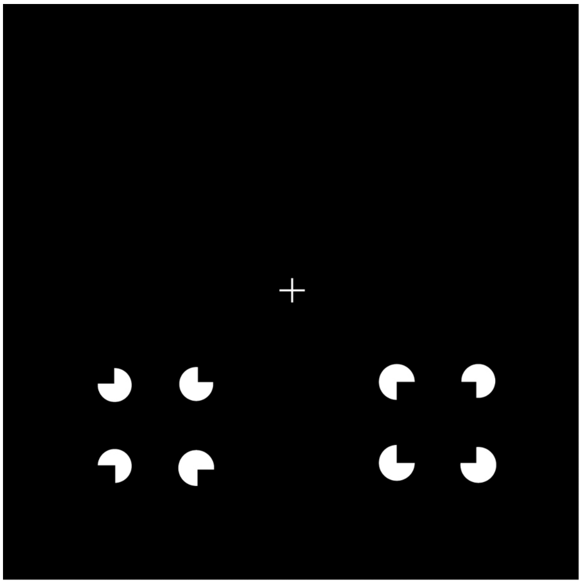

Fig. 1. Task display.
Example of a target-present display that shows the two possible stimulus locations in the experiment. In the global task, the target was a Kanizsa square (right) and the corresponding distracter was the non-Kanizsa configuration (left). Conversely, in the local task, the non-Kanizsa configuration was the target, and the Kanizsa square was the distracter. Target-absent displays would always present two distracters, either two Kanizsa squares or two non-Kanizsa configurations, depending on the local or global task, respectively.

ing illusory contours (Conci, Gramann, Müller, & Elliott, 2006; Conci, Müller, & Elliott, 2007; Conci et al., 2009).

Although selection of global illusory figures vs. local configurations would, thus, provide a powerful manipulation for examining age-related changes in attentional selectivity, there are no studies to date that have systematically explored its effects. According to the inhibition-deficit theory of aging (Hasher, Lustig, & Zacks, 2007), one might expect older, as compared to younger, adults to display increased difficulty to select a local configuration, and suppress a task-irrelevant global object. Indeed, age-related decline in inhibitory processes has been suggested to account for age-dependent changes in the global-local processing of other, Navon-type (Navon, 1977) hierarchical stimuli (Tsvetanov, Mevorach, Allen, & Humphreys, 2013). However, recent findings suggest that the increased global processing advantage (or local processing disadvantage) with age is rather task-specific and not consistent across different global-local paradigms (Lux, Marshall, Thimm, & Fink, 2008; Staudinger, Fink, Mackay, & Lux, 2011)—arguing against an account of age differences in global-local processing in terms of a general deficit of inhibitory control in older adults (Bruyer and Scailquin, 2000). Thus, from the available literature, it remains controversial what type of neuro-cognitive mechanisms contribute to the ostensibly relatively specific age effects on global-local processing (Georgiou-Karistianis et al., 2006).

In younger participants, recent neuroimaging studies provided deeper insights into the neural substrates of global-local processing (Murray and Herrmann, 2013; Seghier and Vuilleumier, 2006). In particular, activations in the lateral occipital complex (LOC) have been linked to the processing of coherent objects, and preferential processing of closed shapes via feedback to lower-level striate and extrastriate visual areas (Altschuler et al., 2012; Murray et al., 2002; Lee and Nguyen, 2001; Stanley and Rubin, 2003). In addition, event-related potentials (ERPs) provide a complementary view of the temporal processing dynamics of illusory-figure processing and a means to investigate how pre-selective global shape integration influences subsequent attentional processing stages. ERPs in response to illusory figures start to differ in the time range of the posterior N1, which is typically enhanced for Kanizsa figures compared to local-level baseline configurations (e.g., Herrmann and Bosch, 2001; Murray, Foxe, Javitt, & Foxe, 2004; Proverbio and Zani, 2002; Senkowski, Röttger, Grimm, Foxe, & Herrmann, 2005; see Murray et al., 2002, for even earlier effects). In accordance with the imaging literature, the global-local N1 effect has been interpreted to reflect global shape processing in the LOC (He, Fan, Zhou, & Chen, 2004; Martinez, Ramanathan, Foxe, Javitt, & Hillyard, 2007; Murray, Imber, Javitt, & Foxe, 2006). This initial processing advantage for global shapes, as reflected in the N1, has been suggested to influence the attentional priority assigned to competing objects under visual selection conditions (Senkowski et al., 2005). In a subsequent time window, the actual spatial-attentional selection of global vs. local configurations is indexed by the posterior contralateral negativity (PCN; Conci et al., 2006; Conci, Töllner, Leszczynski, & Müller, 2011; Töllner, Conci, & Müller, 2015), where the event-related lateralization (ERL) is quantified as the differential activity over the hemispheres contra- vs. ipsilateral to the visual hemifield in which a target stimulus is presented (Corriveau et al., 2012; Luck, Woodman, & Vogel, 2000; Wascher and Wauschkuhn, 1996). The PCN (also referred to as N2pc) is an established ERP marker for focal-attentional selection of task-relevant items in visual space (e.g., Eimer, 1996; Woodman and Luck, 1999; Töllner et al., 2011, 2012a,b), with generators residing in posterior parietal and ventral occipito-temporal cortex (Hopf et al., 2000, Hopf, Boelmans, Schoenfeld, Heinze, & Luck, 2002). For younger participants, we recently showed that the PCN varies with global-local properties of target and distracter stimuli under different selection conditions (Conci et al., 2011). In our study, participants were presented with Kanizsa squares and non-Kanizsa configurations appearing at two possible locations in a bilateral display (see Fig. 1). Participants were instructed to make a target-present vs. target-absent decision under two conditions: In the “global” condition, participants had to detect the Kanizsa figure and ignore the non-Kanizsa distracter. In the “local” condition, participants were presented with identical stimuli, but now had to detect the non-Kanizsa target configuration while ignoring the Kanizsa figure distracter. A behavioral global-precedence effect – that is: faster and more accurate selection of global as compared to local targets – was accompanied by an earlier peaking PCN in the global compared to the local task, indicative of a faster shift of focal attention to the target when the global target had to be detected, compared to when the local configuration was the target.

In the present study, we adopted the approach introduced by Conci et al. (2011) to provide deeper insight into the mechanisms underlying age differences in global-local processing. We assessed behavioral performance measures (reaction times [RTs] and response error rates [ERs]) and ERLs[1] of groups of younger and older adults in tasks in which either Kanizsa-squares were targets and non-Kanizsa configurations distracters, or, conversely, non-Kanizsa configurations were targets and Kanisza-squares distracters. Besides a general decline in performance with age (Salthouse, 1996), we expected qualitative differences between younger and older adults to become manifest in terms of an over-additive influence of global-local task conditions on age effects (Age × Task interaction). Following our previous study (Conci et al., 2011), we expected global precedence, and potential age differences in this effect, to be mirrored in the PCN. To preview the main results, as hypothesized, we observed a global-local PCN

[1] As we were specifically interested in effects of age on the attentional selection of global vs. local stimuli, we focused on ERLs; see the Supplement for analyses of non-lateralized effects on visual ERPs.

modulation in both age groups. Furthermore, we found a – not a-priori expected – positivity posterior contralateral (PPC) in the time window of 150–225 ms. This additional ERL preceding the PCN[2] was reported in several recent studies (e.g., Corriveau et al., 2012; Fortier-Gauthier, Moffat, Dell'Acqua, McDonald, & Jolicœur, 2012; Jannati, Gaspar, & McDonald, 2013; Gokce, Geyer, Finke, Müller, & Töllner, 2014; Wascher and Beste, 2010) and has been suggested to reflect selective visual processing under conditions with relative saliency differences between target and distracter stimuli. The PPC modulation observed in the present study indicates that the component is further sensitive to age differences in the selection of global vs. local configurations.

2. Method

2.1. Participants

Twelve younger (10 male, 2 female; mean age: 25.2 years) and twelve older (7 male, 5 female; mean age: 67.7 years) right-handed participants were included in the sample. All observers received payment for taking part in the study and provided written informed consent according to the Helsinki II declaration. The experimental procedure was approved by the ethics committee of the Department of Psychology, Ludwig-Maximilians-Universität München (LMU Munich). The younger participants' data was obtained for, and has already been reported in, a previous study (Conci et al., 2011). The data for the older participants was newly collected. The latter were comprehensively screened for potential age-related pathologies: none of the older participants reported any history of neurological (e.g., traumatic brain injury, stroke), psychiatric (e.g., depression, anxiety disorders), chronic somatic (e.g., hypertension, diabetes), or chronic eye diseases (e.g., glaucoma, cataract). All participants were confirmed to have normal or corrected-to-normal vision, and their visual acuity was 0.63 or better (Snellen, 1868). A Mini Mental State Examination (Folstein, Folstein, & McHugh, 1975) ruled out any symptoms prognostic of dementia: all participants achieved a score of 27 points or higher.

2.2. Apparatus and stimuli

Stimulus generation, event timing, and trigger signals were controlled by an IBM-PC-compatible computer. Stimuli were presented in grey (1.83 cd/m^2) against a black background (0.02 cd/m^2) in the bottom left and right quadrants of a 19-inch computer monitor (1024 × 768 pixel screen resolution, 85-Hz refresh rate). Stimuli were presented in the lower half of the visual field, (1) because the PCN is larger for stimuli presented in the lower, compared to the upper, visual field due to the anatomy of the visual pathways (Luck, Chelazzi, Hillyard, & Desimone, 1997; Eimer, 1996) and (2) because the perceptual illusion in Kanizsa figures is known to be stronger for lower- as compared to upper-hemifield presentations (Rubin, Nakayama, & Shapley, 1996). Each stimulus configuration, composed of four pacman inducers with a diameter of 0.7° of visual angle, was presented in the lower left and right quadrants of the display, 4.1° from the centrally presented fixation cross (see Fig. 1 for an example display). At a viewing distance of approximately 80 cm, each candidate grouping subtended a viewing angle of 2.3° × 2.3°. In the global task condition, in target-present trials, the target was defined as a global Kanizsa square, and a local non-Kanizsa configuration (with pacman inducers rotated outwards by 180°) was the distracter. This was reversed in the local task condition, with the Kanizsa square being the distracter and the non-Kanizsa configuration being the target. In target-absent trials, displays contained the respective non-target configurations only i.e., presenting either two identical Kanizsa square or two non-Kanizsa configurations.[3] Both global and local configurations consisted of a symmetric stimulus representation; that is, physical stimulus characteristics, inducer orientations, and object complexities (measured in terms of the possible object rotations and reflections; see Garner and Clement, 1963) were identical. Similarly, the feature contrast between the target and distracter was identical for both conditions, with equal changes in inducer orientation for a target relative to a given distracter configuration. Thus, the only major difference between the global and local task was whether the target configuration or the distracter configuration induced an illusory square.

2.3. Procedure

Participants were seated in a dimly lit, soundproof experimental chamber. The experiment was divided into two consecutive sessions of either the global or the local task. Each session started with 50–100 practice trials for participants to become familiar with the task. For each session, 360 experimental trials were presented in six blocks of 60 randomized trials each. Participants were instructed to maintain central fixation throughout the whole block. Displays contained a target on 2/3 (and no target on 1/3) of all trials, with targets presented equally likely in the left and right lower quadrants, resulting in 120 trials per condition.

Each trial started with the presentation of a fixation cross for a randomized period of 500–600 ms at the screen center. Following this, two configurations were presented in the bottom left and right quadrants of the display. Participants were required to make a speeded target-present vs. target-absent response via mouse keys. Stimuli were presented for 200 ms, after which a blank screen with a central fixation cross was presented until a response was issued. In case of an erroneous response or time-out after 2500 ms, feedback was provided by a computer-generated tone and an alerting message ('Error' or 'Time-out') was presented for 1000 ms at the center of the screen. Each trial was followed by an inter-stimulus interval of 1000 ms. The order of sessions (global or local task) and the response mapping (i.e., left/right-hand responses to target presence/absence) was counterbalanced across both halves of the experiment and participants, so as to control for practice and compatibility effects between stimulus position and response hand (Fitts and Seeger, 1953).

2.4. EEG recording

The electroencephalogram (EEG) was recorded continuously, at a sampling rate of 1 KHz, using 61 Ag/AgCl electrodes, including those corresponding to the extended 10–10 system (American Electroencephalographic Society, 1994). The electrodes were mounted on an elastic cap. Horizontal and vertical eye movements were monitored by electrodes placed at the outer canthi of the

[2] ERLs in this time range have sometimes been referred to as "N1-posterior-contralateral" (N1pc; e.g., Wascher and Beste, 2010). Similarly, the PCN is also referred to as "N2-posterior-contralateral" (N2pc; e.g., Eimer, 1996). We refrain from using these terms, however, to emphasize the difference waves' independence of the non-lateralized N1/N2 components, and to avoid misinterpretations owing to its varying polarity. For the sake of consistency, we calculate contralateral-minus-ipsilateral activity relative to the location of the *target* stimulus in each condition.

[3] Note that another, much more difficult condition with distracter items of higher similarity to the target object was also included in the experiment (see Conci et al., 2011 for a detailed description). However, we excluded this condition from the present analyses because high error rates in the older sample (mean: 18.5%, range: 5–40%) reduced the number of trials available, and so led to substantially imbalanced trial numbers across groups and conditions. Both reduced and imbalanced trial numbers affect the signal-to-noise ratio, substantially limiting the ERP analyses (Keil et al., 2014; Picton et al., 2000).

eyes and, respectively, the inferior orbit and Fp1. Electrophysiological signals were amplified using a 0.1–100-Hz bandpass filter via BrainAmps (Brain Products, Munich). All electrodes were referenced to Cz and re-referenced off-line to averaged mastoids. ERPs were averaged off-line over an 800-ms epoch; including a 600 ms post-stimulus and a 200-ms pre-stimulus period, which was used for baseline correction. Eye movements were corrected by means of independent-component analyses as implemented in the Brain Vision Analyzer software (Brain Products, Munich). Epochs with artifacts, specifically, containing any signals exceeding $\pm 60\,\mu$V, bursts of electromyographic activity (with the permitted maximum voltage steps between sampling points being $50\,\mu$V), and activity lower than $0.5\,\mu$V within intervals of 500 ms or more, were excluded from averaging on an individual-channel basis. In total, 15.2% of the trials were rejected. The mean number of accepted trial did not differ significantly between task conditions [$F(1,22) = 1.18$, $p = .289$] or age groups [$F(1,22) = 3.03$, $p = .096$]. The mean number of trials was 215 (SD: 28) in the younger group, and 193 (SD: 34) in the older group. As horizontal eye movements are a serious issue when investigating ERLs, we confirmed that the amount of potential, residual eye movements (activity in F9/10) did not differ between groups and task conditions for the PPC and PCN: there were no significant main effects of Task or Task × Age interactions [all $F(1,22) < 1.18$; all $p > .25$].

2.5. Data analysis

Trials on which a response error was made (younger [older] participants: 2.8% [8.4%]; target misses: 3.1% [10.0%], respectively) were removed from the data set prior to the RT and ERP analyses. Trials with RTs more than 2.5 standard deviations above or below each participant's condition mean were also excluded as 'outliers' (3.2% [5.2%] of all trials for younger [older] participants, respectively). In addition, to control for age-related slowing, we examined individually z-transformed RTs (zRTs; Faust, Balota, Spieler, & Ferraro, 1999); that is, for each individual, the mean across all conditions was subtracted from each condition's mean and divided by the standard deviation of the condition mean. The z-transformation effectively rescales the differences between conditions relative to each individual's performance, thus eliminating mean differences in RTs between individuals, including age-related slowing. Target-present RTs, ERs, and zRTs were analyzed by mixed analyses of variance (ANOVAs) with the within-subject factor Task (global, local) and the between-subject factor Age (young, old). Significant interactions were further examined by follow-up ANOVAs and pairwise contrasts (*t*-tests).

Lateralized brain electrical activity, was quantified by subtracting ERPs recorded at lateral posterior electrodes PO7/8 ipsilateral to the target location from contralateral ERPs. These electrodes are in accordance with previous studies examining similar ERLs (Conci et al., 2011; Jannati et al., 2013; Töllner, Rangelov, & Müller, 2012a; Wascher, Hoffmann, Sänger, & Grosjean, 2009; Wascher and Beste, 2010). We did not expect the PPC component a priori; accordingly, our analyses were driven by the visual inspection of the data. We explored the presence of this early lateralization by testing its difference from baseline activity, and further examined whether the component varied with the global-local task conditions and participant's age. Mean amplitudes of the difference waves in the baseline period (200 ms pre-stimulus to stimulus onset) and the time window in which the PPC was most prominent (150–225 ms post-stimulus)[4] were entered into a mixed ANOVA involving the within-subject factors Time Window (−200 to 0 ms, 150–225 ms) and Task (global, local), and the between-subject factor Age (young, old). With regard to the PCN, similar to our prior study (Conci et al., 2011), we focused on peak amplitude and latency, because we expected substantial component timing differences between task conditions and groups. PCN latencies were determined individually at the time point of the maximum negative deflection in the 250–500-ms time window post-stimulus. PCN amplitudes were calculated by averaging five sample points before and after the maximum deflection. Note that even though all statistical analyses were based on the contralateral-minus-ipsilateral differences waves, the reliability of peak measures of grand-averaged potentials could still be affected by temporal variance across trials (Luck, 2014), and the degree of variability could potentially further vary with age and task in the present design. Given this, in order to examine the robustness of the effects observed for the PCN measures, we analyzed additional measures. First, besides our initial peak amplitude analyzes, we also calculated PCN mean amplitudes in the time window 310–410 ms; in this window, the component was clearly present in both groups and both conditions (Fig. 3). Second, as a further measure sensitive to component timing differences, we analyzed the 50% onset latencies using a jackknifing procedure (Ulrich & Miller, 2001). In this procedure, in each condition (global, local), each participant's ERL is replaced by the average across the other, *n*–*1* participants in the group (young, old). The variability among the *n* sub-averages still reflects the variability among the individual ERLs, but with a substantially larger signal-to-noise ratio than the individual participants' waveforms, facilitating reliable determination of ERL latencies. Mixed ANOVAs were performed on all PCN measures with the within-subject factor Task (global, local) and the between-subject factor Age (young, old).

3. Results

3.1. Behavioral data

3.1.1. RTs

The ANOVA performed on the RTs revealed significant main effects of Task [$F(1,22) = 45.84$, $p < .001$] and Age [$F(1,22) = 12.29$, $p < .003$]: responses were 124 ms slower in the local as compared to the global condition, and older participants took 138 ms longer to respond than younger participants. In addition, the Task × Age interaction was significant [$F(1,22) = 9.17$, $p < .007$], due to a marked increase in RTs, of 179 ms, from the global to the local task for the older participants ($p < .001$), compared to an increase of 69 ms for the younger participants ($p < .007$) (see Fig. 2A).

3.1.2. ERs

The ANOVA on the ERs also revealed significant main effects of Task [$F(1,22) = 5.76$, $p < .03$] and Age [$F(1,22) = 7.58$, $p < .02$]. Errors were increased by 3.5% for the local as compared to the global condition, and older observers made 6.3% more errors overall than younger observers. The Task × Age interaction did not reach statistical significance ($p = .13$), though the ER pattern qualitatively mirrored that of the RTs: the increase in errors from the global to the local task was numerically larger for older than for younger adults (5.8% vs. 1.3%; see Fig. 2B).

3.1.3. zRTs

The ANOVA performed on the zRTs confirmed the main effect of Task [$F(1,22) = 59.68$, $p < .001$] and the Task × Age interaction [$F(1,22) = 7.17$, $p < .02$] to be significant, but not the main effect of Age ($p = .4$). zRTs were negative in the global condition (−.590) and

[4] Because the difference waves in the PPC time range exhibited no discernible peaks on a single-participant basis, we did not conduct latency analyses on this component, and amplitude analyses were conducted on mean amplitudes (see also Wascher et al., 2012).

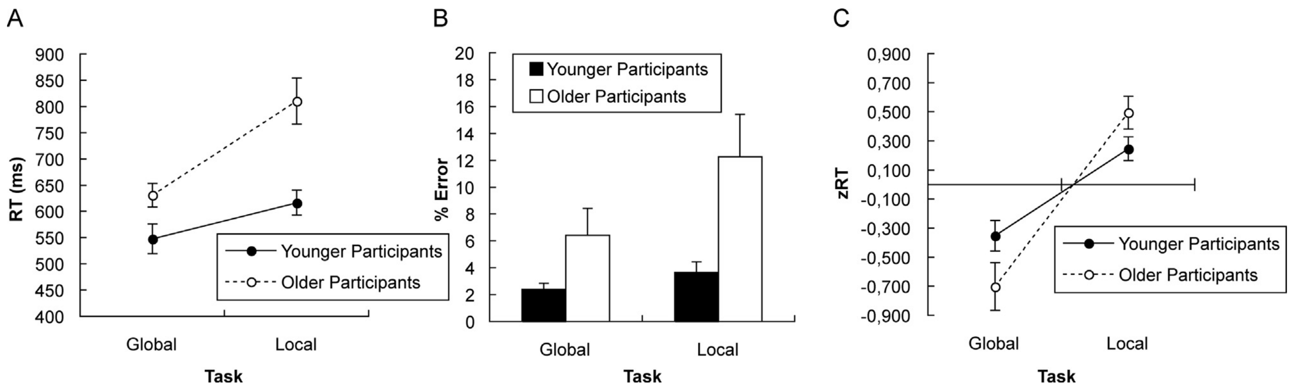

Fig. 2. Behavioral performance.
Mean target-present reaction times (RTs) (A), associated error rates (ERs) (B), and corresponding z-transformed RTs (zRTs) (C) as a function of the task (global: left; local: right), and age group (young: solid lines, black bars; old: dashed lines, white bars). Error bars indicate the standard errors of the mean.

positive in the local condition (.326), and the difference in zRTs between the global and local conditions was larger for older than for younger participants (1.234 vs. .598) (see Fig. 2C). This interaction demonstrates that the stronger global precedence effect in the older, compared to the younger, group cannot simply be attributed to a general age-related slowing.

3.2. Electrophysiological data

Visual inspection of the ERLs revealed the expected PCN across conditions and age groups. In addition, only older participants displayed a PPC, preceding the PCN wave, in the local condition (see Fig. 3).

3.2.1. PPC

In the local task, a larger positivity contralateral to target was elicited only in the group of older participants (Fig. 3B). The ANOVA revealed the two-way interaction Age × Task [$F(1,22) = 14.21$, $p = .001$], and the three-way interaction Age × Time Window × Task [$F(1,22) = 14.46$, $p = .001$] to be significant. Separate follow-up ANOVAs for the two age groups yielded no significant main effects or interactions for the younger participants [all $F(1,11) < 2.5$; all $p > .15$]. In contrast, for the older participants, there was a highly significant Task main effect [$F(1,11) = 18.15$, $p = .001$] and a significant Time Window × Task interaction [$F(1,11) = 18.35$, $p = .001$]. In the older group, difference waves were significantly more positive in the local than in the global condition within the post-stimulus time window of 150–225 ms [$t(11) = 4.27$, $p = .001$], with activity being comparable between the global and local conditions in the baseline period of −200 to 0 ms [$\underline{t}(11) = .89$, $p = .39$] (Fig. 4A).

3.2.2. PCN

The PCN was elicited earlier when participants had to select a global compared to a local configuration; furthermore, the component appeared both reduced and delayed for older relative to younger participants (Fig. 3). The ANOVA on the PCN peak latencies yielded a main effect of Age [$F(1,22) = 7.83$; $p = .010$] and a main effect of Task [$F(1,22) = 19.96$; $p < .001$], resulting from the overall faster elicitation of the PCN for younger compared to older participants, and for global relative to local task conditions (Fig. 4C). The main effect of Task was confirmed by an additional ANOVA on onset latencies [$F_c(1,22) = 4.96$; $p = .046$]; however, the main effect of Age failed to approach statistical significance [$F_c(1,22) = .198$; $p = .661$].

The ANOVA on PCN amplitudes revealed a significant main effect of Age [$F(1,22) = 4.83$; $p = .039$], with a higher negativity for younger than for older participants. Furthermore, the Task × Age interaction was significant [$F(1,22) = 7.83$; $p = .010$], attributable to a larger PCN in the global than in the local task for younger participants [$F(1,11) = 6.71$; $p = .025$], but not for older participants [$F(1,11) = 1.48$; $p = .25$] (Fig. 4B). The same interaction was found in an additional ANOVA on mean amplitudes in the 310–410-ms time window [$F(1,22) = 19.48$, $p < .001$]. However, the main effect of Age was not significant in this analysis either [$F(1,22) = 2.07$, $p = .16$].

4. Discussion

In the present study, we investigated age differences in global-local processing by analyzing behavioral performance data and ERLs in a visual selection task. Younger and older participants were required to discern the presence (vs. absence) of either a Kanizsa square or a non-Kanizsa arrangement of physically identical local elements in a bilateral display. We found the global processing advantage (or local processing disadvantage) to be more pronounced for the older than the younger group, over and above a general performance decline with age. Analyses of two functionally distinct ERLs disclosed brain activity dynamics associated with age-specific differences in selecting stimuli under varying global-local task conditions.

4.1. Age-related impairment in suppression of global form distracters

First, we found early lateralized brain activity to vary as a function of task condition and age: only older participants showed a reliable PPC 150–225 ms post-stimulus towards the non-Kanizsa target in the local task. We propose that this activity indicates processing of the global distracter object in the hemifield opposite to the non-Kanizsa target configuration, which manifests in a larger negativity contralateral to the Kanizsa square (see Fig. 3). A possible mechanism reflected by this PPC modulation might be older participants' difficulty to relinquish the default state of attending to global objects, even though the task required them to focus consistently, for an entire trial block, on the local configuration.

Nie, Müller, & Conci (2015, see also Conci, Nie, & Müller, 2013) introduced the concept of a "comfort" default global state, in which an initial analysis of visual input in terms of global display characteristics provides the observer with a broad gist of the scene. The extraction of local details, in turn, requires a time-consuming disengagement from this state and a controlled "zooming-in" to set the system to a level of local resolution (see also Stoffer, 1993). In light of the current results, the process of zooming-in from a global to a local state of attentional resolution appears to become less effective with age: the PPC indicates that the global form unintentionally summoned older participants' attention at early stages

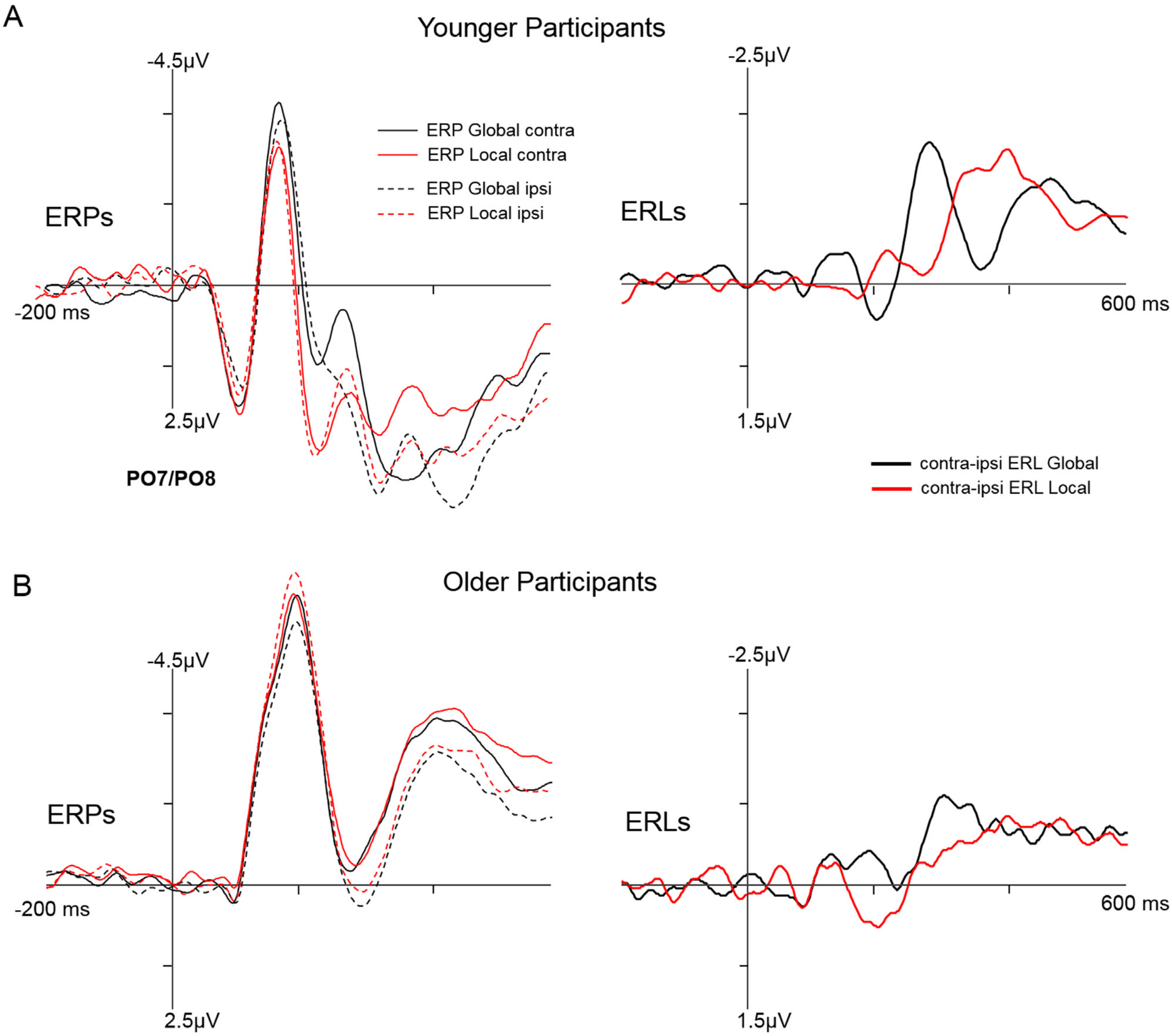

Fig. 3. Event-related potentials and lateralizations. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.) Grand-average event-related potentials (ERPs, left) and event-related lateralizations (ERLs, right) at electrodes PO7/PO8 for groups of younger participants (A) and older participants (B). ERLs were computed by subtracting ERPs ipsilateral (dashed lines) from ERPs contralateral (solid lines) to the target in the global task (black lines) and the local task (red lines).

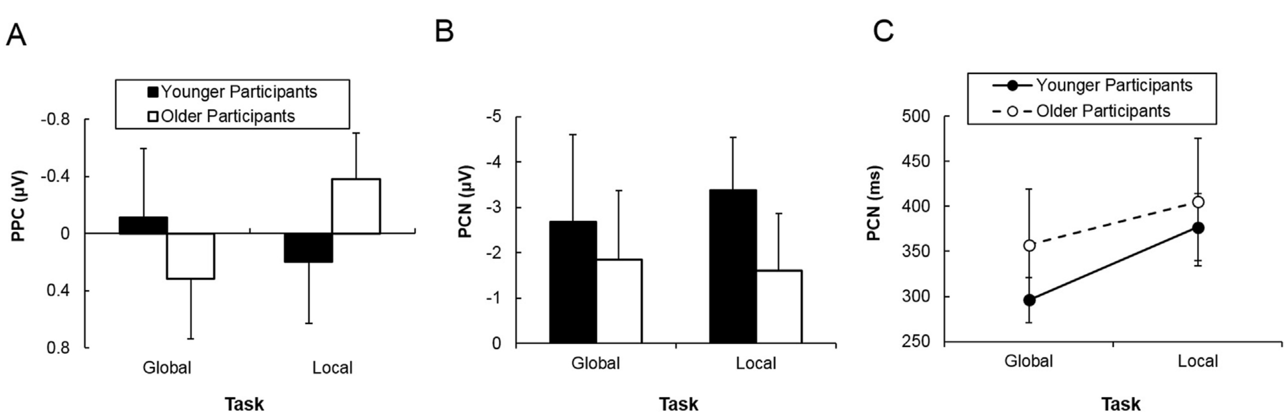

Fig. 4. Mean-plots of ERL measurements.
Mean values of PPC mean amplitudes in the 150–225 ms post-stimulus time window (A), PCN peak amplitudes (B), and PCN peak latencies (C) as a function of the task (global: left; local: right), and age group (young: black bars; old: white bars). Error bars indicate the standard errors of the mean.

of spatially specific coding. This impairment seems to have disrupted, or at least delayed, their intention-guided spatial allocation of attention to the consistently task-relevant, local stimulus configuration reflected in the PCN. In this view, our results support the inhibition-deficit theory of aging, more specifically, age deficits in inhibiting distracter processing at early stages in the processing stream (Hasher et al., 2007; Kim, Hasher, & Zacks, 2007). Within this framework, the PPC effect might be interpreted to reflect older individuals' deficit in suppressing the default salient attracter signal of the coherent shape, which requires them to perform an effortful switch from a global to the task-relevant local state.

PPC-like activations have been reported in previous ERP studies (Akyürek and Schubö, 2011; Corriveau et al., 2012; Fortier-Gauthier et al., 2012; Jannati et al., 2013; Gokce et al., 2014), though their functional interpretation is not entirely clear. Some of these studies focused on relative saliency differences between target and distracter stimuli (but not global-local processing), demonstrating a positive-going deflection contralateral to the target (or a negative-going deflection contralateral to the distracter) under conditions in which the distracter was more salient than the target in the opposite hemifield (Fukuda and Vogel, 2009; Wascher and Beste, 2010; but see Töllner, Müller, & Zehetleitner, 2012b). Interestingly, this effect was found to increase with age, which was attributed to older adults' impaired resistance to interference from conspicuous distracters (Wascher, Schneider, Hoffmann, Beste, & Sänger, 2012). Along these lines, older participants' PPC in the local task may be seen as an indicator of age-specific difficulties in inhibiting the strong bottom-up signal generated by the task-irrelevant, salient illusory figure (Senkowski et al., 2005). The fact that younger participants in our study did not show a reliable PPC suggests that they – in contrast to the older group – were able to adjust and maintain their attentional settings according to prevailing task demands. This enabled them to override the strong bottom–up signal of the Kanizsa square instantly when focally attending to the square conflicted with the selection requirements of the task (cf. Mevorach, Hodsoll, Allen, Shalev, & Humphreys, 2010). Taken together, we propose that the PPC in the present task design marks older participants' stickiness to global default processing at early stages, which, at least in part, explains the age-related increase in global-local differences in the behavioral data.

The PCN was reliably elicited in each of the task conditions for both age groups. This indicates that, at subsequent stages, older as well as younger participants were able to allocate their focal attentional resources to the task-relevant configuration, whether or not the target induced a global percept. The PCN timing was dependent on the task conditions: across age groups, participants showed shorter PCN latencies in the global, as compared to the local, task (52 ms), indicative of faster allocation of attention to the Kanizsa, relative to the non-Kanizsa, configuration. This neurophysiological effect mirrors the faster RTs observed for global, as compared to local, selection across the two age groups. Furthermore, the PCN was overall reduced (0.9 μV) and delayed (59 ms) in older, relative to younger, participants. In agreement with previous studies that reported comparable age-dependent PCN modulations (Li, Gratton, Fabiani, & Knight, 2013; Lorenzo-López, Amenedo, & Cadaveira, 2008; Wiegand, Finke, Müller, & Töllner, 2013), our results add to the mounting evidence that older adults are generally less efficient in, and require more time for, shifting focal attention to target objects in visual space. However, we interpret these age effects tentatively as the age differences were evident for peak measures, but failed to approach statistical significance for onset measures. This pattern of effects is most probably due to age modulating trials of relatively intermediate processing speed (as indexed by peak measures), whereas no such influence seems to affect the relatively fastest trials (as indexed by onset measures) in a given condition.

On a more general level, our results are in agreement with recent studies indicating that the selection of grouped objects involves multiple, sequential stages of processing that can be traced using ERPs (Kasai, Takeya, & Tanaka, 2015). While the N1 component is sensitive to preferential processing of a coherent global object, as compared to local fragments, on early processing stages (Martinez et al., 2007; Murray et al., 2002), the subsequent spatial-attentional selection of a given globally grouped configuration seems to be indexed by the PCN (Conci et al., 2006, 2011; Töllner et al., 2015). Of note, the PPC modulation occurs within a similar time range to the N1: it might as well be described as a lateralization of the N1 contralateral to the global shape (for a detailed analysis and discussion of global-local and age effects on the non-lateralized N1 in the present study, see also the Supplement). It was previously suggested that an N1 lateralization reflects interactions between perceptual global shape integration in the ventral pathway, and preferential spatial target processing of the dorsal pathway (Senkowski et al., 2005). In light of the present results, in the older group, this processing advantage of the global shape occurs irrespective of whether or not it is beneficial for the task at hand. We therefore assume that the PPC might be an neurophysiological marker of older observers' difficulty in overriding involuntary preferential processing of the global shape by top-down task settings. By contrast, the subsequent allocation of spatial attention to the task-relevant (global or local) shape, as marked by the PCN, seems to reflect an obligatory process for both age groups to accomplish the present task.

4.2. Implications for age differences in hierarchical processing

There is an ongoing discussion about whether and how hierarchical processing changes with aging (e.g., Staudinger et al., 2011). Prior research produced inconsistent results, reporting enhanced global-precedence effects (Roux and Ceccaldi, 2001), no differences (Bruyer, Scailquin, & Samson, 2003), or even a reversal to 'local precedence' (Lux et al., 2008) with increasing age. There is, as yet, no clear-cut understanding as to which aspects of hierarchical object processing can account for this inconsistent pattern, though the different task designs and types of global-local manipulation employed are likely key factors (Dale and Arnell, 2013). In a selection task using hierarchical letter stimuli, Tsvetanov et al. (2013) showed that older adults were particularly impaired in selecting low- over high-salient stimuli, supporting the view that age differences in hierarchical processing are dependent on the relative salience of global vs. local target and distracter stimuli in a display. Our findings are consistent with this idea and suggest a putative, underlying neurophysiological mechanisms, according to which the difficulty to suppress the Kanizsa-square distracter in older adults originates at relatively early, probably sensory-driven processing levels.

Note that, when using Kanisza-type arrangements, the relative salience between global and local configurations can be manipulated only one way: the global configuration is invariantly more salient than the local configuration, with emergent properties of the Kanisza figure generating 'pop-out'. The degree to which the ERP results can be generalized towards neural mechanisms underlying age differences in global-local processing of other hierarchical stimuli is therefore limited. The fact that similar N1 modulations have been reported for both Kanizsa-type (Martinez et al., 2007; Murray et al., 2002) and Navon-type stimuli (Beaucousin et al., 2013; Heinze and Münte, 1993; Heinze, Hinrichs, Scholz, Burchert, & Mangun, 1998; Proverbio, Minniti, & Zani, 1998) suggests that early object completion mechanisms may, at least to a certain degree, compare for various hierarchical stimuli. Future ERP studies may specifically investigate the relative salience of global-local target-distracter relations and their interactions with age using different stimulus types. For the time being, however, we limit our conclusions to contending that age differences in global-local processing depend on the degree to which the task draws on functions that are specifically affected by aging, such as the suppression of preferentially processed, global distracter objects (Georgiou-Karistianis et al., 2006; Lien, Gemperle, & Ruthruff, 2011).

5. Conclusions

We found that increased global precedence in older age resulted from stronger susceptibility to distracting global object information, beyond a general slowing of information processing. By examining ERLs, we observed older participants to display a specific deficit in suppressing the initial spatially specific processing of salient distracting (i.e., task-interfering) *global* shapes at early processing stages, prior to being able to allocate attention to the task-relevant *local* information. We argue that older participants have difficulties to switch from a default global to a local attentional state when the task requires them to select local details.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biopsycho.2015.10.006.

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Supplement

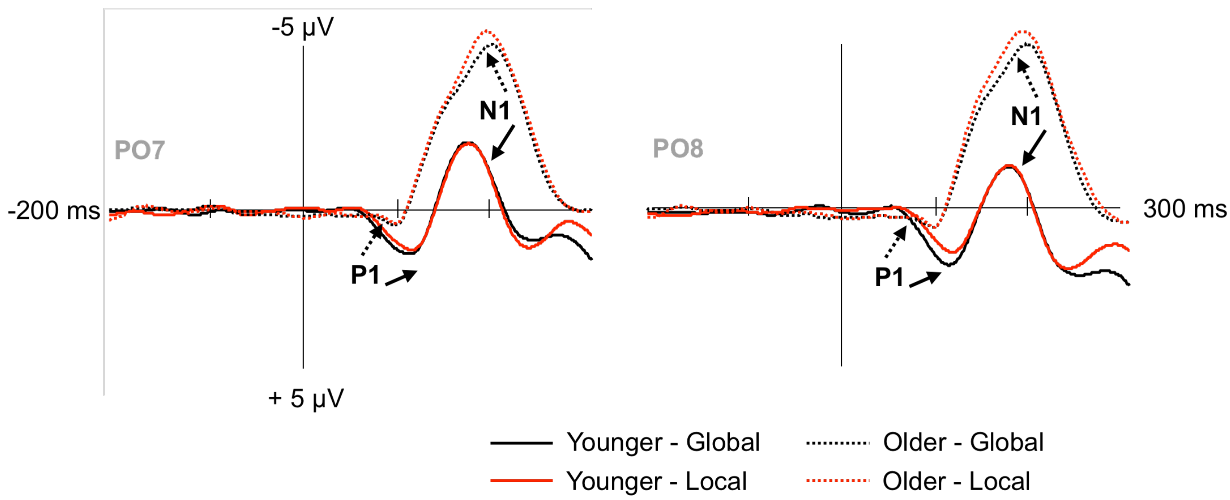
BIOPSY-D-15-00324

Age-related decline in global form suppression

Wiegand, I., Finke, K., Töllner, T., Starman, C., Müller, H.J., Conci, M.

Analyses of early visual P1 and N1 event-related potentials

In addition to the event-related lateralizations reported in the main manuscript, we analyzed early visual components as a function of the participants' age and the global-local task condition. Mean amplitudes of the P1 and N1 were calculated in the post-stimulus time windows of 75–125 ms and 150–200 ms, respectively, as determined by visual inspection of the grand-average waveforms at the lateral posterior electrodes PO7 and PO8 (see Figure below). Mixed ANOVAs on P1 and N1 amplitudes were performed with the within-subject factors Task (global, local) and Electrode (PO7, PO8), and the between-subject factor Age (young, old).



P1. The ANOVA of the mean P1 amplitudes revealed a significant main effect of Age [F(22,1)=7.21; p=.01], due to the P1 being larger for younger than for older participants. There was also a significant main effect of Task [F(22,1)=5.25; p=.03], reflecting a more pronounced P1 in the global as compared to the local condition. Furthermore, the Task × Electrode interaction was borderline-significant [$F(22,1)=3.12$; $p=.09$], with the difference between global and local task conditions tending to be more pronounced at the right [PO8: $t(23)=2.70$, $p=.013$] compared to the left electrode [PO7: $t(23)=1.46$, $p=.158$]. No other main effect or interaction reached significance [all $F(1,22)<2.82$; all $p>.10$].

N1. The ANOVA on mean N1 amplitudes revealed only a significant main effect of Age [$F(22,1)=9.88$; $p=.005$], due to a stronger deflection in the older compared to the younger participants. There was also a marginally significant main effect of Task [$F(22,1)=3.26$; $p=.09$] and a Task × Age interaction [$F(22,1)=3.97$; $p=.059$]. Separate ANOVAs in the two age groups revealed a borderline-significant effect of Task [$F(11,1)=4.66$; $p=.054$] for the older participants, who showed a slightly higher N1 amplitude in the local compared to the global task. There were no significant main effects or interactions for the young participants [all $F(1,11)<1.76$; all $p>.20$].

Discussion

The age effects in visual ERPs are indicative of generally altered visual processing in older age, which likely contributed to the overall behavioral performance decline (slower RTs and higher error rates) in the older, relative to the younger, group. In accordance with this, age-dependent variations in the P1 and N1 amplitudes have previously been attributed to slower and less accurate visual discrimination abilities in older age (Kutas et al., 1994). However, the reported age effects on early visual processes are not uniform across studies, with some studies showing enhanced, and others reduced or no differences between age groups (Czigler & Balázs, 2005; Ceponiene et al., 2008; Falkenstein et al., 2006; Wiegand et al., 2014; Yordanova et al., 2004). This irregular pattern has been explained by differences between the tasks employed (DeSanctis et al., 2008). Presumably, subjective difficulty, decline in low-level sensory visual processes, and attentional resource requirements for a given task depend on participants' age, resulting in interactive effects of age and task conditions in visual ERPs (Curran, Hills, Patterson, & Strauss, 2001).

In the present study, we found the P1 to be reduced in the older compared to to the younger group. The P1 is assumed to reflect processing of sensory stimulus characteristics in extrastriate areas, and its facilitation by selective attention (e.g., Hillyard, Vogel, & Luck, 1998). Accordingly, we take the age-related P1 reduction to indicate that initial sensory encoding of both global and local configurations was attenuated in the older group. Furthermore, in line with previous studies in younger participants (Brodeur et al., 2008; Murray et al., 2002), the component varied with task condition: the P1 was enhanced when observers were required to detect a Kanizsa square, relative to when the local configuration was the target. In light of the global processing advantage, the P1 modulation might be taken to indicate that global targets attracted a larger amount of resources than local targets (reflected in the P1 amplitude difference), facilitating the coding of the global form at early stages in young adults (see Conci et al., 2011). The (borderline) right-sided distribution of the global-local P1 effect is further in accordance with a right-hemispheric specialization for global object information, as, for example, indicated by studies of patients with right-hemispheric lesions (Fink et al., 1997; Robertson and Lamb, 1991).

The N1 component was enhanced for older relative to younger participants. The N1 amplitude has been linked to the amount of resources required to discriminate task-relevant stimuli (Vogel & Luck, 2000). Accordingly, we suggest that the age-related increase reflects older participants needing to recruit comparatively more resources in order to perform the global-local selection task, maybe because they have to compensate an age-related decline of low-level visual processes.

Unlike many previous ERP studies, we did not find an N1 enhancement for the global relative to the local task (Brodeur et al., 2006; Herrmann and Bosch, 2001; Martinez et al., 2007;

Murray et al., 2002, 2004; Pegna et al., 2002; Proverbio and Zani, 2002). Importantly, these studies typically compared ERP responses to the presence versus the absence of illusory contours in single, centrally presented stimuli. The global-local N1 effect is known to decrease for laterally, compared to centrally, presented stimuli (Murray et al., 2002; see also Abu Bakar et al., 2008). As we focused on the selection of global versus local stimuli in the presence of the respective other configuration in lateral displays (see also Conci et al., 2006), we may not have been able to isolate the global-local N1 effect. Furthermore, inter-individual variability within and across age groups in the present study might have been relatively higher than that in studies with one, more homogenous participant sample, as supported by the trend we found towards an age-dependent change in the pattern of the global-local N1 effect. The pattern of the ERLs depicted more reliably competitive perceptual and attentional selection processes depending on the global-local properties of target-distracter relations and their interactions with observer's age.

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