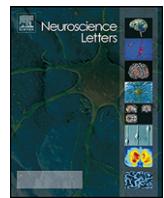




Contents lists available at ScienceDirect

Neuroscience Letters

journal homepage: www.elsevier.com/locate/neulet

Feature-selective attention: Evidence for a decline in old age

Cliodhna Quigley^a, Søren K. Andersen^a, Lars Schulze^{a,b}, Martin Grunwald^c, Matthias M. Müller^{a,*}^a Institut für Psychologie I, Universität Leipzig, Seeburgstrasse 14–20, 04103 Leipzig, Germany^b Klinik für Psychiatrie und Psychotherapie, Universität Rostock, Germany^c Haptik-Forschungslabor, Paul-Flechsig-Institut für Hirnforschung, Medizinische Fakultät, Universität Leipzig, Germany

ARTICLE INFO

Article history:

Received 22 December 2009

Received in revised form 10 February 2010

Accepted 19 February 2010

Keywords:

Ageing

Feature-selective attention

SSVEP

EEG

ABSTRACT

Although attention in older adults is an active research area, feature-selective aspects have not yet been explicitly studied. Here we report the results of an exploratory study involving directed changes in feature-selective attention. The stimuli used were two random dot kinematograms (RDKs) of different colours, superimposed and centrally presented. A colour cue with random onset after the beginning of each trial instructed young and older subjects to attend to one of the RDKs and detect short intervals of coherent motion while ignoring analogous motion events in the non-cued RDK. Behavioural data show that older adults could detect motion, but discriminated target from distracter motion less reliably than young adults. The method of frequency tagging allowed us to separate the EEG responses to the attended and ignored stimuli and directly compare steady-state visual evoked potential (SSVEP) amplitudes elicited by each stimulus before and after cue onset. We found that younger adults show a clear attentional enhancement of SSVEP amplitude in the post-cue interval, while older adults' SSVEP responses to attended and ignored stimuli do not differ. Thus, in situations where attentional selection cannot be spatially resolved, older adults show a deficit in selection that is not shared by young adults.

© 2010 Elsevier Ireland Ltd. All rights reserved.

The ability to shift and direct spatial attention seems mostly intact in old age [6,13,18,4]. However older adults are slower and display distinct difficulties, in particular in suppressing the processing of task-irrelevant stimuli [7,15]. Indeed it has been postulated that an inhibitory deficit is at the core of age-related changes in cognitive processing [16], for example decline in working memory performance [11]. Although spatial aspects are a central part of visual processing, attentional selection can also operate on visual features and objects and there may be age-related differences in non-spatial selection. Here we investigate whether cued shifts in feature-selective attention are subject to change in old age.

To separately examine cortical responses to simultaneously presented attended and ignored stimuli, we used frequency tagging, which is based on the finding that repetitive sensory stimulation evokes a regular, oscillatory cortical response [23]. In the visual modality such a response is known as the steady-state visual evoked potential (SSVEP), the amplitude of which can be estimated using spectral methods. It is possible to separate responses to several simultaneously presented stimuli if they have different presentation rates, allowing for 'frequency tagging' of different spectral regions of the recorded electroencephalogram (EEG). In addition, SSVEP amplitudes have been shown to be robustly modulated by

the allocation of attention to a stimulus [19]. To date, few cognitive ageing studies have measured SSVEPs (see [17] for a recent memory study) and the frequency tagging approach has not yet been applied to the study of attention and ageing. This study also serves as a first test of this method with an older sample of participants.

Here, the participants' task was to detect coherent motion (target motion) in one of two superimposed differently coloured random dot kinematograms (RDKs) while ignoring coherent movement events in the other RDK (distracter motion). An RDK consists of a group of dots, each moving independently in a random direction; when enough dots simultaneously move in the same direction, this global motion is detectable by an observer. Previous research by our group has demonstrated that young adults are able to shift their attention to such stimuli, as reflected in behavioural performance and modulation of SSVEP by attention [1–3,20]. In these earlier experiments, the sources of the SSVEP modulations were localised to early visual areas, suggesting that the attentional selection of such stimuli on the basis of features is the result of a top-down enhancement of feed-forward visual processing, in line with other recent results [30]. Using a similar experimental paradigm, we investigated whether there are age-related changes in the ability to shift attention non-spatially, namely to a cued feature, colour.

10 older and 11 young adults participated in the experiment. Of these, 1 older and 1 younger adult were rejected prior to data analysis due to excessive EEG artifacts and low steady-state response barely above noise level, respectively, leaving 9 older (age 67.2 ± 7.1 (mean \pm standard deviation), range: 55–75 years, all right-handed,

* Corresponding author. Tel.: +49 341 973 5962; fax: +49 341 973 5969.

E-mail address: m.mueller@rz.uni-leipzig.de (M.M. Müller).

3 females) and 10 young adults (age 24.1 ± 3.9 , range: 19–32 years, all right-handed, 8 females). It should be noted that the term 'older adults' is often reserved for individuals of more than 60 or 65 years of age and that we use it here in a more descriptive sense. Younger adults were students at the University of Leipzig. 6 of the older adults were recruited from the out-patient Memory Clinic at the University Hospital, where they had voluntarily attended dementia screening (interview and range of cognitive tests including the Mini-Mental-State exam [10]) and were judged to be free of any signs of cognitive impairment. The remaining older subjects were family or friends of the experimenters. All subjects reported no history of neurological illness, normal or corrected-to-normal vision and were tested for colour-blindness using Ishihara plates. Subjects gave informed written consent and received payment or course credit for their participation. The experiment was conducted in accordance with the Declaration of Helsinki and local ethical guidelines and was approved by the local ethics committee.

The experiment was conducted in a dimly lit, electrically shielded recording chamber. Participants were seated approximately 80 cm from a 19" CRT monitor with 72 Hz (13.89 ms) refresh rate and resolution of 800×600 pixels. The stimuli, red and blue random dot kinematograms (RDKs), were photometrically isoluminant (6.75 cd/m^2) and presented using pure colour phosphors on a white background (77 cd/m^2). Each contained 125 dots (squares of 8 pixels, or 15 arcmin, width) distributed randomly within a circle of radius approximately 5.5° of visual angle (175 pixels). Each dot moved 2 arcmin from frame to frame in any of the four cardinal directions, selected randomly. To allow for separate analysis of steady-state evoked responses to each stimulus, frequency tagging was used. The red dots flickered at 8 Hz (5 frames on, 4 frames off) and blue at 12 Hz (4 frames on, 2 frames off). Target or distracter motion consisted of coherent movement of 85% of the dots of a given colour in a single direction for 556 ms, corresponding to a total displacement of approximately 1.2 visual degrees.

Subjects were familiarised with the task in a training session before EEG cap and electrodes were applied. Participants were instructed to respond as accurately as possible and completed a minimum of two training blocks of 20 trials, each containing target and/or distracter motion. Initial blocks were without flicker, and when it was clear that the task was understood, training with flicker began and continued until performance stabilised. After training, participants were informed that half of the trials would contain no coherent motion.

The experiment consisted of 8 blocks containing 55 trials of variable duration (3.18–3.58 s) with 1.2 s inter-trial interval. Each block lasted approximately 4 min. Feedback regarding hit rate, false-alarm rate and reaction time was given during a break after each block. Subjects were instructed which hand to use for button presses, and this was changed after four blocks and counterbalanced over subjects. During each trial subjects maintained fixation on a centrally presented cross, and the target RDK colour was cued with variable onset (0.96 and 1.36 s after trial onset) by fixation cross colour change from black to red or blue (Fig. 1). One, two, or no coherent motion events occurred in each trial, and could appear at any time after cue onset, with a minimum of 830 ms between events. Trial order and coherent motion onsets were randomised so the occurrence of coherent motion was not predictable. Only trials without coherent motion were submitted to EEG analysis.

EEG data were recorded from 32 channels in a custom layout (see [1] for more details; approximate electrode locations are shown in the topographic maps in Fig. 2) using a BioSemi ActiveTwo system (BioSemi, Amsterdam, The Netherlands) at a sampling rate of 256 Hz, re-referenced off-line to the algebraic average of the mastoid channels. 4 further electrodes were used in bipolar montages to measure vertical and horizontal electrooculogram. Pre-processing

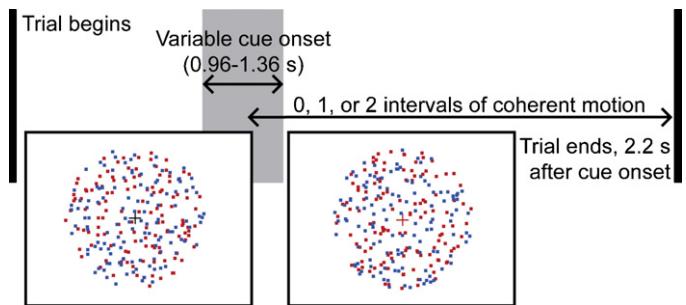


Fig. 1. Schematic representation of the sequence of events within a trial. A fixation cross colour change indicated to the subject which RDK was to be attended, and the onset of this cue varied across trials. Two example frames depict the RDK stimuli, with black fixation cross before cue onset on the left, and coloured (here red) fixation cross after cue onset shown on the right. Each dot moved in a random direction from frame to frame (monitor refresh rate was 72 Hz). Blue dots flickered at a rate of 8 Hz, red dots at 12 Hz. Participants' task was to respond to coherent motion in the attended RDK (targets) while ignoring analogous motion in the unattended RDK (distracters). One, two, or no events (target or distracter) could occur after cue onset, and the trial ended 2.2 s after cue onset. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

and analysis were carried out using EEGLAB [8] and custom functions written in MatLab (The MathWorks, Natick, MA). Epochs of 3.1 s duration were extracted and trials which contained target or distracter motion were discarded, leaving only data from trials without coherent movement for further analysis. Rejection of trials containing eye movements or muscle artifact was performed by hand. The average rejection rate was 15% for younger and 25% for older subjects. One older subject had frequent blink artifacts; these were corrected using a standard regression method [12]. Condition means were calculated for each subject with the constraint that equal numbers of trials from each condition were used, with random selection applied in case of unequal number.

Steady-state visual evoked potential (SSVEP) amplitudes were calculated by Fourier transform of trial-averaged EEG data for each condition and channel separately. Spherical-spline interpolated topographic maps of the steady-state amplitudes for each stimulation frequency (8 and 12 Hz, calculated over a 2.5 s window beginning before cue onset, with the first 500 ms of trials excluded to avoid contamination by stimulus onset VEP) were inspected in order to determine which channels to subject to further analysis. In both subject groups, a clear peak was found at the occipital pole (Oz, marked with a larger dot in the topographic maps in Fig. 2), and this electrode was used for further analysis. Previous work in our group with similar stimuli [3,20] has consistently found greatest amplitudes at this recording site.

The first 7 older subjects had steady-state stimulation phase-locked to trial onset (i.e. both frequency's cycles began at trial onset). The stimulation program was then changed to allow for time-course analysis, and the remaining subjects had stimulation phase-locked to cue onset. This analysis approach was however not pursued because of the nature of the results reported here. In order to estimate the SSVEP, individual trials must be aligned relative to the phase of both stimulation frequencies before averaging. Epoching during pre-processing was carried out accordingly: relative to trial onset (0–3.1 s) in the case of the first 7 subjects, and relative to cue onset (−0.9 to 2.2 s) for the remaining participants. Pre- and post-cue analysis windows were defined (trial-locked epochs: pre-cue window 0.4–0.9 s, post-cue 1.5–2.5 s; cue-locked epochs: pre-cue −0.5 to 0 s, post-cue 1.2–2.2 s), and SSVEP amplitudes were calculated for each window and experimental condition ('attend red' or 'attend blue'). Each subject's amplitudes for a given frequency were normalised to baseline by dividing by their pre-cue condition mean for that frequency. As the results were similar for both frequencies and the behavioural data also showed no dif-

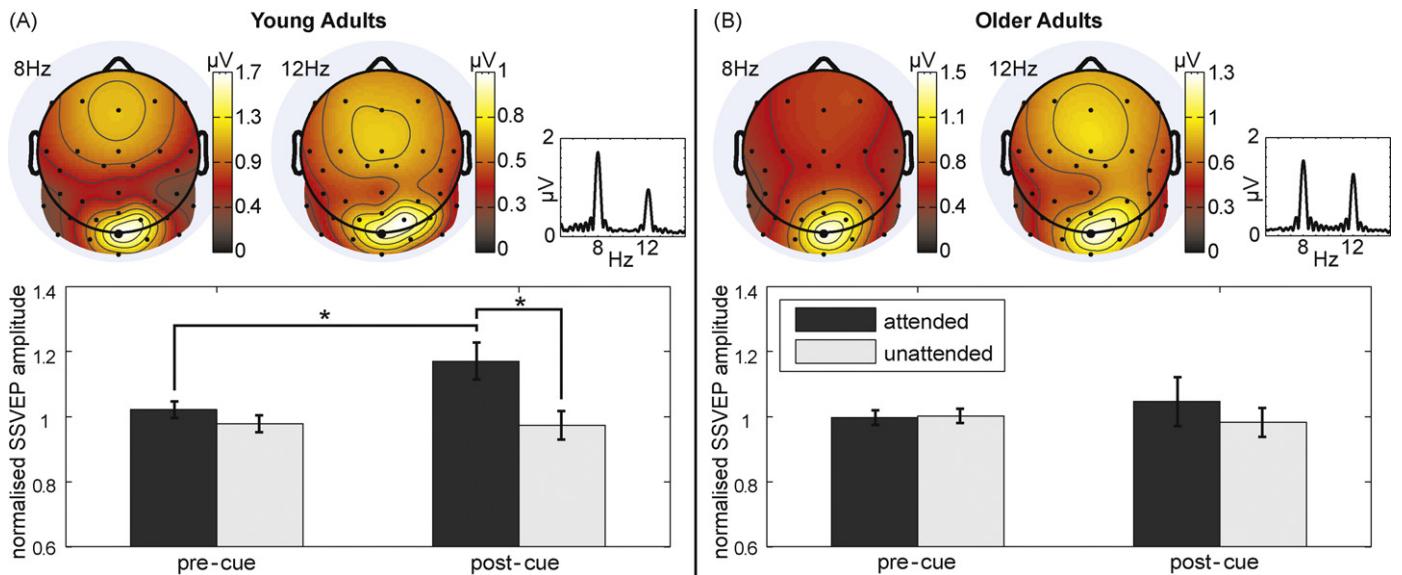


Fig. 2. SSVEP results. (A) Young adult group: grand average topographic distributions of SSVEPs elicited by red (8 Hz, top left) and blue (12 Hz, top centre) RDKs, calculated over 2.5 s of trial. Grand average amplitude spectra measured at the occipital pole (Oz) over the same time interval (top right). The bottom row shows normalised SSVEP amplitudes for 'attend' and 'ignore' in the pre- and post-cue intervals. Stars indicate significant differences ($p < 0.05$), error bars are standard error of the mean. (B) Results for older adult participants, depicted as in (A). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

ference, the two experimental conditions were averaged to yield 'attend' and 'ignore' conditions (as in [1–3]).

Three within-group paired comparisons were performed on the normalised SSVEP data for each subject group: amplitudes from the 'attend' condition before and after cue onset in order to test for attentional enhancement; the 'ignore' condition before and after cue onset to test for suppression of unattended stimuli; and 'attend' and 'ignore' in the post-cue interval to test for an overall attentional effect.

For analysis of behavioural data, a response window from 300 to 1100 ms after the onset of target or distracter motion was used to classify button presses as hits or false alarms. Reaction times (hits only) were measured as time from motion onset to key-press. Hit and false-alarm rates were used to compute sensitivity (d'), the magnitude of which reflects the observer's ability to discriminate between targets and distracters, with 0 indicating chance performance [28]. No difference in d' was found between 'attend blue' and 'attend red' conditions in either age group (paired t -tests, older adults: $t(8) = -0.288$, $p = 0.780$; young adults: $t(9) = -0.195$, $p = 0.850$), so a single d' was calculated over conditions.

Additionally, in order to evaluate whether participants could discriminate between the presence and absence of coherent motion, we calculated their sensitivity to any coherent motion – target or distracter. To do so we calculated a further d' from the "hit" rate of response on trials containing coherent motion and the "false-alarm" rate of response for the trials with no coherent motion. If subjects were responding in an arbitrary fashion then this measure of motion sensitivity should be approximately zero. Furthermore, to test for any fatigue-related performance decline, we calculated hit rates for the first and second half of the experiment for each subject and compared these within age groups using a paired t -test. All other statistical tests were carried out using one or two sample two-tailed t -tests and an alpha of 0.05.

In our test for effects of fatigue no difference was found in either group (young adults: $t(9) = 0.774$, $p = 0.459$; older adults: $t(8) = -0.880$, $p = 0.404$). In addition, the mean of our measure of motion sensitivity (see above) was significantly greater than zero for both groups (young: 3.356 ± 0.576 (mean \pm standard deviation), $t(9) = 18.425$, $p < 10^{-7}$; older: 3.053 ± 0.800 , $t(8) = 11.451$, $p < 10^{-5}$) and there was no significant difference between age

groups ($t(17) = -0.955$, $p = 0.353$). Thus, both groups could reliably detect motion events, and the similarity of hit rates in experiment halves strongly suggests participants were actively attempting to complete the task.

Regarding task performance, the difference between age groups is pronounced. d' was significantly greater than zero for both groups (young: 2.665 ± 0.872 , $t(9) = 9.660$, $p < 10^{-5}$; older: 0.932 ± 0.780 , $t(8) = 3.582$, $p < 0.01$) but younger subjects were significantly better than older adults in discriminating targets from distracters, as seen in the group difference in d' values ($t(17) = -4.542$, $p < 10^{-3}$). There was however no significant difference in mean reaction times (young: 719 ± 77 ms, older: 746 ± 65 ms, $t(17) = 0.841$, $p = 0.412$).

The grand mean SSVEP topographies of both groups show a clear peak centred at Oz for each flicker frequency, and the mean amplitude spectra for both groups also show well-defined peaks at the stimulation frequencies (Fig. 2, top row). Normalised amplitudes for the 'attend' and 'ignore' conditions in pre and post-cue windows are shown for each subject group (Fig. 2, lower row). Young adults showed a significant effect of attentional cueing: post-cue 'attend' amplitudes were significantly greater than pre-cue amplitudes ($t(9) = -2.368$, $p < 0.05$), while no difference was found in the 'ignore' comparison ($t(9) = 0.078$, $p = 0.939$), but as expected, there was a significant difference between 'attend' and 'ignore' amplitudes in the post-cue interval ($t(9) = 2.489$, $p < 0.05$). In the older group, no difference was seen in 'attend' amplitudes before and after cueing ($t(8) = -0.588$, $p = 0.573$) or in the 'ignore' comparison ($t(8) = 0.467$, $p = 0.653$). Critically, no overall attentional effect was seen in the older group in the post-cue interval ($t(8) = 1.340$, $p = 0.217$).

Looking at the behavioural data, a clear difference in task ability was seen between the two age groups, which was not due to fatigue. Although older adults could detect occurrences of coherent motion equally as well as young adults, they had difficulty discriminating between target and distracter motion events. Based on the behavioural data alone, it is not clear whether this is due to a failure in perceptually discriminating between the two kinds of motion events, or in adequately suppressing responses to distracter motion. This can however be elucidated by the SSVEP results, which provide a measure of attentional selection.

Although no attentional effect was seen in the older adult group, the overall topographic distribution and amplitude of the steady-state response is almost identical in younger and older adults, and corresponds well to previous results [3,20]. As such, we can report that a robust SSVEP is measurable in older adults, and propose that the frequency tagging method represents a useful approach for future cognitive ageing research. Comparing SSVEP amplitudes before and after the appearance of the attentional cue, in younger adults there is an enhancement of the amplitude corresponding to the attended RDK, and no change in the amplitude corresponding to the RDK that should be ignored. The post-cue amplitudes for attended and ignored stimuli also differ significantly, replicating the results of earlier studies [2,3,20]. Older adults, however, show no modulation of SSVEP amplitude by attention—although there is indeed a robust steady-state response to each of the stimuli, there is no difference in amplitude for attended or ignored stimuli when compared before and after cue onset, and there is no difference in amplitudes elicited by attended and ignored stimuli in the post-cue analysis window. Earlier work using similar stimuli localised the cortical sources of the SSVEP attentional modulations to early visual areas including V1, V2 and V3 [2,3]. Thus, it seems that the deficit in feature-selective attention in older adults is due to a deficit in selection at an early stage of visual processing, which is a failure at the level of perceptual rather than response selection.

The changes in visual processing that occur in old age have been well investigated. Colour perception is subject to optical changes, in particular the perceived luminance of blue tones due to yellowing of the crystalline lens [21]. There is no evidence however that this had an impact here, as no difference was found for older adults between 'attend blue' and 'attend red' conditions in terms of behavioural measures or SSVEP results. Age-related changes in motion processing have also been reported, but our measure of motion sensitivity suggests that older adults could detect motion events. In addition, the stimuli used were well within psychophysically determined detection limits for older adults, both in terms of duration [5] and the proportion of dots moving coherently [27]. The deficit in selection does not seem to be due to impaired processing of the stimuli themselves, rather to an impairment in attentional selection of the cued stimulus.

Our results indicate that for older subjects there is a deficit in attentional selection of a feature when this selection cannot be mediated by spatial attention. Feature-selective attention is a top-down modulation of processing in early visual areas [2,3,30], so is the age-related deficit reported here due a problem in the top-down, cue-related "instruction" to attend to a certain feature, or is it rather a deficit in the enhancement of bottom-up processing required to maintain selection of the feature? The top-down component of spatial attention seems to be intact in old age, as shown in endogenous spatial cuing studies [6] and visual search [18]. In younger subjects, common areas in the fronto-parietal network have been shown to be involved in feature-based and spatial attentional deployment [9,26], but there are differences [14,24] and it may be that the frontal decline associated with normal ageing [22] selectively affects the top-down aspect of non-spatial feature-selective attention. Regarding bottom-up processing in older visual cortex, single-cell studies in macaque have revealed a decline in feature selectivity [25,29] which could also impact feature-selective attention. Future work will have to disentangle the relative contributions of top-down and bottom-up processes to this age-related decline in feature-selective attention.

Acknowledgements

We thank Renate Zahn for assistance with data acquisition. This experiment was realised using Cogent Graphics developed by John

Romaya at the LON at the Wellcome Department of Imaging Neuroscience. Thanks also to Matthias Ihrke for his implementation of the Gratton ocular correction EEGLAB plug-in. CQ was supported by the Deutsche Forschungsgemeinschaft, graduate program "Function of Attention in Cognition".

References

- [1] S.K. Andersen, S. Fuchs, M.M. Müller, Effects of feature-selective and spatial attention at different stages of visual processing, *J. Cogn. Neurosci.* (2009), doi:10.1162/jocn.2009.21328.
- [2] S.K. Andersen, S.A. Hillyard, M.M. Müller, Attention facilitates multiple stimulus features in parallel in human visual cortex, *Curr. Biol.* 18 (2008) 1006–1009.
- [3] S.K. Andersen, M.M. Müller, S.A. Hillyard, Color-selective attention need not be mediated by spatial attention, *J. Vis.* 9 (2009) 1–7.
- [4] M.G. Baxter, M.L. Voytko, Spatial orienting of attention in adult and aged rhesus monkeys, *Behav. Neurosci.* 110 (1996) 898–904.
- [5] P.J. Bennett, R. Sekuler, A.B. Sekuler, The effects of aging on motion detection and direction identification, *Vis. Res.* 47 (2007) 799–809.
- [6] T. Curran, A. Hills, M.B. Patterson, M.E. Strauss, Effects of aging on visuospatial attention: an ERP study, *Neuropsychologia* 39 (2001) 288–301.
- [7] J.W. de Fockert, A. Ramchurn, J. van Velzen, Z. Bergström, D. Bunce, Behavioral and ERP evidence of greater distracter processing in old age, *Brain Res.* 1282 (2009) 67–73.
- [8] A. Delorme, S. Makeig, EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including Independent Component Analysis, *J. Neurosci. Methods* 134 (2004) 9–21.
- [9] T. Egner, J.M. Monti, E.H. Tritschuh, C.A. Wieneke, J. Hirsch, M.-M.M. Mesulam, Neural integration of top-down spatial and feature-based information in visual search, *J. Neurosci.* 28 (2008) 6141–6151.
- [10] M.F. Folstein, S.E. Folstein, P.R. McHugh, "Mini-Mental State". A practical method for grading the cognitive state of patients for the clinician, *J. Psychiatr. Res.* 12 (1975) 189–198.
- [11] A. Gazzaley, J.W. Cooney, J. Rissman, M. D'Esposito, Top-down suppression deficit underlies working memory impairment in normal aging, *Nat. Neurosci.* 8 (2005) 1298–1300.
- [12] G. Gratton, M.G. Coles, E. Donchin, A new method for off-line removal of ocular artifact, *Electroencephalogr. Clin. Neurophysiol.* 55 (1983) 468–484.
- [13] P.M. Greenwood, R. Parasuraman, J.V. Haxby, Changes in visuospatial attention over the adult lifespan, *Neuropsychologia* 31 (1993) 471–485.
- [14] B.Y. Hayden, J.L. Gallant, Time course of attention reveals different mechanisms for spatial and feature-based attention in area V4, *Neuron* 47 (2005) 637–643.
- [15] M.K. Healey, K.L. Campbell, L. Hasher, Cognitive aging and increased distractibility: costs and potential benefits, *Prog. Brain Res.* 169 (2008) 353–363.
- [16] C. Lustig, L. Hasher, R.T. Zacks, Inhibitory deficit theory: recent developments in a "new view", in: D.S. Gorfein, C.M. MacLeod (Eds.), *The Place of Inhibition in Cognition*, American Psychological Association, Washington, DC, 2007, pp. 145–162.
- [17] H. Macpherson, A. Pipingas, R. Silberstein, A steady state visually evoked potential investigation of memory and ageing, *Brain Cogn.* 69 (2009) 571–579.
- [18] D.J. Madden, S.L. Connelly, T.W. Pierce, Adult age differences in shifting focused attention, *Psychol. Aging* 9 (1994) 528–538.
- [19] S.T. Morgan, J.C. Hansen, S.A. Hillyard, Selective attention to stimulus location modulates the steady-state visual evoked potential, *Proc. Natl. Acad. Sci. U.S.A.* 93 (1996) 4770–4774.
- [20] M.M. Müller, S. Andersen, N.J. Trujillo, P. Valdés-Sosa, P. Malinowski, S.A. Hillyard, Feature-selective attention enhances color signals in early visual areas of the human brain, *Proc. Natl. Acad. Sci. U.S.A.* 103 (2006) 14250–14254.
- [21] D. Nguyen-Tri, O. Overbury, J. Faubert, The role of lenticular senescence in age-related color vision changes, *Invest. Ophthalmol. Vis. Sci.* 44 (2003) 3698–3704.
- [22] A. Pfefferbaum, E. Adalsteinsson, E.V. Sullivan, Frontal circuitry degradation marks healthy adult aging: evidence from diffusion tensor imaging, *Neuroimage* 26 (2005) 891–899.
- [23] D. Regan, Some characteristics of average steady-state and transient responses evoked by modulated light, *Electroencephalogr. Clin. Neurophysiol.* 20 (1966) 238–248.
- [24] B. Schenkluhn, C.C. Ruff, K. Heinen, C.D. Chambers, Parietal stimulation decouples spatial and feature-based attention, *J. Neurosci.* 28 (2008) 11106–11110.
- [25] M.T. Schmolesky, Y. Wang, M. Pu, A.G. Leventhal, Degradation of stimulus selectivity of visual cortical cells in senescent rhesus monkeys, *Nat. Neurosci.* 3 (2000) 384–390.
- [26] H.A. Slagter, A. Kok, N. Mol, J.L. Kenemans, Spatio-temporal dynamics of top-down control: directing attention to location and/or color as revealed by ERPs and source modeling, *Brain Res. Cogn. Brain Res.* 22 (2005) 333–348.
- [27] R.J. Snowden, E. Kavanagh, Motion perception in the ageing visual system: minimum motion, motion coherence, and speed discrimination thresholds, *Perception* 35 (2006) 9–24.
- [28] T.D. Wickens, *Elementary Signal Detection Theory*, Oxford University Press, New York, 2001.
- [29] S. Yu, Y. Wang, X. Li, Y. Zhou, A.G. Leventhal, Functional degradation of extrastriate visual cortex in senescent rhesus monkeys, *Neuroscience* 140 (2006) 1023–1029.
- [30] W. Zhang, S.J. Luck, Feature-based attention modulates feedforward visual processing, *Nat. Neurosci.* 12 (2009) 24–25.