# Consequences of Video Games on Oculomotor Behavior and Attention and Additional Implications for Healthy Aging

Dissertation

zur Erlangung des Grades eines
Doktors der Naturwissenschaften

der Mathematisch-Naturwissenschaftlichen Fakultät
und
der Medizinischen Fakultät
der Eberhard-Karls-Universität Tübingen

vorgelegt
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Juli - 2015

Tag der mündlichen Prüfung: 20. November 2015

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# Summary

Video games are a wide-spread leisure activity and are consumed around the world. There is increasing evidence that playing video games shortens reaction times in many tasks. A possible explanation is an alteration in the control of visual attention.

In the first part of this dissertation, I will provide evidence that playing video games also shortens the reaction times in eye movements, that this reduction is not accompanied by reduced impulse control and that it is not explained by a faster shift of covert attention. Probably, playing video games increases the ability to extract visual information. In the second part, the eye movements in the elderly are analyzed. I will show that age has a profound impact on eye movements, decreasing performance in many ways. Finally I will try to connect these two areas, and show how video games could be used to counteract age-related decline.

## Zusammenfassung

Videospiele sind mittlerweile eine allgegenwärtige Freizeitbeschäftigung weltweit. Aus Sicht der Wissenschaft herrscht Konsens, dass Videospielekonsum zu kürzeren manuellen Reaktionszeiten führt. Dem könnte eine effizientere visuelle Aufmerksamkeitskontrolle zu Grunde liegen.

Der erste Teil dieser Dissertation zeigt, dass Videospieler schnellere Augenbewegungen haben. Dies ist jedoch nicht auf eine reduzierte Impulskontrolle oder schnellere Aufmerksamkeitsverlagerungen zurückzuführen. Vielmehr besitzen Videospieler vermutlich eine effizientere visuelle Informationsverarbeitung. Der zweite Teil der Dissertation beschäftigt sich mit dem Einfluss gesunden Alterns auf Augenbewegungen und zeigt eine deutliche, nicht-pathologische Abnahme in verschiedenen Parametern. Insgesamt soll am Ende eine Brücke zwischen beiden Themengebieten geschlagen und über die Möglichkeit der Anwendung von Videospielen zur Kompensation der altersbedingten Nachteile nachgedacht werden.

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# List of Acronyms

| | |
|---|---|
| **BS** | brainstem saccade generator |
| **DLPFC** | dorsolateral prefrontal cortex |
| **EBN** | excitatory burst neuron |
| **ERP** | event-related potential |
| **FEF** | frontal eye field |
| **fMRI** | functional magnetic resonance imaging |
| **LATER** | linear approach to threshold with ergodic rate |
| **LIP** | lateral intraparietal area |
| **MN** | motoneuron |
| **MT** | mediotemporal area |
| **MST** | mediosuperiotemporal area |
| **NOT** | nucleus of the optic tract |
| **NVGP** | non-video game player |
| **OKN** | optokinetic nystagmus |
| **OPN** | omnidirectional pause neuron |
| **RT** | reaction time |
| **SC** | superior colliculus |
| **SPEM** | smooth pursuit eye movement |
| **SRT** | saccadic reaction time |
| **TN** | tonic neuron |
| **TREND** | Tübinger evaluation of risk factors for early detection of neurodegeneration |
| **VGP** | video game player |
| **VOR** | vestibuocular reflex |

# 1 An introduction to video games, age and the movements of the eyes

## 1.1 Video games

Video games have been a subject of examinations since their early beginnings in the amusement arcades (Lowery and Knirk, 1982; Rushton, 1981). Nowadays, they are still highly discussed in media and science. Especially in the younger population, playing video games is nearly ubiquitous. In Germany and the U.S., for example, more than 50% of the teenagers play several times a week, with average gaming times amounting to over one hour per day (Feierabend et al., 2014; Gentile, 2009; Lenhart et al., 2008; Rideout et al., 2010). A similar trend is already present in children (Feierabend et al., 2012; Gentile, 2009; Olson et al., 2007). The implications of this high prevalence are dividing parents and children (Kutner et al., 2008) and the scientific community (Ferguson, 2013) alike. Unfortunately, if we do not undertake serious efforts, there seems to be little hope of overcoming this digital divide (Greitemeyer, 2014). Therefore, although this thesis is concerned with a positive outcome associated with video game playing, I will also give a short overview on the negative effects literature to shed light on both sides of the coin.

### 1.1.1 Negative effects

From their first appearances on, video games have been of concern for public health. Early studies focused on concrete risks like “Space Invader” epilepsy (Rushton, 1981) – the first report of “video game epilepsy” (for a review see Shoja et al., 2007) – or curiosities like “Nintendinitis” (Brasington, 1990). Nowadays, especially action video games[1] have been repeatedly associated with desensitization, increased aggression and impairments in pro-social behavior (Anderson and Carnagey, 2009; Anderson et al., 2010; Carnagey et al., 2007; DeLisi et al., 2013; Gentile et al., 2004; Gentile and Gentile, 2008; Greitemeyer and Mügge, 2014).

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[1] I will not use the popular term *violent video game* since it implies a general negative outcome from this sort of games (Ferguson and Garza, 2011). Although the term *action video game* includes sports and racing games commonly accepted as non-violent, it still seems to be superior to the negative connotation accompanying *violent video games*. In addition, the definition of violence in video games itself can be quite vague. For example, *Super Mario Bothers*, a platform game, involves “considerable violence in the sense that the player typically spends a considerable amount of time destroying other creatures” (Anderson and Dill, 2000, p.779).

Although there seems to be plenty of evidence for the negative effects of action video games, problems with the methodology in these studies were pointed out early on (Ferguson and Kilburn, 2010; Griffiths, 1999; Mitrofan et al., 2009). “Anti-social” effects vanish if confounds are properly controlled (Ferguson and Garza, 2011; Valadez and Ferguson, 2012) and instead of game violence, difficulty (Engelhardt et al., 2015) or competitiveness (Adachi and Willoughby, 2011) may, at least in part, account for the detrimental outcomes. Most important, non-competitive violent video games do not increase aggressive behavior, whereas competitive but non-violent games do (Adachi and Willoughby, 2011). The authors of this study suggest that instead of violence, competition might heighten aggression through an increase in physiological arousal. Since action video games are often more competitive, this factor may have confounded the results of studies showing an aggression increasing effect of action video games. In general, other factors, like depressive symptoms, are much stronger predictors of violence than playing action video games itself (Ferguson, 2011). Supporting this view, reduced psychosocial well-being seems to cause video game playing instead of being caused by it (Kowert et al., 2015).

Indeed, the deleterious effects of action video games can actually be negated or even turned into positive ones if played together with others (Coyne et al., 2011; Ferguson and Garza, 2011; Greitemeyer et al., 2012; Velez et al., 2014). In addition, “bad” behavior in the virtual world might even sensitize us for moral behavior in real life (Grizzard et al., 2014).

Despite these controversial results regarding violent content, many video games are highly immersive. They exert a strong motivational pull on the player by addressing basic needs for self-determination (Ryan et al., 2006; for a review see Przybylski et al., 2010). In addition, a main reason for young people to play is competing with and winning against others (Olson, 2010). From monkey studies it is known that game competition with a real opponent increases activity in the prefrontal cortex as compared to non-competition or a virtual opponent (Hosokawa and Watanabe, 2012). This frontal activity is most likely associated with reward expectation (Watanabe, 1996). Similarly, winning against a human competitor supersedes computer opponents in men (Kätsyri et al., 2013b) and the active part of playing is more rewarding than observing someone play (Kätsyri et al., 2013a). Taken together with the fact that game playing releases dopamine (Koepp et al., 1998), addiction is a potential risk associated with video games (Gentile, 2009; Gentile et al., 2011; Rehbein et al., 2010).

Finally, another quite obvious negative effect is that video gaming time cannot be spent on homework or other educational activities (Cummings and Vandewater, 2007; Weis and Cerankosky, 2010).

### 1.1.2 Positive effects

> Deliberately allocating attention to one part of the environment, ignoring other sources of distraction is a quality known as attentional control, and is not obviously associated with chasing zombies.
>
> *(Bavelier and Davidson, 2013, p.426)*

The world would be an easier place if things were just black and white and only negative effects were associated with (action) video games[2]. But quite the opposite is the case. The first wave of video game research in the 1980s already attributed some positive outcomes to gaming (Dorval and Pepin, 1986; Gagnon, 1985; Lowery and Knirk, 1982; McClurg and Chaillé, 1987; Orosy-Fildes, 1989). These early studies were focused mainly on improvements in spatial cognition but were also subject to some methodological concerns, like the lack of proper control conditions or proof of generalization (Boot et al., 2011; Sims and Mayer, 2002).

In 2003, the Rochester-based research group of French biologist Daphne Bavelier sparked the second wave of research on the positive effects of video games. This study found that action video game playing enhances several aspects of visuospatial attention, like subitizing[3], the useful field of view and the attentional blink (Green and Bavelier, 2003).

In contrast to the literature on negative effects, many of the positive outcomes have been *causally* linked through training studies to video game playing. The following aspects are improved after training participants on a video game:

- Backward masking (Li et al., 2010)
- Dual-tasking and task-switching (Chiappe et al., 2013; Green et al., 2012; Strobach et al., 2012)
- Spatial cognition (Cherney, 2008; de Lisi and Wolford, 2002; Feng et al., 2007; Okagaki and Frensch, 1994; Sanchez, 2012; Terlecki et al., 2008)
- Visual search (Wu and Spence, 2013)
- Visual working memory (Blacker et al., 2014; Boot et al., 2008)

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[2] It is still unclear which game features exactly are beneficial. Additionally, the field lacks a clear definition of *action video games*. Attempts have been made (Dye et al., 2009; Franceschini et al., 2013; Green et al., 2010a; Hubert-Wallander et al., 2011), but some definitions “could apply equally well to Frogger as it does Call of Duty” (Ferguson, 2014, p.1). Moreover, several genres have positive and possibly disjunct outcomes (Dobrowolski et al., 2015; Oei and Patterson, 2013). Thus, in the context of beneficial effects, I will refrain from genre specific definitions.

[3] In contrast to the slow incremental counting every one of us has mastered, subitizing is the ability to judge the number of items only with a brief look at nearly constant reaction time. In “normal” people subitizing ranges from 0 up to 3-4 items (Mandler and Shebo, 1982), whereas video game players reach 5 items.

- Visuospatial attention (Green and Bavelier, 2003, 2006a; Greenfield et al., 1994; Spence et al., 2009; Wu et al., 2012)

Besides these cognitive changes, video games also cause enhancements in low-level visual functions like contrast sensitivity (Li et al., 2009) and spatial resolution (Green and Bavelier, 2007).

It has been argued that many of these results stem from “esoteric laboratory tasks” and that it “is not clear [if] practical values of these laboratory effects” can be demonstrated (Ferguson, 2014, p.1). Although not vast in numbers, studies showing “real-life” applications of video game effects do exist. Video game training attenuates ataxia (Ilg et al., 2012) as well as dyslexia in children (Franceschini et al., 2013) and induces plasticity in the visual system of adult amblyopic patients (Fricker et al., 1981; Jeon et al., 2012; Li et al., 2011). The performance of laparoscopic surgeons can be enhanced with video game training (Schlickum et al., 2009) as well as “putting force” in golf players (Fery and Ponserre, 2001) and flying skills in pilots (Gopher et al., 1994). Relating the “real-life” to brain changes, Kühn et al. (2013) showed a substantial increase in gray matter volume of the dorsolateral prefrontal cortex (DLPFC) after two months of 30-minutes-per-day video game training, indicating a causal role of gaming in these alterations [4].

In addition, cross-sectional studies have shown that video game players (VGPs) outperform non-video game players (NVGPs) on various aspects as different as:

- Attentional capture (Chisholm et al., 2010)
- Change detection (Clark et al., 2011)
- Line bisection (Latham et al., 2014)
- Multiple-object tracking (Sungur and Boduroglu, 2012; Trick et al., 2005)
- Multisensory processing (Donohue et al., 2010)
- Time perception (Rivero et al., 2013)
- Visual field size (Buckley et al., 2010)
- Visual sensitivity (Appelbaum et al., 2013)
- Visual short-term memory (Blacker and Curby, 2013; Wilms et al., 2013)

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[4] Oddly, the DLPFC is one of the key areas for moral behavior (Anderson et al., 1999). Since Kühn et al. used *Super Mario* as a training game, it would be interesting to see if the trained participants show improved moral judgments – similar to the results of Grizzard et al. (2014), but without the use of “violence”.

A concise summary of the positive-effects literature covering the last 30 years has been done by Latham et al. (2013). For a general review see Bavelier et al. (2012b) and for a more psychological perspective Granic et al. (2014). A critical meta-analysis is provided by Powers et al. (2013).

Disregarding the actual outcome variable in the task, VGPs show faster reaction times (RTs) across the board (Dye et al., 2009). Given the huge diversity of tasks in which video game benefits are observed, a broad generalization rather than a multitude of specialized perceptual learning events may be at work. Thus, video game effects are probably not a task-specific or motor change, but an alteration of attentional abilities. Indeed it has been suggested, that video game playing alters the ability of "learning to learn" (Bavelier et al., 2012b; Green et al., 2010a). Modeling studies support this idea by showing that VGPs can flexibly adapt to new tasks (Bejjanki et al., 2014; Green et al., 2010b).

A similar but more manageable idea is an enhancement of top-down attention in VGPs. Support for this notion comes from the field of neurophysiology. In studies using electroencephalography VGPs showed changes in occipital activity. Training with a video game increased the amplitudes of late-occurring event-related potentials (ERPs) but did not change early ERPs in an attentional visual field task (Wu et al., 2012). The early ERPs are associated with bottom-up processes, whereas the late ERPs measure the top-down control aspects of attention like resource allocation and selection. Therefore, these results implicate that video game playing enhances top-down control, most likely by improving distractor suppression. VGPs also show decreased amplitudes in the late component of steady-state evoked potentials to unattended stimuli in a rapid serial visual presentation task (Mishra et al., 2011). This supports the view of improved distractor suppression and enhanced top-down control of attention. Several neuroimaging studies provide further evidence for this hypothesis. VGPs seem to have a thicker cortex in frontal areas (Kühn et al., 2014) as well as overall decreased activity in the frontoparietal attention network (Bavelier et al., 2012a; Granek et al., 2010) – a decrease causally linked to video game playing (Prakash et al., 2012). Additionally, VGPs show lower activity in the motion processing mediotemporal area (MT) in response to moving distractors (Bavelier et al., 2012a). Taken together, these studies indicate less cognitive demands and thus superior attentional skills in VGPs. The apparent discrepancy between increased occipital ERP amplitudes and decreased frontal functional magnetic resonance imaging (fMRI) activity may be brought together in terms of efficiency. In the first imaging study on video game playing, an overall decrease in glucose metabolism in the brain was found after video game training (Haier et al., 1992). This study concluded that the training group developed a more efficient top-down strategy for the game, which in turn led to a decreased number of recruited brain circuits and thus reduced metabolic activity.

Another explanation for the general RT benefits found in VGPs are faster discrimination abilities. One study found shorter early ERPs in VGPs supporting this view (Bailey et al., 2010). Unfortunately, this study used a cross-sectional design and thus might just show preexisting differences between VGPs and NVGPs (Boot et al., 2011; Kristjánsson, 2013).

Finally, it has also been proposed, that the faster RTs of VGPs stem from more efficient stimulus-response mappings (Castel et al., 2005). This would defy better top-down attentional control but would explain the RT benefits.

More light will be shed into these questions through the studies included in this thesis (see Section 2.1 on page 27).

## 1.2 Aging

The careful reader may now ask where aging comes into (video game) play. By 2050 the generally falling fertility rates will triple the proportion of people aged 65 years and older with respect to the global population (Harper, 2014; United Nations, 2013a). In addition, life expectancy will reach 82 years by the end of the century (United Nations, 2013b). Therefore, the consequences of aging will become an ever more important question. On the one hand, neurodegenerative diseases, which are best predicted by age, are of concern. On the other hand, increased life expectancy is postponing and not prolonging senescence (Vaupel, 2010), thereby increasing the number of *healthy* years of life.

Unfortunately, even normal aging has some undesirable side effects: processing speed is slowed (Cerella and Hale, 1994; Salthouse, 2000), RT variability increased (Hultsch et al., 2002; Morse, 1993) and inhibitory control impaired (Dempster, 1992). For saccadic eye movements (see Section 1.4 on page 11) this decline starts around 30 years of age with a slow, but steady linear decrease in performance (Klein et al., 2005). An fMRI-focused review on the effects of aging on cognition is given by Grady (2012).

This conglomerate of detrimental phenomena has been termed *cognitive decline.* Frontal areas like the DLPFC are especially vulnerable to aging (Morrison and Baxter, 2012). One might speculate that the aging brain simply loses neurons over the years and thus cognitive decline arises. From monkey studies it is known that the number of neurons in their homologue of DLPFC is fairly stable after maturation, but the amount of dendritic spines and synapses substantially decreases with senescence (Luebke et al., 2010). Thus, not the neurons are lost, but their connectivity is reduced. Although obtained in macaques, these results are probably also applicable to humans due to our close phylogenetic proximity.

Despite the fact that these changes are quite pronounced, it is still not known if they actually cause cognitive decline. Indeed, the negative connotation of this term was recently challenged by an alternative explanation. The “decline” in cognitive functions may just be a consequence of lifelong learning (Ramscar et al., 2014). Over the years we acquire a multitude of different behaviors, which steadily increases our decision space. Selecting an adequate option will thus take longer the older we get. Therefore the term *cognitive aging* might be better to describe these effects.

Whatever the “true” reason for cognitive aging might be, its outcome detrimentally influences the lives of the elderly. For example, slower RTs lead to an increased risk of falling (van den Bogert et al., 2002). Impairments in processing speed are major reasons for older people having to cease driving (Marie Dit Asse et al., 2014) and if they do not, decreased visuospatial attention and visual sensitivity intensifies the risk of traffic accidents (Ball and Owsley, 1991). Therefore it would be advantageous to be able to attenuate the effects of cognitive aging.

Many video games have a high degree of enjoyment and even the elderly seem to relish playing games more than mere perceptual training (Belchior et al., 2012). Thus it is not surprising that several researchers used video games to temper the effects of cognitive aging on RTs (Clark et al., 1987; Drew and Waters, 1986; Dustman et al., 1992; Goldstein et al., 1997), visual attention (Belchior et al., 2013), cognitive control (Anguera et al., 2013; Basak et al., 2008), distraction (Mayas et al., 2014) and indeed, driving skills (Belchior, 2007). For a meta-analysis on video game training in the elderly see Toril et al. (2014).

Neurophysiology emphasizes the potential of video game training in older adults. As already mentioned, playing video games leads to a decrease in frontal activity probably as a consequence of more efficient attentional resource allocation. In older adults however, frontal activity is increased as compensation for a decreased functioning of the early visual areas (Grady et al., 1994) – a phenomenon termed *posterior-anterior shift with aging* (Davis et al., 2008). Therefore it seems that video game training might hold the power to reverse this effect.

Nevertheless, placing every grandparent in front of a PC might not be the ultimate solution to "curing" cognitive aging; for example driving relies on a multitude of skills that are all affected by age. Particularly, the perception of motion is indisputably important in driving and one would expect especially the fast-paced action video games to improve this ability. Alas, it seems that this is only the case for contracting radial motion patterns – a type of optic flow induced by *backward* movements (Hutchinson and Stocks, 2013). Therefore, it is fundamental to conduct research that links video game benefits in the young population to the drawbacks of cognitive aging in the elderly. The studies included in this thesis provide such a comparison in the oculomotor domain (see Section 2.2 on page 31). Since vision is the primary sense of most primates the analysis of eye movements provides deep insights into the function of the brain. The following chapter will show us why.

## 1.3 The (goal-directed) movement of the eyes

> Our eyes are parts of our brain sticking out.
>
> *(Cleveland, ECEM 2013)*

Eye movements have been of interest to mankind for a long time. Already the Greek philosopher Aristotle was concerned with the coordinated movement of our eyes (Wade, 2010). Nevertheless, it took until the end of the 19th century before eye movement research really started to gain speed with the introduction of more quantitative measurement methods (earlier studies had used afterimages or auditory methods). One of the first successful visualization attempts used a kymograph and a lever construction connected to a contact lens made of plaster-of-Paris (Huey, 1898). Obviously, this was not the most pleasant recording technique[5] since it affected the eye and its movements through the lever. Only three years later did the American psychologist Raymond Dodge introduce the first contact-free eye tracker which was able to record horizontal eye movements on a photosensitive plate (Dodge and Sparks Cline, 1901). Since then eye movement research gained a lot of momentum with new methods, like limbus tracking or videooculography, which have made eye tracking an inexpensive and easy-to-use technique. An extensive overview on the history of eye movement research is given by Wade and Tatler (2011).

But what do we actually measure when we are looking at the eyes? In his seminal work Dodge (1903) introduced five types of eye movements: (I) Saccades, (II) smooth pursuit, (III) vestibuocular reflex (VOR), (IV) rotatory nystagmus and (V) vergence. Whereas this is a rather phenomenological division, it has already separated slow (Type II and IV) from fast (Type I) eye movements and outlined the category of compensatory eye movements. Nowadays, three larger classes of eye movements are distinguished based on their functions.

1. *Compensatory eye movements* reduce the influence of head and body movements on vision by canceling self-induced motion blur. The VOR is driven by the vestibular system and induces short-latency eye movements in the opposite direction to the head movement. For longer, slowly-accelerating movements, the optokinetic nystagmus (OKN) is induced by the resulting retinal image motion (e.g. when sitting in a train and looking out of the window). The OKN has a ten times longer latency than the VOR, since it “computes” self-motion from the movement of the image on the retina. A concise review on compensatory eye movements in the context of slow eye movements is given by Ilg (1997).

2. *Goal-directed eye movements* move and keep an important detail of the retinal image on the fovea. This spot has the highest resolution in the retina but covers

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[5] The participant’s eye had to be “rendered anæsthetic by the use of cocaine” (Huey, 1898, p.585).

only a tiny fraction of our visual field – in humans roughly 1 °, which corresponds to the size of a thumbnail at the outstretched arm. Goal-directed eye movements enable us to sample flexibly our whole visual environment with this high spatial resolution. They can be further separated in fast (saccades) and slow (pursuit) movements. Since these eye movements are the main research subject of this thesis, Section 1.4 on the next page and Section 1.5 on page 23 will be dedicated exclusively to saccades and smooth pursuit eye movements (SPEMs).

3. *Fixational eye movements* (Barlow, 1952) like ocular drift and microsaccades occur during fixation. Although the eyes seem stationary, very small movements are still at work. Especially microsaccades seem to be important for the avoidance of image fading during sustained fixation (McCamy et al., 2012) and can indicate the orientation of covert attention shifts (Hafed and Clark, 2002). Although their actual function is highly debated, it seems that there is only little difference in microsaccades and their larger counterparts (for an overview see Hafed, 2011). Microsaccades elicit similar perceptual changes (Hafed, 2013), have equally stereotyped kinematics (Zuber et al., 1965) and compensate for inequalities in foveal resolution, just as saccades do for the retina (Poletti et al., 2013). A general review on microsaccades is given by Martinez-Conde et al. (2013).

## 1.4 Saccades

Saccades (from French for *jerk*) are fast, jerky eye movements between two phases of fixation. Dodge (1916) suggested using this term uniformly for his “Type I” eye movements. The word was coined by the French ophthalmologist Louis Émile Javal, although he was only referring to work done by his technician Lamare (Wade et al., 2003).

Saccades can be haptically observed when two fingers are put on a closed eyelid and one starts to look from right to left. During this experiment the jerky nature of the saccade is palpable.

The purpose of these eye movements is to project quickly a detail of the retinal image to the fovea, thereby enabling spatial high-resolution sampling of the whole visual environment. Fig. 1.1 on the next page shows the eye movement pattern (“scanpath”) of a participant during free viewing of an image. It can be seen that the eyes are really “scanning” the image and that saccades are always separated by fixations.

The advantage of studying saccades is their close connection to attention (see Section 1.4.1) and their highly stereotypical time course. Time-of-day effects on saccadic reaction times (SRTs) and peak velocities are relatively small and test-retest variability is virtually absent (Wilson et al., 1993). Even on a trial-by-trial basis, saccades show markedly similar time courses (see the position and velocity traces in Fig. 1.2 on page 14). Therefore, saccades can be regarded as an “oculomotor fingerprint”[6].

In addition, saccades are incredibly accurate: Even when participants are instructed to make “inaccurate” saccades, their average accuracy is not affected (Mosimann et al., 2004). This is not surprising, since the main purpose of saccades is the projection of peripheral image details directly onto the fovea. In consequence, saccades should be fairly straight – which is true only for purely horizontal saccades. Unfortunately, asynchronous co-activation of the horizontal and vertical eye muscles during oblique saccades and attentional processes are affecting the saccades mid-flight. Therefore, the trajectories of saccades during free viewing can become quite curved (e.g. Viviani et al., 1977; reviewed by van der Stigchel et al., 2006).

### 1.4.1 Attend to the eyes! – Saccades and attention

> Every one knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of several simultaneously possible objects. It implies withdrawal from some things in order to deal effectively with others.
>
> *(James, 1890, pp.403-404)*

In the scanpath example shown in Fig. 1.1 on the following page, the saccade landing positions are not scattered randomly over the image – which would also adhere to high-resolution sampling – but are rather distinctly distributed. The participant looked

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[6] Wilson et al. (1993) reports anecdotal data for monozygotic twins who had almost identical peak velocities in their saccades.

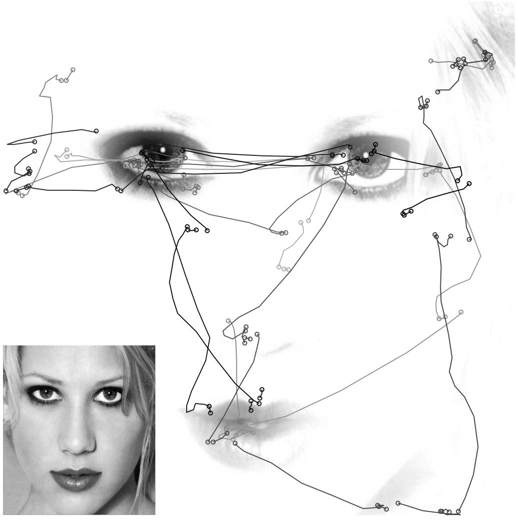

**Fig. 1.1:** Scanpath during free viewing of an image. Image lightness is adjusted according to fixation duration. Saccades (thin lines; circles: start-/endpoints) are scaled in lightness according to time of occurrence (black: first, gray: last). The data were collected in the *Schülerlabor Neurowissenschaften*, Tübingen (see Ilg, 2015). The inset depicts the original image which was taken from the picture pool of the *Schülerlabor*.

mainly at the eyes, mouth and nose. This seems to be a quite distinct pattern for faces within species (Dahl et al., 2009). This distinct pattern implies a close relationship between saccades and spatial attention, guiding our eyes to the interesting parts.

In the famous spotlight-of-attention model (Posner, 1980), spatial attention is imagined as a spotlight shedding light on events in the darkness of available information (see James' quote in the dictum above; for a review consult Petersen and Posner, 2012). This attentional spotlight can be covertly shifted to a location without moving the eyes (e.g. try to fixate the following parenthesis, and direct your attention to the lower border of the page). If the locus of attention has to be further analyzed (e.g. spell the page number at the attended location), the spatial resolution of the fovea is needed and thus, a saccade or overt shift of attention is executed.

This close relationship between covert (internal) and overt (saccadic) attention shifts has been confirmed in several experiments. Discrimination performance at the landing position of an upcoming saccade is improved compared to unattended positions and SRTs to attended locations are shortened (Kowler et al., 1995). This implies that covert attention has been shifted to the landing position prior to the saccade. Similarly, detection as well as discrimination performance are best at the saccade endpoint, regardless of the previously attended position (Deubel and Schneider, 1996; Hoffman and Subramaniam, 1995). The latter studies also show the necessity of shifting attention prior to the saccade to its future endpoint, or "that while it is possible to make attention movements without making corresponding eye movements, it is not possible to make an eye movement without making a corresponding shift of attention" (Shepherd et al., 1986, p.475).

Using a modeling approach Clark (1999) found that many task-dependent alterations in SRTs, like the effects of target eccentricity (Kalesnykas and Hallett, 1994) or fixation condition (Dorris and Munoz, 1995; Kalesnykas and Hallett, 1987), can be explained by combining an attentional all-or-nothing mechanism with a simple trigger for saccades. This lends further support to a close link between covert attention and overt saccades. Results from neuroimaging studies and neurophysiology support this idea. Covert and overt attention shifts activate nearly identical frontoparietal networks (Corbetta et al., 1998; de Haan et al., 2008) and show similar single-cell activity in the superior colliculus (SC) as well as in the frontal eye fields (FEFs; Ignashchenkova et al., 2004; Schall, 2004).

Finally, if we accept that each saccade is preceded by a covert attention shift, saccades can be separated on the basis of this underlying shift. If attention is captured by a sudden transient onset like a flash, the saccade towards this stimulus is a reflexive, bottom-up driven saccade. If, on the other hand, attention is allocated based on a rule like "look up to the upper right corner of the current page", the according saccade is voluntary and top-down controlled. Saccades towards simple onset cues, so-called visually-guided saccades, are reflexive saccades (e.g. Westheimer, 1954), whereas saccades to the mirror position of such an onset cue are voluntary (anti-) saccades (Hallett, 1978; for a review consult Munoz and Everling, 2004).

A review on reflexive and voluntary attention is given by Corbetta and Shulman (2002), while attention models are reviewed by Itti and Koch (2001).

### 1.4.2 The faster, the better? – Saccade kinematics

> It should be pointed out, that even the fastest woman does not reach the velocities achieved by monkeys.
>
> *(Becker and Fuchs, 1969, p.1249)*

Saccades are one of the fastest movements in our body. Depending critically on their size (and also the sampling rate of the eye tracker, Juhola et al., 1985), they can reach peak velocities of up to 900 °/s (see for example Fig. 3 in Bahill et al., 1975b). Saccades show a stereotypical relationship between duration and amplitude[7], as well as peak velocity and amplitude. This relationship is linear up to amplitudes of 15 °, after which a soft saturation limit is reached[8](Bahill et al., 1975b; Baloh et al., 1975). Because of its distinctiveness this property of saccades has been labeled *main sequence*, "a term borrowed from our astronomer friends" (Bahill et al., 1975b, p.201). In astronomy, it describes a distinct class of stars which lie on a pronounced band when stellar brightness is plotted against color in the Hertzsprung-Russell diagram (for a historical review see Nielsen, 1964). An example of the amplitude-velocity main sequence for horizontal saccades obtained in a visually-guided saccade task is shown in Fig. 1.2 on the next page.

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[7] A fact already observed by Dodge in 1903: "The duration of eye movements [...] varies directly with the angle of displacement, but is approximately constant for each individual under the same conditions" (Dodge, 1903, p.184).

[8] Interestingly, most naturally occurring saccades do not exceed amplitudes of 15 ° (Bahill et al., 1975a).

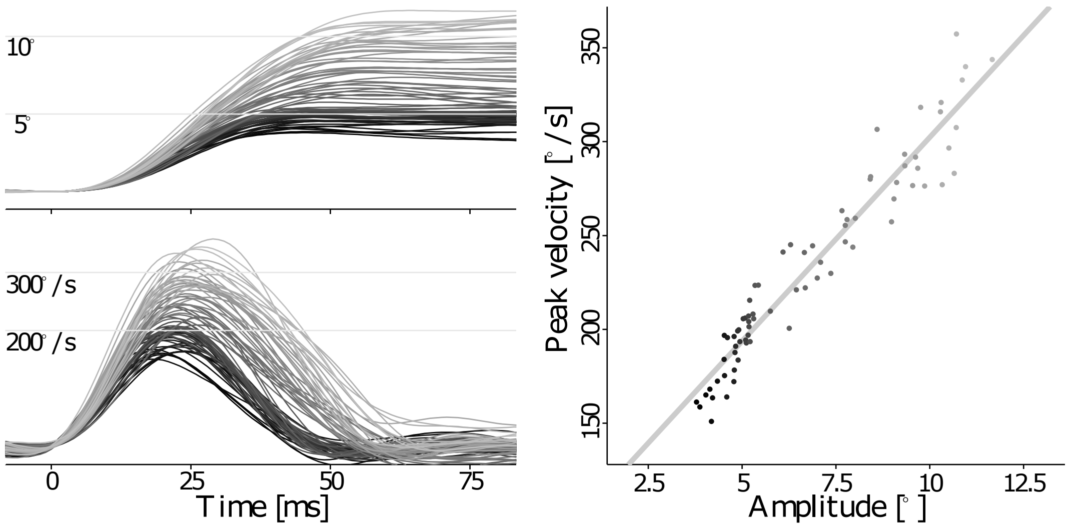

**Fig. 1.2:** Saccades of one participant in a visually-guided saccade task. The left side shows recorded eye position (upper panel) and velocity (lower panel) aligned to saccade onset. The right side shows the amplitude-velocity main sequence. Color lightness is adjusted according to saccade amplitude (dark: small, light: large). The data were collected in the *Schülerlabor Neurowissenschaften*, Tübingen (see Ilg, 2015).

The main sequence is such a prominent feature of saccades that it even reveals commonalities with other eye movements. Saccades, fast phases of rotatory VOR (Ron et al., 1972), OKN (Kaminiarz et al., 2009; Mackensen and Schumacher, 1960) and microsaccades (Zuber et al., 1965) all show the same main sequence indicating a common mechanism of generation (see Section 1.4.3 on the following page).

To understand how the main sequence arises, two key features are important:

1. The saccadic system suffers from signal-dependent noise: Stronger motor commands for the extraocular muscles increase saccadic peak velocity, but also add proportionally more noise to the signal. This results in an increased endpoint variability for faster saccades. Therefore, the motor command should not be too strong and thus the movement duration not too short, to avoid imprecise saccades.

2. During saccades, we are essentially motion blind – a phenomenon termed *saccadic suppression*. More precisely, motion sensitivity is drastically reduced during an ongoing saccade to avoid self-induced motion blur (Burr et al., 1994; Ross et al., 1996; details on the neuronal basis are given by Thiele et al., 2002). Therefore, the duration and number of saccades should be kept at a minimum to maximize visibility.

Obviously, these are two contradictory goals and this inherent problem has been framed clearly by Carpenter (1981, p.238):

> "A typical saccade of 10 ° lasts about 50 ms, during which the high rate of visual slip renders the visual system all but blind. Thus, paradoxically, the more frequently the oculomotor system tries to improve things by getting the fovea exactly on target, the less time remains actually to see: so that a suitable balance must be struck between not seeing quite what we want, and not seeing at all."[9]

More precisely, faster saccades reduce the influence of saccadic suppression, but increase endpoint variability, which in turn increases the need for corrective saccades and thus the time with impaired motion perception. In an optimal-control strategy, the main sequence is a simple consequence of the speed-accuracy trade-off inherent in these two properties (Harris and Wolpert, 2006; Tanaka et al., 2006). The model of Harris and Wolpert niftily incorporates these problems in a simple two-termed cost function. The first term reflects the costs for moving the eyes and is basically proportional to duration. The second term subsumes "fixation costs" like endpoint accuracy and scatter. With this in mind, some phenomena regarding saccadic peak velocities can be easily explained. Normally, velocity profiles are highly idiosyncratic as shown in Fig. 1.2. However, there are also

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[9] This quote reflects the older view that during saccades all visual information is suppressed. Indeed, only motion perception is impaired and to the contrary, the available visual information might even be crucial to maintain perceptual stability (Bremmer et al., 2009).

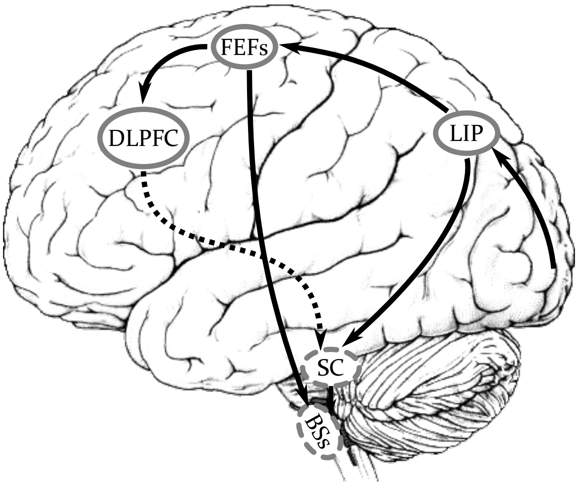

**Fig. 1.3:** Neuronal network involved in the generation of reflexive pro- and voluntary anti-saccades. Solid lines indicate excitatory, dotted lines inhibitory connections. BSs*: brainstem saccade generators*: (see Fig. 1.4 on page 19), *DLPFC*: dorsolateral prefrontal cortex, *FEFs*: frontal eye fields, *LIP*: lateral intraparietal area, *SC*: superior colliculus. Brain image modified from Image1 (2015).

considerable differences. Reflexive saccades are faster than voluntary ones (Edelman et al., 2006; Smit et al., 1987). Target properties like luminance (Becker and Fuchs, 1969) and intrinsic value for the participant (Montagnini and Chelazzi, 2005; Takikawa et al., 2002; Xu-Wilson et al., 2009) alter peak velocities, as do arousal (di Stasi et al., 2013) and reinforcement learning (Madelain et al., 2011). In Harris' and Wolpert's model, many of these effects alter either the movement cost through emphasizing speed or the fixation cost through inducing scatter. Thus, changes in the main sequence can be seen as a simple reweighing of the underlying control parameters.

### 1.4.3 Neuronal basis of saccades

The saccadic system recruits a brain-wide control network, involving areas in the occipital, parietal and frontal cortex, as well as subcortical areas in the midbrain and the brainstem (see Fig. 1.3). Especially the anti-saccade task, in which participants have to execute a voluntary saccade to the mirror position of a visual stimulus (Hallett, 1978; reviewed by Munoz and Everling, 2004), activates this network almost in its entirety.

One of the most important subcortical areas for the execution of reflexive and voluntary saccades is the SC. This tectal area consists of seven different layers (Gandhi and Katnani, 2011). The superficial layers are responsive to visual stimuli. The intermediate and deeper layers either react to multimodal stimuli or produce premotor bursts, prior to the onset of saccades. Since the superficial layers have sensory inputs and the deep layers premotor output, the SC is the most relevant site for sensorimotor transformation in the saccadic system. Microstimulation in the SC elicits saccades with highly reproducible amplitudes and directions, unveiling the retinotopic organization of the SC (Robinson, 1972). In a more general view, the SC is not only relevant for eye movements, but for arbitrary orienting responses towards particular goals (Krauzlis et al., 2004). For example, microstimulation in the SC of head-free monkeys causes combined eye-head movements (Freedman et al., 1996) and similar stimulation in echolocating bats elicits directed ear movements (Valentine et al., 2002). Finally, even the orienting of covert attention elicits activity in the SC (Ignashchenkova et al., 2004).

Although quite important, the SC is not the only part of the brain where premotor commands for saccades are generated. The lateral intraparietal area (LIP; see Fig. 1.3 on the preceding page) is connected to other oculomotor regions such as the SC and the FEFs and is only one step away from the visual cortex (Andersen et al., 1990). This suggests that LIP also plays an important role in sensorimotor transformation in the saccade network. But how can such a sensorimotor nature be revealed? In ordinary visually-guided saccade tasks, the neuronal response to the target and the saccade is intermingled. Barash et al. (1991a) used a delayed saccade task to separate these two responses. In this task, *memory-guided saccades* are executed to a previously shown target after some delay or "memory" period. This enables the needed separation of the sensory activity associated with the appearance of the target and the motor activity linked to the execution of the saccade. Single-cell recordings during this task showed that many LIP-neurons indeed were active from the beginning of the target until the end of the saccade (Barash et al., 1991a). Importantly, this activity was not just a prolonged reaction to the offset of the fixation target, since the neurons' activities were correlated with the length of the delay period (Barash et al., 1991a). These results clearly demonstrate the sensorimotor nature of LIP. Nevertheless, LIP is not just a simple relay station. LIP-neurons are also active when no target is present but an upcoming saccade is directed into their movement field[10] (Barash et al., 1991b). This implies that LIP is involved in the planning of future saccades.

In the case of the anti-saccade task, the signal from the LIP is sent to the SC, where activity starts to build up at the location of the target. Simultaneously, LIP computes the position for the anti-saccade through vector inversion (Zhang and Barash, 2000, 2004) and sends the corresponding output to the FEFs. These areas in the prefrontal cortex behave very similar to the SC: they exhibit presaccadic build-up activity (Hanes and Schall, 1996), send signals to the brainstem saccade generators (Segraves, 1992) and show activity during covert attention shifts (Schall, 2004). A causal relationship between these signals and the execution of saccades has been established by microstimulation in awake monkeys, which elicited saccades of different amplitudes and directions (Robinson and Fuchs, 1969). In addition to generating a premotor command, the FEFs, together with the DLPFC, send inhibitory signals to the SC to suppress reflexive saccades to the target (Guitton et al., 1985; Hasegawa et al., 2004; Johnston and Everling, 2006; a review is given by Pierrot-Deseilligny et al., 2005).

Many of these findings have been confirmed in lesion studies with humans (Pierrot-

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[10] A neuron's movement field is defined by the range of eye movements which affect its firing rate (Sparks et al., 1976).

Deseilligny et al., 1991): Cerebral infarctions close to the LIP impair the execution of reflexive saccades, whereas lesions in the DLPFC compromise the suppression of such saccades in the anti-saccade task. Similarly, combined lesions in the FEFs and the SC in monkeys completely prevent the execution of visually-guided saccades (Schiller et al., 1980). This emphasizes again the crucial role of these regions in the saccadic system.

The beauty of the rise-to-threshold activity in the SC and the FEFs is the resulting all-or-nothing behavior. Whichever neuronal unit first sends the command also executes the saccade. Thus, there is no “intermediate” anti- or pro-saccade. This behavior is nicely captured when a linear approach to threshold with ergodic rate (LATER) is used to model the decision-making process (Carpenter, 1981, 1988). In such a model, the rate-of-rise of neuronal activity has a Gaussian distribution – a simple assumption which captures the heavily skewed SRT-distributions observed in many saccade tasks (e.g. Hanes and Carpenter, 1999; Noorani and Carpenter, 2013). The model is also able to dissociate the effects of different task alterations on the various decision making stages like baseline activity, rate-of-rise and decision criterion. For example, high certainty about target position as well as the urgency of a decision both shorten SRTs. But where target certainty increases baseline activity (Carpenter and Williams, 1995; Carpenter, 2004), does urgency lower the decision criterion (Reddi and Carpenter, 2000; Reddi et al., 2003). Thus, the LATER model shows that the neurophysiological findings of build-up activity in the SC and the FEFs can be explained by competing decision processes. Inversely, the LATER model also predicts how changes in task instructions alter SRTs by increasing the baseline activity or lowering the decision threshold (Taylor and Hutton, 2009).

As already mentioned, only the winner of this decision process creates a premotor command for saccade generation. The proper execution of a saccade needs to accomplish two crucial tasks. First, the inertia of the oculomotor plant [11] has to be overcome by ensuring high initial acceleration and follow-up velocities. Second, the eye has to be kept at the intended final position. One of the earliest models of the oculomotor plant proposed a *pulse-step* signal to achieve these goals (Robinson, 1964). The “pulse” overcomes the inertia and accelerates the eye and the “step” keeps it at the new position. Indeed, this behavior has later been directly observed in the firing patterns of motoneurons in the oculomotor nuclei (Fuchs and Luschei, 1970).

These motor commands are caused by the saccade generators located in the brainstem (see Fig. 1.4 on the facing page). More specifically, neurons in the paramedian pontine reticular formation and the medullar nucleus prepositus hypoglossi are involved in the generation of horizontal saccades. Vertical saccades are controlled by neurons situated in the frontal part of the midbrain, namely the rostral interstitial nucleus of the medial longitudinal fasciculus and the interstitial nucleus of Cajal. A review on brainstem

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[11] This subsumes all the to-be-controlled parts of the eye. Namely, the globe, the orbital tissues and the extraocular muscles (Sparks, 2002).

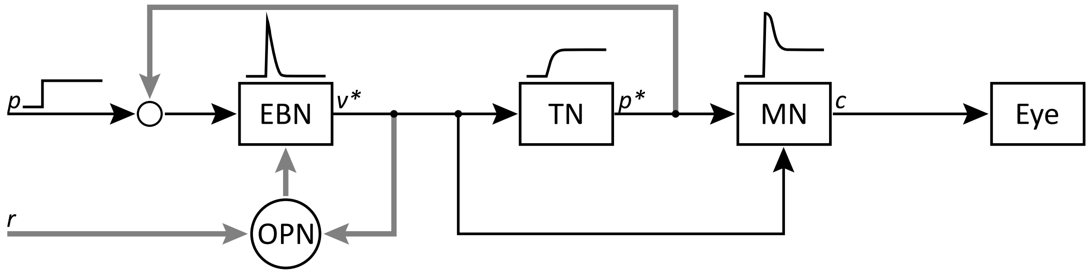

**Fig. 1.4:** The bang-bang controller for the brainstem saccade generator as proposed by Robinson (1975). A release signal $r$ shuts down the activity of omnidirectional pause neurons *OPN*, which inhibit the excitatory burst neurons *EBN*. Simultaneously, intended eye position $p$ is fed to the *EBN*, which generate a vigorous pulse of activity related to eye velocity $v*$. As long as $v*$ is not zero, the *OPN* are inhibited. On the direct pathway, $v*$ is sent to the motoneurons *MN*. On the indirect pathway, tonic neurons *TN* integrate $v*$ to obtain an estimate of the current eye position $p*$. The *MN* combine $p*$ with $v*$ to create the innervation command $c$ for the extraocular muscles. Using a negative feedback loop, $p*$ is compared to $p$ at the input level of the saccade generator. When $p$ and $p*$ are equal, the eye has reached its intended position and the *EBN* cease firing. This stops the inhibition of the *OPN* and the saccade has finished. Thin black lines indicate excitatory, thick gray ones inhibitory connections. Small insets outline the neurons' firing patterns. Modified from Sparks (2002).

saccade control is given by Sparks (2002).

Both saccade generators consist of three different kinds of neurons. During fixation, omnidirectional pause neurons (OPNs) are actively inhibiting the saccade generators. These neurons can be shut down through a disinhibitory release signal (a “trigger”), which immediately causes a vigorous increase in firing rate of the second class of neurons in the generator. So-called burst neurons show a pulse-like behavior and create the acceleration needed to overcome the inertia of the oculomotor plant. Indeed, it has been shown that the duration and intensity of the burst in these neurons is proportional to the duration and velocity of the saccade (Luschei and Fuchs, 1972). Burst neurons can be further divided into excitatory burst neurons (EBNs), which are active during ipsilateral saccades, and inhibitory burst neurons, which suppress contralateral EBNs during these saccades. Nevertheless, the saccade generator still has to solve the task of keeping the eye in the final position. This is accomplished by tonic neurons which create the constant “step”-activity through firing rates directly correlated to eye position. The activity patterns of all three neuron types have been described by Luschei and Fuchs (1972).

Early models of the brainstem generators assumed a ballistic nature of saccades and thus no possibility for online error correction. This is a valid assumption, since the latency of the visual system is longer than the duration of most saccades and can therefore not provide any feedback. However, the purely ballistic view was challenged by results from patients with spinocerebellar degeneration. Saccades in these patients are substantially slowed with velocities saturating around 80 °/s (Robinson, 1975). Using a double-step paradigm with two successively presented targets, Zee et al. (1976) showed that these patients aborted currently executed saccades mid-flight when the second target appeared. These results clearly oppose a ballistic nature, in which saccades are determined before their start and cannot be changed during execution. To solve this problem, Robinson (1975) proposed a simple, internal negative feedback mechanism (see Fig. 1.4 on the previous page) which compares the current eye position to the intended eye position. This idea elegantly circumvents the need for an external visual feedback signal. The current eye position is estimated from an efference copy of the output of the saccade generator. But why does this signal contain the current eye position? Since the firing rate of the EBNs is proportional to the current eye velocity (Luschei and Fuchs, 1972), its integral is a reasonable estimate of eye position (Fuchs and Kaneko, 1981).

A useful side effect of the internal feedback mechanism is that it explains alterations in the main sequence (see Section 1.4.2 on page 13) through fatigue or drowsiness (Robinson, 1975). Fatigue causes saccades to be slower and of longer duration (Bahill and Stark, 1975). This automatic trade-off is driven by the feedback mechanism in the saccade generator, since it only stops when the current eye position is equal to the final position. To reach the same goal, a slower saccade would therefore just have to travel longer – a fact which is not easily incorporated in a purely ballistic model.

Newer models changed the position encoding from a headcentric to an oculocentric coordinate system, which reflects the neuronal signals found in the FEFs and the SC. In addition, cortical signals can be incorporated to account for other observations like curved saccade trajectories and the prolonged SRTs of anti-saccades (Meeter et al., 2010). Still, most models are built upon the simple controller proposed by Robinson in 1975.

Girard and Berthoz (2005) provide a summary of the models for saccade generation and Sparks (2002) gives a comprehensive review on the general role of the brainstem in saccade generation. A complete overview on the neuronal circuitry of the saccadic system is established in the seminal work of Moschovakis et al. (1996). A good review on the motor function of the SC is given by Gandhi and Katnani (2011).

## 1.5 Smooth pursuit eye movements

> Every one would say without hesitation that he could move his eyes rapidly or slowly at will. This is, however, an illusion. The effort to move the eyes slowly from one point to another always results in one or more complete stops, of which, however, the subject is almost never directly conscious.
>
> *(Dodge, 1903, p.311)*

Where saccades are all about speed, SPEMs belong to the slow eye movement class; together with VOR, OKN, the ocular following response and vergence movements (for an extensive review see Ilg, 1997).

Saccades quickly project the image of an object onto the fovea. The high speed during this movement induces a considerable amount of retinal image motion. To deal with the resulting image blur, saccadic suppression attenuates intrasaccadic motion perception (Burr et al., 1994; Ross et al., 1996; Thiele et al., 2002). This in turn, prohibits the use of the saccadic system for motion tracking – the task of keeping a moving target on the fovea [12]– since a prolonged sequence of saccades would reduce motion perception into oblivion (see Carpenter's quote on page 15).

An interesting property of the pursuit system arises from this fact: SPEMs critically depend on the presence of a stimulus in motion. In general, it is not possible to shift the eyes in a smooth fashion without a moving target, which has been framed nicely by Dodge (see dictum above). This can be easily observed by putting two fingers on a closed eyelid and trying to pursue an imaginary line on a wall with the other, open eye. This will result in a palpable, jerky sequence of saccades. In contrast, if one uses one's own thumbnail of the free hand to create a moving stimulus, eye motion becomes smooth and is barely palpable any more, since now a SPEM is executed.

The motion input for the pursuit system in general is the relative motion of the target image on the retina ("retinal slip"). The pursuit system minimizes the retinal slip to stabilize the target's image using a local negative feedback loop similar to saccades (Robinson et al., 1986). Nevertheless, the motion signal does not have to be visual. Proprioceptive, tactile and, to a lesser extent, also auditory stimuli can elicit SPEMs (Berryhill et al., 2006). In a laboratory setting, pursuit can even be voluntarily controlled by self-induced local motion signals (Lorenceau, 2012). These results clearly show that besides the main input of retinal slip, the pursuit system also incorporates extra-retinal information.

On a neuronal level, pursuit relies on two cortical key areas. Retinal motion signals are mainly processed in the MT, whereas extra-retinal signals are incorporated in the mediosuperiotemporal area (MST). Unilateral MT-lesions cause specific retinotopic pursuit deficits contralaterally to the affected site (Dürsteler and Wurtz, 1988).

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[12] Although this is the main purpose of the pursuit system, extra-foveal and imaginary visual motion stimuli also elicit near-optimal pursuit performance (Ilg and Thier, 1999; Wyatt et al., 1994). Thus, it is not retinal location, e.g. a foveal target, which drives SPEMs.

Similar lesions in the MST elicit retinotopic deficits, which are extended to the whole contralateral field. In addition, such lesions evoke directionally selective impairments for stimuli moving towards the affected hemisphere ("ipsiversive" motion; Dürsteler and Wurtz, 1988). The extended retinotopic pursuit impairments after MST-lesions indicate sequential signaling in the pursuit system: Motion information is handed over from the MT to the MST but cannot be processed any further. Moreover, the loss of ipsiversive motion selectivity reveals extra-retinal signal processing in the MST. If no extra-retinal signals were present, the impairments should be constrained to a visual field and not a specific direction. These ipsiversive deficits have been explained by the grouping of the cortical projections. Ipsiversively selective cells directly signal to the nucleus of the optic tract (NOT) in the pretectum (Ilg and Hoffmann, 1993). This is somehow surprising, since in primates the ipsilateral visual field is mainly processed in the contralateral hemisphere. Hoffmann et al. (1992) showed that the necessary ipsilateral information is cortically exchanged via callosal connections. Therefore, a unilateral MST-lesion removes specifically the ipsiversive output to the NOT, which in turn causes the direction selective pursuit deficit for ipsiversive motion.

More support for the presence of extra-retinal signals in the MST comes from a study with moving imaginary targets (Ilg and Thier, 2003). Such targets do not induce retinal motion in a neuron's receptive field. Consequently, MT-neurons do not respond to these targets. A subset of neurons in the MST ("visual tracking neurons") on the other hand, are activated by such stimuli, ruling out retinal signals in these cells (Ilg and Thier, 2003). Similarly, during anticipatory pursuit, eye velocity is higher before the reappearance of a target (Freyberg and Ilg, 2008) and in parallel, the visual tracking neurons exhibit shorter latencies to the target's return (Ilg, 2003). Since, by definition, anticipatory pursuit is not related to the presence of a visual target, the shortening of the MST-response cannot be caused by retinal signals. In summary, these findings show that the activity in the MST is related to general and not retinal motion. A review on the role of the MT and the MST in the generation of SPEMs and in motion processing is given by Ilg (2008).

Besides the aforementioned parietal areas, the frontal lobes, too, are part of the pursuit system. Similar to the FEFs for saccades, the pursuit-related frontal eye fields exert top-down control on SPEMs for trajectory anticipation and prediction (Fukushima et al., 2002).

Since the close connection of pursuit to the presence of motion, SPEMs are an ideal behavioral probe for motion processing (Ilg, 1997) as well as anticipatory and predictive mechanisms in the brain. This close connection works in both ways. Not only does pursuit rely on motion perception, but also motion perception is improved during pursuit. When participants have to predict the location-of-impact of a moving target on a stationary goal, performance is significantly better during pursuit of the target compared to stationary fixation (Spering et al., 2011). Most likely, the motion estimate of the target is refined by the internal motion signal generated from the SPEM, whereas during fixation, this estimate is based on retinal signals alone. Participants also incorporate this melioration automatically into their own behavior. During trajectory interception, participants execute SPEMs without being instructed to do so (Mrotek and Soechting, 2007).

# 2 Summary of our studies

The work presented in this thesis analyzes the effects of video gaming (Mack and Ilg, 2014; Mack et al., 2015c) and age (Mack et al., 2015a,b) on oculomotor behavior and attention. In the first part, video game effects were quantified and a possible alteration in attention was examined (see Section 2.1). In the second part, the influence of age on saccades and SPEMs was tested in a very large sample of elderly people (see Section 2.2 on page 31).

## 2.1 Video game studies

Many video games require fast responses to suddenly appearing events and indeed, VGPs exhibit generally shorter RTs (Dye et al., 2009). This can be achieved through a speed-accuracy trade-off, where a lower response threshold, e.g. reduced inhibitory control, leads to shorter reflexive RTs at the cost of a higher rate of incorrect responses. On the other hand, improvements in visual attention, for example the faster allocation and orientation of the covert spotlight of attention (Posner, 1980), may provide an RT benefit without such a drawback and may also improve reflexive, as well as voluntary, responses.

### 2.1.1 Video games and saccades

Using the anti-saccade task (Hallett, 1978), which probes inhibitory control and simultaneously provides reflexive as well as voluntary SRTs, we were able to show that the superior performance of VGPs is not due to a speed-accuracy trade-off (Mack and Ilg, 2014). The tested VGPs did not make more reflexive saccades, but instead tended to even show lower error rates, clearly ruling out reduced inhibitory control as an explanation. This result is in line with a neuropsychological study showing improved executive functioning, without increased risk behavior in VGPs (Buelow et al., 2015), pointing to an improvement in cognitive control. In addition, the reflexive as well as voluntary SRTs of VGPs were shortened in our study (Mack and Ilg, 2014), resembling the previous results for manual RTs (Dye et al., 2009). Since the pathways for the execution of reflexive and voluntary saccades separate in the parietal cortex (LIP, Fig. 1.3 on page 16) and only join on the level of the brainstem after the SC, these results point towards an early attentional enhancement or a late motor improvement.

Due to the cross-sectional nature of our study, a causal relationship between video game playing and faster SRTs cannot easily be inferred. Therefore, we conducted a training study with ten NVGPs who had never consumed video games before (Neuhaus, 2011). The training group played *Super Mario Galaxy* for two hours a day over the course of seven consecutive days, whereas the control group received no intervention at all. Anti-saccade task performance of the training group was examined before ("pre-test") and after the training period ("post-test"). The control group was similarly tested over the course of one week but without the intervention. Both groups exhibited shorter SRTs and lower error rates in the post-test compared to the pre-test. Although pre-post-test gains in SRTs were positively correlated with game success in the training group, the general pre-post-test improvements did not differ between groups. These results seem to indicate that the SRT differences between NVGPs and VGPs result from preexisting group dissimilarities and self-selection, with faster individuals tending to play more video games. The small number of participants however, limits the explanatory power of this study. In addition, *Super Mario Galaxy* does not rely on very fast RTs and thus the training period might have been too short to reveal any training effects. Future research is needed to shed more light into this issue.

### 2.1.2 Video games and attention

Previous studies had used manual RTs which are closely related to the motor behavior required in many video games, e.g. "button pressing". Our results revealed that also reflexive and voluntary saccades are improved in VGPs, indicating an attentional enhancement in this group (Mack and Ilg, 2014). Nevertheless, SRTs involve a motor component as well, which makes it hard to disentangle attentional from motor effects. As pointed out by Castel et al. (2005), faster RTs may simply be caused by a more efficient stimulus-response mapping – the ability to connect a given input stimulus to a specific motor output behavior. Although this explanation implies a separate improvement for each new task and several studies found superior performance of VGPs in purely perceptual tasks like multiple-object tracking (Green and Bavelier, 2006b), subitizing (Green and Bavelier, 2003, 2006b), direction and orientation discrimination (Bejjanki et al., 2014; Green et al., 2010a), faster stimulus-response mappings cannot be ultimately ruled out in studies involving motor behavior.

An additional unresolved issue is the similar improvement in reflexive as well as voluntary saccades, found in our eye movement study (Mack and Ilg, 2014). This would either need a very late motor adaptation, since the pathways of these saccade types join only at the level of the brainstem, or an early sensory improvement at the level of LIP or earlier (see Section 1.4.3 on page 16). The latter can be caused by enhanced attentional control. More specifically, VGPs may have faster covert attention shifts, which underlie their superior performance. This would explain many of the improvements found in VGPs, including a similar benefit for reflexive and voluntary saccades, since presaccadic target selection relies on attention (Deubel and Schneider, 1996). Additionally, this explanation would easily apply to any task involving some form of visuospatial attention.

Employing the *Nakayama task* (Nakayama and MacKeben, 1989), which is a perceptual task probing exactly this aspect of attentional control, we found better performance in VGPs, but interestingly no evidence for faster shifting speeds (Mack et al., 2015c). The superior performance of VGPs is in line with the studies showing improved performance in perceptual tasks mentioned above. In addition, it lends further support against a better stimulus-response mapping and towards an attentional enhancement in VGPs. The complete lack of a difference in shifting speed between VGPs and NVGPs however, speaks against faster covert attention shifts as an explanation.

Two main alternatives are possible. First, VGPs may have a higher rate of information acquisition. This hypothesis explains both, gains in time-limited perceptual tasks, as well as improvements in information-limited reaction time tasks. In perceptual tasks, stimuli are typically shown only very briefly and thus the time to gather information is constrained. A higher acquisition rate leads to more information gathered during the stimulus presentation. This in turn, causes a more informed decision and better performance. In reaction time tasks, individuals are normally asked to react as fast as possible. Thus, an “information limit” can be assumed at which the participant is convinced that his decision will be correct and a response is initiated. A higher rate of information acquisition would enable individuals to reach this limit faster, leading to shorter response times. Both outcomes have been observed in VGPs (e.g. Bejjanki et al., 2014; Dye et al., 2009).

The second explanation is more specifically related to the Nakayama task. VGPs may not possess faster covert shifts of attention, but their spotlight of attention might be larger, e.g. their “perceptual span” might be increased. This would reduce the total number of attention shifts needed, since information can be gathered from a larger area without moving the spotlight again. Such an alteration would result in similar improvements to the first explanation, but the they would be dependent on the closeness of the stimuli.

In a follow-up study to Mack et al. (2015c), we developed a dual-task (similar to Palomares et al., 2011; Vetter et al., 2008) to test the size of the attentional spotlight. This paradigm involved a central discrimination task to assure that attention is not shifted around and a peripheral enumeration task to measure the size of the perceptual span. In the enumeration task, participants had to judge the number of circles presented at different eccentricities. The size of the perceptual span can be inferred in a drop in performance at a specific eccentricity. Small eccentricities elicit nearly perfect performance, whereas very large eccentricities result in the participants guessing the number of circles. Therefore, we expected NVGPs and VGPs to perform equally at these two extremes. On the contrary, VGPs should be able to show higher performance at higher eccentricities in-between the two extreme eccentricities if their perceptual span is indeed larger. We tested 19 VGPs and 27 age-matched NVGPs in this paradigm. The VGPs showed generally higher performance at all eccentricities, indicating no differences in perceptual span, but again pointing to a higher rate of information acquisition (Henz et al., 2015).

### 2.1.3 Summary of the video game studies

In summary, the studies on video games comprised in this thesis show that the faster reaction times found in VGPs (Dye et al., 2009) are also found in the oculomotor domain and are not caused by reduced inhibitory control or a speed-accuracy trade-off. In addition, the superior performance of VGPs is not a mere consequence of a faster stimulus-response mapping, but is also not caused by faster covert attention shifts or increased perceptual span. Probably, VGPs possess a top-down attentional enhancement in information acquisition.

## 2.2 Aging studies

Age-related cognitive decline will become an ever more pressing topic in our aging society (see Section 1.2 on page 7) and thus methods to tackle these impairments are needed. Video games may be one promising way to go (Basak et al., 2008; Belchior et al., 2013; Goldstein et al., 1997). To assess the success of potential video game training regimens, one has to first know what age-related changes occur and if these can be altered by video game playing at all.

For the comparison of the effects found in our saccade study (Mack and Ilg, 2014) with age-related changes in the saccadic system, we measured the performance of a large sample of elderly participants recruited from the Tübinger evaluation of risk factors for early detection of neurodegeneration (TREND) (Berg, 2012; Berg and Eschweiler, 2015) in the anti-saccade task. In young and old participants comparable differences arose to those found between VGPs and NVGPs (Mack et al., 2015a). Such changes in anti-saccade performance have been shown to indicate the ability to drive in the elderly (Schmitt et al., 2015), emphasizing the importance of our result for activities in daily life.

In addition to saccadic eye movements, we also probed perceptual learning and motion processing in the elderly with a simple pursuit task (Mack et al., 2015b). Improvements in motion processing have been causally linked to video game playing (Green and Bavelier, 2006b; Green et al., 2010b) and this ability is an important aspect in everyday activities such as driving a car. Perceptual learning is important to adapt quickly to new tasks. Our results show an age-related decline in pursuit performance and behavioral variance, but no difference in perceptual learning.

Due to their large scale nature, these two studies might serve as a basis for further evaluation of video game training regimens to overcome the impairments imposed by cognitive aging.

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# 4 Manuscripts included in this thesis

## 4.1 Study 1: The effects of video game play on the characteristics of saccadic eye movements

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| **Authors** | David J. Mack and Uwe J. Ilg |
| **Journal** | *Vision Research* |
| **Reference** | Mack and Ilg, 2014 |

### Abstract

Video game play has become a common leisure activity all around the world. To reveal possible effects of playing video games, we measured saccades elicited by video game players (VGPs) and non-players (NVGPs) in two oculomotor tasks. First, our subjects performed a double-step task. Second, we asked our subjects to move their gaze opposite to the appearance of a visual target, i.e. to perform anti-saccades. As expected on the basis of previous studies, VGPs had significantly shorter saccadic reaction times (SRTs) than NVGPs for all saccade types. However, the error rates in the anti-saccade task did not reveal any significant differences. In fact, the error rates of VGPs were actually slightly lower compared to NVGPs (34% versus 40%, respectively). In addition, VGPs showed significantly higher saccadic peak velocities in every saccade type compared to NVGP. Our results suggest that faster SRTs in VGPs were associated with a more efficient motor drive for saccades. Taken together, our results are in excellent agreement with earlier reports of beneficial video game effects through the general reduction in SRTs. Our data clearly provides additional experimental evidence for an higher efficiency of the VGPs on the one hand and refutes the notion of a reduced impulse control in VGPs on the other.

### Statement of contributions

This study consists of a full reanalysis of the data from my diploma thesis (Mack, 2010). The new analysis was conducted by myself and the manuscript was created together with Uwe J. Ilg.

Vision Research 102 (2014) 26–32

Contents lists available at ScienceDirect

Vision Research

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

# The effects of video game play on the characteristics of saccadic eye movements

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ARTICLE INFO

*Article history:*
Received 14 April 2014
Received in revised form 2 July 2014
Available online 1 August 2014

*Keywords:*
Video game play
Saccade
Attention
Latency
Main sequence
Anti-saccades

ABSTRACT

Video game play has become a common leisure activity all around the world. To reveal possible effects of playing video games, we measured saccades elicited by video game players (VGPs) and non-players (NVGPs) in two oculomotor tasks. First, our subjects performed a double-step task. Second, we asked our subjects to move their gaze opposite to the appearance of a visual target, i.e. to perform anti-saccades. As expected on the basis of previous studies, VGPs had significantly shorter saccadic reaction times (SRTs) than NVGPs for all saccade types. However, the error rates in the anti-saccade task did not reveal any significant differences. In fact, the error rates of VGPs were actually slightly lower compared to NVGPs (34% versus 40%, respectively). In addition, VGPs showed significantly higher saccadic peak velocities in every saccade type compared to NVGP. Our results suggest that faster SRTs in VGPs were associated with a more efficient motor drive for saccades. Taken together, our results are in excellent agreement with earlier reports of beneficial video game effects through the general reduction in SRTs. Our data clearly provides additional experimental evidence for an higher efficiency of the VGPs on the one hand and refutes the notion of a reduced impulse control in VGPs on the other.

## 1. Introduction

Nowadays, playing video games is a widespread leisure activity. A recent survey (Rideout, Foehr, & Roberts, 2010) indicates that 60% of young people between the ages of 8 and 18 years in the U.S. play video games at least 1 h per day. Despite this general dissemination, the consequences of video game play are still heavily debated. On the one hand, negative effects like decreased prosocial and increased aggressive behavior were reported (Anderson et al., 2010). However, if parental involvement was assured, pro-social behavior and civic engagement of subjects increased – which was explained by the team-oriented multiplayer options in action video games (Ferguson, 2011).

On the other hand, playing video games is associated with multiple enhancing effects: amongst others, a better control of the negative effects of bottom-up attentional capture (Chisholm et al., 2010), improved working memory (Colzato et al., 2012), a superior contrast sensitivity function (Li et al., 2009), better signal detection (West et al., 2008), more precise multisensory temporal processing (Donohue, Woldorff, & Mitroff, 2010), enhanced change detection (Clark, Fleck, & Mitroff, 2011) and even better laparoscopic surgical skills (Rosser et al., 2007). Even an increase of grey brain matter after 2 months of video game playing (30 min per day) was recently reported (Kuhn et al., 2013).

Besides documenting a correlation between beneficial effects on performance and video game play, some studies have also established a causal relationship by comparing the performance of subjects before and after training periods (Green & Bavelier, 2003; Li et al., 2009). However, extensive video game practice did not always improve the performance of subjects, for example in an enumeration task (Boot et al., 2008). In summary, video game players (VGPs) react faster than non-video game players (NVGPs) in a variety of tasks (Dye, Green, & Bavelier, 2009).

Despite this large body of evidence, reasons for the short reaction times of VGPs are still unknown. This reduction is most likely of attentional nature, since VGPs are faster in tasks ranging from spatial cueing over n-Back to visual search. Indeed, a recent study showed an altered attentional network in VGPs compared to NVGPs (Bavelier et al., 2012), especially an increased activation of the fronto-parietal network.

Interestingly, most of the above mentioned studies used rather indirect measures of the attentional mechanisms based on costs or benefits in perceptual tasks. It has been shown that subjects express perceptual benefits at the location of the target of subsequently executed saccadic eye movements (Deubel & Schneider,

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http://dx.doi.org/10.1016/j.visres.2014.07.010
0042-6989/

1996; Hoffman & Subramaniam, 1995; Kowler et al., 1995). These findings suggest that even without explicitly measuring perceptual thresholds there might exit a possibility to monitor the shifts of attention directly by simply measuring the saccadic eye movements. The above mentioned studies allow the conclusion that these fast jerky eye movements are always preceded by a shift of the spotlight of attention towards the future landing point of the eyes (Posner, 1980). In addition to the possibility of observing the shift of attention directly, it is feasible to monitor the competing attentional control systems in a special saccade paradigm: the anti-saccade task (Hallett, 1978). In this task, subjects are asked to perform a saccade in the opposite direction to the presentation of a visual target (the "*anti-saccade*"). However, since the appearance of the visual target itself attracts attention (Posner, 1980), subjects sometimes fail to suppress the reflexive saccade towards the target (the "*pro-saccade*").

The execution of saccades is controlled by circuits involving the superior colliculus, the parietal eye field, the frontal eye field and, ultimately, the two saccade generators in the brain stem responsible for horizontal and vertical saccades, respectively. These generators cause a fixed linear relationship between the saccade amplitude and its duration and peak velocity – known as the main sequence (Bahill, Clark, & Stark, 1975; Sparks, 2002). Data from animal experiments suggest that the correct execution of anti-saccades depends critically on the frontal cortex: single-unit activity in the supplementary and frontal eye fields of rhesus monkeys is increased during anti-saccades compared to pro-saccades (Munoz & Everling, 2004). Analogously, patients with frontal lobe lesions show an increased frequency of pro-saccades (Guitton, Buchtel, & Douglas, 1985). Therefore, the frequency of pro-saccades ("*error rate*") can be used as a measure for the efficiency of the impulse control mediated by the frontal cortex. In normal subjects, saccadic reaction times (SRTs) are negatively correlated with the error rate: subjects with shorter SRTs show higher error rates (Evdokimidis et al., 2002). The contrary is shown in a study about the effects of ethanol: ethanol caused longer SRTs hand in hand with decreased error rates (Khan et al., 2003).

For these reasons, we addressed the effects of video game play upon eye movements as a handle to the orienting of attention with two different saccade paradigms. The double-step task (Becker & Jurgens, 1979; Lisberger et al., 1975) was used to enforce reflexive saccades with very short reaction times. The anti-saccade task (Hallett, 1978) allowed us to measure the ability to withhold the fast reflexive pro-saccades towards a visual target. We hypothesized that VGPs display shorter SRTs compared to NVGPs in general. This reduction may be caused by an impaired impulse control or alternatively by an increased efficiency of the visuo-motor system of VGPs. Independent of the exact nature of the second possibility, if the first explanation were true, the error rates of VGPs should be increased compared to NVGPs. Identical error rates in VGPs and NVGPs on the other hand would definitively exclude the explanation of impaired impulse control in VGPs. Finally, we asked whether the dynamic properties of the gaze shifts, determined by brainstem circuits, display any differences between VGPs and NVGPs.

## 2. Material and methods

### 2.1. Participants

All subjects were classified according to their daily video gaming time. The time was self-reported in a questionnaire before the measurement. Subjects who reported less than 1 h per day were classified as non-video game players (NVGPs), whereas subjects with equal or more than 1 h per day were classified as video game players (VGPs). The subjects were not told to which group they belong before the experiment. This was done to avoid differential motivation effects which could have led to better performance in VGPs, simply because they think that they will perform better due to their expertise.

We measured a total of 67 subjects of whom 46 participated in both tasks. Some subjects completed only one of the two tasks. Therefore, the sample sizes are slightly different. In the anti-saccade task, a total of 56 subjects (26 NGVPs, 30 VGPs) were tested. The mean age of NVGPs was 18.6 ± 0.6 years (mean ± SE) and that of VGPs 19.5 ± 0.6 years. In the double-step task, 57 subjects were measured (27 NVGPs, 30 VPGs). The NVGPs in this task were aged 18.6 ± 0.6 years and the VGPs 19.8 ± 0.7 years. There were no significant group differences regarding age in neither task (1-factorial ANOVA: $p = 0.318$ in the anti-saccade and $p = 0.191$ in the double-step task). All experiments were performed in accordance with the Declaration of Helsinki.

The analysis of the reported daily gaming times showed that there were similar amounts of video game consumption in each task. VGPs in the anti-saccade task played on average 1.3 ± 0.1 h per day (mean ± SE) whereas VGPs in the double-step task played and 1.4 ± 0.1 h per day. All subjects had normal or corrected to normal vision.

### 2.2. Experimental setup

The experiments were performed on a PC (AMD Athlon 64 X2 4800+, 1 GiB DDR2 RAM, ATI Radeon Xpress 1150) with two 19 in. screens (HP L1950, refresh rate: 60 Hz, resolution: 1280 × 1024 pixels). The main control screen was connected via the DVI-Port and the stimulus screen via the VGA-Port of the graphics adapter. Data analysis and stimulus presentation was done with Matlab 2008a (The Mathworks, Natick, MA) and the Psychophysics Toolbox Version 3 (Brainard, 1997; Pelli, 1997).

Horizontal eye position was recorded with an infrared limbus tracker in front of the subject's left eye. The eye position was sampled at 1 kHz with a spatial resolution of approximately 6 arcmin (Ilg et al., 2006). Viewing distance in all experiments was kept at 57 cm and the stimuli were presented in white (luminance 60 cd/m$^2$) on a black background.

### 2.3. Saccade tasks

The duration of the entire experimental session was at most 1 h and consisted of the anti-saccade task and/or the double-step task. In both tasks, a trial began with a random fixation time between 500 and 1000 ms. A white cross with 18 arcmin edge length was presented as the fixation target at the center of the screen. Saccade targets were filled white squares with an edge length of 7 arcmin.

#### 2.3.1. The double-step task

In the double-step task, two consecutive targets were presented with an inter-stimulus interval (ISI) of 50, 100, 250 or 500 ms. Targets could appear at 5 and 10 deg to the left and right of the fixation spot. The second target always appeared at a different position as the first target, resulting in twelve target position combinations. The subjects were asked to perform saccades towards these targets as fast as possible. A measurement consisted of two blocks of 144 trials (three repetitions for each of the four ISIs and the twelve target position combinations). For the evaluation, the datasets from the two blocks were merged. The duration of each trial was fixed to 2000 ms. Saccades towards the first target ("*saccade 1*") were defined as being closer to this target than to the second target. Otherwise they were considered saccades towards the second target ("*saccade 2*"). Corrective saccades towards either target were also detected but not include in this analysis. Entire trials were excluded from analysis if no saccade 2 was found, either saccade

1 or 2 was anticipatory (e. g. had a reaction time of less than 90 ms) or its amplitude gain was outside the range of 0.4–1.6. In addition, trials were excluded if eye position changed more than 2.5 deg in a 250 ms interval prior to saccade onset.

### *2.3.2. The anti-saccade task*

In the anti-saccade task, subjects were asked to perform a saccade towards the mirror position of a presented target. A measurement consisted of 240 trials (40 repetitions for each of the six target positions at 5, 10 and 15 deg to the left and right of the fixation spot). The trial duration was fixed to 1500 ms. The first saccade in each trial after target presentation was considered as anti-saccade if its end point was opposite to the target eccentricity otherwise it was considered as pro-saccade. Trials were discarded if eye position changed more than 2.5 deg in a 250 ms interval prior to saccade onset, if this saccade occurred before 90 ms after target presentation (anticipatory response) or if the absolute amplitude gain was outside the range of 0.4–1.6. The error rate was calculated as the number of pro-saccades divided by the number of valid saccades.

## *2.4. Data processing*

Eye velocity was computed by differentiation of the eye position; acceleration was computed by differentiation of eye velocity. Saccades were detected based on an acceleration threshold (3.500 deg/s$^2$) on a trial-by-trial basis. In a first step, all acceleration peaks were selected from smoothed acceleration data (running average across 31 ms) and peaks with opposing signs were paired. Then, pairings were rated according to their temporal distance and similarity – with close and similar peaks being preferred. In the last step, each two pairings with a time distance smaller than 20 ms were considered to be blinks and removed. The remaining pairings were the detected saccades. For these, saccadic reaction time, amplitude, duration and peak velocity were determined. To prevent artificial prolongation of the duration through smoothing, the start and end time of the saccades were computed from the only very slightly smoothed velocity data (running average across 5 ms). In order to determine the SRT of a given subject in a given condition, we calculated the median values across the SRTs of all valid trials.

We used saccade duration, peak velocity and amplitude to calculate the main sequence for each subject independently. The linear regression equation describing the peak velocity as a function of saccade amplitude was determined through robust linear regression with iteratively reweighted least-square (Holland & Welsch, 1977) to diminish any outlier influence of single saccades on the individual equations. To compare saccadic peak velocities in VGPs and NVGPs, we evaluated the peak velocity of a 10 deg saccade from this individual linear regression equation.

## 3. Results

### *3.1. The double-step task*

The double-step task forced our subjects to perform reflexive saccades as fast as possible. Fig. 1 shows single-trial eye position traces of a typical subject (Subject 64, 18 years old, male, played between 1 and 2 h per day VGP) together with the resulting median traces for all four ISI values.

The probability to actually execute two saccades clearly increased from short to long ISI values. The SRT for saccades towards the first target are rather independent of the ISI whereas the reaction times of the saccades directed towards the second target are clearly prolonged for the 50 ms and 100 ms ISI condition. We analyzed the SRTs of all subjects with respect to ISI and video game play and performed appropriate statistical testing. We pooled our data obtained from different target positions. For saccades directed towards the first target (see Fig. 2A), a 2-factorial ANOVA showed significant effects of ISI ($p = 0.002$) and video game play ($p = 0.011$), while the interaction of both factors was not significant ($p = 0.859$). Therefore, VGPs had shorter SRTs independent of the specific ISI and short ISIs evoked short SRTs in both groups equally.

For saccades directed towards the second target (see Fig. 2B), a different pattern emerged. The 2-factorial ANOVA revealed significant differences only for ISI ($p < 0.001$). Video game play had no significant effect on the SRTs ($p = 0.115$). But the interaction of both factors was significant ($p = 0.006$). SRTs for the short ISIs were clearly longer than for the long ISIs. Shortest SRTs (which were comparable to the SRTs from the first target) in both groups were only found in the 500 ms ISI condition. Interestingly, VGPs had shorter SRTs for long ISIs and longer SRTs for the shortest ISI than NVGPs.

In case of the short ISIs, subjects often omitted the saccade towards the first target. Instead, they only performed a single saccade targeted towards the second target. Fig. 2C shows the

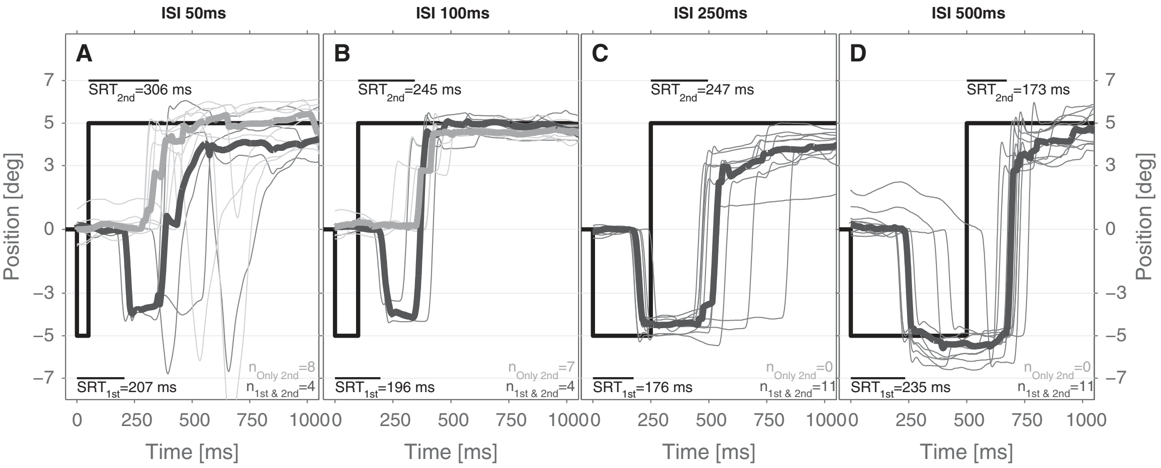

**Fig. 1.** Single trial eye position traces of subject 64 in the double-step paradigm. Exclusively trials were the first target appeared at 5 deg left followed by the second target at 5 deg right or vice versa are shown for all four ISI conditions (A–D). Trials were the subject performed saccades towards both targets are shaded dark gray whereas trials with only saccades towards the second target are shaded light gray. Bold lines represent medians; SRTs are given as median across all trials for each condition. Subject 64 was 18 years old, male, and played between 1 and 2 h per day (VGP).

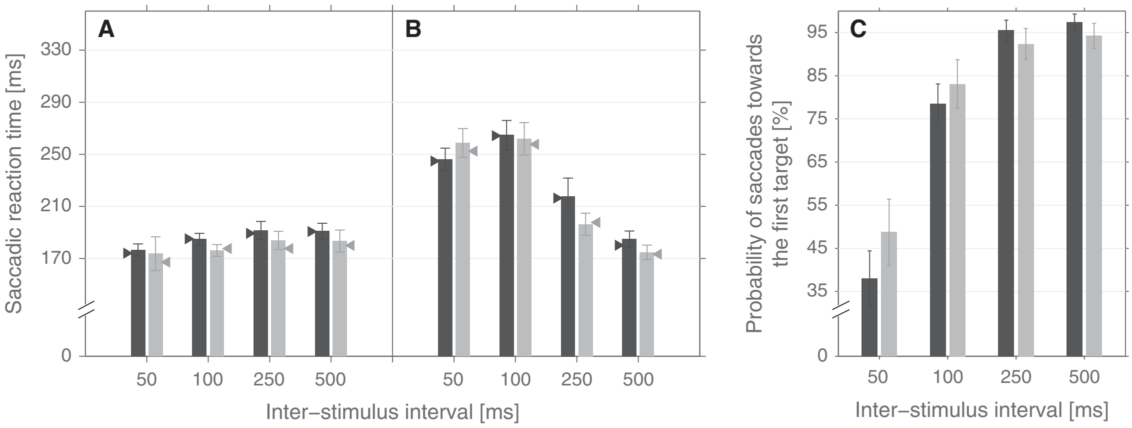

**Fig. 2.** Comparison of saccadic parameters obtained from VGP and NVGPs, respectively, in the double-step paradigm. In (A), the saccadic reaction times for all four ISI conditions towards the first target are shown (all possible target positions were pooled). In (B), saccadic reaction times toward the second target are shown. In (C), the probability of saccades directed towards the first target is shown. Bars show mean values across subjects; error bars represent 95% confidence intervals; triangles in (A and B) indicate median values across subjects.

probability that a saccade towards the first target was executed. At the 50 ms ISI condition, the probability dropped down substantially, even more pronounced in the case of NVGPs. For the long ISIs, no difference in saccade probability was present. The 2-factorial ANOVA revealed a significant effect of ISI on saccade probability ($p < 0.001$); the influence of video game play was not significant ($p = 0.178$). However, the interaction of both factors was significant ($p = 0.008$). This suggests that a video game play effect was only present for the short ISIs, for which the VGPs were more able to catch the first target despite its brief presentation. A ceiling effect for longer ISIs may have prevented any differences between VGPs and NVGPS becoming visible.

### 3.2. The anti-saccade task

Fig. 3 gives single-trial eye position traces of our typical subject 64 (VGP) obtained from the anti-saccade experiment. The target was presented 5 deg to the right, and the subject was asked to execute a saccade towards the left. These anti-saccades are shown in black; the erroneous pro-saccades are shown in grey.

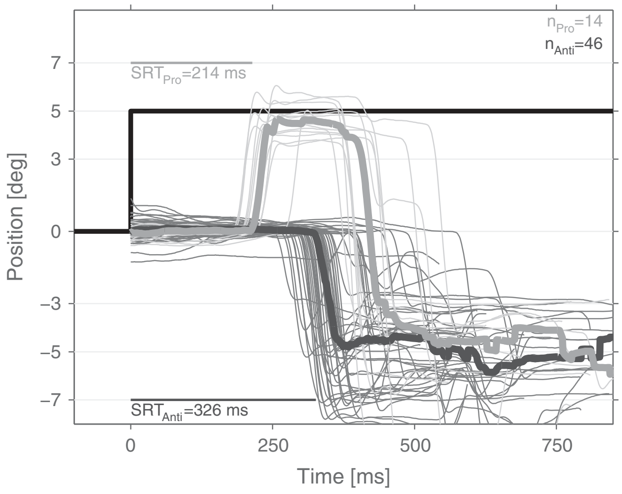

**Fig. 3.** Single trial eye position traces of subject 64 in the anti-saccade paradigm. Only trials are shown in which the target appeared 5 deg (left and right pooled). Trials where the subject performed an anti-saccade are shown in dark gray; pro-saccades are shown in light gray. Bold lines represent medians; SRTs are given as median across all given trials.

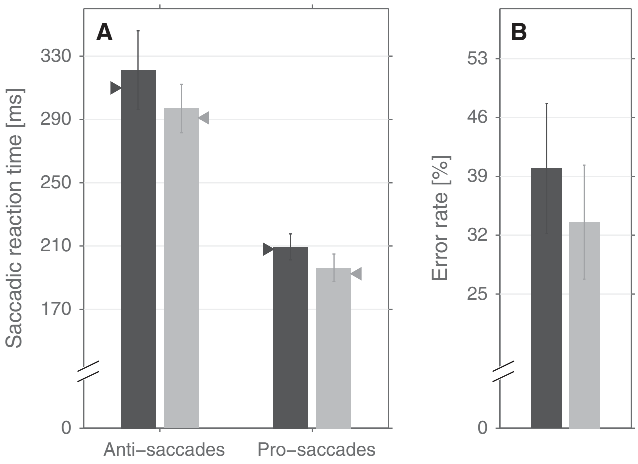

**Fig. 4.** Comparison of saccadic parameters obtained from VGPs and NVGPs, respectively, in the anti-saccade paradigm. In (A), saccadic reaction times for anti- and pro-saccades are shown. (B) Gives the error rate expressed as the frequency of pro-saccades. Bars show mean values across subjects; error bars represent 95% confidence intervals; triangles in (A) indicate median values across subjects.

The SRT of pro-saccades (214 ms) are clearly shorter compared to anti-saccades (326 ms). The error rate of this subject was 14/(46 + 14) = 23% in this example.

The SRTs of all subjects in the anti-saccade task were in agreement with the literature (Hallett, 1978; Munoz & Everling, 2004): Reflexive pro-saccades had shorter SRTs than anti-saccades in both groups (see Fig. 4A). More interestingly, VGPs showed shorter reaction times for both saccade types compared to NVGPs. The 2-factorial ANOVA revealed a significant effect of saccade type ($p < 0.001$) and video game play ($p < 0.014$), whereas the interaction of both factors was not significant ($p = 0.466$).

Shorter SRTs were in line with our first hypothesis. To decide whether this effect is due to impaired impulse control, we determined the error rates of both groups shown in Fig. 4B. A linear regression analysis across all subjects revealed a negative slope ($\text{error}_{(\text{SRT pro-saccade})} = -0.2 * \text{SRT} + 70.0$; $R^2 = 0.044$), so there is a non-significant tendency that subjects with long SRT express rather low error rates. However, in support of the latter explanation, a 1-factorial ANOVA showed no significant differences in error rates between NVGPs and VGPS. ($p = 0.207$). In fact, there was even a tendency that VGPs (34%) produced slightly less errors than NVGPs (40%).

### 3.3. SRT comparison

In order to compare SRTs obtained from all experiments in our study, we plotted SRT of VGPs versus SRT of NVGPs, usually known as a Brinley plot (not shown). The resulting linear ordinary least squares regression ($R^2 = 0.946$) had a slope of 0.95 and was significantly different from unity ($p = 0.003$). Therefore, SRTs of VGPs are shorter than that of NVGPs in general. This result is in perfect alignment with earlier reported data (Dye, Green, & Bavelier, 2009; Hubert-Wallander et al., 2011).

### 3.4. Dynamic properties of the saccades

So far, we analyzed the latencies of the elicited saccades. However, since we measured the eye movements with high spatial and temporal resolution, we were also able to analyze the dynamic saccade properties, especially the maximal eye velocity during each saccade (peak velocity). The dependence of the peak velocity on saccade amplitude (main sequence) for typical subject 64 (VGP) is shown in Fig. 5.

Pro-saccades were characterized by higher peak velocities compared to anti-saccades. The peak velocity of saccades directed to the first or second target, respectively, was not different.

To be able to compare the peak velocities of different types of saccades executed by VGPs and NVGPs, we determined the peak velocity of saccades with amplitude of 10 deg for each subject independently (see Section 2.4). The linear robust regression yielded $R^2$ values between 0.51 and 0.83. The mean values across all subjects are shown in Fig. 6.

The peak velocity of anti-saccades was clearly lower compared to that of pro-saccades and saccades elicited in the double-step task. Moreover, VGPs had higher peak velocities than NVGPs. The 2-factorial ANOVA showed a significant effect of saccade type ($p < 0.001$) and video game play ($p < 0.001$). The interaction of both factors was non-significant ($p = 0.754$). This suggests that faster SRTs in VGPs were also associated with a more efficient motor drive for saccades.

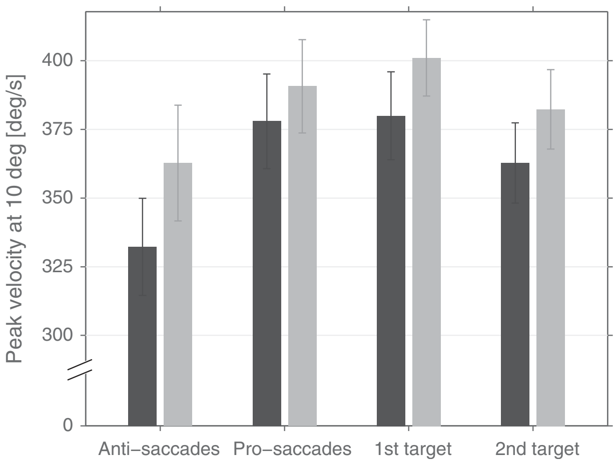

**Fig. 6.** Comparison of peak velocities of 10 deg saccades performed by VGPs and NVGPs. Bars show mean values across subjects; error bars represent 95% confidence intervals.

Finally, we analyzed the correlation of peak velocity and saccadic reaction times for all our subjects. It is important to note that we included all saccade types, pro- and anti-saccades as well as saccades towards the first and second target, in this analysis. As Fig. 7 shows, the peak velocity is inversely related to the SRT. However, the correlation obtained from VGPs is clearly different from the correlation obtained from NVGPs. This is another support for the notion of higher efficiency of the visuo-motor system of VGPs.

## 4. Discussion

Using two different saccade tasks, we found several differences between NVGPs and VGPs. VGPs showed shorter saccadic reaction times for voluntary as well as reflexive saccades. The error rate of VGPs and NVGPs was not different in the anti-saccade task. Surprisingly, the saccades of VGPs had higher peak velocities than those of NVGPs.

### 4.1. VGPs react faster

In line with our first hypothesis, we found reduced SRTs in VGPs. This reduction was not restricted to reflexive or cognitively driven saccades and was present in data obtained from both saccade tasks. Hence, this speed-up seems not to be related to the generation of a specific saccade type. Instead, it appears to occur earlier in processing. One possibility is that it happens in the selection of a possible saccade target, a mechanism relying on attentional control. Consequently, the shorter reaction times of VGPs may be attributed to faster attentional processing since the spot-

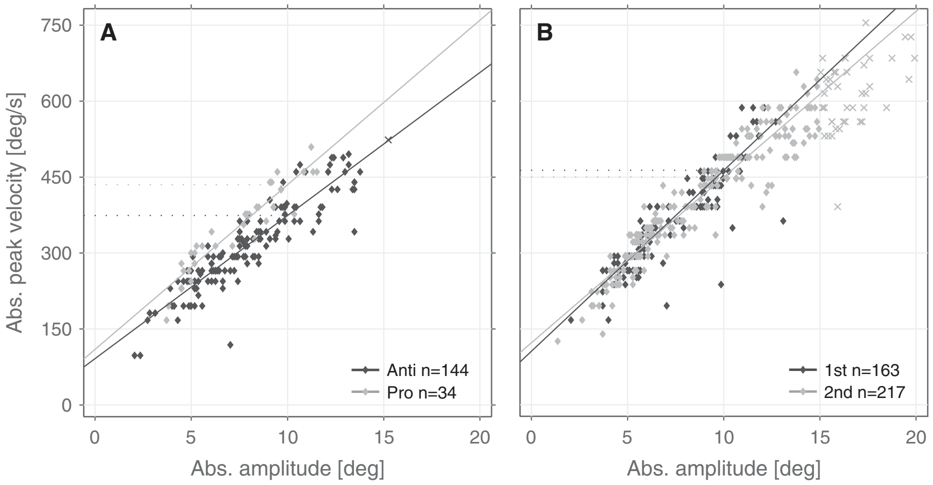

**Fig. 5.** Main sequence of saccades performed by subject 64. (A) Gives anti- and pro-saccades, (B) shows all saccades executed in the double-step paradigm. Lines show robust linear regressions, computed only for saccades with amplitudes between 0 and 15 deg indicated by dots. Saccades with larger amplitudes are shown by crosses and were not used for the regression, since these large amplitude saccades were mainly performed towards the second target.

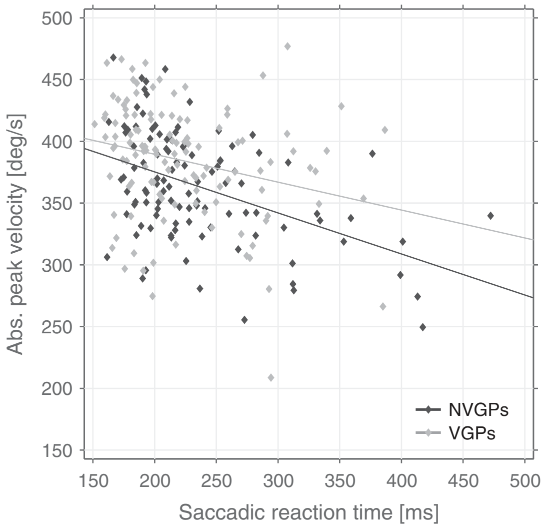

**Fig. 7.** Correlation of peak velocity and saccadic reaction time. Peak velocity is plotted as a function of SRT for each subject and every experimental condition (dark and light gray dots). Linear regressions were computed for VGPs and NVGPs, respectively (dark and light gray lines). $R^2$ of VGPs was 0.065 whereas $R^2$ of NVGPs was 0.207. For both groups, the regression slopes are negative, showing a tendency that peak velocity is inversely correlated with SRT. Importantly, the resulting linear regressions are clearly different for VGPs and NVGPs.

light of attention is shifted prior to the execution of saccades (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler et al., 1995). However, we do not have the experimental data to proof faster attentional processing in VGPs. Attentional enhancement would result in faster reaction times and in lower perceptual thresholds. Since we did not address perceptual thresholds, we cannot attribute our effects to superior attentional processing in VGPs. So the differences in VGPs and NVGPs definitively represent the higher efficiency of the specifically trained visuo-motor system which may be explained by increased attentional mechanisms, increased motor effects, or by arousal effects, to name the most likely reasons.

Nevertheless, the shorter reaction times for VGPs are consistent with a recent report from Chisholm and colleagues (Chisholm et al., 2010). They analyzed the effects of video game play on attention and also found decreased reaction times in VGPs. This was attributed to a better endogenous control over the attentional orienting response. The authors proposed that VGPs assess the relevance of a stimulus faster. The results of our study would support this view, since this is the common processing step in which the speed-up is possible for all saccade types.

Short ISIs (50 and 100 ms) result in a substantial prolongation of the SRT towards the second target. This effect can be explained by a suppressive effect of the first target on the execution of the second saccade. It is known that suddenly appearing stimuli block the execution of successive saccades which was described as "*saccadic inhibition*" (Reingold & Stampe, 2002). This effect seems to cancel the overall pattern of shorter reaction times in VGPs compared to NVGPs.

### *4.2. No impaired impulse control in VGPs*

We had two alternative explanations for the reduced reaction times in VGPs: first, impaired impulse control; second, higher efficiency of the visuo-motor system. The fact that the error rates of VGPs are slightly lower than that of NVGPs clearly contradicts the notion of impaired impulse control in VGPs. The higher efficiency of the visuo-motor system is in perfect agreement with a recent study combining perceptual performance and EEG recordings (Mishra et al., 2011). In that study, subjects had to report the presence of a target either in the central or peripheral visual field. VGPs performed better and reacted faster than NVGPs. In addition, the amplitude of steady-state visual evoked potentials elicited by peripheral non-attended stimuli was smaller in VGPs. Once more, this argues in favor of a better control of the reflexive allocation of attention in this group.

### *4.3. VGPs have increased saccadic peak velocities*

Higher peak velocities of pro-saccades compared to anti-saccades have been reported earlier (Smit, Van Gisbergen, & Cools, 1987). There is general agreement that saccades directed towards a visual target reach highest peak velocities whereas saccades directed to targets presented in a different modality, recalled from memory, or reconstructed by spatial transformation, reach lower peak velocities. However, the mechanism responsible for this dichotomy is still unknown.

Recently, it was suggested that the lower peak velocities of memory-guided saccades compared to visually-guided saccades can be traced back to the increased probability of blinks accompanying memory-guided saccades (Powers, Basso, & Evinger, 2013). Although the blink-induced curvature of saccade trajectories is able to explain the difference in peak velocities of visual and memory-guided saccade, this explanation is not able to explain the difference of peak velocities of pro- and anti-saccades since there is no reason to assume that the blink frequency is different for pro- and anti-saccades. In addition, we excluded trials with blinks form our analysis.

The brainstem circuitry for the motor generation of saccades is well understood and consists of a few specialized neuronal circuits. These neurons generate the pulse-step characteristic of the firing rate of extra-ocular-motoneurons observed during the execution of saccades. It is unknown how these circuits are modulated for the different saccade types on the one hand and what the difference between VGPs and NVGPs is on the other. VGPs produce higher peak velocities during all types of saccades. It has been shown earlier in monkeys that the saccadic peak velocity can be altered by the anticipated amount of reward (Takikawa et al., 2002). In humans it was shown that the peak velocity increases with the intrinsic value of the stimulus (Xu-Wilson, Zee, & Shadmehr, 2009). Saccades towards targets which have to be discriminated are faster compared to targets without behavioral significance (Bieg et al., 2012; Montagnini & Chelazzi, 2005). Finally, the peak velocity of saccades can be altered by reinforcement learning; for a review see (Madelain, Paeye, & Darcheville, 2011). The latter review emphasizes a correlation of short SRTs with higher peak velocities, which is in perfect agreement with our data shown in Fig. 7. In addition to the general correlation between SRT and peak velocity, our data additionally document the increased efficiency of the visuo-motor system of VGPs compared to NVGPs.

### *4.4. Differences due to different motivation of VGPs and non-players?*

Recently, it was argued that the beneficial effects of video games may be due to methodological flaws (Boot, Blakely, & Simons, 2011). The major criticism was that most studies recruited specifically VGPs. This may cause the selection process itself to act as motivation for the VGPs to outperform NVGPs. We are convinced that our study is not affected by this, because we did not search explicitly for VGPs when we recruited our subjects. In addition, the subjects did not know in advance how they were classified according to their daily gaming time.

Finally, the benefits of playing video games might be explained by perceptual learning (Censor, Sagi, & Cohen, 2012). Perceptual learning during video game play might affect saccade execution in our study. However, perceptual learning was shown to be specific for simple stimulus attributes and depends on the specific task (Sagi & Tanne, 1994). Therefore, there is no reason to assume that the benefits of playing video games in our saccade tasks can be explained by perceptual learning.

## Acknowledgments

We like to thank Ziad Hafed for fruitful discussions and Simon Parker for careful proof-reading. DJM was financially supported by a stipend of the Werner Reichardt Centre of Integrative Neuroscience. In addition, the study was supported by the German Research Foundation (DFG IL 34/6-1).

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## 4.2 Study 2: Video game players show higher performance but no difference in speed of attention shifts

**Authors** David J. Mack, Helene Wiesmann and Uwe J. Ilg
**Journal** Submitted to *Acta Psychologica*
**Reference** Mack et al., 2015c

### Abstract

Video games have become both a widespread leisure activity and a substantial field of research. In multiple tasks, video game players (VGPs) show superior performance compared to non-video game players (NVGPs). An enhancement in the visuospatial attention of VGPs, particularly faster covert attention shifts, may explain this phenomenon. Since improved visuospatial attention cannot be disentangled from faster stimulus-response mappings in reaction time (RT) based measurements, we used a spatial cueing task, with varying cue lead times (CLTs), to investigate the speed of covert attention shifts of 98 male participants independent of RTs. VGPs exhibited increased maximum as well as better average performance than NVGPs. Surprisingly, no differences in shifting speed, as measured by the CLT needed for maximum performance, were found. In line with previous studies, our results clearly rule out faster stimulus-response mappings as underlying the higher performance of VGPs. More importantly, our data do not support faster covert attention shifts as a possible explanation. Instead, we suggest that VGPs have a more efficient top-down control over attentional mechanisms compared to NVGPs.

### Statement of contributions

The hypothesis and the experimental paradigm were developed by myself with support from Uwe J. Ilg and Ziad M. Hafed. All data collection was done by Helene Wiesmann and myself. The analysis of the data was done by myself with support from Uwe J. Ilg. Parts of the data were used in the graduation thesis of Helene Wiesmann (Wiesmann, 2012). The manuscript was created by myself and Uwe J. Ilg.

# VIDEO GAME PLAYERS SHOW HIGHER PERFORMANCE BUT NO DIFFERENCE IN SPEED OF ATTENTION SHIFTS

David J. Mack, Helene Wiesmann, Uwe J. Ilg

## 1. Introduction

Video games have been a controversial topic in both the media and science over the past decade. Despite a high prevalence in the younger population – 60 % of juveniles in the U.S. play at least one hour a day (Rideout, Foehr, & Roberts, 2010) – there still is no consistent evidence about the consequences of video game play. Some studies have shown detrimental effects like increased aggression and decreased prosocial behavior (Anderson et al., 2010), or the development of addiction symptoms (Gentile et al., 2011). Obviously, too much screen time displaces other activities like doing homework or sports (Cummings & Vandewater, 2007). However, it remains unclear whether or not violence in video games can be blamed for aggressive behavior (Ferguson, San Miguel, Garza, & Jerabeck, 2012), or if being "bad" in a video game improves moral sensitivity in the real world (Grizzard, Tamborini, Lewis, Wang, & Prabhu, 2014). In addition, cooperative video game play even negates the aggression-increasing effects of video games (Velez, Greitemeyer, Whitaker, Ewoldsen, & Bushman, 2014).

This last result reflects a bright side of the coin: video game play has been linked to more precise temporal processing (Donohue, Woldorff, & Mitroff, 2010; Rivero, Covre, Reyes, & Bueno, 2013), superior contrast sensitivity (Li, Polat, Makous, & Bavelier, 2009) and spatial resolution (Green & Bavelier, 2007), enhanced control over selective attention (Cain, Prinzmetal, Shimamura, & Landau, 2014; Chisholm & Kingstone, 2012; Green & Bavelier, 2003), faster information integration (Green, Pouget, & Bavelier, 2010) and even real-life ameliorations such as better surgical skills (Rosser et al., 2007), or improved reading abilities in dyslexic children (Franceschini et al., 2013). Latham, Patston, and Tippett (2013) have done a thorough review of video game research in the last decades.

In general, video game players (VGPs) show shorter reaction times than non-video game players (NVGPs) in a multiplicity of tasks (Dye, Green, & Bavelier, 2009). The superior performance of VGPs is independent of the gaming platform and is even observed when games are played on mobile devices (Oei & Patterson, 2013). Moreover, two months of daily 30-minute video game play increases gray matter volume (Kuhn, Gleich, Lorenz, Lindenberger, & Gallinat, 2014), and the size of the striatum is correlated with the extent of improved video game performance (Erickson et al., 2010). We have recently shown that VGPs have shorter reaction times but do not produce more errors in an anti-saccade task (Mack & Ilg, 2014) that is highly controlled, since it involves only the presentation of a single target. Our results indicate that inhibitory control is not altered in VGPs. In a similar study using saccade targets and distractors defined by line color and orientation, it was also demonstrated that VGPs have shorter saccadic reaction times compared to NVGPs (Heimler, Pavani, Donk, & van Zoest, 2014). In contrast to our report, a slight increase in error rates of VGPs was found in this study.

Recently, Bavelier, Green, Pouget, and Schrater (2012) proposed that VGPs exhibit an enhanced ability in "learning to learn", that is, the ability to adapt swiftly to new tasks. More specifically, allocation of attentional resources is increased, thereby enhancing the signal in question for the task. Currently, it is debated whether attentional improvements are related to exogenous, bottom-up control through improved distractor inhibition (Bavelier, Achtman, Mani, & Focker, 2012; Cain et al., 2014; Mishra, Zinni, Bavelier, & Hillyard, 2011), or to endogenous, top-down control of attention (Chisholm, Hickey, Theeuwes, & Kingstone, 2010; Chisholm & Kingstone, 2012; Clark, Fleck, & Mitroff, 2011). Based on the results from our eye movement study, we wanted to explore a third alternative: the faster allocation of attentional resources in VGPs, as suggested by Bavelier, Green, et al. (2012). We hypothesized that, in the framework of visuospatial attention, not just the allocation, but the mere attentional orienting response is faster in VGPs. Within the famous "spotlight of attention" metaphor, this orienting is achieved through a covert attention shift (Posner, 1980;

Posner, Snyder, & Davidson, 1980). These attention shifts can either be driven in a bottom-up manner through exogenous signals (e.g. sudden onset cues) or by top-down control through endogenous signals (e.g. symbolic or rule-based cues). It has been argued that bottom-up processes precede top-down control of attention (for a review see Theeuwes, 2010) and that feature-based attention is closely related to bottom-up priming (Theeuwes, 2013). In our own study (Mack & Ilg, 2014), we found faster reaction times for exogenously as well as endogenously driven saccadic eye movements. These eye movements are believed to be preceded by covert attention shifts (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995). Since we found similar effects for both saccade types, we hypothesized that a speeded allocation and a faster covert shift of attention might be the best explanation for these results. In addition, this would account for the shorter reaction times of VGPs in any task which involves some form of spatial attention.

However, in reaction time based experiments, the faster responses of VGPs (Dye et al., 2009) can be explained alternatively by a more efficient stimulus-response mapping (Castel, Pratt, & Drummond, 2005). An examination of purely attentional effects must therefore use a paradigm without any motor involvement. Although there have been perceptual studies using performance based signal detection tasks (e.g. Green & Bavelier, 2003; West, Stevens, Pun, & Pratt, 2008), none of them have explicitly looked at the speed of covert attention shifts. An elegant way to measure the speed of these shifts without motor involvement, is the spatial cueing task introduced by Nakayama and Mackeben (1989). In this paradigm (called the "Nakayama task") the shifting speed is derived from discrimination performance. As in other spatial cueing tasks, the participant has to detect the presence of an oddball in a search array. In principle, the oddball is defined by a feature conjunction of orientation and color (Treisman & Gelade, 1980). In contrast to normal conjunction search tasks, the location of the oddball is cued, reducing the conjunction search to a simple neighbor comparison. The crux of the task is the very brief presentation of the search array for only 17 ms. The duration of the cue indicating the location of the oddball in the upcoming search array (the cue lead time; CLT), is systematically varied between trials (see section 2.2 and figure 1 for a detailed description of the task). With increasing CLT, an attentional enhancement of the signal and thus better discrimination performance can be observed until a certain point. For longer CLTs, the attentional enhancement decays and performance drops substantially. At a specific CLT, the attentional enhancement will be strongest, resulting in a performance peak. This CLT for peak performance is a direct measure for the speed of covert attention shifts.

Nakayama and Mackeben (1989) hypothesized that the overall time course of performance reflects an early peaking bottom-up as well as a late plateauing top-down component. At short CLTs, the orientation response is **transient** and bottom-up triggered. At long CLTs, the response is **sustained** and under top-down control. It has been shown that the selective part of attention (e.g. the selection of the signal before the covert attention shift) is actually responsible for the transient component (Wilschut, Theeuwes, & Olivers, 2011). The authors of this study also found that task difficulty is echoed in a transition from shorter to longer CLTs for peak performance. They proposed that this reflects a shift from a bottom-up defined to a top-down controlled strategy in the participants. In summary, the CLT for peak performance in the Nakayama task may reflect differences in subjective task difficulty, type and speed of attention shift.

## Research questions

For the reasons mentioned above, we used the Nakayama task to pursue three research questions:

(1) Do VGPs also perform better in the Nakayama task, thereby lending further support against a simply faster stimulus-response mapping?
(2) Does a potential attentional benefit in VGPs result from faster shifts of attention?
(3) Are there differences in the balance between top-down and bottom-up control of attentional mechanisms in VGPs and NVGPs?

# 2. Methods

## 2.1 Experimental setup

The experiments were conducted on a PC (AMD Athlon 64 X2 173 4800+, 1 GiB DDR2 RAM, ATI Radeon Xpress 1150) running Windows XP in dual-screen setup (HP L1950; screen diagonal: 19 “, refresh rate: 60 Hz, resolution: 1280 x 1024 pixels). The control screen for the investigator was connected via the DVI-port and the stimulus screen via the VGA-port of the graphics adapter. All stimuli were presented using the Psychophysics Toolbox Version 3 (Brainard, 1997; Pelli, 1997) and MATLAB R2008a (The Mathworks, Natick, MA). Viewing distance of the participants was kept constant at 57 cm through a chin and forehead rest.

## 2.2 Task procedure

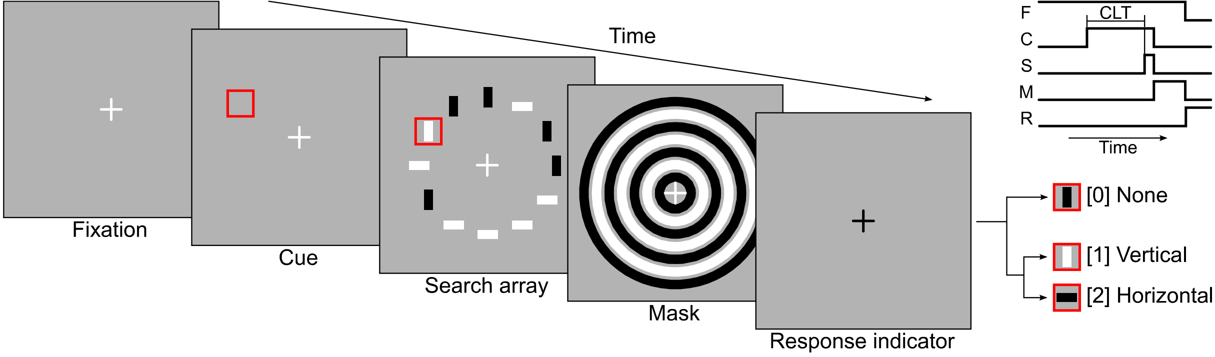

**Fig. 1: Sequence of events in the Nakayama task used in the current study**. The three possible responses are indicated at the right (the correct response in this example would be “1”). The inset in the upper right shows the timing of the stimulus.
*F*: Fixation, *C*: Cue, *S*: Search array, *M*: Mask, *R*: Response indicator.

Figure 1 shows the sequence of events in our version of the Nakayama task (i.e. “Experiment 5: effect of retinal eccentricity” in Nakayama & Mackeben, 1989). The participants had to indicate if the bar at the cued location matched the other bars in its feature combination. These features were ‘orientation’ (horizontal/vertical) and ‘color’ (black: luminance ≤ 1 cd/m$^2$; white: luminance 125 cd/m$^2$). All stimuli were presented on a gray background (luminance 30 cd/m$^2$). A trial began with a white fixation cross (size: 19 x 19 arcmin, line width: 2 arcmin) at the center of the screen. After a random fixation time (250 - 500 ms), a red square (size: 44 x 44 arcmin, line width: 4 arcmin) cued the oddball location. The CLT was parametrically chosen from 14 values (0, 17, 33, 50, 67, 83, 100, 117, 133, 150, 200, 300, 400 and 600 ms). Subsequently, the search array, consisting of 12 bars (each sized 30 x 16 arcmin) in a circular arrangement of 4 degree radius, was shown for 17 ms. The bar centers were equally spaced at the 12 clock positions with a center-to-center distance of 2.1 degree of visual angle. Six bars were randomly assigned to one feature combination (e.g. “horizontal-black”) and the remaining six to the opposite feature combination (e.g. “vertical-white”). Thus, the two groups of bars were always different in both feature dimensions. The bar at the cued location (aka the oddball) either differed in its orientation from the rest (e.g. “vertical-black” or “horizontal-white”) or not at all (e.g. “horizontal-black” or “vertical-white”). All other bars were randomly assigned to any of the 11 remaining positions. The cue stayed on the screen during the presentation of the search array to avoid any offset transient. After the search array, a black-and-white concentric circle pattern was shown for 250 ms to mask the search array and diminish the influence of afterimages. Finally, the mask disappeared and the fixation cross changed its color from white to black, signaling that the participant should now respond to the oddball orientation (horizontal, vertical or none). All responses were collected via keyboard button presses. Non-numeric keypad digits were used to indicate if the oddball was horizontal (button “1” press; middle finger of the left hand), vertical (button “2” press; index finger of left hand), or wasn’t an oddball at all, i.e., matched the other bars (button “0” press; index finger of the right hand). The three oddball types assured that mere guessing was not a rewarding strategy, since chance level was reduced to 33 %. Each trial ended only after the participant pressed the button. Therefore, the measurement was self-paced and could be halted in between two trials. After the response, the next trial started with an inter-trial interval of 300 ms.

Each participant performed three training blocks of 42 trials each (1 repetition for the 14 CLTs and the 3 oddball types), each with decreasing search array durations (117, 83 and 50 ms), in order to familiarize the participants with the task and avoid learning effects in the subsequent full measurement block (294 trials; 7 repetitions for each CLT and oddball type). Training and measurement blocks were preceded by an additional demonstration of the whole sequence of events and response options. The entire experiment took between 40 and 75 minutes.

## 2.3 Data processing

A trial was considered 'correct' if the response of the participant matched the oddball type. For each participant, the performance at each CLT was then defined as the mean correct performance at that CLT. Baseline performance was derived from performance at 0 ms CLT and was designed to measure performance without attentive influences. Mean performance was computed over all CLTs as a general measure of the participant's task achievement. Peak performance was calculated as the maximum performance, and the corresponding CLT was used as a measure for the speed of the covert attention shift. In some participants, more than one peak performance was found. In these cases, we always took the first CLT for peak performance to get a lower limit on the speed of the attention shift. Based on the proposal of Nakayama mentioned in the Introduction, we separated the participants according to their CLT results into a **transient** class (CLT for peak performance < 150 ms) and a **sustained** class (CLT for peak performance ≥ 150 ms). This threshold was derived from the trough in the distribution of the CLTs for peak performance, which can be seen in figure 3.

## 2.4 Participants

98 male participants were enlisted from German high school senior classes. The recruitment procedure was covert and did not mention the video game aspect of the study to avoid differential motivation effects. Before the experiment, participants were only told that it was a study on attention in juveniles. No further information was given until they had finished the experiment, when the whole purpose of the study was revealed. Afterwards, each participant completed a questionnaire (see supplemental material S1 for a translated version), which included date of birth, sex, and a self-report of the time per week spent playing video games (weekly gaming time; WGT) as well as doing sports (weekly sports time; WST). In addition, participants had to mark on a checklist all the game genres they play ('Puzzle', 'First Person Shooter', 'Sport', 'Action', 'Jump 'n' Run', 'Adventure', 'Strategy', 'Other') and name their favorite video game. All values had to be given over the course of the last 12 months. The WST was used to control for a potential confound of sports. Based on the WGT, participants were classified as either NVGPs (WGT < 4 hours) or VGPs (WGT ≥ 4 hours) irrespective of the genre they played. From anecdotal reports of our participants, VGPs tend to play in one long session once per week, rather than in several short ones every day. Thus, we chose a threshold of 4 hours to include also moderate VGPs who might play only for one evening per week.

Of the NVGPs who indicated they play video games, the three most reported favorite games were Fifa Soccer (n = 4; action video game), Call of Duty (n = 2; action video game) and Pro Evolution Soccer (n = 2; action video game). For the VGP group, the favorite games were Battlefield (n = 11; action video game), Call of Duty (n = 8; action video game) and Fifa Soccer (n = 7; action video game). In addition, we used the genre of the reported favorite game to classify VGPs into two subgroups of non-action-VGPs (naVGPs) and action-VGPs (aVGPs). Following the definition of Green, Li, and Bavelier (2010), action video games had to be fast, unpredictable and perceptually as well as cognitively challenging. Thus, first person shooters like Battlefield, sports games like Fifa Soccer, and action games like Assassin's Creed were put into the action video game category. Games like League of Legends or StarCraft were classified as non-action video games. Similarly, the game genres from the questionnaire checklist were grouped into action video games ('First Person Shooter', 'Action', 'Sport') and non-action video games ('Puzzle', 'Jump 'n' Run', 'Adventure', 'Strategy', 'Other'). The classification of the action video game-related subgroups was repeated with this checklist. VGPs were defined as aVGPs if they marked any of the action video game categories and as naVGPs otherwise.

Originally we measured both sexes, but failed to find enough female VGPs. To avoid confounding any effects of video game play with effects of gender, we did not include data of female participants in the analysis. All participants had normal or corrected to normal vision. All experiments were performed in accordance with the Declaration of Helsinki.

## 2.5 Statistics

The data were processed and analyzed using self-written Matlab scripts. To compare the effects of the two main factors, attention type (transient/sustained) and video game play (NVGPs/VGPs), full 2-factorial ANOVAs were computed.

Since many studies define VGPs based on action video game play, we also computed full 2-factorial ANOVAs within the VGP group for the main factors attention type and action video game play (naVGPs/aVGPs). We performed this test with the favorite-game-based as well as the genre-checklist-based definitions.

All post-hoc tests were performed using the Tukey-Kramer method. Results were considered significant at an alpha level of 0.05.

An initial analysis to check the validity of the attention type division was carried out as a 3-factorial ANOVA with 1st-order interactions for the main factors CLT (0, 17, 33, 50, 67, 83, 100, 117, 133, 150, 200, 300, 400 and 600 ms), attention type (transient/sustained) and video game play. An additional post-hoc t-test was performed for each CLT between the two attention types to reveal specific differences. Significance for this test was considered at the Bonferroni-corrected alpha level (0.004).

# 3. Results

The performances of typical VGPs and typical NVGPs for both attention types are shown in figure 2. For these examples, the VGPs outperformed the NVGPs with respect to peak, mean, and baseline performances. However, all reached their peak performance at the same CLTs with respect to attention type. Whereas both transient participants have a clear early peak at 33 ms (figure 2 a), this transient component is much less pronounced in the sustained participants, who show a late plateau around 300 ms instead (figure 2 b).

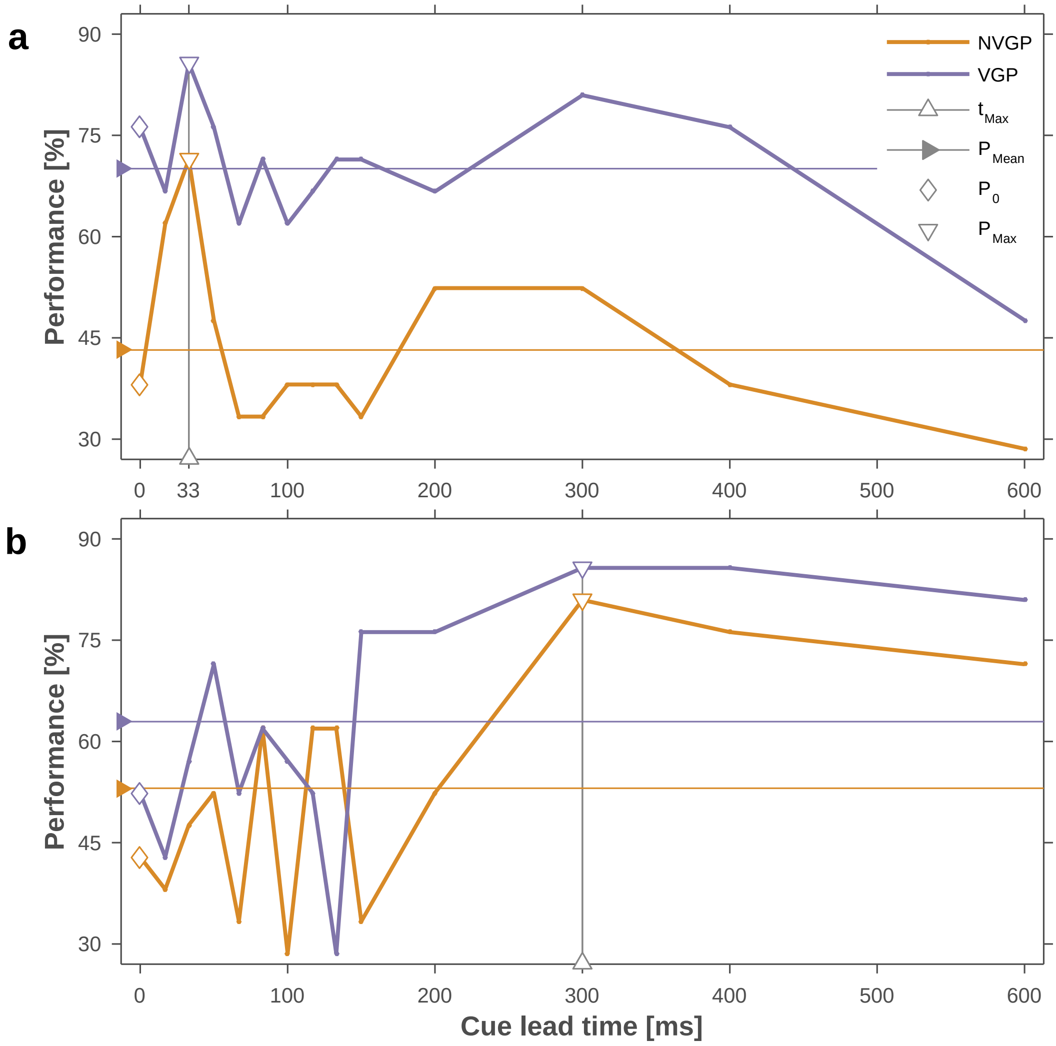

**Fig. 2: Single participant data. (a)** Examples of transient attention types: a NVGP (age: 17 years, WGT: 0 hours, WST: 4 hours, $P_0$: 38 %, $P_{Mean}$: 43 %, $P_{Max}$: 71 %, $t_{Max}$: 33 ms) and a VGP (age: 17 years, WGT: 7 hours, WST: 6 hours, $P_0$: 76 %, $P_{Mean}$: 70 %, $P_{Max}$: 86 %, $t_{Max}$: 33 ms). **(b)** Examples of sustained attention types: a NVGP (age: 18 years, WGT: 2 hours, WST: 5 hours, $P_0$: 43 %, $P_{Mean}$: 53 %, $P_{Max}$: 81 %, $t_{Max}$: 300 ms) and a VGP (age: 17 years, WGT: 10 hours, WST: 2 hours, $P_0$: 52 %, $P_{Mean}$: 63 %, $P_{Max}$: 86 %, $t_{Max}$: 300 ms).

$P_0$: Performance at 0 ms CLT, $P_{Mean}$: Mean performance, $P_{Max}$: Peak performance, $t_{Max}$: CLT for peak performance, *WGT*: Weekly gaming time, *WST*: Weekly sports time.

Table 1 shows the statistics of our 98 male participants, separated into 36 NVGPs and 62 VGPs. According to action video game play (defined by favorite game genre), the VGP group consisted of 18 naVGPs and 44 aVGPs. With respect to attention type, we observed proportionally more sustained VGPs (34 %) than NVGPs (22 %), but this difference did not reach significance ($p = 0.223$; asymptotic Fisher test). 2-factorial ANOVAs revealed no significant differences in age or WST with respect to attention type or video game play (all p’s ≥ 0.115). For WGT, the influence of attention type ($p = 0.998$) was not significant, whereas the effect of video game play was significant ($p < 0.001$). The analysis of the number of individual peak performances showed a significant effect of attention type ($p = 0.017$) with fewer peaks in the sustained attention types. Video game play had no influence on the number of peaks ($p = 0.535$).

| | | # | Age [years] | WST [hours] | WGT [hours] | $n_{Max}$ |
|---|---|---|---|---|---|---|
| **All** | | 98 | 18 ± 0.2 (15-27) | 6 ± 0.4 (0-22) | 8 ± 0.8 (0-30) | 1.6 ± 0.1 (1-5) |
| **NVGPs** | **transient** | 28 | 18 ± 0.2 (16-20) | 6 ± 0.9 (0-22) | 1 ± 0.2 (0-3) | 1.8 ± 0.2 (1-4) |
| | **sustained** | 8 | 17 ± 0.4 (15-18) | 5 ± 1.1 (1-12) | 1 ± 0.4 (0-3) | 1 ± 0 (1-1) |
| **VGPs** | **transient** | 41 | 18 ± 0.3 (16-27) | 6 ± 0.6 (0-18) | 13 ± 1.3 (4-30) | 1.7 ± 0.2 (1-5) |
| | **sustained** | 21 | 18 ± 0.3 (15-20) | 5 ± 0.9 (0-16) | 12 ± 1.3 (5-25) | 1.4 ± 0.1 (1-3) |

**Table 1:** Descriptive statistics of our 98 male participants. Values are given as: mean ± standard error (Minimum-Maximum).

*#*: Number of participants, $n_{Max}$: Number of individual peak performances, *WGT*: Weekly gaming time, *WST*: Weekly sports time.

The distribution of the CLTs for peak performance across all participants is shown in figure 3. The distribution was clearly bimodal, with a transient peak at 33 ms, a sustained peak around 300 ms and a trough around 150 ms.

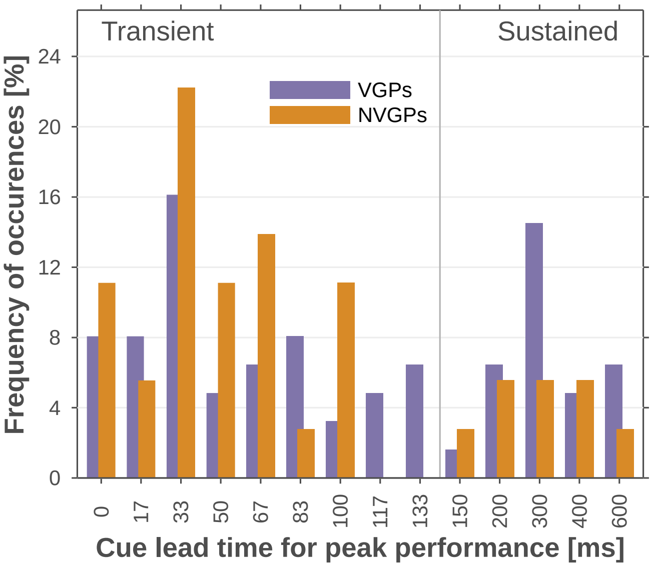

**Fig. 3: Distribution of the cue lead times for peak performance** across all 98 subjects. Note the non-uniform scaling of the x-axis. Bars represent relative frequency of occurrences within each group. The thin gray vertical line indicates the threshold for the division of the two attention types.

To see if the performance curves of the transient and sustained participants were different, we computed a 3-factorial ANOVA for CLT, video game play and attention type. The results are shown in figure 4. The CLT had no significant influence on its own ($p = 0.153$) but formed a significant interaction with attention type ($p < 0.001$). This indicates differential performance of attention types at different CLTs. A point-wise post-hoc comparison for each CLT showed that the sustained attention type performed better at the longer CLTs. Independent of attention type or CLT, video game play had a significant effect ($p < 0.001$), with VGPs showing an overall higher performance.

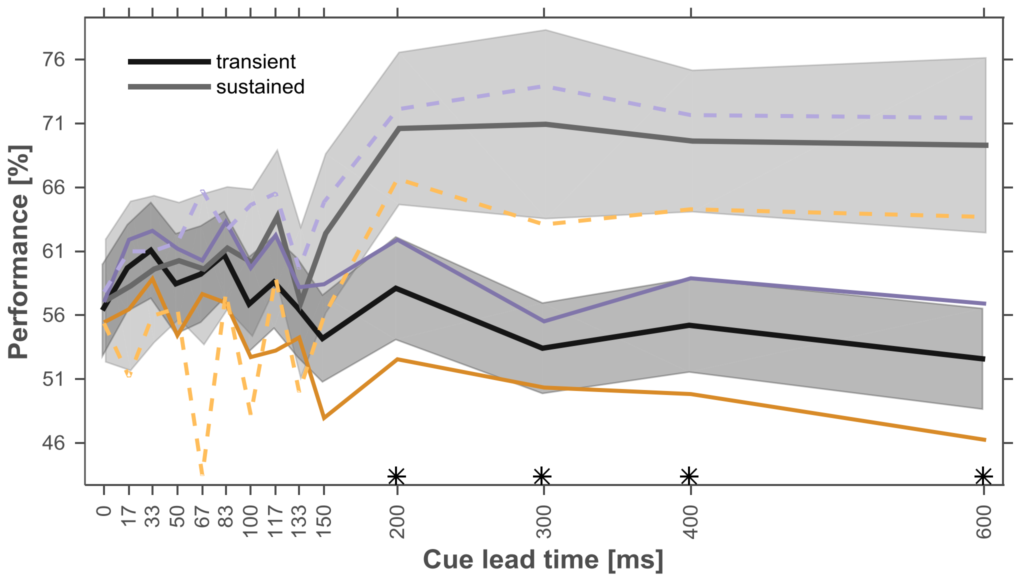

**Fig. 4: Performance for each CLT and attention type** across all 98 subjects. The gray shaded areas indicate 95% confidence intervals. The stars indicate significant differences between the two attention types for particular CLTs. The red and blue lines indicate the means for NVGPs and VGPs, respectively. The attention type is marked by the line style (solid: transient, dashed: sustained).

As shown in figure 5 a, there was no difference in baseline performance with respect to attention type (p = 0.919) or video game play (p = 0.562). The mean performance shown in figure 5 b revealed that sustained attention types were slightly better than transient ones, although this difference was not significant (p = 0.111). However, video game play had a significant influence on mean performance (p = 0.005): VGPs of both attention types performed better than NVGPs. This confirms the results from the previous 3-factorial ANOVA.

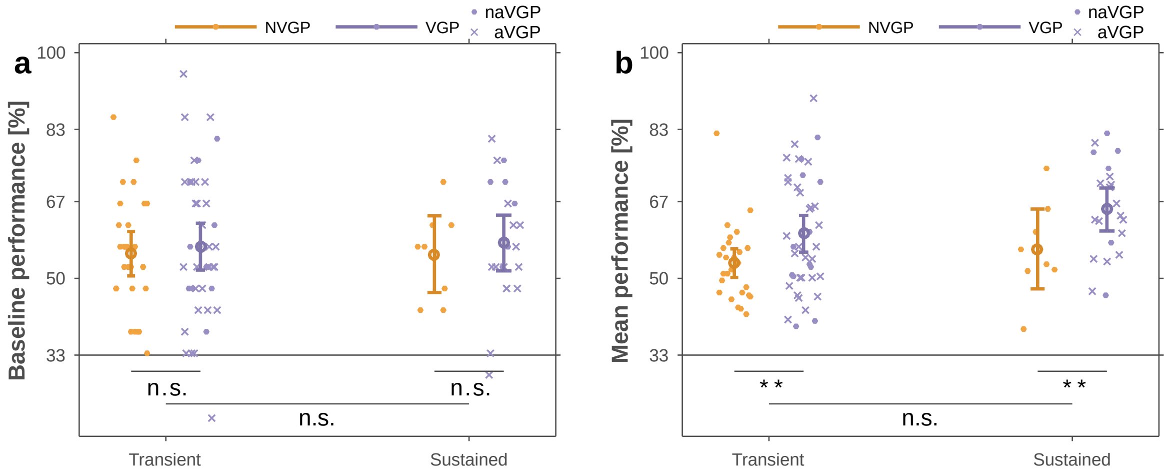

**Fig. 5: (a) Baseline performance** at 0 ms CLT and **(b) mean performance** across all CLTs. ANOVA results are depicted by dark horizontal lines and symbols (n.s.: p > 0.05, **: p ≤ 0.01). Error bars show group means and 95 % confidence intervals. The small markers represent single participants. Chance level is marked by the horizontal gray dotted lines.
*aVGP/naVGP*: Action-/non-action-VGP, *n.s.*: not significant.

In the case of peak performance shown in figure 6 a, the effect of attention type was significant ($p = 0.007$). The sustained group had higher peak performances than the transient one. The influence of video game play was also significant ($p = 0.005$): VGPs performed better than NVGPs. Since attention type had a significant influence on peak performance, we confirmed these results in an additional regression analysis:

NVGPs : $P_{Max} (t_{Max}) = 0.028 \cdot t_{Max} + 68\ \%$, $R^2 = 0.118$, $p = 0.04$

VPGs : $P_{Max} (t_{Max}) = 0.019 \cdot t_{Max} + 76\ \%$, $R^2 = 0.067$, $p = 0.042$

In both groups, peak performance ($P_{Max}$) was significantly correlated with the CLT for peak performance ($t_{Max}$). VGPs' peak performance was approximately 9 % higher. The comparison of the slopes of the two linear regressions revealed no significant difference ($p = 0.303$).

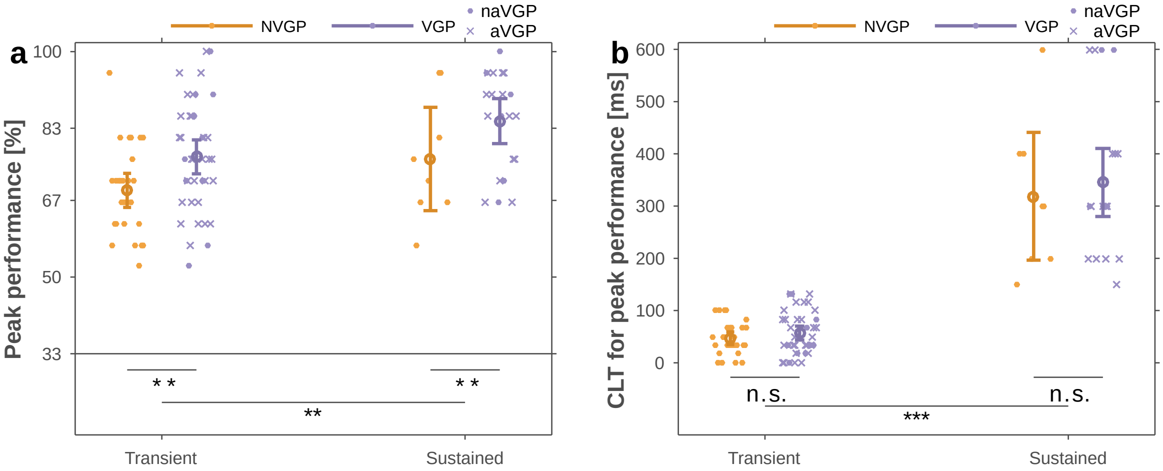

**Fig. 6: (a) Peak performance** and **(b)** the **corresponding cue lead time for peak performance**. ANOVA results are depicted by dark horizontal lines and symbols (n.s.: $p > 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$). Error bars show group means and 95 % confidence intervals. The small markers represent single participants. Chance level in **(a)** is marked by the horizontal gray dotted line.
*aVGP/naVGP*: Action-/non-action-VGP, *n.s.*: not significant.

The results from the CLTs for peak performance can be seen in figure 6 b. The influence of attention type was significant (by definition; $p < 0.001$). But surprisingly, there was no effect of video game play ($p = 0.167$).

Finally, within the VGP group, we compared baseline, mean, and peak performance as well as CLT for peak performance, with respect to action video game play (non-action vs. action). We did not observe any significant differences between the two subgroups for the favorite-game-based definition (p's ≥ 0.195), nor for the genre-checklist-based definition (p's ≥ 0.236).

All unreported factor interactions of the computed ANOVAs in the results section were not significant (p's ≥ 0.113).

## 4. Discussion

According to our initial research questions, we obtained three main results:

(1) VGPs performed significantly better than NVGPs in mean as well as peak performances.
(2) There were no significant differences in the CLTs for peak performance of VGPs and NVGPs.
(3) There was a tendency for the proportion of VGPs using top-down control of attention to be higher compared to NVGPs. However, this difference did not reach significance.

In the following discussion, we try to interpret our results in view of improved attentional mechanisms in VGPs.

## 4.1 VGP benefits cannot be explained by more efficient "button pressing"

Based on the present findings, we can exclude a faster stimulus-response mapping for the general ameliorations found in VGPs, as proposed previously (Castel et al., 2005). Since we did not measure any reaction times, but still found superior performances in VGPs, our results lend further support against the notion of VGPs just being faster in "pressing the button". Therefore, the benefits displayed by VGPs in the present study have to result from improvements in the attentional system, in agreement with earlier findings. Two studies employing the useful field of view task, found better overall performance in VGPs (Green & Bavelier, 2003, 2006). The authors concluded that VGPs possess an enhanced allocation of spatial attention. They also demonstrated a causal relationship between video game play and performance benefits in a training study. In another paper by the same lab, visual motion discrimination was analyzed with respect to video game play (Green, Pouget, et al., 2010). By modelling the underlying neuronal processes, this study showed that there is no difference in the time necessary for motor preparation and execution with respect to video game play. Instead, VGPs actually integrated the necessary information faster than NVGPs.

## 4.2 VGPs do not shift their spotlight of attention in a faster manner

Initially, we hypothesized that VGPs show faster shifts of attention from which measured reaction time benefits arose. Contrary to this idea, VGPs in our study did not exhibit faster covert attention shifts, as indicated by the lack of differences in the CLTs for peak performance. Still, we found profoundly better performances in VGPs and offer three possible explanations for these results:

i) Increased rate of information processing in VGPs

Attention not only increases the discriminability of stimuli through distractor inhibition or signal enhancement, but also accelerates the rate of visual information processing (Carrasco & McElree, 2001). It has been shown that attention is needed to form precise representations in visual short term memory (Persuh, Genzer, & Melara, 2012), and VGPs show improved visual sensitivity (Appelbaum, Cain, Darling, & Mitroff, 2013). Since VGPs have a more precise representation of the stimulus, they have more information available than NVGPs in the same time epoch. Taken together, this could lead to the higher performance seen in VGPs without the need for faster attention shifts.

ii) Higher rate of information accumulation

More specifically, VGPs may not only have an increased rate of information processing, but a higher rate of information accumulation. Probabilistic inference is increased by action video game play and yields an improvement, for instance, in a simple motion discrimination task (Green, Pouget, et al., 2010). These authors estimated an approximately 20 % higher rate of information accumulation for VGPs, which could also account for the better performance of VGPs.

iii) Reduced backward masking in VGPs

Another explanation would be reduced backward masking in VGPs (Li, Polat, Scalzo, & Bavelier, 2010). An attenuated inhibitory effect of the mask would give VGPs more time to extract crucial information from the search array that was only presented for 17 ms.

With the data presented here, we cannot ultimately distinguish between these alternatives, but we clearly exclude a speeded attention shift, or an improved stimulus-response mapping, as reasons for the superior performance of VGPs.

## 4.3 Balance between bottom-up and top-down control

Nakayama and Mackeben (1989) previously concluded that the response functions observed in their task are the sum of a transient, bottom-up component and a sustained, top-down component. When we separated our participants by attention type and plotted the mean performance for each CLT, this became clearly visible. Nakayama speculated that the lack of a downturn in the performance curve of some participants may be due to ceiling effects. A high mean performance would result in the flattening out of the transient component, which is not supported by our data since the mean performance in the sustained group of VGPs and NVGPs was not significantly different from the transient group. Moreover, Wilschut et al. (2011) proposed that greater task difficulty leads observers to rely more on top-down control at longer CLTs, thus leading to an increase in the late plateauing component of the performance curve.

In the present study, the proportion of participants expressing the sustained attention shift was higher in VGPs, although this difference was not significant. Previous studies found enhanced top-down control of attention in VGPs (Cain et al., 2014; Chisholm et al., 2010; Chisholm & Kingstone, 2012; Clark et al., 2011), which supports our observation. Nevertheless, further research is required to make more definitive conclusions concerning this issue.

## 4.4 No difference in baseline performance

We included the baseline performance (observed at 0 ms CLT) in our analysis to have a control condition without any attentional influences. We observed no differences in baseline performance of VGPs and NVGPs. From monkey physiology, it is known that attention is only able to boost the neuronal response if a stimulus is present in the receptive field (Treue & Maunsell, 1996). Directed attention without a stimulus is not able to elicit a neuronal response. At 0 ms CLT, the cue cannot attract attention to the location of the oddball since it is shown simultaneously with the stimulus, thus preventing a possible attentional benefit from affecting performance in this condition. Since our results clearly point in the direction of attentional benefits in VGPs, the lack of difference in baseline performance also supports this notion.

## 4.5 Basic considerations for the comparison of VGP and NVGPs

Due to the cross-sectional nature of our study, we cannot determine if the differences between VGPs and NVGPs are causally related to the consumption of video games or are mere reflections of preexisting group disparities. One might speculate that people with superior attentional abilities perform better in video games and thus play more often (Boot, Blakely, & Simons, 2011; Kristjansson, 2013). In this line of thought, the reported differences between VGPs and NVGPs would be the consequence of a sampling bias. However, this idea is disputed by increasing evidence from multiple training studies, showing a causal relationship between superior performance of VGPs and video game play (Franceschini et al., 2013; Green & Bavelier, 2003, 2006, 2007; Kuhn et al., 2014; Li et al., 2009; Li et al., 2010; Oei & Patterson, 2013). The main focus of our study was not if video game play leads to superior performance (question of causality), but how the performance benefits of VGPs over NVGPs can be explained (question of effect). Nevertheless, to causally relate the better performance of VGPs observed here to video game play, a training study is needed.

Another problem with cross-sectional studies is expectation bias. The knowledge that VGPs are recruited due to their expertise might affect their motivation and thus their performance (and vice versa for NVGPs; Boot et al., 2011). We are convinced that our results were not influenced by expectation biases because our participants had no prior knowledge about the experiment's real purpose (i.e., they were initially only asked to join a study on attention). They also could not infer the purpose from the video game questionnaire, since it was administered after completion of the experiment. Thus, participants could not build up any group-related expectations, which might have otherwise influenced their performance.

We also did not include the data of female participants in our analysis to avoid confounding gender effects in the NVGP and VGP groups.

The last point addresses action video games. It has been increasingly emphasized that only action video games elicit the beneficial effects found in VGPs (Appelbaum et al., 2013; Bavelier, Achtman, et al., 2012; Blacker & Curby, 2013; Cain, Landau, & Shimamura, 2012; Chisholm et al., 2010; Green & Bavelier, 2003; Green, Li, et al., 2010). This is a valid claim, since most action video games are visually complex, fast paced and often involve the parallel execution of several tasks. The successful player is significantly challenged both perceptually and cognitively. Nonetheless, the exact features needed to elicit beneficial effects are unknown. The striking lack of dissimilarities between naVGPs and aVGPs for two different types of action video game play definitions in the current study indicates that a simple discrimination with respect to game genre may not be enough to capture the myriad features characteristic of different games. A recent study also showed that players of real-time strategy games, which commonly not defined as action video games, are better than players of first person shooter games, which are generally accepted as the archetype of action video games, in multiple-object tracking (Dobrowolski, Hanusz, Sobczyk, Skorko, & Wiatrow, 2015), a task previously associated with superior performance only in aVGPs (Green & Bavelier, 2006).

# 5. Conclusion

All together, we provide further evidence against faster stimulus-response mappings as an explanation for higher task performance found in VGPs. Most importantly, our results do not support a role for faster covert orienting responses in VGPs underlying their enhanced performance. Most likely, VGPs have an enhanced attentional system.

# 6. Acknowledgement

We like to thank Ziad Hafed for his valuable support during the initial phase of the study. DJM was financially supported by a stipend of the Werner Reichardt Centre of Integrative Neuroscience.

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# Supplemental material

## Questionnaire

**Questionnaire**

Schülerlabor
Neurowissenschaften
Universität Tübingen

Investigator:

Station:

Sex: ☐ male ☐ female

Date of birth: ______________________________

Self-assessment: very good ☐ ☐ ☐ ☐ ☐ ☐ very bad

Do you play video games? ☐ no ☐ yes

**Weekly gaming time ca.:** ______________ hours

**Which gaming platform(s) do you use?**

| | | | |
|---|---|---|---|
| ☐ Computer | ☐ Playstation 2 | ☐ Playstation 3 | ☐ XBox 360 |
| ☐ Nintendo Wii | ☐ PSP | ☐ Nintendo DS | ☐ Other: ____________________ |

**Which game genre(s) do you play?**

| | | | |
|---|---|---|---|
| ☐ Sport | ☐ Puzzle | ☐ First Person Shooter | ☐ Action |
| ☐ Jump 'n' Run | ☐ Adventure | ☐ Strategy | ☐ Other: ____________________ |

**Which is your favorite game (name only one)?** ______________________________

What are your hobbies? ____________________________________________________________

____________________________________________________________

Do you do sports? ☐ no ☐ yes

**Weekly sport time ca.:** ______________ hours

**Name your sports:** ____________________________________________________________

Would you participate in a voluntary follow-up study? ☐ no ☐ yes

E-Mail address: ____________________________________________________________

## 4.3 Study 3: Influence of healthy aging and sex on anti-saccade performance in elderly individuals: Results from the TREND study

| | |
|---|---|
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| **Journal** | Submitted to *European Journal of Neuroscience* |
| **Reference** | Mack et al., 2015a |

### Abstract

Until 2050, the global population of people aged 65 or older will triple, emphasizing the need for proper knowledge about the consequences of age on health and cognition. One such effect is a general slowing of processing speed. Although well documented in many domains, the eye movement literature is still controversial. Some studies found a slowing of voluntary and reflexive eye movements in the anti-saccade task, whereas others found differential effects or no effects at all. The anti-saccade task is appealing, since its proper execution involves areas in parietal and frontal cortex, midbrain and brainstem and thus can reveal age-related changes on a larger scale. We went out to clarify the effects of healthy aging on anti-saccade task-performance by measuring a large sample of 731 healthy, non-demented individuals (51–84 years). Such a large sample also enabled us to investigate possibly hideous effects of sex. We found detrimental outcomes of age on the number of valid trials, reaction times, behavioral variability and the number as well as peak velocity pro-saccades. In addition, males outperformed females with respect to anti-saccadic reaction time, number and peak velocity of pro-saccades and reaction time variability. Due to the large sample size, our results can serve as a fundamental basis for early differentiation of normal and pathological aging processes in the brain in future studies and provide further documentation of the changes related to healthy aging.

### Statement of contributions

This study includes data collected in the framework of the TREND study under the aegis of Daniela Berg, Walter Maetzler and Gerhard W. Eschweiler. The experimental course of action was developed by myself with the support of Uwe J. Ilg and Karin Srulijes. The data collection was done by Lena Stetz, Sandra Lachenmaier and Leonie Gugolz. The data were analyzed by myself with support from Uwe J. Ilg and Sebastian Heinzel. The manuscript was created by myself and Uwe J. Ilg with support from Sebastian Heinzel and Andrea Pilotto.

# INFLUENCE OF HEALTHY AGING AND SEX ON ANTI-SACCADE PERFORMANCE IN ELDERLY INDIVIDUALS: RESULTS FROM THE TREND STUDY

David J. Mack, Sebastian Heinzel, Andrea Pilotto, Lena Stetz, Sandra Lachenmaier, Leonie Gugolz, Karin Srulijes, Gerhard W. Eschweiler, Walter Maetzler, Daniela Berg, Uwe J. Ilg

## 1. Introduction

### 1.1 Age-related changes in brain functions and cognitive processing

Life expectancy is steadily rising all over the world, leading to a continuous increase of elderly people (Vaupel, 2010). Therefore, age-related changes in brain functions, cognitive processing as well as motor control, are in the focus of public interest. Such changes related to non-pathological, healthy aging occur particularly in the seventh decade of life and manifest as a slowing of processing speed (Cerella & Hale, 1994; Salthouse, 2000) often termed "cognitive decline". One reason for this general slowing might be the decreased connectivity in the frontoparietal and the default mode network of the elderly brain (Grady *et al.*, 2010; Koch *et al.*, 2010; Madden *et al.*, 2010). Age also adversely affects memory, another aspect of cognition, through changes in synaptic plasticity of the hippocampus and the prefrontal cortex (Morrison & Baxter, 2012). Besides cognitive processing, the control of motor actions declines with age, manifesting as a deficit in balance, gait, movement speed and coordination (Seidler *et al.*, 2010).

### 1.2 The anti-saccade paradigm

Many of these age-related changes affect the frontal cortex, which is the last part of the brain to develop (Fuster, 2002) and seems to be first one to undergo changes later in life. An oculomotor paradigm which heavily relies on the integrity of the frontal cortex is the anti-saccade task (Hallett, 1978). In an ordinary saccade task participants execute a visually-guided saccade towards a suddenly appearing target. In contrast, the anti-saccade task requires participants to perform a voluntarily driven "anti-saccade" towards the mirror position of such a target. Sometimes, participants will fail to suppress the erroneous, reflexively driven, visually-guided "pro-saccade" towards the target. The frequency of these erroneous pro-saccades (e.g. "error rate") can be used as a measure for inhibitory control associated with the frontal cortex. Single-unit recordings in awake rhesus monkeys have revealed that the execution of pro- and anti-saccades depend on the recruitment of two distinct neural networks (Munoz & Everling, 2004). The generation of an anti-saccade depends on the frontal and supplementary eye fields (FEF and SEF). High activity of neurons in the FEF, which project directly to the superior colliculus (SC) and the brainstem, indicate an upcoming anti-saccade (Everling & Munoz, 2000). During the preparation for an anti-saccade, an additional inhibitory signal from the dorsolateral prefrontal cortex (dlPFC) is sent to the SC to suppress any pending pro-saccade (Johnston & Everling, 2006). On the other hand, the execution of a pro-saccade is mainly driven by the SC: High pre-stimulus activity of SC build-up neurons signals the occurrence of an erroneous pro-saccade (Everling *et al.*, 1998).

This difference in the underlying pathways is also reflected in the saccade parameters: Anti-saccades have longer saccadic reaction times (SRTs; Hallett, 1978; Evdokimidis *et al.*, 2002) and lower peak velocities (Smit *et al.*, 1987) compared to ordinary visually-guided saccades or erroneous pro-saccades.

In summary, anti-saccade task performance relies on the integrity of the parietal and frontal cortex, the midbrain and the brainstem and the according neuronal circuitry is well understood. In addition, this task contrasts reflexive and cognitive functions, is reliable and easy-to-use. Therefore it is a perfect starting point in the search for age-related changes in the brain.

## 1.3 Age effects on the anti-saccade paradigm

So far, there have been several studies analyzing aging effects in the anti-saccade task. Table 1 summarizes the outcomes of these studies.

| | | | | Age-related changes | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | SRT | | | SRT variability | | Accuracy | | Velocity | | Error rate | Validity |
| | | Participants | Age | AS | VS | Δ | AS | VS | AS | VS | AS | VS | | |
| Grouped comparison | **Alichniewicz 2013** | Y: 13<br>O: 23 | 25 ± 2<br>59 ± 7 | + | + | | | | | | | | +[a] | =[b] |
| | **Butler 1999** | Y: 16<br>O: 16 | 17-23<br>65-80 | + | + | = | | | =[c] | =[c] | | | +[a] | =[b] |
| | **Fujiwara 2010** | Y: 22<br>O: 96 | 20-29<br>60-85 | + | + | | + | + | | | | | + | |
| | **Harsay 2010** | Y: 18<br>O: 18 | 18-36<br>64-85 | + | | | | | | | | | =[d] | |
| Age correlation | **Klein 2005** | 327 | 9-88 | + | + | | | + | | | | | +[e] | |
| | **Mirsky 2011** | 48 | 48-79 | = | = | | | | = | = | = | - | | =[b] |
| | **Munoz 1998** | 168 | 5-79 | + | + | = | = | = | | | = | = | = | |
| | **Olincy 1997** | 42 | 19-79 | + | + | + | | | = | - | | | + | |
| | **Peltsch 2011** | 81 | 60-85 | + | + | + | + | + | | | | | +[e] | -[f] |
| | **Raemaekers 2006** | 31 | 18-72 | + | + | | | | | | | | =[a] | -[b] |
| | **Shafiq-Antonacci 1999** | 238 | 44-85 | + | + | | + | + | = | = | = | = | + | |

*Δ*: Anti-effect (difference between AS and VS SRT), *AS*: Anti-saccade, *O*: Old age group, *SRT*: Saccadic reaction time, *VS*: Visually-guided saccades, *Y*: Young age group

[a] Derived from the reported percentage of correct AS [b] Derived from the reported percentage of correct VS [c] Derived from the reported AS & VS amplitude

[d] Reported as percentage of hits [e] Reported as percentage of AS direction errors [f] Derived from the percentage of VS direction errors

**Table 1:** Previous work on the influence of healthy aging on anti-saccade task performance. Age-related changes are indicated by symbols (+: increase, =: no change, -: decrease). *Accuracy* subsumes measures of the proximity between final eye position and target position. *Validity* subsumes measures of the number of valid trials.

In general, no age-related improvements have been found. Most studies reported longer SRTs and increased error rates in older compared to younger individuals. However, the findings for reflexive and voluntary saccade are heterogeneous. Some studies found equal age-related increases in SRTs for both saccade types (Butler *et al.*, 1999; Klein *et al.*, 2005; Raemaekers *et al.*, 2006), whereas others found a stronger effect on anti-saccades (Olincy *et al.*, 1997; Fujiwara *et al.*, 2010; Peltsch *et al.*, 2011). Three major points contribute to this disagreement. First, the sample sizes are quite different and especially correlational studies suffer from a small number of participants. Second, although often controlled for, sex is not uniformly handled and might be a confound especially in grouped studies. Third, anti-saccades are often compared to visually-guided saccades measured in a separate, ordinary saccade task (Olincy *et al.*, 1997; Munoz *et al.*, 1998; Klein *et al.*, 2005; Peltsch *et al.*, 2011). This allows for a clear separation of the age-related effects on purely visually evoked saccades and anti-saccades. However, ordinary saccade tasks are much easier for the participant than the anti-saccade task and the resulting difference in cognitive load may influence the outcome parameters. The elderly might find the anti-saccade task more demanding and thus might need more resources to accomplish the task. This in turn, might show up as a differential effect of age on reflexive and voluntary saccade, when they are measured in separate tasks.

To overcome the mentioned limitations, we examined a very large sample of 731 healthy elderlies in the anti-saccade task and pursued two main research questions:

1. Does healthy aging affect the saccade network differentially and if so, is the frontal part more affected?
2. Is there a noteworthy effect of sex?

To avoid the confound of cognitive load, we explicitly refrained from comparing anti-saccades to separately-measured, visually-guided saccades, but took the erroneous pro-saccades (the “direction error”; Munoz & Everling, 2004) to equate the influence of cognitive load on both saccade types.

# 2. Material and methods

## 2.1 Participants

All participants (n=731, age 51 to 84 years) were measured as part of the **T**übinger evaluation of **R**isk factors for **E**arly detection of **N**euro-**D**egeneration (TREND) study (Berg & Eschweiler). For this study, only healthy non-demented elderly individuals were recruited. All participants were pre-screened and excluded if any history of psychiatric diseases, dementia, epilepsy, stroke, multiple sclerosis or encephalitis was reported. Additional exclusion criteria were based on disorders which would have prevented study completion, like paresis, severe sensory dysfunction or the inability to walk without assistance (Hobert *et al.*, 2011). For a more detailed description of inclusion/exclusion criteria to the TREND study see Berg (2012). The experiments were performed in accordance with the Declaration of Helsinki and approved by the Ethic Commission of the local Medical Faculty. All participants gave informed consent.

## 2.2 Experimental setup

We measured horizontal eye movements of the left eye with a limbustracker (Skalar IRIS, Skalar Medical B.V., Delft, Netherlands). The IRIS has a resolution of 2 arcmin and eye position was digitized at 1 kHz. Stimuli were presented on a 23 “ LED screen (Fujitsu P23T-6; 1920x1080 px resolution, 60 Hz refresh rate) and generated using the Psychophysics Toolbox version 3 (Brainard, 1997; Pelli, 1997; Kleiner *et al.*, 2007) under Matlab R2008a (The MathWorks Inc., Natick, MA, 2008). The fixation and saccade targets were presented in white (luminance 58 cd/m$^2$) on a black background (luminance ≤ 0.1 cd/m$^2$). Fig. 1 shows a sketch of our setup. Viewing distance was held constant at 57 cm through a chin- and head-rest. The participants' head was strapped to the head rest during the whole measurement to keep movement artefacts to a minimum.

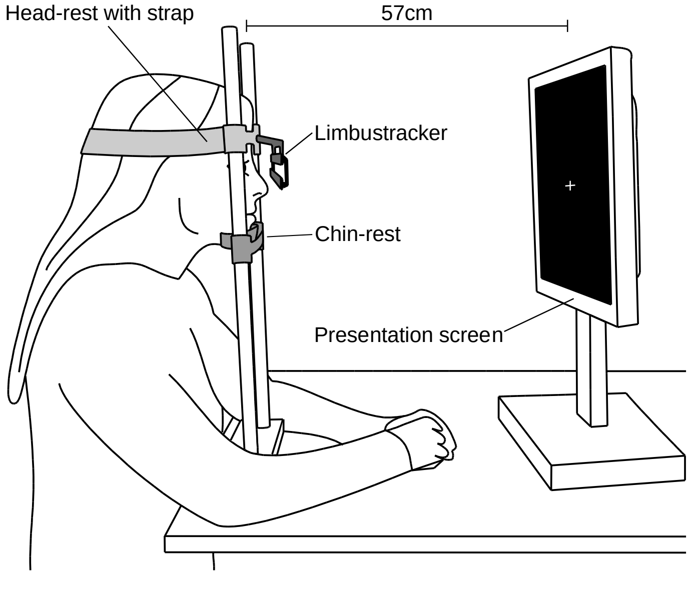

**Fig. 1:** Experimental setup. The head- and chin-rest assured the viewing distance of 57 cm and reduced movement artifacts. All eye movements were recorded with a limbustracker from the left eye of the participant.

## 2.3 The anti-saccade task

Participants were instructed to look at the horizontal mirror position of an appearing square target (size: 10x10 arcmin, color: white), i.e. the position opposite on the horizontal axis. The target appeared randomly at 5 ° or 10 °, respectively, left or right to the initial fixation cross (size: 16x16 arcmin, color: white) at the center of the screen. The fixation duration was randomly chosen between 500 to 1000 ms on a trial-by-trial basis, after which the target appeared until the end of the trial at 1500 ms. The next trial started immediately thereafter. In total, 160 trials were conducted (40 repetitions for each of the 4 target positions). The erroneous pro-saccades towards the target were used as to get a grip on the reflexive saccades (see Section 1.4). This necessarily led to a variable number of pro- and anti-saccades in each individual (see Section 2.4). The entire measurement was standardized through the use of a fixed protocol to avoid differential influences from the experimenter (see Supplemental material M 1).

## 2.4 Data processing

Eye position was first low-pass filtered with a 5th order Butterworth filter (cut-off frequency 45 Hz) and subsequently differentiated to obtain eye velocity (1st differentiation) and eye acceleration (2nd differentiation), respectively. A central difference was used to compute the differentiations.

All eye movements (including, e.g. drifts and blinks) were detected with a velocity threshold of 40 °/s. Saccades were defined as eye movements with peak velocities larger than 80 °/s and peak accelerations above 4000 $°/s^2$.

Based on the properties of the first detected saccade after target onset, a trial was considered invalid according to six exclusion criteria (see Supplemental table T 1):

a) No such saccade was detected.
b) The eye position trace changed more than 2.5 ° in a 250 ms window prior to the onset of the saccade.
c) The saccade was grossly inaccurate, e.g. the saccadic gain (saccade amplitude divided by target position), was outside the range of 0.4 to 1.6.
d) The saccade was preliminary, e.g. it occurred within 90 ms after target onset.
e) The absolute peak velocity was greater than 1000 °/s.
f) The absolute acceleration/deceleration peaks exceed 100.000 $°/s^2$.

Criteria b), e) and f) mainly covered artifacts like blinks, whereas c) and d) excluded anticipatory responses.

Each valid saccade was classified as anti-saccade if its end point was horizontally opposite to the target position; otherwise it was classified as pro-saccade. If a participant made less than seven valid saccades of either type (e.g. anti- or pro-saccade) in total, the according parameters (see Section 2.5) of this type were excluded from the analysis. This exclusion criterion was chosen to be saccade-type specific, because removal of all data of a participant would have artificially narrowed the distribution of error rates, e.g. perfect performance with 0 pro-saccades may then also have been removed from the entire analysis. In total, 8 participants (1.1 %) were removed from the pro-saccade analysis, 46 (6.3 %) from the anti-saccade analysis and one participant (0.1 %) was excluded from the whole analysis because he failed to produce enough valid saccades of either type.

## 2.5 Statistics and saccade parameter computation

For each valid saccade the following parameters were determined: SRT as time from target presentation to saccade onset, saccade amplitude as difference between saccade start- and end-position, gain as saccade amplitude divided by target eccentricity, and saccadic peak velocity as the maximum velocity between on- and offset of the saccade. To obtain the SRTs and gains for each saccade type and each individual, the median was computed from all valid saccades and used for the further analysis. The median was chosen since especially SRTs tend to have skewed distributions (see Supplemental figure F 1). For the SRTs also the “anti-effect” – the difference between anti- and pro-SRTs – was computed. To analyze the variance in our parameters, we calculated the intra-individual variability of the SRTs and gains as the standard deviation (SD) of the respective values. The error rate was calculated by ($n_{Pro}$ / ($n_{Anti}$+ $n_{Pro}$)) * 100 where $n_{Anti}$ and $n_{Pro}$ are the numbers of valid anti- and pro-saccades, respectively.

To compare the kinematics of the saccades, we computed the main sequence for peak velocity versus amplitude using a robust linear regression with iteratively reweighted least-squares (Holland & Welsch, 1977; see Supplemental table ST 1). From the resulting equations, exemplary peak velocities of 10 °-saccades were computed for each participant.

To quantify how many valid saccades of either type were recorded for a participant, we computed the validity (e.g. proportion of valid trials) as (($n_{Anti}$+ $n_{Pro}$) / 160) * 100, where 160 is the number of trials presented to each participant.

For the analysis of the influence of aging on the saccade parameters, a linear ordinary least-squares regression between age and the respective measures was calculated. Additionally, the Pearson correlation coefficient and the corresponding p-value were derived from the linear regression. We also tested whether the slopes of resulting regressions were significantly different (Sachs, 2002). Throughout the entire article, significant regressions are shown by solid lines, whereas non-significant ones are indicated by dashed lines.

Any possible sex effects on saccade performance measures were analyzed using analysis of covariance (ANCOVA) with age as a covariate. Only the resulting population marginal means (PMM) which were adjusted for the effects of age are reported in the context of sex effects. All results were considered significant at an alpha level of 0.05.

# 3. Results

With respect to our research questions, two main findings of our study can be given:

1. SRTs and their SDs increased linearly with age, as did the variability of saccadic gains and the error rate. Validity and pro-saccadic peak velocities decreased with age. Saccadic gains, anti-saccadic peak velocities and the anti-effect were not affected by age.
2. Gender had no influence on validity, saccadic gains, pro-SRTs and the anti-effect. However, males had shorter anti-SRTs, less variability in SRTs of both saccade types and a lower error rate compared to females. In addition, the peak velocities of males were higher for both saccade types, although the difference only reached significance for pro-saccades.

## 3.1 Descriptive statistics

Descriptive values of our entire sample are shown in table 2.

| | | Mean | SD | Min. | Max. | Participants |
|---|---|---|---|---|---|---|
| **Age [years]** | **All** | 67 | 7 | 51 | 84 | 731 |
| | **Females** | 66 | 7 | 51 | 83 | 369 |
| | **Males** | 68 | 7 | 53 | 84 | 362 |
| **Number of saccades** | **Total** | 81 | 28 | 14 | 149 | 731 |
| | **Anti** | 37 | 25 | 0[a] | 126 | 731 |
| | **Pro** | 44 | 26 | 0[a] | 147 | 731 |
| **Validity [%]** | | 51 | 17 | 9 | 93 | 731 |
| **Error rate [%]** | | 55 | 23 | 0 | 100 | 731 |
| **Gain** | **Anti** | 0.85 | 0.16 | 0.47 | 1.39 | 685 |
| | **Pro** | 0.87 | 0.15 | 0.48 | 1.32 | 723 |
| **Gain SD** | **Anti** | 0.31 | 0.05 | 0.15 | 0.48 | 685 |
| | **Pro** | 0.25 | 0.06 | 0.1 | 0.4 | 723 |
| **SRT [ms]** | **Anti** | 345 | 62 | 187 | 615 | 685 |
| | **Pro** | 219 | 41 | 119 | 404 | 723 |
| **SRT SD [ms]** | **Anti** | 108 | 38 | 42 | 275 | 685 |
| | **Pro** | 89 | 38 | 21 | 228 | 723 |
| **Peak velocity [°/s]** | **Anti** | 328 | 67 | 88 | 646 | 685 |
| | **Pro** | 369 | 55 | 167 | 554 | 723 |
| **Anti-effect [ms]** | | 124 | 63 | -261 | 351 | 684 |

SD: Standard deviation, SRT: Saccadic Reaction Time

[a] The number of saccades for the computation of most of the other saccade parameters was at least 7 (see section 2.4).

**Table 2:** Descriptive statistics.

As Fig. 2 shows, there was a small but significant difference in the age distribution of the participants: The males (M) were on average 2 years older than females (F; ANOVA: $p < 0.001$).

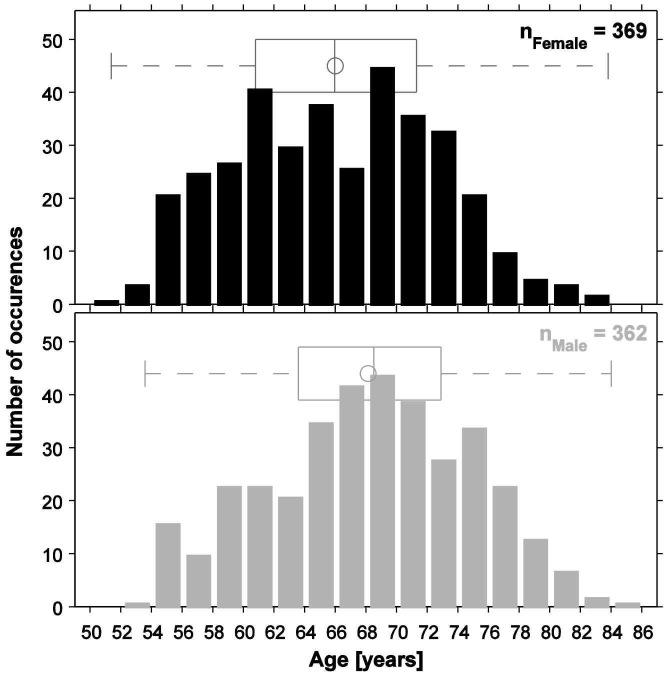

**Fig. 2:** Age distribution of the participants grouped by sex (black: females, light gray: males). The age difference between males and females is statistically significant ($p < 0.001$). Boxplots show 1st, 2nd and 3rd quartiles (box) and most extreme ages within 1.5 interquartile ranges from ends of the box (whiskers). Circles depict means. *n*: Number of participants.

## 3.2 Effects of age

Fig. 3 a depicts single eye position traces for all trials with a target at 5 ° eccentricity of a typical younger participant (M, age: 54 years, error rate: 13 %). Fig. 3 b shows according data for an older participant (M, age: 82 years, error rate: 70 %). The older participant made more pro-saccades and had longer and more variable SRTs compared to the younger participant.

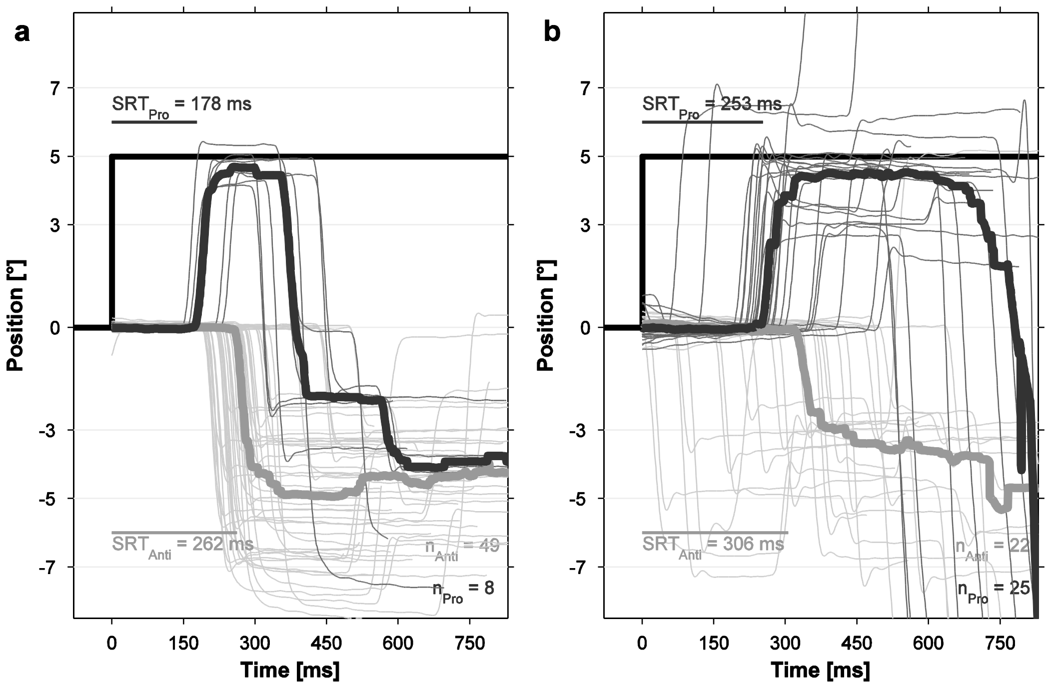

**Fig. 3:** Single trial eye position traces of **(a)** a younger participant (male, 54 years, validity 74 %, error rate 13 %) and **(b)** an older participant (male, 82 years, validity 46 %, error rate 70 %).Only valid trials are shown, where the target appeared at 5 ° (left and right trials are pooled). Trials in which the participants performed anti-saccades are shown in light gray; pro-saccade trials in dark gray. Bold lines represent medians. The thin black line shows the target. *n*: Number of valid saccades, *SRT*: Saccadic Reaction Time.

Over all participants, a significant positive correlation between age and validity was observed (slope: -0.3 %/year, intercept: 69 %, $R^2 = 0.011$, $p = 0.004$; see Supplemental figure F 2). A closer look at the exclusion criteria revealed that this effect was mainly driven by a significant age-related increase in the proportion of trials where the participants' either made a preliminary saccade (slope: 0.1 %/year, intercept: 8 %, $R^2 = 0.009$, $p = 0.013$; see Supplemental figure F 3) or no saccade at all (slope: 0.1 %/year, intercept: -0.9 %, $R^2 = 0.007$, $p = 0.02$; see Supplemental figure F 3).

The accuracy, as measured by the gain, on the other hand did not change with age (Anti: $p = 0.275$; Pro: $p = 0.452$; see Fig. 4 a). In contrast, the variabilities of the gains increased with age as shown in Fig. 4 b. This effect was weaker in anti-saccades (slope: 0.0006/year, intercept: 0.3, $R^2 = 0.008$, $p = 0.017$) than in pro-saccades (slope: 0.001/year, intercept: 0.2, $R^2 = 0.019$, $p < 0.001$), however, the slopes were not significantly different ($p = 0.102$).

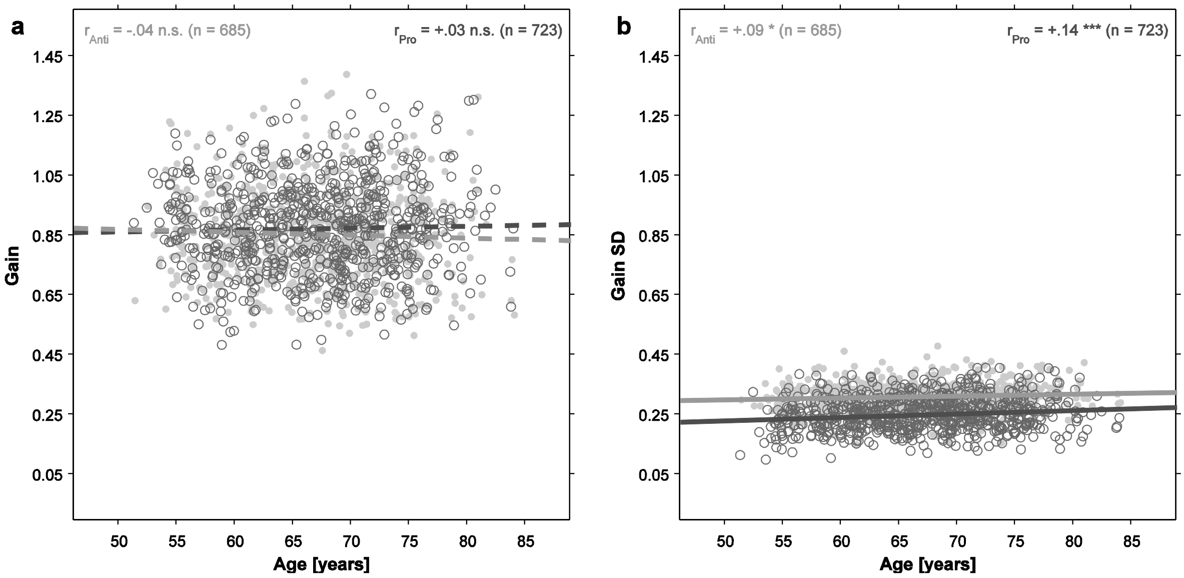

**Fig. 4:** Age correlation of **(a)** gain (not affected by age) and **(b)** intra-individual standard deviation of the gain. The linear regression slopes did not differ between saccade types. Anti-saccades are indicated by filled light gray circles; pro-saccades by open dark gray circles. Bold lines represent the resulting linear regressions (dashed: non-significant correlation, solid: significant correlation). *r*: Pearson correlation coefficients with according p-values (*n.s.*: $p > 0.05$, ***: $p \leq 0.05$, *****: $p \leq 0.001$), *n*: Number of participants, *SD*: Standard deviation.

With increasing age, SRTs increased for both anti-saccades (slope: 1.5 ms/year, intercept: 246 ms, $R^2 = 0.025$, $p < 0.001$) and pro-saccades (slope: 1.4 ms/year, intercept: 123 ms, $R^2 = 0.055$, $p < 0.001$) as shown in Fig. 5 a. The influence of age was equal for both saccade types and therefore the regression slopes were not significantly different ($p = 0.47$). As a consequence, the anti-effect did also not change with age as shown in Fig. 5 c ($p = 0.69$).

Fig. 5 b shows that the variabilities of SRTs also increased with age for anti-saccades (slope: 0.8 ms/year, intercept: 52 ms, $R^2 = 0.021$, $p < 0.001$) and pro-saccades (slope: 0.8 ms/year, intercept: 36 ms, $R^2 = 0.02$, $p < 0.001$). Again, the regression slopes were not differentially influenced by age ($p = 0.441$).

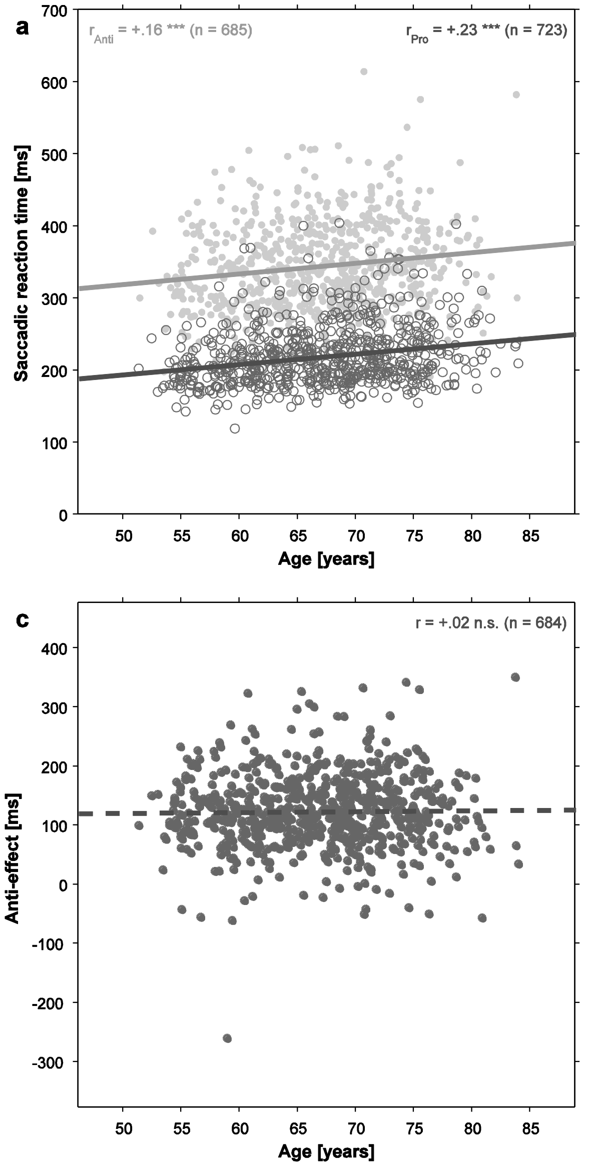

**Fig. 5:** Age correlation of **(a)** saccadic reaction time, **(b)** intra-individual standard deviation of the SRT and **(c)** anti-effect (e.g. difference of anti- and pro-SRT; not affected by age). The linear regression slopes did not differ between saccade types. Anti-saccades are indicated by filled light gray circles; pro-saccades by open dark gray circles. Bold lines represent the resulting linear regressions (dashed: non-significant correlation, solid: significant correlation). *r*: Pearson correlation coefficients with according p-values (*n.s.*: $p > 0.05$, *****: $p \leq 0.001$), *n*: Number of participants, *SD*: Standard deviation.

The analysis of the error rates shown in Fig. 6 a revealed a significant increase with age (slope: 0.6 %/year, intercept 18 %, $R^2 = 0.026$, $p < 0.001$).

With respect to the dynamic properties of saccades, a differential effect of age was found as shown in Fig. 6 b. Anti-saccadic peak velocities were not affected by age ($p = 0.896$), whereas pro-saccadic peak velocities decreased with age (slope: -0.7 °/(s·year), intercept: 417 °/s, $R^2 = 0.008$, $p = 0.019$). However, the difference in slopes did not reach significance ($p = 0.06$).

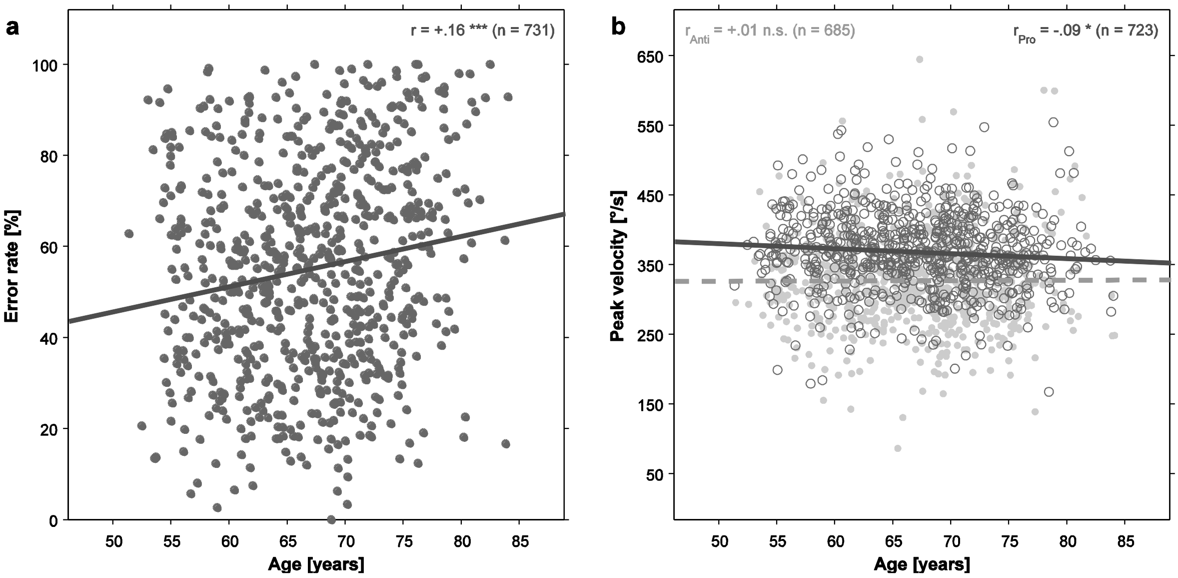

**Fig. 6:** Age correlation of **(a)** error rate and **(b)** saccadic peak velocity (only pro-saccadic peak velocities were affected by age). The linear regression slopes did not differ between saccade types. Anti-saccades are indicated by filled light gray circles; pro-saccades by open dark gray circles. Bold lines represent the resulting linear regressions (dashed: non-significant correlation, solid: significant correlation). *r*: Pearson correlation coefficients with according p-values (*n.s.*: p > 0.05, ***: p ≤ 0.05, *****: p ≤ 0.001), *n*: Number of participants.

## 3.3 Effects of sex

The effects of sex were determined by removing any influence of age by treating it as a covariate in an ANCOVA. In the following, only the age-adjusted PMM ± SE are reported.

There was no difference between the sexes in validity (F: 50 ± 1 %, M: 51 ± 1 %, p = 0.178; see Supplemental figure F 4 a), the gain of anti-saccades (F: 0.86 ± 0.01, M: 0.85 ± 0.01, p = 0.203; see Supplemental figure F 4 c) or the gain of pro-saccades (F: 0.88 ± 0.01, M: 0.86 ± 0.01, p = 0.107; see Supplemental figure F 4 c).

However, as Fig. 7 a shows, a differential influence of sex was found in the SRTs. Anti-saccades exhibited longer SRTs in females (F: 350 ± 3 ms, M: 338 ± 3 ms, p = 0.016), whereas pro-SRTs were not affected by sex (F: 221 ± 2 ms, M: 218 ± 2 ms, p = 0.338). Consequently, the anti-effect was higher in females, but this difference failed to reach significance (F: 128 ± 3 ms, M: 118 ± 3, p = 0.051, see Supplemental figure F 4 b).

In contrast, the variabilities of SRTs were equally influenced by sex as can be seen in Fig. 7 b. Females had higher SRT SDs for anti-saccades (F: 113 ± 2 ms, M: 104 ± 2 ms, p = 0.004) as well as pro-saccades (F: 93 ± 2 ms, F: 85 ± 2 ms, p = 0.007). The error rate of females was also higher compared to males as depicted in Fig. 7 c (F: 58 ± 1 %, M: 52 ± 1 %, p = 0.001).

Finally, as Fig. 7 d shows, the peak velocities of females were slower than that of males. This difference, however, was significant only in pro-saccades (F: 364 ± 3 °/s, M: 374 ± 3 °/s, p = 0.016) but not in anti-saccades (F: 323 ± 4 °/s, M: 332 ± 4 °/s, p = 0.07).

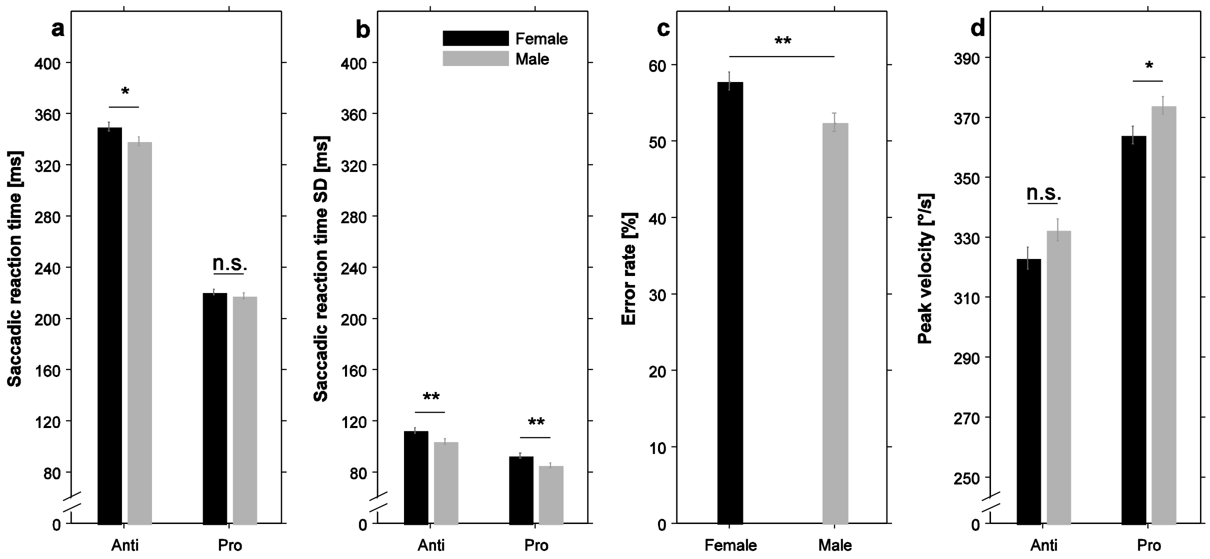

**Fig. 7:** Sex effects on **(a)** saccadic reaction time (only anti-saccades were affected by sex), **(b)** intra-individual SD of the saccadic reaction time, **(c)** error rate and **(d)** saccadic peak velocity (only pro-saccades were affected by sex). Bars show population marginal means obtained from the ANCOVA. Error bars represent the resulting standard errors of the means. *n.s.*: $p > 0.05$, ***: $p \leq 0.05$, ****: $p \leq 0.01$, *SD*: Standard deviation.

# 4. Discussion

## 4.1 Effects of age

### 4.1.1 General aspects

A very general finding of our study is that the ability to perform saccades, expressed as validity, decreased with age. Similar findings have also been reported by Butler *et al.* (1999). This detrimental effect could possibly hamper a careful analysis of any specific oculomotor parameter. In order to ensure the robustness of our analysis, we only included data with at least seven pro- or anti-saccades, respectively. In general, it seems that older subjects have more problems to maintain fixation and to suppress unwanted eye movements (Faust & Balota, 1997; Gottlob *et al.*, 2007) which is supported by the age-related increase in preliminary saccades found in our study. These fixation errors might be related to the increased sensitivity for distractors in older participants (Guerreiro *et al.*, 2010).

### 4.1.2 Saccadic reaction times and their variability relate to slowing of processing speed

In line with previous findings, SRTs increased with age (Abel *et al.*, 1983; Bono *et al.*, 1996; Olincy *et al.*, 1997; Munoz *et al.*, 1998; Butler *et al.*, 1999; Shafiq-Antonacci *et al.*, 1999; Klein *et al.*, 2005; Irving *et al.*, 2006; Raemaekers *et al.*, 2006; Fujiwara *et al.*, 2010; Harsay *et al.*, 2010; Peltsch *et al.*, 2011; Bonnet *et al.*, 2013). The effects found in the present study were equal for anti- and pro-SRTs and their SDs. Inconsistent evidence has been previously found, suggesting age-dependent differences between reflexive and voluntary saccades (Olincy *et al.*, 1997; Munoz *et al.*, 1998; Peltsch *et al.*, 2011) or the lack thereof (Butler *et al.*, 1999; Klein *et al.*, 2005). It is important to note that pro-saccades reported here are erroneously executed visually-guided saccades in the anti-saccade task, whereas in the other studies pro-saccades are measured in a separate visually-guided saccade task. Since different task instructions affect SRTs (Mosimann *et al.*, 2004; Taylor & Hutton, 2009), a comparison of ordinary visually-guided saccades and anti-saccades might be confounded by cognitive load differences between both tasks. Therefore, we are convinced that our method is not prone to such a confound, and enables an unambiguous comparison of pro- and anti-saccades without the disadvantage of different instruction.

The general increase in reaction times found in the elderly is accompanied by a shift in activity from posterior to frontal brain areas for pro- and anti-saccades (Raemaekers *et al.*, 2006). Cortical processing of visual information starts in the primary visual cortex (Brodmann area 17) until it reaches the eye movement related areas such as FEF, SEF or PEF as well as the midbrain SC. In monkeys, it has been shown that saccades can be elicited by intra-cortical micro-stimulation as early as in the primary visual cortex (Tehovnik *et al.*, 2003). Studies exploring the anatomical and neurophysiological age-related changes in monkeys found that the neurons in the primary visual cortex show decreased selection selectivity (Schmolesky *et al.*, 2000; Fu *et al.*, 2013). This may lead to a worse signal-to-noise ratio quite early in visual processing and therefore may ultimately increase RTs in all visual tasks. Neuro-imaging evidence in humans suggests that the elderly exhibit decreased parietal activation underlying the anti-saccade task compared to young individuals (Alichniewicz *et al.*, 2013). Taken together, the changes in SRTs related to healthy aging may not be specifically attributed to pronounced changes of the function of a certain brain area, but rather reflects the general slowing of processing in the entire elderly brain (Salthouse, 2000).

A last comment relates to the existence of this slowing. Recently, it was proposed that the slowing might not represents cognitive decline, but rather reflects the consequence of lifelong learning (Ramscar *et al.*, 2014). As attractive the idea of a lifelong increase of vocabulary is, it does not apply to the age-related decline of saccadic eye movements. There is definitively no lifelong accumulation of possible target locations for saccadic eye movements.

### 4.1.3 Error rates as a measure of frontal lobe function

Increased error rates in the elderly have been found in the current study and have been reported before (Olincy *et al.*, 1997; Butler *et al.*, 1999; Shafiq-Antonacci *et al.*, 1999; Raemaekers *et al.*, 2006; Fujiwara *et al.*, 2010; Peltsch *et al.*, 2011; Bonnet *et al.*, 2013). In all anti-saccade studies, the error rate is a direct measure for inhibitory control of the frontal lobe. Therefore, the increased error rates clearly indicate a general decline of frontal function in the elderly (Madden *et al.*, 2010), especially in inhibitory control (Dempster, 1992; West, 1996).

An open question at present is whether the increased error rate might reflect age-related changes in the posterior parietal cortex, as it was proposed that this area might be important with respect of the inhibition of the reflexive saccades towards the target (Pierrot-Deseilligny *et al.*, 2005).

### 4.1.4 Saccade accuracy and variability indicate loss in resolution

While mere visuo-motor demands in the anti-saccade task might increase at higher age, the accuracy of saccades, as measured by the gain, did not change. This corresponds to previous findings (Bono *et al.*, 1996; Olincy *et al.*, 1997; Butler *et al.*, 1999; Shafiq-Antonacci *et al.*, 1999; Irving *et al.*, 2006; Pratt *et al.*, 2006; Gottlob *et al.*, 2007; Harsay *et al.*, 2010; Klein *et al.*, 2010) and shows that the core function of the saccadic system, i.e. precisely moving the eyes to a target location, is preserved. Although the accuracy of the system remains intact, it seems that its precision decreases, since the saccadic endpoint variability, as measured by the gain SDs, increased with age. It is difficult to disentangle whether the increase in variability is related to age-related changes in sensory processing or motor preparation. In favor of changes in the sensory processing are the above mentioned changes in the selectivity in primary visual cortex. Changes in motor preparation on the other hand could be due to age-related changes in the cerebellum (see below). In summary, the oculomotor control does not differ from the skeletal control which is also characterized by an age-related increase in spatial and temporal variability (Seidler *et al.*, 2010).

### 4.1.5 Dynamic saccade parameters are determined by the brainstem

It is important to note that the selection of saccade direction as well as the SRTs are a direct outcome of the cortical eye fields and the SC. The kinematic saccade properties like the peak velocity are determined by the saccade generators located in the paramedial pontine reticular formation (PPRF) and rostral interstitial medial longitudinal fasciculus (riMLF), respectively (Scudder *et al.*, 2002; Sparks, 2002). With respect to the influence of age on saccadic peak velocities, results in the literature do not give a consistent image. On one hand, there are reports of unchanged peak velocity emphasizing that the function of the saccade generators is resistant to aging (Munoz *et al.*, 1998; Shafiq-Antonacci *et al.*, 1999; Pratt *et al.*, 2006; Bonnet *et al.*, 2013). On the other hand, some studies have shown slowed saccades in the elderly (Abel *et al.*, 1983; Wilson *et al.*, 1993; Bono *et al.*, 1996; Irving *et al.*, 2006; Velazquez-Perez *et al.*, 2009; Mirsky *et al.*, 2011).

Somehow, our own results parallel this inconsistency: We found that pro-saccadic peak velocity was slightly negatively affected by age, whereas there was no change in anti-saccadic peak velocity. Theoretical considerations about the control strategy for saccade trajectory might help to clarify this issue. Recently, it was suggested that the main sequence results from an optimal control model according to a kinematic speed-accuracy trade-off and confronted to signal dependent noise (Harris & Wolpert, 2006). Interestingly, since the variability of the anti-saccadic gain (expressed in the model as fixation error) is much larger compared to pro-saccades, this model is able to explain the generally higher pro-saccadic peak velocities (Smit *et al.*, 1987) also found here. From the stronger increase in pro-saccadic gain variability, the model also predicts the observed age-related reduction in the peak velocity of pro-saccades only, since the fixation cost increase.

Finally, it must be noted that the output of the brainstem saccade generator is modulated by the cerebellum (Thier *et al.*, 2000). The possibilities to adapt the amplitude of saccades as well as to counteract fatigue are two additional functions of the cerebellum (Prsa & Thier, 2011). Hence, the age-related changes in the dynamic saccade properties clearly demonstrate that cerebellar function is also influenced by age, which could be explained by an age-related cerebellar grey matter loss (Good *et al.*, 2001; Raz *et al.*, 2001).

## 4.2 Effects of sex

Our study is, to our knowledge, the first which analyzed sex effects on oculomotor behavior in a large sample of elderly participants. We applied an ANCOVA to remove the pronounced effect of age on the saccade parameters, which may hide potential sex effects in other studies. Li *et al.* (2012) reported higher error rates in females but no differences in SRTs, whereas Bonnet *et al.* (2013) failed to find any influences of sex. The small but differential effect of sex on SRTs and peak velocities presented here might only be visible because of the large sample size used. Although small, it is an important observation and emphasizes the need to control for sex when planning group comparisons using the anti-saccade task.

## 4.3 Methodological considerations

A general problem with the anti-saccade task is the speed-accuracy trade-off, i.e. participants with long SRTs have lower error rates compared to participants with short SRTs. Indeed, it has been explicitly shown that there are two groups of anti-saccade performers: those with short SRTs and higher error rates and vice versa (Li *et al.*, 2012). In the same vein, we recently reported that there was a negative slope in the regression between error rates and SRTs in the comparison of video-game players and non-players (Mack & Ilg, 2014). In theory, participants could voluntarily change their strategy from shorter reaction times and higher error rates to longer reaction times and lower error rates. Our approach to measure only a single block of trials and to define pro-saccades as the erroneous saccades directed towards the visual target was intended to avoid this strategy change. Nevertheless, if the age effects presented here would have been caused by a mere strategy change in the elderly, error rates should have declined with increasing SRTs. Obviously, our results speak to the contrary, since both SRTs and error rates increased with age.

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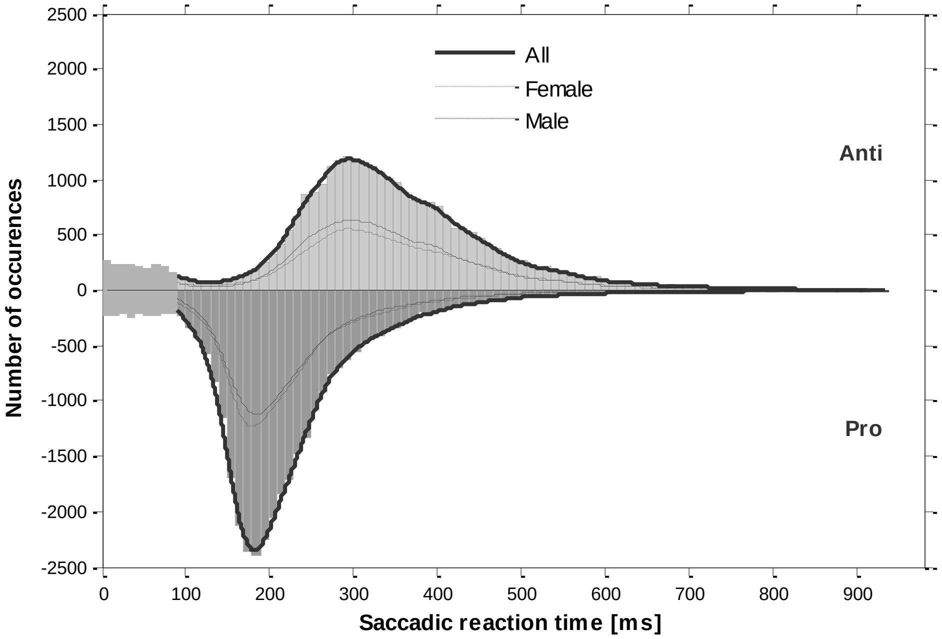
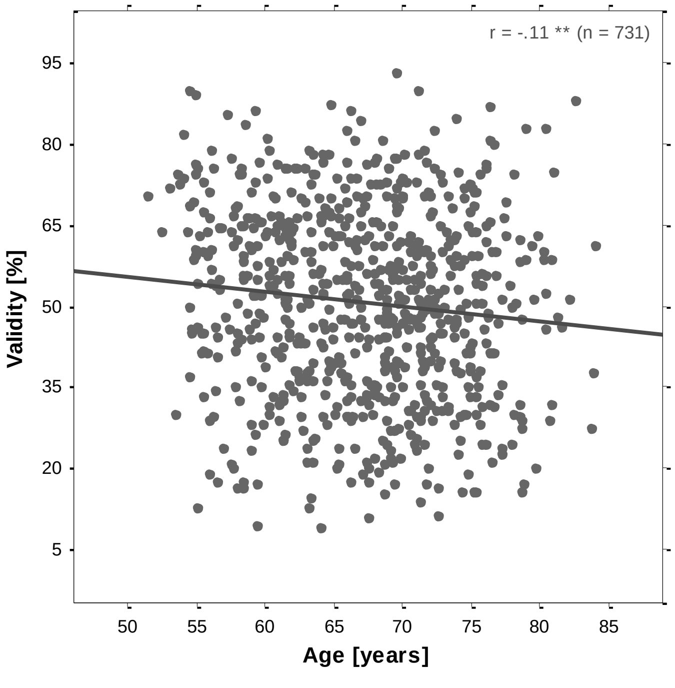
# Supplemental figures

## F 1: SRT distribution



Black lines show the smoothed distribution for the valid saccades (nAnti = 26705, nPro = 32511). The gray area below 90 ms shows excluded preliminary saccades (nAnti = 2004, nPro = 2052).

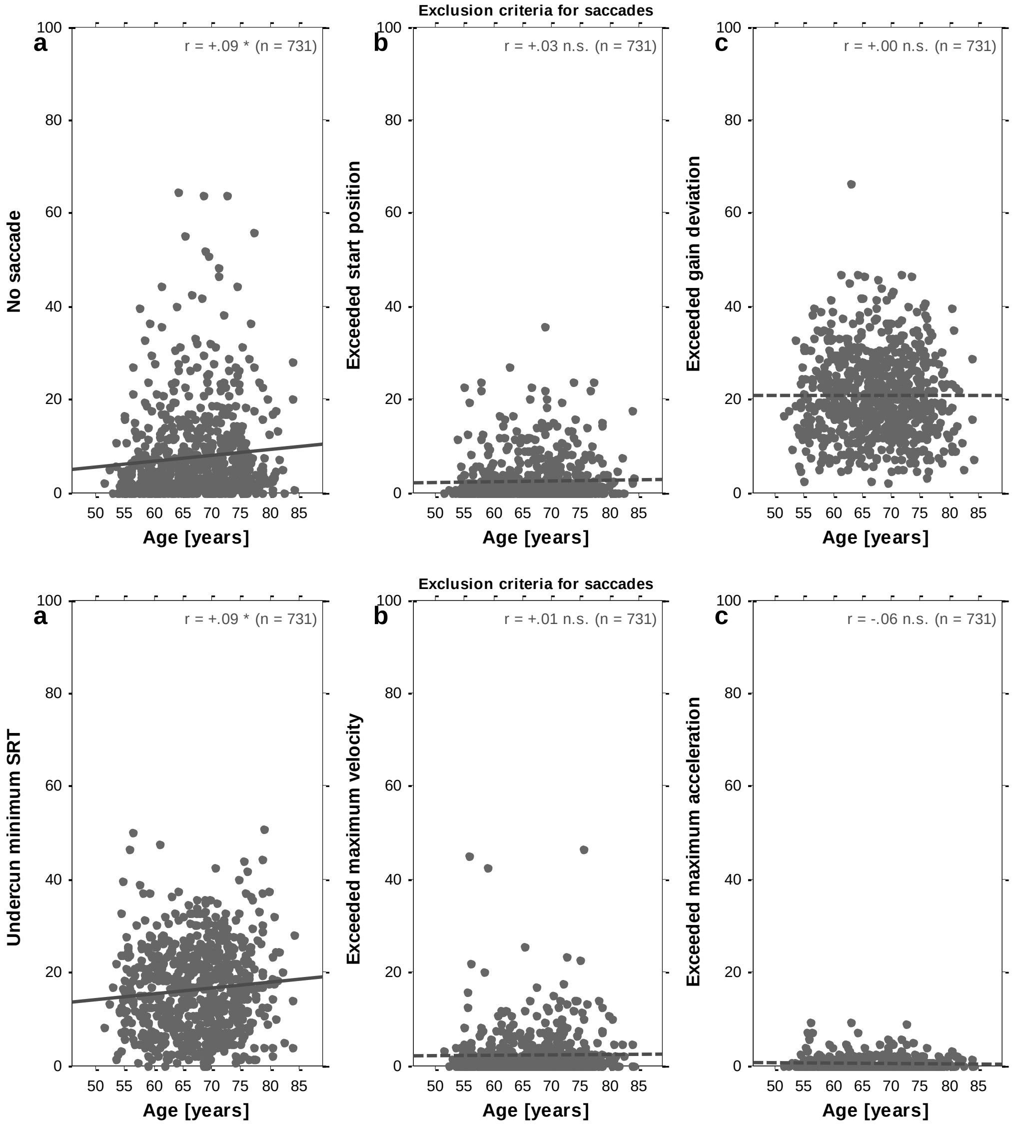
## F 2: Validity



*r*: Pearson correlation coefficient with according p-value (****: p ≤ 0.01), *n*: Number of participants.

| | **Slope [%/year]** | **Intercept [%]** | **$R^2$** | **p** |
|---|---|---|---|---|
| **Validity** | -0.3 | 69 | 0.011 | 0.004 |

# F 3: Saccade exclusion criteria

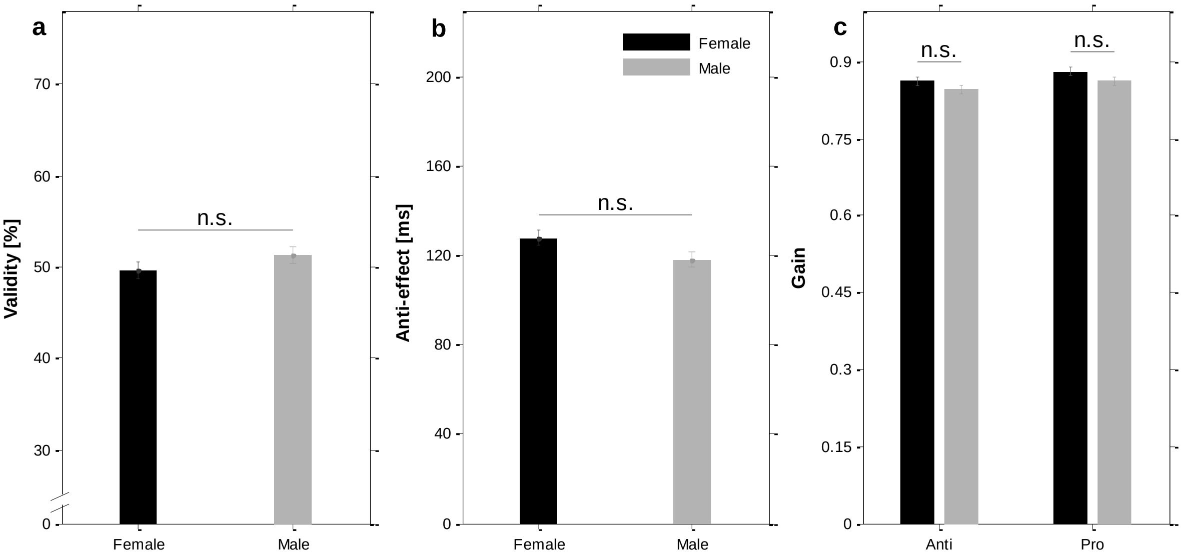


*r*: Pearson correlation coefficients with according p-values (*n.s.*: p > 0.05, ***: p ≤ 0.05), *n*: Number of participants.

The lower row corresponds to the exclusion criteria d), e), f).

| Exclusion criterion | Slope [%/year] | Intercept [%] | $R^2$ | p |
|---|---|---|---|---|
| **a) No Saccade** | 0.1 | -0.9 | 0.007 | 0.02 |
| **b) Position** | - | - | - | 0.43 |
| **c) Gain** | - | - | - | 0.915 |
| **d) SRT** | 0.1 | 8 | 0.009 | 0.013 |
| **e) Velocity** | - | - | - | 0.693 |
| **f) Acceleration** | - | - | - | 0.105 |

## F 4: Sex effects



*n.s.*: p > 0.05

| | | PMM ± SE | | p(F≠M) |
|---|---|---|---|---|
| | | **Female** | **Male** | |
| **Validity** | | 50 ± 1 | 51 ± 1 | 0.178 |
| **Anti-effect** | | 128 ± 3 | 118 ± 3 | 0.051 |
| **Gain** | **Anti** | 0.86 ± 0.01 | 0.85 ± 0.01 | 0.203 |
| | **Pro** | 0.88 ± 0.01 | 0.86 ± 0.01 | 0.107 |
| PMM: Population marginal mean from ANCOVA, SE: Standard error, p(F≠M): P-value from ANCOVA for the difference between females and males | | | | |

# Supplemental tables

## T 1: Additional descriptive statistics

| | | Mean | SD | Min. | Max. | Participants |
|---|---|---|---|---|---|---|
| **Calibration duration [s]** | | 256 | 146 | 65 | 2239 | 732 |
| **Number of invalid saccades** | | 77 | 28 | 11 | 151 | 732 |
| **$R^2$ for peak velocity regression[a]** | **Anti** | 0.67 | 0.21 | 0.01 | 1 | 692 |
| | **Pro** | 0.8 | 0.14 | 0.03 | 0.98 | 724 |
| **Trial exclusion[b] [%]** | **a) No Saccade** | 8 | 10 | 0 | 64 | 732 |
| | **b) Position** | 3 | 5 | 0 | 36 | 732 |
| | **c) Gain** | 22 | 9 | 3 | 66 | 732 |
| | **d) SRT** | 13 | 8 | 0 | 43 | 732 |
| | **e) Velocity** | 2 | 4 | 0 | 46 | 732 |
| | **f) Acceleration** | 0 | 1 | 0 | 9 | 732 |

SD: Standard deviation, SRT: Saccadic Reaction Time

[a] See section 2.5 for details on the computation of the linear regression.

[b] See section 2.4 for a detailed description of the exclusion criteria.

# Supplemental material

## M 1: Study protocol

Der Proband soll das Kinn gut auf die Kinnstütze auflegen und die Stirn muss an das Stirnband angelegt sein. Die Unterarme sollen locker auf dem Tisch liegen. Das Gewicht sollte nach vorne auf die Kopfstütze und die Arme verlagert werden. Zur weiteren Fixierung wird das Kopfband um den Kopf des Patienten gelegt.

***„Ich unterstütze jetzt Ihren Kopf mit einem Band. Dadurch wird Ihr Nacken während der Messung entlastet. Außerdem wollen wir verhindern, dass die Messung durch kleine Bewegungen verfälscht wird, der Augenpositionssensor ist nämlich sehr empfindlich."***

### *Kalibration*

Der Sensor wird vor dem linken Auge des Patienten eingestellt.

***„Ich stelle jetzt den Augenpositionssensor vor ihrem linken Auge ein. Bitte schauen Sie dabei in die Mitte des Bildschirms."***

Hierbei sollte darauf geachtet werden, dass der Proband auch beim Einstellen des Sensors auf den Bildschirm sehen kann und nicht durch den Kopf des Versuchsleiters blockiert wird. Danach wird der Offset und die Verstärkung der IRIS eingestellt.

***„Ich stelle jetzt die Empfindlichkeit der Apparatur ein. Bitte fixieren Sie zunächst das weiße Kreuz in der Mitte, jetzt das linke, jetzt das rechte…Lassen Sie sich nicht durch den roten Punkt irritieren, dieser wird von mir eingestellt, bitte nur auf die Kreuze schauen"*** usw. beliebig wiederholen.

Nach erfolgter Kalibration:

***„Ab jetzt bitte nicht mehr sprechen und nicht mehr bewegen. Stellen Sie sich am besten vor, Sie wären eine Salzsäule."***

Bei langwieriger Kalibration vor nächster Messung:

***„ Schließen Sie kurz die Augen, damit Sie sich erholen können."***

### *Erklärung smooth pursuit*

***„Wir bitten Sie nun, dem Punkt auf dem Bildschirm ganz genau hinterher zu schauen, ohne dabei den Kopf oder Körper zu bewegen. Versuchen Sie dabei bitte nicht zu blinzeln. Wir machen die Messung 5 Mal."***

### *Erklärung Antisakkaden Task anhand Demo*

***„Bitte schauen Sie zunächst auf das Kreuz in der Mitte. Sobald ein kleines weißes Kästchen links oder rechts davon erscheint, schauen sie bitte genau in die spiegelbildlich entgegen gesetzte Richtung .Wenn das Kreuz also 5cm links des Kreuzes erscheint, schauen Sie bitte 5cm rechts des Kreuzes.***

***Wenn Sie einen Fehler gemacht haben, macht das überhaupt nichts, einfach weiter machen. Selbst unser Professor, der den Versuch entworfen hat, hat eine Fehlerquote von 70%, vielleicht machen Sie es sogar besser!***

***Schauen sie erst wieder zurück in die Mitte, wenn das Kreuz wieder erscheint."***

### *Erklärung Testdurchlauf Antisakkaden*

***„Ich zeige Ihnen jetzt noch, in welcher Geschwindigkeit die Messung ablaufen wird.***
***Haben Sie noch Fragen? Wenn ja stellen Sie sie bitte jetzt!"***

### *Erneute Kalibration*

***„Ich überprüfe jetzt noch einmal die Einstellung der Apparatur. Bitte schauen Sie in auf das Kreuz in der Mitte, nach links, nach rechts …."*** **(siehe oben)**

Nach erfolgter Kalibration:

***„Sie sind jetzt wieder eingestellt, bitte ab jetzt nicht mehr sprechen und nicht mehr bewegen.“***

### *Antisakkadenmessung*

**„Wir machen nun die Messung, diese dauert 6 Minuten.“**

Alle 40 Durchläufe „Anfeuern“ des Probanden

1. ***„Sie haben jetzt das erste Viertel geschafft. Bleiben Sie dran, weiter so!“***
2. ***„Jetzt ist Halbzeit. Bitte schauen Sie auch weiterhin immer in die entgegengesetzte Richtung der Kästchen.“***
3. ***„Prima, Sie haben schon drei Viertel geschafft. Jetzt kommt noch der Endspurt!“***

## 4.4 Study 4: Influence of healthy aging on perceptual learning and performance in a predictive pursuit task: Results from the TREND study

| | |
|---|---|
| **Authors** | David J. Mack, Lena Stetz, Sandra Lachenmaier, Leonie Gugolz, Karin Srulijes, Gerhard W. Eschweiler, Walter Maetzler, Daniela Berg and Uwe J. Ilg |
| **Journal** | Prepared for submission to *Experimental Brain Research* |
| **Reference** | Mack et al., 2015b |

### Abstract

Pursuit eye movements enable us to analyze moving targets with the high spatial resolution of our fovea. Pursuit is closely linked to motion processing and is controlled by parietal and frontal cortex as well as brainstem and cerebellum. The pursuit system is an ideal model for the examination of age-related changes in the human brain. Unfortunately, there is large inter- and intra-individual variability in pursuit performance, making it difficult to pin down the sometimes small age-related alterations. Therefore, we analyzed pursuit performance in 976 healthy, non-demented participants (51–85 years). To see the stability of pursuit performance, and if short-term plasticity is altered by age, we quantified fast learning trajectories over the course of 5 trials. We found general improvements in number and amplitude of catch-up saccades (CUS) as well as the latency of the initial CUS. Peak velocity of CUS decreased, too. Pursuit gain and duration were not affected. Most importantly, learning trajectories did not differ with age. Overall however, age impaired number, amplitude and peak velocity of CUS, pursuit gain and duration. No change in initial CUS latency was found. The intra-individual variability increased with age for all parameters except for CUS peak velocity and initial CUS latency. Our results provide normative data for a simple and easy-to-use pursuit task, and shows clearly the age-dependency of the pursuit system. These data may be used for early identification of normal and pathological aging processes in the brain.

### Statement of contributions

The data for this study were collected together with the data for the third study (Mack et al., 2015a) and similar contributions apply, except for the analysis, which was done by myself, and the manuscript, which was created by myself and Uwe J. Ilg.

# INFLUENCE OF HEALTHY AGING ON PERCEPTUAL LEARNING AND PERFORMANCE IN A PREDICTIVE PURSUIT TASK: RESULTS FROM THE TREND STUDY

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# 1. Introduction

## 1.1 Smooth pursuit and saccadic eye movements

Many animals possess a fovea, primates, for example but not rabbits (Hughes 1977). This central part of the retina has an enormously high spatial resolution. Smooth pursuit eye movements (SPEM) keep a moving part of the retinal image in the fovea to optimally exploit the high resolution of this tiny part of the retina. The “delivery” system, which project peripheral images onto the fovea, generates fast, jerky eye movements called saccades. These eye movements are highly optimized for speed as well as accuracy. Their peak velocity and amplitude form a characteristic, near-linear relationship known as the *main sequence* (Bahill et al. 1975; Baloh et al. 1975). Thus, in contrast to other goal-directed body movements, saccades exhibit similar peak velocities for similar amplitudes. Where the saccade system tries to minimize landing error and flight time (Harris and Wolpert 2006), the pursuit system mainly minimizes retinal slip (e.g. relative retinal target velocity) but also involves retinal image position and acceleration (Blohm et al. 2005; Lisberger et al. 1987). It can even be modeled with non-retinal controllers (Dicke and Thier 1999; Robinson et al. 1986) or combining retinal and extra-retinal predictive information in two Kalman filters (Orban de Xivry et al. 2013).

From the external motion signal, an internal representation of target motion in space is generated. In primates it has been shown, that specialized tracking neurons code object motion in world coordinates independently of retinal slip (Ilg et al. 2004; Thier and Erickson 1992). This internal representation is influenced by top-down information, like anticipation and prediction (Fukushima et al. 2002; Ilg 2003; Kattoulas et al. 2011; Sprenger et al. 2011), even enabling pursuit in the absence of a target. The presence of an internal representation of target motion shows the close relationship between movement perception and the SPEM. In patients with extensive saccadic intrusions during pursuit, movement perception is severely impaired (Haarmeier and Thier 1999) and direction prediction is improved if a moving target is traced with SPEM (Spering et al. 2011).

In general the saccade and pursuit systems are behaviorally and cortically separated. During SPEM, catch-up saccades are only executed in the initial phase, when the target has to be place on the fovea, and during the closed-loop stage, if the target cannot be brought back to the fovea by sole SPEM (de Brouwer et al. 2002b). Although these are two different systems, there is a strong interaction between them. In contrast to saccades to stationary targets, which only compensate for retinal position error, catch-up saccades also incorporate retinal slip and thus show, that the saccade and pursuit system are intermingled (de Brouwer et al. 2002a).

With respect to the neuroanatomy, proper execution of saccades involves the posterior parietal cortex (PPC) and its parietal eye field (PEF), the superior colliculus (SC) in the midbrain and the saccade generators in the brain stem (Pierrot-Deseilligny et al. 1991). Pursuit control on the other hand depends on two key areas in the parietal cortex. The middle temporal area (MT/V5) codes retinal image motion (Lisberger and Movshon 1999), whereas middle superior temporal area (MST) represents target motion in extra-personal space (Ilg et al. 2004). In addition, the frontal pursuit area creates top-down signals for trajectory prediction (Fukushima et al. 2002). Subcortically, pursuit control involves cerebellar and pontine regions, where the parietal and frontal signals converge. For a detailed review on the neuronal basis of pursuit eye movements see (Ilg and Thier 2008; Thier and Ilg 2005).

## 1.2 Perceptual learning in aging

In many visual tasks, participants' performance improves rapidly over several trials and after some time also between trials. These two learning processes have been termed fast and slow perceptual learning and may pertain for several years (Fahle and Edelman 1993; Karni and Sagi 1993; Poggio et al. 1992). Perceptual learning has been associated with plasticity in early visual processing areas of the adult brain (e.g. (Ball and Sekuler 1987)). Recently, it was found that this plasticity is retained with age, e.g. there is no decline in perceptual learning in the elderly (Chang et al. 2014). Supporting this idea, no age-related differences in learning trajectories have been found (Fahle and Daum 1997; McKendrick and Battista 2013).

Since pursuit performance relies on global cortical functioning and is closely related to motion perception, it may be especially susceptive to age-related decline. Therefore we wanted to see how fast learning in a pursuit task is affected by age. A potential effect may then be visible in different learning trajectories.

## 1.3 Oculomotor aging

Since, the two systems for goal directed eye movement involve brain-wide networks, we turned towards pursuit eye movements to identify changes in normal, healthy aging. Sharpe and Sylvester (1978) have already pointed out that "smooth pursuit is an age dependent motor system". Several studies showed age-related changes in pursuit performance in a variety of different tasks. Table 1 gives a quite extensive review on the literature on aging in the pursuit system.

| | | | | | | Age-related changes | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | **#** | **Age** | **Stimulus** | **Gain** | **Latency** | **$n_{Saccades}$** | **Variability** |
| Grouped comparison | **Kuechenmeister** | **1977** | 20[f] | 20-30 | Sin, Tri | –[g] | | | |
| | | | 20[f] | >50[3] | | | | | |
| | **Sharpe** | **1978** | 15 | 19-32 | Tri | – | + | +[b] | |
| | | | 10 | 65-77 | | | | | |
| | **Spooner** | **1980** | 25 | 22-64 | SR | –[a] | | | +[2] |
| | | | 14 | 50-85 | | | | | |
| | **Hutton** | **1983** | 19 | 23-36 | Sin | –[e] | | + | +[2] |
| | | | 32 | 56-84 | | | | | |
| | **Kaufman** | **1986** | 13 | 21-34 | Tra | –[5] | | | |
| | | | 12 | 64-88 | | | | | |
| | **Zackon** | **1987** | 10 | 35-63 | Sin, Tri | – | | | |
| | | | 11 | 66-87 | | | | | |
| | **Larsby** | **1988** | 10 | 7-15 | Sin | – | | +[c] | |
| | | | 10 | 22-56 | | | | | |
| | | | 10 | 62-85 | | | | | |
| | **Curthoys** | **1992** | 20 | 18-34 | SR | –[a,2] | | +[2] | |
| | | | 17 | 35-49 | | | | | |
| | | | 14 | 50-64 | | | | | |
| | | | 8 | ≥ 65 | | | | | |
| | **Morrow** | **1993** | 6 | 29-35 | SR | –[a] | = | | [4] |
| | | | 5 | 60-76 | | | | | |
| | **Kanayama** | **1994** | 10 | 23-33 | Sin | – | | | |
| | | | 10 | 50-59[3] | | | | | |
| | | | 10 | 60-69[3] | | | | | |
| | | | 10 | >70[3] | | | | | |
| | **Moschner** | **1994** | 23 | 18-43 | Sin | – | | | + |
| | | | 57 | 75-93 | | | | | |
| | **Paige** | **1994** | 30 | 18-44 | Sin | – | | | |
| | | | 23 | 45-69 | | | | | |
| | | | 20 | 70-89 | | | | | |
| | **Handke** | **1999** | 11 | 21-30 | SR | –[6] | +[6] | | |
| | | | 10 | 53-72 | | | | | |
| | **Sakuma** | **2000** | 26 | 22-46 | SR | –[h] | +[2] | | +[2] |
| | | | 23 | 50-72 | | | | | |
| | **Knox** | **2005** | 10 | 19-26 | SR | | + | | +[2] |
| | | | 15 | 64-81 | | | | | |
| | **Fukushima** | **2014** | 14 | 19-24[3] | Mem, SR | –[a] | + | | |
| | | | 11 | 65-89 | | | | | |
| Age correlation | **Langenegger** | **1988** | 21 | 8-74 | Sin, Tri | = | | = | [4] |
| | **Bono** | **1996** | 66 | 5-90 | Sin | –[a] | | | |
| | **Ross** | **1999** | 64 | 18-70 | Tra | – | | +[b] | |
| | **Ettinger** | **2004** | 24 | 16-40[3] | Tra | | | +[b,6] | |
| | **Kattoulas** | **2011** | 1187 | 18-25 | Tri | (=[d]) | (=[d]) | | |
| | **Sprenger** | **2011** | 45 | 20-75 | SR, Tri | –[a,1] | +[1] | | |
| | **Bonnet** | **2013** | 145 | 19-82 | Sin | = | | | |
| * | **Kerber** | **2006** | 53 | 75-84 | Sin | = | | | |

* Longitudinal study (9-years follow-up), *#*: Number of participants, *Mem*: Memory-based, *$n_{Saccades}$*: Number of saccades, *Sin*: Sinusoidal, *SR*: Step-Ramp, *Tri*: Triangular, *Tra*: Trapezoidal

[a] Derived from velocity
[b] Derived from frequency of saccades
[c] Derived from frequency of saccades with higher amplitude
[d] Reported in relation to target blanking
[e] Derived from cross-correlation coefficient
[f] Pooled over sex groups
[g] Derived from five-point scoring method
[h] Derived from retinal slip velocity correlation

[1] Only for step-ramp
[2] Only by trend/anecdote
[3] No detailed information given
[4] Found to be generally high
[5] Only for fast targets
[6] Only for slow targets

**Table 1: Previous work on the influence of healthy aging on pursuit performance.** Age-related changes are indicated by symbols (+: increase, =: no change, −: decrease). For grouped comparisons, the age groups are indicated independently. In studies with patients, only the results for healthy controls are considered.

Most of the studies agree, that pursuit performance (measured by eye velocity or velocity gain) decreases with age (Bono et al. 1996; Curthoys et al. 1992; Fukushima et al. 2014; Handke and Buttner 1999; Hutton et al. 1983; Kanayama et al. 1994; Kaufman and Abel 1986; Kuechenmeister et al. 1977; Larsby et al. 1988; Morrow and Sharpe 1993; Moschner and Baloh 1994; Paige 1994; Ross et al. 1999; Sakuma et al. 2000; Sharpe and Sylvester 1978; Spooner et al. 1980; Sprenger et al. 2011; Zackon and Sharpe 1987), whereas pursuit latency (Fukushima et al. 2014; Handke and Buttner 1999; Knox et al. 2005; Sakuma et al. 2000; Sharpe and Sylvester 1978; Sprenger et al. 2011) and the number of catch-up saccades increase (Curthoys et al. 1992; Ettinger et al. 2004; Hutton et al. 1983; Larsby et al. 1988; Ross et al. 1999; Sharpe and Sylvester 1978). On a closer look, there have also been negative findings for some of these parameters (Bonnet et al. 2013; Kattoulas et al. 2011; Kerber et al. 2006; Langenegger and Meienberg 1988; Morrow and Sharpe 1993). With respect to the inter-individual variability of the parameters, there seems to be an increase with age (Hutton et al. 1983; Knox et al. 2005; Moschner and Baloh 1994; Sakuma et al. 2000; Spooner et al. 1980) but most reports are either anecdotally or only briefly mentioned. This is interesting, since high inter-individual variability may be a main cause for some of the negative findings. In this line of thought, Langenegger and Meienberg (1988) called for “data from a representative number of adolescent subjects”. Since then, there has been only one study that examined pursuit performance in a huge sample (Kattoulas et al. 2011). This study however was confined to young adults and thus, age-related data from a huge sample is still missing.

### 1.4 Research Agenda

We wanted to supply normative data from a large number of participants to overcome the high inter-individual variability in pursuit performance measures and thus clarify some of the controversial findings. Since our data should be of use in every-day clinical examinations, we chose a very simple, easily applicable predictive pursuit task for our study. In addition, we carefully analyzed catch-up saccades to tap into age-related changes in the saccade system. We also examined perceptual learning trajectories in old age by looking at the change in parameters over repeated trials. If plasticity is retained with age and pursuit impairments are compensated only in the beginning, we expected to see different learning trajectories over several trials in younger and older participants.

## 2. Methods

### 2.1 Participants

From the **T**übinger evaluation of **R**isk factors for **E**arly detection of **N**euro-**D**egeneration (TREND) study (Berg and Eschweiler), 976 healthy non-demented elderly participants (472 females, 504 males) were measured. To be included in the TREND-study, participants had to lack any reported history of psychiatric diseases, dementia, epilepsy, stroke, multiple sclerosis or encephalitis. In addition, participants were only evaluated, if no disorder was assessed, which would have prevented study completion, like paresis, severe sensory dysfunction or the inability to walk without assistance (Hobert et al. 2011). A detailed description of inclusion/exclusion criteria to the TREND-study can be found in (Berg 2012).

All experiments were performed in accordance with the Declaration of Helsinki and approved by the Ethic Commission of the local Medical Faculty.

## 2.2 Experimental setup

Horizontal eye movements were recorded from the left eye with a limbustracker (Skalar IRIS, Skalar Medical B.V., Delft, Netherlands; spatial resolution 2 arcmin, sampling rate 1 kHz). All stimuli were generated with the Psychophysics Toolbox version 3 (Brainard 1997; Kleiner et al. 2007; Pelli 1997) under Matlab R2008a (The MathWorks Inc., Natick, MA, 2008) and presented on a 23 " LED screen (Fujitsu P23T-6 LED; resolution: 1920x1080 px, pixel pitch: 0.265 mm, refresh rate: 60 Hz, response time: 5 ms). The pursuit target was a white square (luminance 58 cd/m$^2$, size 13 x 13 arcmin) on a black background (luminance ≤ 0.1 cd/m$^2$). Viewing distance to the screen was kept constant at 57 cm through a head- and chin-rest. Participants' were strapped to the head rest during the whole measurement to minimize movement artefacts (see figure 1).

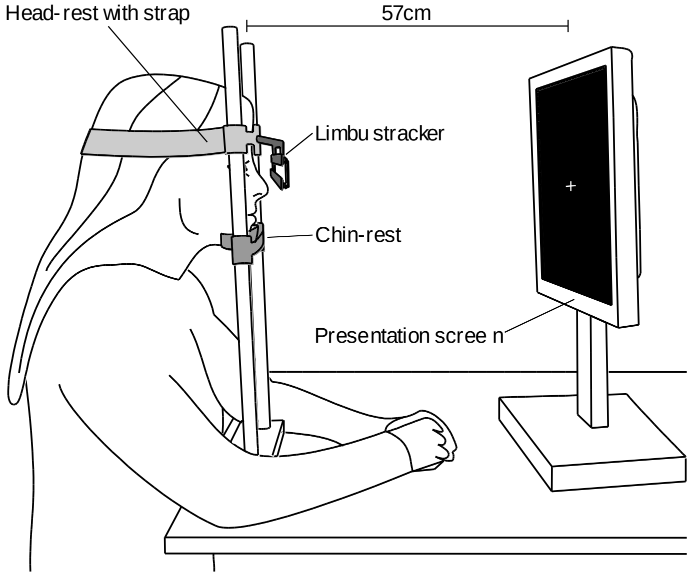

**Fig. 1: Experimental setup.** The head- and chin-rest assured the viewing distance of 57 cm and reduced movement artifacts. All eye movements were recorded with a limbustracker from the left eye of the participant.

## 2.3 The pursuit task

The stimulus was a horizontal, sinusoidal target movement (amplitude 10 °, duration 10 s, frequency 0.5 Hz, velocity 31 °/s; starting from center to the right). After an initial calibration, participants were instructed to look precisely at the moving target for the whole trial and 5 consecutive trials were performed. The entire measurement was standardized through the use of a fixed protocol to avoid differential influences from the experimenter.

## 2.4 Data processing

Eye position was low-pass, zero-phase (to avoid phase distortion) filtered with a Butterworth filter (order 7x2, cut-off frequency 45 Hz). Pursuit and saccades were detected using an eye-velocity based, windowed standard deviation (SD) filter and according thresholds (see Supplemental Methods SM1). Since the ongoing pursuit eye movement component is added to saccades, their amplitude and peak velocity were corrected for mean perisaccadic pursuit velocity according to the method proposed by de Brouwer et al. (2002a). Saccades were validated based on amplitude, duration and kinematic constraints (see Supplemental Methods SM2). The latency of the first saccade occurring within 90 and 1000 ms in the direction of the target (*time to first saccade*) was determined for each trial. If no such saccade was found, the corresponding trial was ignored (leading to fewer overall trials for this parameter). In addition, total number of saccades, median saccade amplitude and an exemplary peak velocity at 5 ° amplitude was identified for each trial. The latter was derived from a robust linear regression (Holland and Welsch 1977) of the main sequence (Bahill et al. 1975; Baloh et al. 1975), for which the coefficient of determination ($R^2$) was also determined (see Supplemental Methods SM2).

To quantify pursuit quality, total valid pursuit duration was computed from second 2 to the end of the trial (to exclude the initial fixation phase). Trials in which the valid pursuit duration was below 2 s were excluded. Pursuit gain was derived from a nonlinear least-squares cosine fit of the de-saccaded eye velocity over the same time window as the valid pursuit duration (see Supplemental Methods SM3).

The resulting gain was also used to verify the calibration quality of each measurement. All trials in which the experimenter reported difficulties during calibration or which had a pursuit velocity gain below 0.5 or above 1.2 were manually inspected. If the gain deviation was a cause of a calibration error, gain was accordingly corrected to be close to 1. If no common gain could be identified for all files of the participants (e.g. 3 trials were ok, but 2 files had a smaller gain, due to, for example, inter-trial head movements), the trials with the smaller gain were excluded. In cases were no common gain could be determined at all, the participant was excluded from the analysis.

In summary, the following saccade parameters were computed for each trial and participant: total number, median amplitude, peak velocity at 5 ° as well as $R^2$ and time to the first saccade. For pursuit the according parameters were velocity gain and valid pursuit duration. Individual values for participants were computed as median and SD over single trials.

In total, we obtained valid trials from 976 participants. Of these participants, 972 had valid 1st trials, 968 valid 2nd, 966 valid 3rd, 956 valid 4th and 954 valid 5th trials.

## 2.5 Statistics

Fast learning trajectories over the course of the five trials using and 5x2 ANOVA with main factors “trial number” (1-5) and “age group” (<66 and >66). The latter factor was a simple median split of our sample into “younger” (age ≤ 66 years, mean age: 61, n = 488) and “older” (age > 66 years, mean age: 72, n = 488) participants.

For the analysis of aging, linear ordinary least-squares regressions between age and the median and SD values over trials were computed. Pearson correlation coefficients and the corresponding p-values were derived from these linear regressions.

Throughout the entire article, significant effects will be shown as solid lines, whereas non-significant ones are dashed.

All results are considered significant at an alpha level of 0.05.

# 3. Results

In summary, there were small but significant improvements in saccade parameters (number, amplitude and peak velocity) over the course of the five trials, whereas pursuit performance (as measured by velocity gain and valid duration) did not change with repeated testing. The improvements were similar in the younger and older group.

Overall, saccade and pursuit parameters as well as their variance were dependent on age. Only the SD of the peak velocity and the time to first saccade were not affected by age.

## 3.1 Descriptive statistics

The means for all measured values in our participants are shown in table 2.

| | | | **Mean** | **SD** | **Min.** | **Max.** | **#** |
|---|---|---|---|---|---|---|---|
| **Age** | **[years]** | **All** | 67 | 7 | 51 | 85 | **976** |
| | | **Female** | 66 | 7 | 51 | 85 | **472** |
| | | **Male** | 68 | 7 | 53 | 84 | **504** |
| **Number of saccades** | | **MDN$_T$** | 25 | 6 | 8 | 67 | **976** |
| | | **SD$_T$** | 3 | 2 | 0 | 16 | |
| **Saccade amplitude** | **[°]** | **MDN$_T$** | 2.3 | 1 | 0.7 | 7 | |
| | | **SD$_T$** | 0.48 | 0.36 | 0.03 | 2.75 | |
| **Saccadic peak velocity at 5°** | **[°/s]** | **MDN$_T$** | 253 | 48 | 126 | 445 | |
| | | **SD$_T$** | 25 | 14 | 2 | 105 | |
| | | **$R^2_T$** | 0.91 | 0.09 | 0.45 | 1 | |
| **Time to first saccade** | **[ms]** | **MDN$_T$** | 253 | 57 | 128 | 639 | |
| | | **SD$_T$** | 76 | 53 | 0 | 328 | |
| **Pursuit velocity gain** | | **MDN$_T$** | 0.7 | 0.19 | 0.08 | 1.09 | |
| | | **SD$_T$** | 0.08 | 0.05 | 0.01 | 0.44 | |
| **Valid pursuit duration** | **[s]** | **MDN$_T$** | 5.9 | 0.7 | 2.3 | 7 | |
| | | **SD$_T$** | 0.29 | 0.21 | 0.01 | 1.74 | |

*#*: Number of participants, *MDN$_T$*: Median over trials, *SD$_T$*: SD over trials, *SD*: Standard deviation, *$R^2_T$*: Median determination coefficient over trials (see section 2.4)

**Table 2: Descriptive statistics.** All values are computed over single trials.

## 3.2 Influences of trial number and age group[1]

Figure 2 a shows the eye position traces for the five trials of an exemplary younger participants. Figure 2 b depicts the five trials of an older. Clearly, the older participants made more and larger saccades. These saccades occurred mostly when target moved at maximum velocity (zero crossings), thus indicating particular pursuit difficulties at higher speed.

As seen in figure 3, age group significantly impaired all saccade and pursuit parameters over all participants (Fig. 3 a-c, e-f) except for time to first saccade (Fig. 3 d). Older participants made more and larger saccades, reached lower peak velocities, had lower pursuit velocity gains and made less valid pursuit.

Trial number on the other hand, had a significant influence only on the saccade parameters (Fig. 3 a-d) with the first trials tending to higher values than the last ones. Contrarily, neither pursuit velocity gain (Fig. 3 e) nor valid pursuit duration (Fig. 3 f) changed significantly over trials.

Most importantly, we did not find any interaction between trial number and age group. Whereas the time to first saccade reached borderline significance ($p = 0.053$; Fig. 3 d), all other parameters were far away from our alpha level ($p$'s $\geq 0.622$; Fig. 3 a-c, e-f).

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[1] For better readability p-values for the main factors of the ANOVA are given directly in the figures.

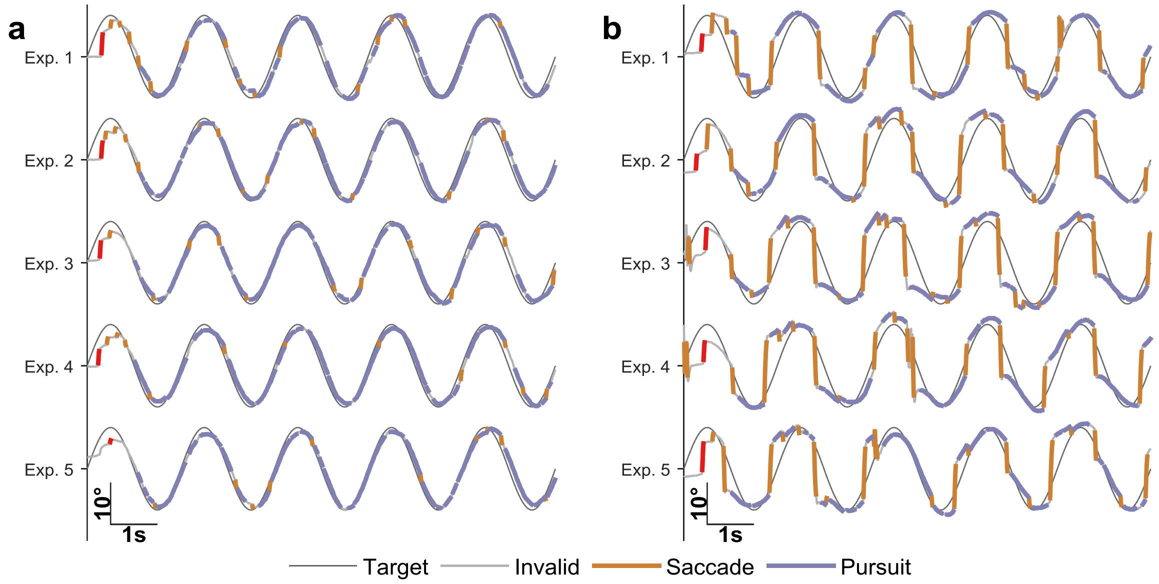

**Fig. 2: Eye position traces for the five consecutive trials** (top to bottom) of **(a)** a younger participant (male, 54 years, $n_s$: 13, $a_S$: 1.1 °, $v_S$: 316 °/s, $R^2$: 0.99, $t_S$: 295 ms, g: 0.88, d: 6.7 s) and **(b)** an older participant (male, 82 years, $n_s$: 20, $a_S$: 4.8 °, $v_S$: 237 °/s, $R^2$: 0.88, $t_S$: 389 ms, g: 0.47, d: 6.1 s). Numbers are medians over trials. The inset in the lower left indicates the axis scaling. $a_s$: Saccade amplitude, $d$: Valid pursuit duration, $g$: Gain, $n_s$: Number of saccades, $R^2$: Coefficient of determination for $v_s$ regression, $t_s$: Time to first saccade, $v_S$: Saccadic peak velocity at 5 °.

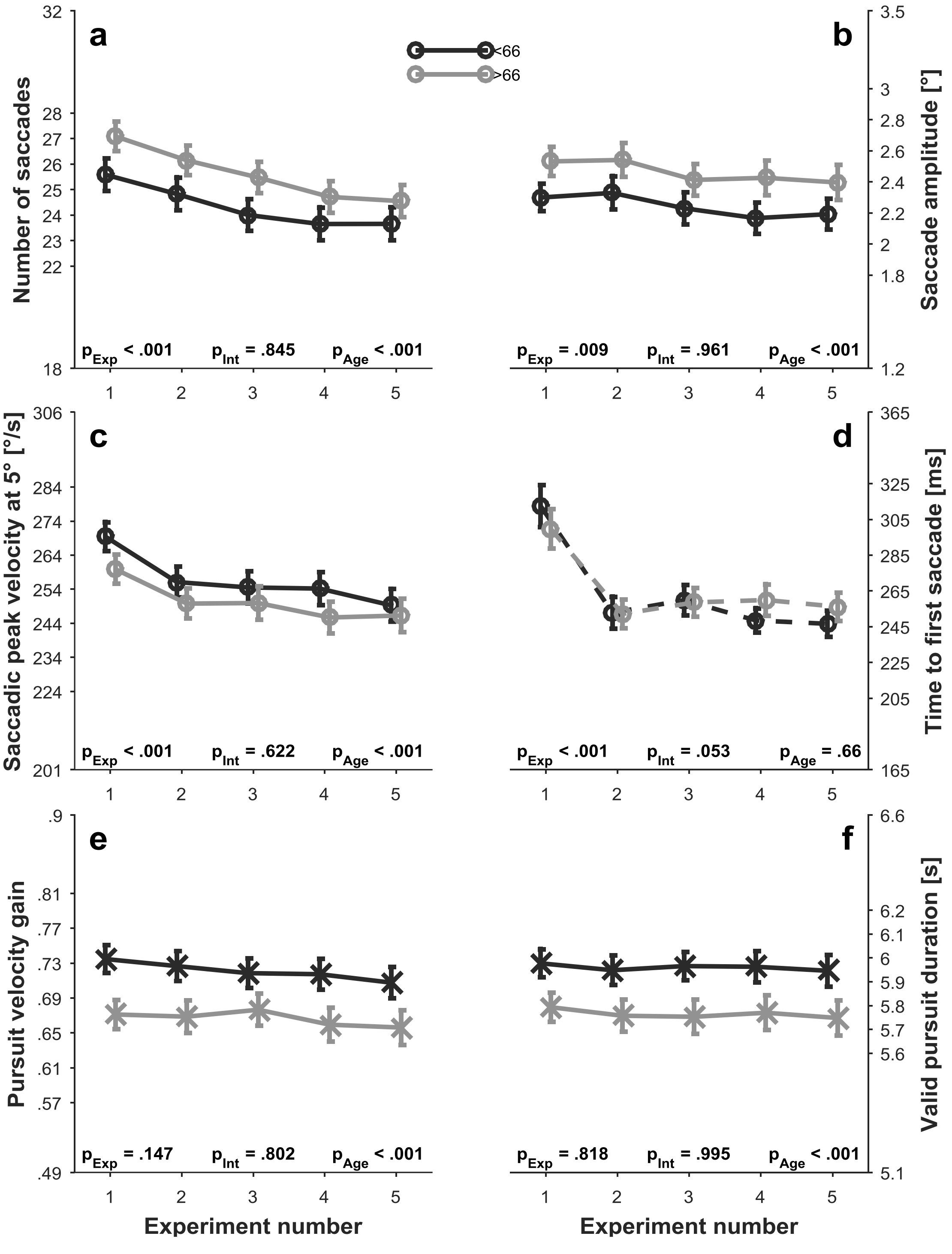

**Fig. 3: Dependency of saccade and pursuit parameters on trial number and age group.** P-values from the 2-factorial ANOVAs are given for main factors (interactions were not significant). Significance at the 0.05-alpha level is indicated for trial number by marker type (cross: not significant, circle: $p \leq 0.05$) and for age group by line style (dotted: not significant, solid: $p \leq 0.05$). Error bars give 95% confidence intervals. Y-axis limits represent mean ± 1 SD over all participants (mean marked by the central y-tick). $p_{Trial}$: P-Value for trial number, $p_{Age}$: P-Value for age, *SD*: Standard deviation.

## 3.3. Effects of age on overall task performance[2]

As already reflected by the grouped analysis before, most of the individual medians over trials were affected by age as depicted in figure 4. The linear regressions were significant for every parameter (Fig. 4 a-c, e-f) except for time to first saccade ($R^2 = 0.002$; Fig. 4 d).

The number of saccades (16 + 0.1/year, $R^2 = 0.019$; Fig. 4 a) and their amplitude (1 ° + 0.02 °/year, $R^2 = 0.016$; Fig. 4 b) both increased with age. Saccadic peak velocity (288 °/s - 0.5 °/(s·year), $R^2 = 0.005$; Fig. 4 c), pursuit velocity gain (1 - 0.005 /year, $R^2 = 0.03$; Fig. 4 e) and valid pursuit duration (7 s - 0.02 s/year, $R^2 = 0.027$; Fig. 4 f) decreased with age.

A similar picture was drawn for the intra-individual variances. Results are shown in figure 5. Significant age correlations were found for every parameter (Fig. 5 a-b, e-f) except for the SDs of peak velocity ($R^2 = 0.002$; Fig. 5 c) and time to first saccade ($R^2 < 0.001$; Fig. 5 d).

SDs of number of saccades (2 + 0.02/year, $R^2 = 0.004$; Fig. 5 a) as well as their amplitude (0.09 ° + 0.006 °/year, $R^2 = 0.011$; Fig. 5 b), pursuit velocity gain (0.0001 + 0.001 /year, $R^2 = 0.025$; Fig. 5 e) and valid pursuit duration (-0.02 s + 0.005 s/year, $R^2 = 0.021$; Fig. 5 f) all increased with age.

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[2] For the simplicity of reading, p-values and correlation coefficients for the linear regressions are given directly in the figures. The linear regression coefficients for significant correlations are abbreviated in the text as (Intercept + Slope, coefficient of determination).

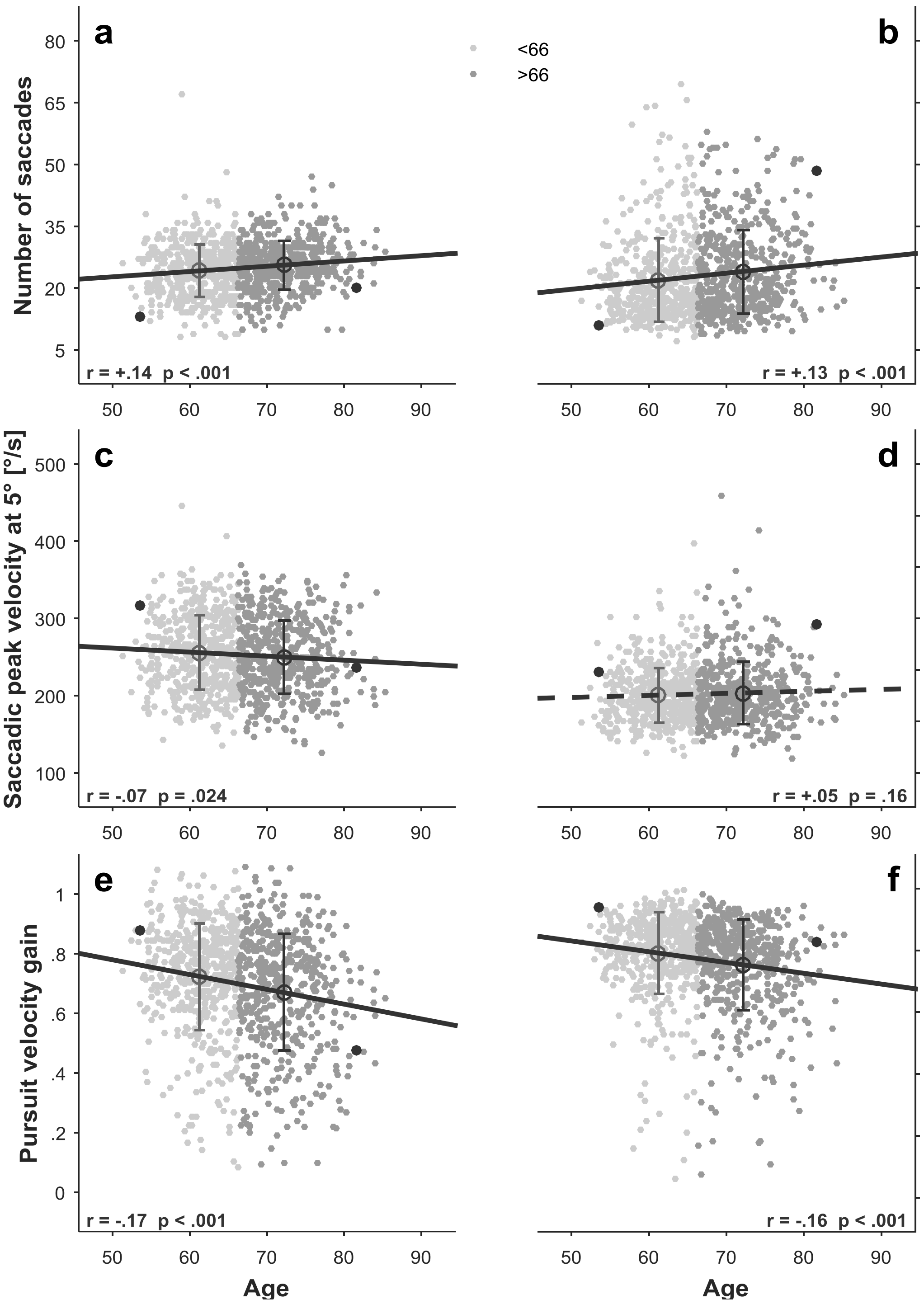

**Fig. 4: Age correlation of saccade and pursuit parameters.** Filled circles indicate single participants (color shows age group). Lines represent linear regressions. Significance of age correlations is indicated by line style (dashed: non-significant, solid: p ≤ 0.05). Error bars indicate age group means and SDs. All values represent medians over trials. *r*: Pearson correlation coefficient with according p-value, *SD*: Standard deviation.

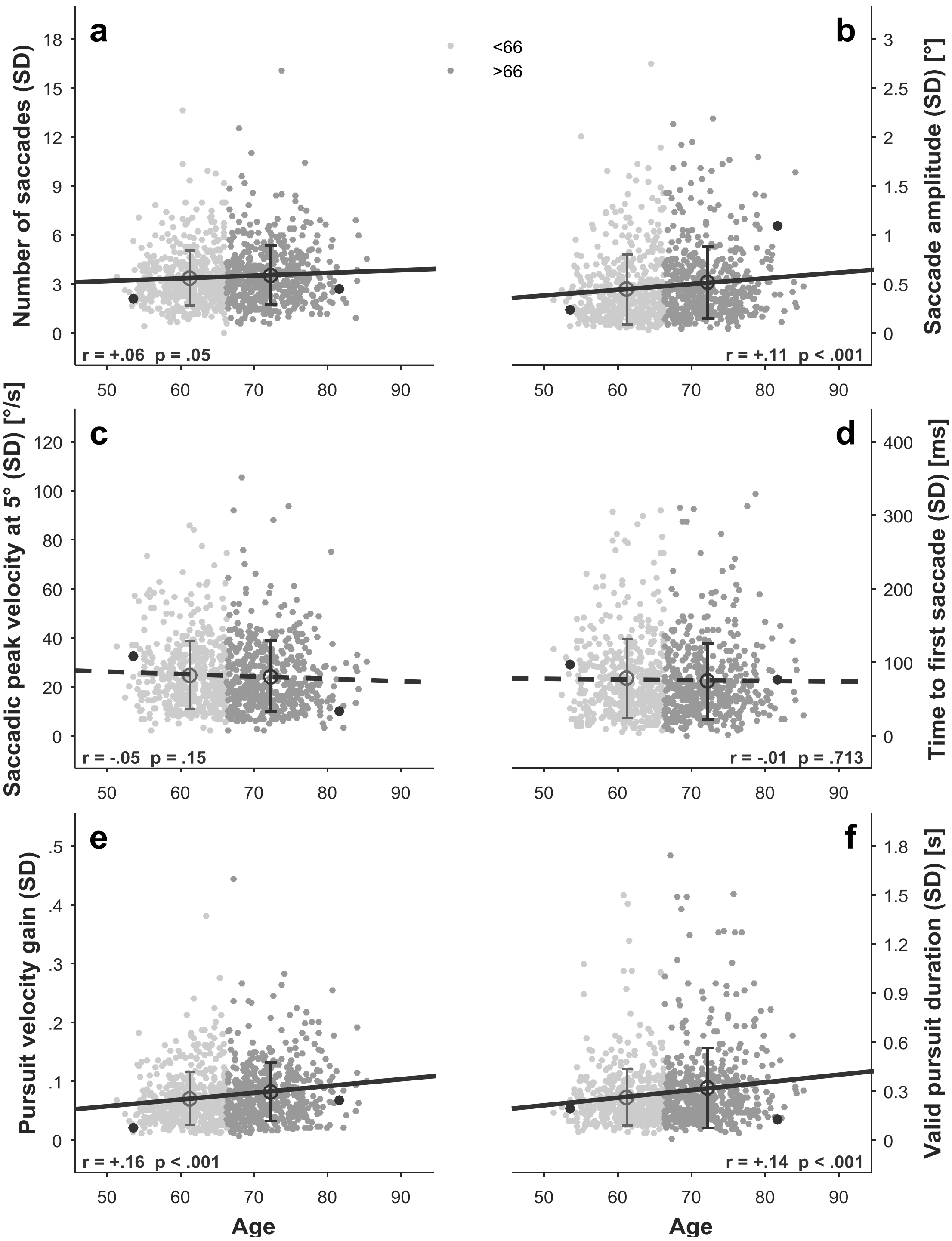

**Fig. 5: Age correlation of saccade and pursuit parameter variance measures.** Filled circles indicate single participants (color shows age group). Lines represent linear regressions. Significance of age correlations is indicated by line style (dashed: non-significant, solid: p ≤ 0.05). Error bars indicate age group means and SDs. All values represent SDs over trials. *r*: Pearson correlation coefficient with according p-value, *SD*: Standard deviation.

# 4. Discussion

## 4.1 Perceptual learning in aging

We did not find any interaction between age group and trial number and thus no difference in the learning trajectories between younger and older participants. This fits well to previous studies, which found no age-related change in perceptual learning (Chang et al. 2014; Fahle and Daum 1997; McKendrick and Battista 2013). Chang et al. (2014) proposed that problems with learning in the elderly are caused by decreased memory stability but not by a decline in plasticity. Our results fully support this notion, since we did not observe changes in fast learning. In addition, since we did not compare young adults with elderly participants, but used an old-to-older approach, our results implicate that even in very high age, plasticity is retained.

With respect to the general learning trajectories, pursuit gain and valid pursuit duration did not change over trials. However, a small but significant improvement in the number of saccades as well their amplitude was present; indicating learning over trials. The lack of an influence on gain and duration of pursuit maybe explained in the sensitivity of these measures. An improvement of 2 saccades at median amplitude of 2.4 ° between the first and the last trials as presented here, amounts to a possible increase in valid pursuit duration of approximately 50 ms over the course of 10 s. Similarly, global gain is not very sensitive to small deviations within short pursuit phases. Thus, an improvement in pursuit performance may not be visible in these two measures. Thus, participants' pursuit performance actually improved over trials. Participants may have adapted to the task by switching from a more retinal, exogenously driven, to a more extra-retinal, prediction-based pursuit strategy over the course of the five trials. This is line with a developmental model by Balkenius and Johansson (2007), which shows that developmental learning changes the weighting from exogenous, saccadic pursuit to prediction-based, smooth pursuit. On a shorter time scale, this may also be the case for fast learning over several trials.

Regarding the change in saccadic peak velocities, it has been shown that perceptual goals (Montagnini and Chelazzi 2005) and arousal (for a review see Di Stasi et al. (2013)) lead to higher peak velocities. In the first trial, the novelty of the task may increase arousal and its perceptual goal might be more pressing than in successive trials. This may explain the increase in saccadic peak velocity found only in the first trial.

In addition to the participants' arousal and perceptual goals, they also lack information about target direction in the first trial. It has been shown that knowledge about movement direction and velocity of an upcoming movement decreases reaction times to its onset (Sekuler and Ball 1977). For saccades, it has been shown that less uncertainty about target location, leads to shorter saccadic reaction times by increasing the initial decision signal (Carpenter 2004; Carpenter and Williams 1995). Therefore, the strong decrease in time to first saccade after the first trial found in the present study might be explained by this decrease in uncertainty.

## 4.2 Aging pursuit

### 4.2.1 An age-dependent motor system

The statement by Sharpe and Sylvester (1978) is fully supported by our results: pursuit eye movements are an "age-dependent motor system". In the present study, all pursuit related parameters showed a significant age-dependency. As pictured by reduced gain and increased saccade number and amplitude, senescence impacts pursuit accuracy and maintenance. Most of the previous reports agree with our results (see table 1). We found a clear age-related decline in pursuit performance, most prominently in the decreased velocity gain. It has been reported that the elderly have longer pursuit latencies (Fukushima et al. 2014) and lower initial eye accelerations (Morrow and Sharpe 1993). The latter study proposed that reduced initial acceleration leads to lower open-loop gain, which again explains the poorer steady-state gain for sinusoidal stimuli. In the present data, lower gain was paralleled by an increased number of saccade and higher amplitudes. Pursuit gain can be modelled in a multiplicative, negative relationship to rate and amplitude of catch-up saccades

(Friedman et al. 1991). An increase in saccade rate and amplitude would thus lead to an even stronger decrease in gain – which is supported by the higher correlation coefficient in our age-dependency of gain. The only variable not affected by age, was the time to first saccade. This fits to recent results obtained with step-ramp stimuli (Fukushima et al. 2014). Since the first catch-up saccade often marks the beginning of the closed-loop stage of pursuit, it seems that this is not delayed in the elderly.

But how is pursuit performance generally impaired by age? In humans there is merely no age-related degeneration in the abducens and vestibular nuclei (Alvarez et al. 2000; Vijayashankar and Brody 1977). Alvarez et al. (2000) speculated that the constant oculomotor activity in everyday life may actually prevent or at least profoundly delay degeneration in the oculomotor nuclei. Thus, the motor portion of the pursuit system is most likely not the defendant for the age-related performance loss (Knox et al. 2005; Morrow and Sharpe 1993).

In senescent monkeys it has been shown, that the direction selectivity, signal-to-noise ratio and response latencies of cells in primary visual cortex (V1) are impaired by age (Schmolesky et al. 2000; Wang et al. 2005). V1 provides the first direction-selective cells projecting to area MT (Movshon and Newsome 1996), where similar age effects have been found (Liang et al. 2010; Yang et al. 2009). Since area MT extracts the crucial retinal motion signals driving the pursuit system (Ilg and Thier 2008), these age-related changes in the brain may lead to a degraded and delayed motion signal and thus impair pursuit performance. Although these results were obtained in monkeys, they are probably also true for humans. Anticipatory SPEM is very similar in humans and primates (Freyberg and Ilg 2008) and area MT (V5) has a human homologue in the lateral occipitotemporal cortex (Barton et al. 1996). Several other studies imply a similar control network as in monkeys for human smooth pursuit; for a review see Lencer and Trillenberg (2008). Supporting the idea of a sensory rather than a motor decline with age, studies have shown that translational motion processing is impaired by age (Bennett et al. 2007; Billino et al. 2008; O'Connor et al. 2010; Snowden and Kavanagh 2006). Measuring reaction times to motion onsets, Porciatti et al. (1999) attributed the their age-related difference specifically to a sensory origin. Thus, decreased pursuit performance is probably caused by a decline in motion processing and not in motor function. The impairment of motion processing is most likely a result of a degraded motion signal from earlier visual processing areas (V1, MT/V5).

This argument could also be used to explain the higher intra-individual variability observed with increasing age in our study. A degraded motion signal may impede the pursuit system from producing an equally consistent response as in the young. The higher variability fits well into the general picture of increased intra-individual variability in reaction times of the elderly (Hultsch et al. 2002)

### 4.2.2 An alternative explanation

Hultsch et al. (2002) pointed out that the higher variability may also be caused by lapses in attention in the elderly. Attention in pursuit is needed for example to suppress the strong self-induced global background motion, which otherwise might trigger optokinesis (Lindner and Ilg 2006; Lindner et al. 2001). Participants' performance in an attention demanding task is closely tied to the pursuit location and rapidly declines behind and ahead of the target (Lovejoy et al. 2009). Vice versa, directing attention to the target decreases catch-up saccade number and amplitude and improves overall pursuit (Van Gelder et al. 1990). Similarly, narrowing the focus of attention increases open-loop velocity gain (Madelain et al. 2005), which leads to higher closed-loop gain. Therefore decreased attention to the task might alternatively explain the increased variability and impaired performance in the elderly.

### 4.2.2 Changes in saccade kinematics

The small but significant decline in saccadic peak velocity parallels previous findings from saccade tasks (Abel et al. 1983; Irving et al. 2006). Since saccade peak velocity is not only a product of the brainstem saccade generators but also the cerebellum (Thier et al. 2000), an age-related decline points also to some cerebellar involvement.

## 5. Methodological considerations

Although only healthy individuals were recruited for our study, we found quite pronounced inter-individual (as opposed to intra-individual) variability. For example pursuit gains ranged from nearly 0 to 1 and valid pursuit duration dropped to the minimum of 2 s in some participants. This high inter-individual variability is well observed in the elderly (Morse 1993). In addition, the annual loss of gain was rather small (0.005 per year of age). Taken together, this makes differences hard to detect in narrow age ranges or smaller sample sizes and should be kept in mind when planning pursuit studies in older participants.

## 6. Conclusion

We found impairments of nearly all pursuit performance measures together with an increase in intra-individual variability in a large healthy sample of elderly individuals. These findings confirm and extend on previous results and stress the fact, that pursuit is an age dependent motor-system. Since pursuit eye movements are commonly used in clinical diagnoses, it is important to take these age-related changes into account. Otherwise decreased performance may be falsely attributed to pathological deterioration. We also found that age does not change the ability to quickly adapt to a new task, namely we did not find any difference in the fast learning trajectories in the elderly. This raises hope, that age does not affect every aspect of daily life. It remains for the future, to see if there are individual difference in these learning trajectories and if participants can be separated into good and bad learners, based on their performance, which might be used to detect early changes related to pathological aging.

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# SUPPLEMENTAL FIGURES

## Figure S1: Sample statistic

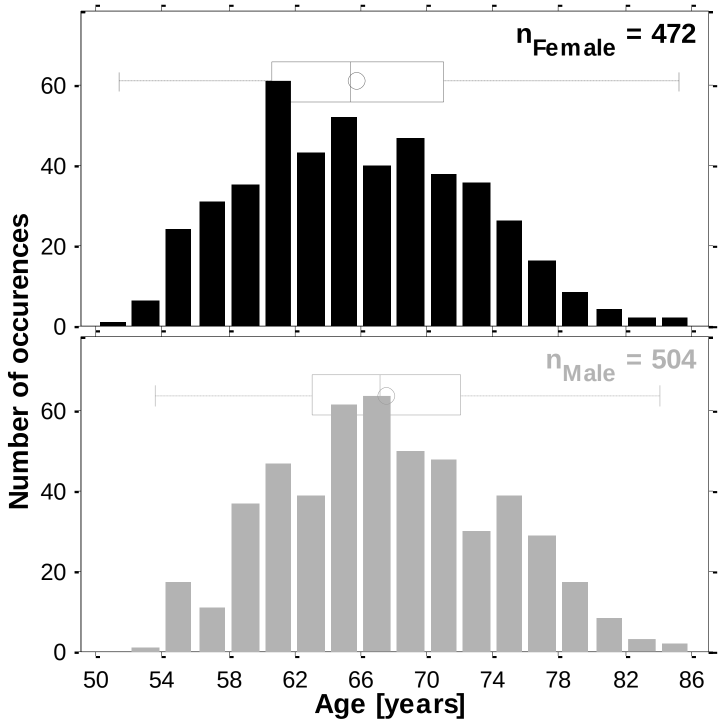

**Fig. S1: Age distribution of the participants** grouped by sex (black: females, light gray: males). The age difference between females and males was statistically significant ($p < 0.001$). Boxplots show 1st, 2nd and 3rd quartiles (box) and most extreme ages within 1.5 interquartile ranges from ends of the box (whiskers). Circles depict means. *n*: Number of participants.

## Figure S2: Single TP main sequences

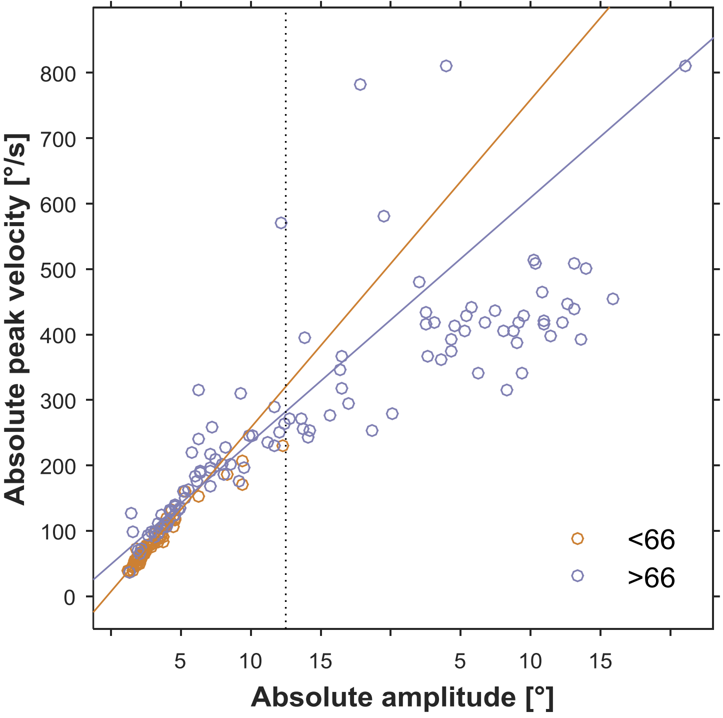

**Fig. S2: Main sequence for the two exemplary participants.** Dots show single saccades. The dotted line indicates the maximum amplitude used for the regressions and the value of the exemplary peak velocity.

# SUPPLEMENTAL METHODS

## SM1: Eye movement detection

The low-pass filtered eye position was differentiated to obtain eye velocity (V) using the GRADIENT function in Matlab. Afterwards a 17 ms-windowed standard deviation (SD) of V was computed (VSD), such that each sample was $VSD_i = SD(V_{i-8}...V_{i+8})$. This procedure removed the low-frequency pursuit-component from the velocity signal. Since large and small saccade produce profoundly different VSD amplitudes, the logarithm of the VSD was taken (LVSD; VSD values < 1 ° were truncated at 1 ° before taking the logarithm). From the resulting signal, a threshold ($T_{LVSD}$) for the detection of non-pursuit eye movements was computed on a trial-by-trial basis as the 90th percentile of all LVSD values ≤ 2 ($LVSD_{Max}$). To avoid overly strict thresholds in low-noise measurements, $T_{LVSD}$ limited to a minimum of 1.

Now, from all LVSD values ≥ $T_{LVSD}$ sub-threshold samples were labeled as pursuit and continuous supra-threshold sample blocks were identified as possible saccades. For each of these blocks, a saccade threshold was computed from the SD of the eye velocity within this block. Using this threshold, saccades were identified as supra-threshold samples. All samples which were neither classified as saccade nor as pursuit were considered invalid and removed.

Figure SM1 gives an example for the detection pattern.

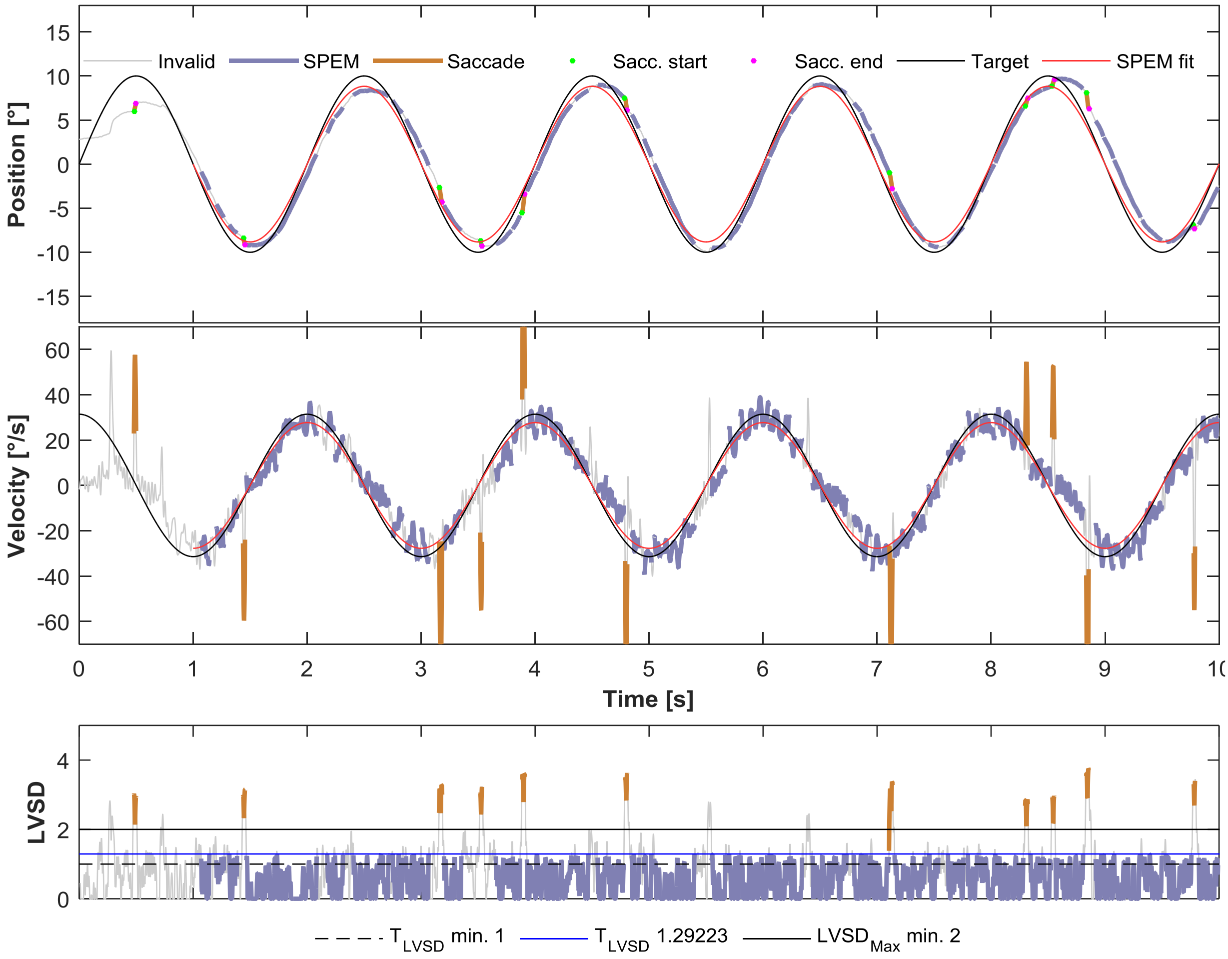

**Fig. SM1: Example trial with detection results.** For a detailed description of the parameters see text.

# SM2: Saccade parameter computation

For each detected saccade, amplitude, duration, peak velocity and peak acceleration/deceleration were computed. Saccades were removed if the endpoint was off screen (e.g. absolute endpoint > 20 °), duration < 9 ms or the kinematics off limits (absolute amplitude < 0.5 or > 30 °; absolute peak velocity < 40 or > 1.000 °/s; absolute peak ac-/deceleration < 3.000 or > 100.000 °/s$^2$).

For the remaining valid saccades, pursuit velocity was removed by correcting saccade amplitude and peak velocity for mean pursuit velocity during the saccade (de Brouwer et al. 2002). Afterwards, the main sequence for peak velocity versus amplitude was calculated, through a robust linear regression (Holland and Welsch 1977) using ROBUSTFIT in Matlab with the ‘bisquare’ weighting function. The coefficient of determination ($R^2$) was computed similar to ordinary least-squares regression (Willett and Singer 1988). Since the main sequence is not linear over the large range of amplitudes observed within our task, we restricted the computation on absolute saccade amplitudes ≤ 5 °. An exemplary peak velocity of 5 ° amplitude was computed for each participant and each trial from the linear regression equation ($V(5\,°) = b_0 + b_1 \cdot 5\,°$, where $b_i$ are the regression parameters).

To quantify pursuit quality, the total duration of pursuit was determined from second 2 to the end of the trial (to exclude the initial fixation phase). Pursuit velocity ($V_{Max}$) was derived from a nonlinear least-squares cosine fit of the de-saccaded eye velocity ($V_{Eye} = V_{Max} \cdot \cos(2\,\pi \cdot V_{Target} \cdot t)$; starting with $V_{Max} = V_{Target} = 31$ °/s) and constrained to non-negative values. Pursuit velocity gain was computed from the resulting eye velocity divided by the target velocity.

# SM3: Pursuit parameter computation

From the valid pursuit samples, the valid pursuit duration was determined. Initial fixation was removed by discarding the first second of each trial in the pursuit analysis (thus maximum valid pursuit duration was 9 s). To obtain pursuit peak velocity ($V_{Max}$), a nonlinear least-squares cosine fit ($V(t) = V_{Max} \cdot cos(2\pi \cdot f_{Target} \cdot t)$, with $f_{Target} = 0.5$ Hz) was performed over the pursuit samples using the LSQNONLIN function from the Optimization Toolbox in Matlab. $V_{Max}$ was initialized with the target velocity ($V_T = 31$ °/s) and constrained to non-negative values. Pursuit velocity gain was computed as $g = V_{Max}/ V_T$. Blue traces in figure SM1 shows the resulting fits.

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# Acknowledgments

I'd like to thank all my friends who accompanied me until this point and especially the following people:

**Akshay, Christiane, Hazel Reister and Nicki** for shedding light into the myths of English punctuation and their valuable input while finishing my thesis.

**My mom** for her unquestioning support and her advice in times when life was being serious.

**My dad** for giving me the love for nature and natural sciences and pointing out that, most often, life should not be taken too seriously.

**Mr. Frits** for showing me that this is especially true, since two hours of continuously playing catch seems also quite fulfilling.

**Uwe**, again, for making this possible and for showing me how to be a good scientist and good person.

**Greate** for much “Quatsch” and her unconditional love even after coming home late and ranting about saccade detection.