Differential Aging effects on visuomotor control:

Evidence for an adaptive aging brain

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Abstract

Aging in psychology has been investigated for decades and general aging declines in behavioral cognitive tasks have been well established. With advances in neuroimaging techniques, some changes have been found in the brain activity patterns of older adults. Their associations with better performance indicate their functions as compensations rather than impairments. The nature of these compensations is unknown: Are they passive responses to structure impairments or active adaptations to the altered environments. Sensorimotor control is supposed to be a pretty good way to explore it because of its natural connections with the external environments and its strong interactions with cognition.

Visuomotor control has been extensively explored with visuomotor adaptation tasks and distinct mechanisms and subcomponents have been identified, such as model based learning and model free learning. In model-base learning, multiple states have been found: fast state, responding strongly to error whereas retaining information poorly, and slow state, responding weakly to error whereas retaining information well. Corroborating these multiple states, fast adaptation and slow adaptation have been identified as well as learning processing and retention processing. For model free learning, recently visuomotor adaptation has been found to be impacted by reward and punishment. How aging impacts these processes has been relative less explored.

Saccadic eye movement is so brief that its online trajectory is resistant to any sensory feedback, making it an especially good way to investigate model-based learning. Saccade adaptation could be induced by different factors, ranging from low-level intrasaccadic step to high-level perceptual task. The first study investigated how aging impacts these two different processing with two different paradigms. A double-step paradigm was used in the first experiment which was designed to trigger primarily low-level, gradual motor adaptation and a perceptual task paradigm was used in the second experiment in which adaptation was induced by a perceptual task that emphasizes high-level, fast processes. Equivalent adaptation of saccadic gain was found in the two age groups in the first experiment whereas the fast, strategic adaptation response was significantly more pronounced in the young adult group in the second experiment.

Reaching movement is with longer duration and less precision so that it is a pretty good complimentary way to investigate model free learning. The second study investigated age-related effects on learning processing and retention processing in reaching adaptation and motivational

modulations of these effects. In the study, a reaching task was used in which participants were asked to make fast shooting movements towards visual targets with their right hand through a robotic manipulandum (vBOT system) allowing to measure reaching trajectories. Adaptation was induced by a 30° screen-cursor visuomotor rotation. Participants were assigned to one of motivational feedback conditions, i.e. neutral, reward, or punishment. Reward and punishment feedback was based on reaching endpoint error. Equivalent retention rate was found in the two age groups whereas learning rate was smaller in older adults. However, the learning rate was equivalently enhanced by reward in the two groups suggesting the benefits from motivational feedback during reaching adaptation so that age-related differences in visuomotor plasticity, though persisting, can be attenuated.

Saccade landing position and saccade latency has been found to be impacted by low-level factor salience and high-level factor value, making saccadic eye movement a good way to explore decision making. Recently the integration of salience and value was found to be dynamic, i.e. their influence on saccade landing position is dependent on saccade latency. The third study investigated how aging impacts these dynamics. In the study, salience and expected value was traded off by asking participants to make saccades to target patches with subregions differing in salience and associated reward. No differences were found between two groups on saccade landing position when only salience was administered. A significant interaction was found between value manipulation and age group on saccade landing position with equivalent reward effects in two groups but weaker penalty effects in senior group. When respecting with saccade latency, reward triggers an average latency decrease in senior adults but not in young adults. These differential reward effects on saccade landing position and saccade latency were also reflected by the less dependence of saccade direction on latency although the dependence exists in both groups.

Taken together, this thesis consistently found reserved low-level processing in older adults, such as equivalent gradual adaptation in the first study, equivalent retention rate in the second study, equivalent influence of salience in the third study. However, the high-level processing was impaired in older adults, such as impaired faster adaptation in the first study, reduced learning rate in the second study, reduced reward effects on saccade latency in the third study. The impairments could be result from impairments in the brain area the high-level processing involved in or from strategy changes.

Contents

Chapter 1: General introduction

According to the census data from Germany government, there were 17.5 million people who were older than 65 years old in Germany in 2016, which was more than 21% of the whole population[1]. Generally most older adults have some kinds of impairments in cognition and movements and more than 15% of them suffered from Alzheimer's disease who do not even remember their grandchildren's names (Hebert et al., 2013). As they get older, they will suffer from more and more illness. Elderly patients (older than 65 years) in 2011 accounted for only 11% of the US population yet they accounted for 34% of health care expenditure (Marik, 2015; Moses et al., 2013). Their medical treatments brought a huge burden for themselves, their family and the society. To make things worse, there will be more and more older adults which will be 28% of the whole population of EU27 countries in 2060 (Harper, 2014). All these facts make it imperative to acquire a comprehensive understanding of aging processing and to find ways to optimize their performance and life.

Psychology of aging has been investigated for several decades and most of these studies focus on aging effects on cognition. General declines have been well established in behavioral cognitive tasks (Cabeza, Nyberg & Park, 2016; Nyberg & Bäckman, 2004; Hultsch et al., 1998; Park et al., 2002; Salthouse, 2010b). Older adults have been found to be bad at various tasks. However, as the neuroimaging techniques advanced, such as the emerging of Positron emission tomography (PET), Magnetic Resonance Imaging (MRI), functional Magnetic Resonance Imaging (fMRI) and Diffusion tensor imaging (DTI), they became widely available and were widely applied in psychology and aging. Several distinct brain activity patterns have been found in older adults' brain and their associations with better performance indicate their functional role as compensation rather than impairments (Park & Reuter-Lorenz, 2009). However, whether these compensations are just passive responses to aging declines or active adaptations to altered environments is unknown (Sugiura, 2016). Potential answers could come from investigations on sensorimotor control because of its natural connections with external environments and strong functional connections with cognition.

Although we look, point, reach and walk in everyday life and although older adults show impairments in movements, aging research on sensorimotor control is rather neglected. Although initially perception and action were supposed to involve in distinct systems (Goodale & Milner,

1992), more and more studies found the strong interactions between them (O'Regan & Noë, 2001). These interactions are even much stronger in older adults (Lindenberger & Baltes, 1994). Sensorimotor control system has been well computed by different models and distinct subcomponents in the system are identified (Hopp & Fuchs, 2004; Krakauer & Mazzoni, 2011; Pélisson et al., 2010; Smith, Ghazizadeh & Shadmehr, 2006; Wolpert & Flanagan, 2016). Comparing to cognitive tasks, sensorimotor tasks are more nature. These characteristics make sensorimotor tasks especially suitable to investigate aging effects on distinct processing. The three studies of this thesis would use different visuomotor tasks to investigate the differential aging processing and reward and punishment effects on these processing.

In the next sections of this chapter, I would introduce what has been found about aging effects on behavioral cognitive tasks and what theories have been proposed to explain them, how aging research with sensorimotor tasks could help reconcile discrepancies in literature, what knowledge has been acquired about visuomotor control and aging effects on it, and finally the outline of the studies included in this thesis.

General but differential aging declines in behavioral cognitive tasks

It is well-established that old adults are worse at various laboratory cognitive tasks than young adults: they have worse capacities of attention, working memory, problem solving, reasoning so on and so forth (Cabeza, Nyberg & Park, 2016; Nyberg & Bäckman, 2004; Hultsch et al., 1998; Park et al., 2002; Salthouse, 2010b). For example, Park and colleagues (2002) found that as people age, except world knowledge, many aspects of information processing become less efficient, such as speed of processing, working memory capacity, and long-term memory (illustrated in Fig. 1).

Speed of Processing
- Digit Symbol
- Letter Comparison
- Pattern Comparison

Working Memory
- Letter Rotation
- Line Span
- Computation Span
- Reading Span

Long-Term Memory
- Benton
- Rey
- Cued Recall
- Free Recall

World Knowledge
- Shipley Vocabulary
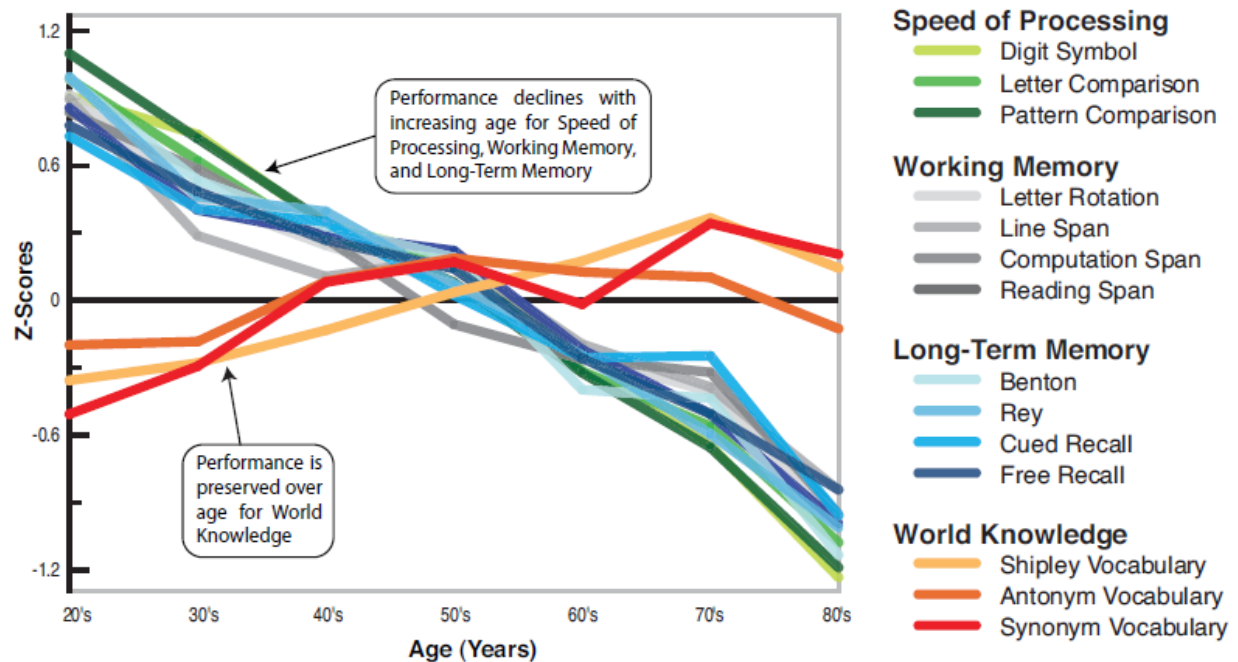- Antonym Vocabulary
- Synonym Vocabulary

Figure 1. Behavioral performance in various cognitive tasks changes with age. Speed of processing, working memory capacity and long-term memory decreases with age while world knowledge is resistant to aging. From Park & Reuter-Lorenz (2009).

However, the extent to which their performance is impaired varies from tasks to tasks so that there are some kinds of tasks in which no aging impairments are found, such as the world knowledge tasks (red and orange lines in Fig. 1). To account for these differential age-related declines in different behavioral cognitive tasks, different theories were proposed. It ranges from resource hypothesis (Craik & Byrd, 1982), inhibition hypothesis (Hasher & Zacks, 1988), processing speed hypothesis (Salthouse, 1996) to not-defined common source hypothesis (Baltes, Staudinger & Lindenberger, 1999). These different hypotheses are proposed based on the understanding of the general cognition. They all agreed on that there were core functions and processing underlying cognition and that this core function or processing was impaired in older adults which lead aging declines in various cognitive tasks. In a word, they posited the general declines of older adults and this generality is based on a common cause. Corroborating with this general decline hypothesis, some damages were found in the structure of older adults' brain in PET and fMRI studies (Cabeza, Nyberg & Park, 2016; Raz, et al., 2005; Raz, et al., 2010).

Common cause hypotheses and their supportive brain structure evidence

At the beginning, differential impairments were found in different memory tasks (Craik, 1977). For example, little aging effects were found in the digit span task, in which subject needed to report a list of digit numbers, whereas a large age difference was found on the free recall of a list of words (Craik, 1977). At that moment, the dominant idea about memory was that different types of memory have discrete mechanisms and structures (Tulving, 1984). Based on this understanding, differential aging effects on various tasks were interpreted as impairments in distinct brain structures or systems. Therefore, Tulving (1984) thought the semantic memory holds up through the life span whereas episodic memory declines.

However, this interpretation could not explain the different performance of older adults in the same type memory but with different materials. For example, older adults' memory of factual knowledge was remembered as well as young adults whereas they remembered recent events much worse (Perlmutter, 1978).

Resource hypothesis

Instead of thinking memory from the system and structure view, Craik (1983; 1984; 1986; Craik & Byrd, 1982) thought it from resource (functions and processes) view, in which he thought "memory" should not be thought of as some attribute or characteristic of the organism along; rather, the activity of remembering, like the parallel activity of perceiving, must be understood as the interaction of different processes, such as external factors as cues (environmental supports from cues and context), and task demands with internal mental operations (self-initiated activity). As illustrated in Fig.2, different memory tasks involve different extends of environmental supports and self-initiated activity. Older adults only had problems with self-initiated activity so that the aging impairment in one task depends only on how much it involves the self-initiated activity.

Task	Environmental support	Self-initiated activity	Age-related decrement
Remembering to remember Free recall Cued recall Recognition Relearning Procedural memory (priming tasks)	increases ↓	↑ increases	↑ increases

Figure 2. Memory tasks showing differential effects of aging. From Craik (1986)

Inhibition hypothesis

Similar to the resource hypothesis, Hasher and Zacks (1979; 1984) postulated that multiple processing operations are assumed to occur in almost every task and they need different resources to reach maximal performance and it is the availability of these resources which constrained cognitive functioning (general capacity hypothesis). They (1988) further specified the main responsibility of inhibition processing for ageing effects on discourse comprehension.

As an especially important capacity in discourse comprehension, working memory was conceived of as a limited capacity mechanism which shares its resources between a storage function and a set of processing functions. At that moment, the processing component of working memory was found to have higher priority than the storage component (Spilich, 1983). These two components were suggested to reduce differentially with aging because older adults showed larger impairments when the demands on storage were high (Cohen & Faulkner, 1984; Light & Anderson, 1988; Wright, 1981). Inhibitory mechanisms were highly related to the contents of working memory because it served to limit entrance into working memory (Neumann, 1987).

In their discourse comprehension studies, old adults were found to have no problems with comprehension and inference of the discourse when it was explicitly described and was self-spaced presented whereas they did have problems if it was described in an unexpected way or it was presented in limited time. In the latter occasion, older adults had more problems with formatting their inference and had less changes of their inference once it was formatted.

Hasher and Zacks (1988) proposed the inhibition theory to account for these differential aging effects. In the inhibition theory (as illustrated in Fig. 3), they proposed that old adults have problems with inhibiting nongoal information and tend to have more self-generated on-line personal values and experience so that they use more working memory resources to maintain activation of nongoal path ideas which leads to their problems in retrieving goal path ideas and / or in comprehension style how they use to understand and inference goal path ideas.

Figure 3. The theoretical framework of inhibition hypothesis. Adapted from Hasher & Zacks (1988).

Processing speed hypothesis

Salthouse (1993; 1994) found strong correlation between age and various measurements of speed (the median correlation was .45, as illustrated in Fig. 4) suggesting the broad phenomenon of age-related slowing in that age-related slowing is not simply attributed to specific and independent processing deficits.

A serial of studies of Salthouse found largely shared age-related variance across various measures of speed and various measures of memory performance (the average is more than 80%, as illustrated in Fig. 5). And the correlation between age and memory performance were eliminated after controlling the speed, suggesting the important mediator function of processing speed in the relations between age and measures of cognitive functioning.

Figure 4. Strong correlations were found among age and various measurements of speed. From Salthouse (1996)

Given these findings, Salthouse (1996) proposed the processing speed hypothesis, in which it was conceived that the main cause of age-related impairments in cognition is due to reduced speed of many processing operations of old adults.
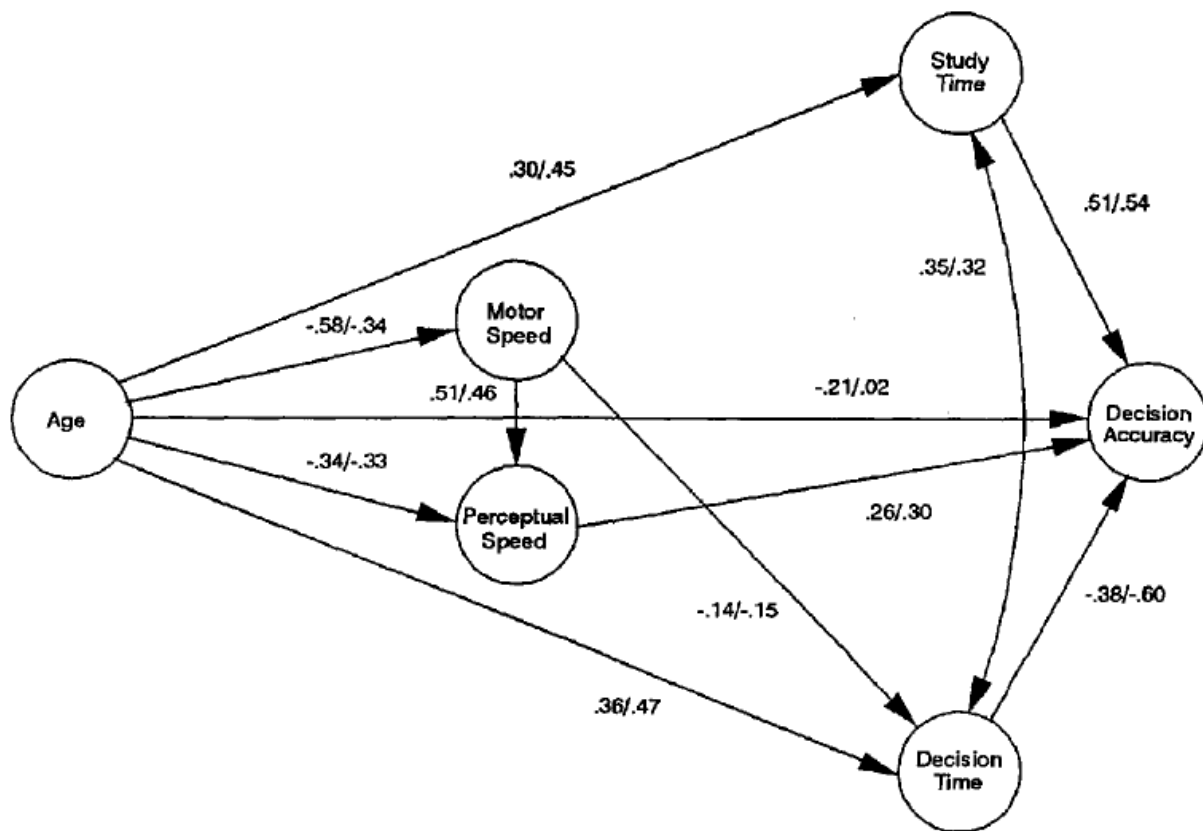
Measure and study	N	Age-related variance			Proportion of shared variance
		Age alone	After reaction time speed	After perceptual speed	
Free recall					
Salthouse (1993d)	305	.162	—	.021	—/.87
Salthouse (1993e)	146[a]	.546	—	.049	—/.91
Salthouse (1995b)	172	.289	—	.013	—/.96
Paired associates					
Salthouse (1993d)	305	.162	—	.024	—/.85
Salthouse (1993e)	146[a]	.596	—	.069	—/.88
Long-term memory for activities					
Earles & Coon (1994)	177	.195	—	.057	—/.71
Associative learning					
Salthouse & Kersten (1993)	104[a]	.152	.016	.025	.89/.84
Salthouse (1994a)					
Study 1	240	.165	.032	.059	.81/.64
Study 2	125	.117	.044	.049	.62/.58
Continuous associative memory					
Letters and Digits					
Salthouse (1994a)					
Study 1	240	.105	.002	.000	.98/1.00
Study 2	125	.038	.004	.000	.89/1.00
Kersten & Salthouse (1993)	78[a]	.265	.046	—	.83/—
Words and Digits					
Salthouse (1994d)					
Study 1	246	.071	.010	.006	.86/.92
Study 2	258	.071	.002	.010	.97/.86
Salthouse (1995d)	100[a]	.369	.087	.061	.76/.83
Working memory					
Paper-and-pencil procedures					
Salthouse & Babcock (1991), Study 2	233	.211	—	.007	—/.97
Salthouse (1991b)					
Study 1	221	.292	—	.050	—/.83
Study 2	228	.254	—	.014	—/.94
Study 3	223	.208	—	.012	—/.94
Computer-administered procedures					
Salthouse (1992a)					
Study 1	180[a]	.279	.081	—	.71/—
Study 2	100	.146	.014	—	.90/—
Salthouse (1995b)	117	.141	.029	.031	.79/.78
Salthouse & Meinz (1995)	242	.033	.001	.001	.97/.97
Combined samples from several studies	184[a]	.155	.031	—	.80/—
Miscellaneous (Salthouse, 1995a)					
Matrix memory					
Verbal	173	.277	.113	.086	.59/.69
Spatial	173	.402	.202	.148	.50/.63
Element memory					
Verbal	173	.087	.040	.005	.54/.94
Spatial	173	.070	.020	.000	.71/1.00
Keeping track					
Verbal	173	.170	.050	.029	.71/.83
Spatial	173	.142	.046	.036	.68/.75

Figure 5. Correlations among age, measurements of speed and various memory performances from results of several studies. Age, speed and memory performances were highly correlated with each other and were highly correlated to age whereas the correlations were largely reduced after control reaction time speed and perceptual speed. Dashes indicate that measures were not available. From Salthouse (1996).

In this theory, Salthouse postulated that there is a general processing constrain so that processing speed is highly responsible for performance of cognitive tasks because 1) if time to perform is limited, slower processing would lead to bad performance in that the operations are not fully executed in simple task or that later processing operations are not fully executed in complex tasks due to large proportion of time occupied by earlier processing (limited time mechanism) and 2) even when time to perform is not limited, slower processing would still lead to bad performance in that different information or processing fail to be integrated because the quality and /or quantity of products of earlier processing is lost due to decay or displacement when the later processing is completed and /or synchronization is disrupted (Simultaneity mechanism). The reduced processing speed is the major factor responsible for declined cognition in older adults.

Common source hypothesis

Consistent with the processing-speed theory, Lindenberger, Mayr and Kliegl (1993) confirmed the powerful predictor role of speed in individual difference in intelligence in old and very old adults (beyond 70 years old). With the structural equation model, they found that the model with speed mediating age and cognition is more prominent than the model without speed between them. Lindenberger and Baltes (1994) found that visual and auditory acuity mediates age and cognition as well as speed. What is more, these sensory functioning accounts for speed better than speed account for sensory functioning, which suggests the more powerful role of sensory functioning. They speculated that these cross-domain relations could be result from a common micro-level factor, such as sensory deprivation or physiological changes with aging. The sensory deprivation, i.e., extensive sensory deprivation may reduce opportunities for intellectually stimulating exchanges with the environment and thus reduce the general level of cognitive abilities. Or maybe they just both reflect the physiological architecture of the brain. The sensory deprivation speculation was ruled out by the following evidence that the powerful association between sensory functioning and intelligence also exits in young adults who have little sensory deprivation (Baltes & Lindenberger, 1997) and that cognitive performance of middle-aged adults is not impaired by artificially reducing their visual and auditory acuity to the levels of old adults (Lindenberger, Scherer & Baltes, 2001).

To summarize, various kinds of cognitive performance are impaired in different degrees in older adults which brought the ideas to think of cognitive performance as results of compounds of different functions or processing. The differential aging effects on different tasks were supposed to be caused by different extents of involvement of some core functions and / or processing, such as self-initiated processing, inhibition processing, speed of processing or common micro-level factors, such as physiological changes with aging. All of the theories point to general factor responsible for aging declines.

Supports from brain structure evidence

Corroborating with the aforementioned hypotheses, neuroimaging studies also found atrophies and shrinkages of brain structure of old adults (Cabeza, Nyberg & Park, 2016; Raz, et al., 2005; Raz, et al., 2010). As illustrated in Fig.6, Caudate Nucleus, lateral Prefrontal Cortex, Cerebellum and Hippocampus diminishes with age at different rates.
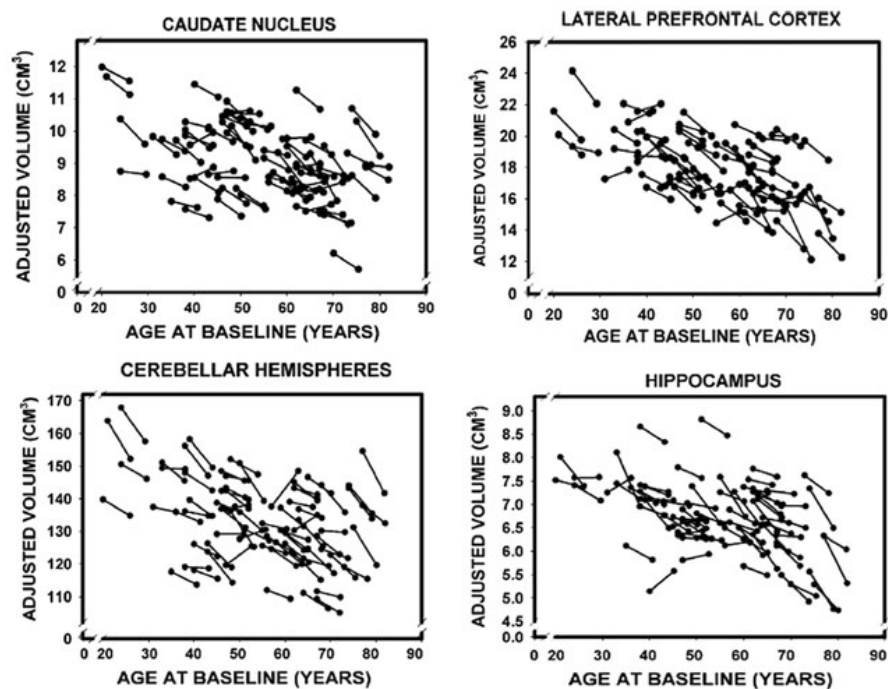

Figure 6. The volume of Caudate Nucleus, lateral Prefrontal Cortex, Cerebellum and Hippocampus diminishes with age. From Raz et al., (2005)

The impaired structures are highly involved in the aforementioned mainly impaired processing. For example, the deficits of white matter integrity found in old adults may reduce conduction speed and slow down processing speed in older adults (Head et al., 2004; Raz, 2000). Both cross-sectional and longitudinal investigations found that there are substantial shrinkages in old adults' brain cortex, especially shrinkage in working memory related cortex caudate, hippocampus and prefrontal cortex (Raz et al., 2005; West, 1996), executive function and inhibition related prefrontal cortex (Haug & Eggers, 1991; Raz et al., 2005; West, 1996). What is more, the shrinkage in older adults in hippocampus (Rosen et al., 2003) and prefrontal cortex (Salat et al., 2002) could predict memory performance.

Function neuroimaging results: compensative and adaptive aging brain

Contrast to the general passive declines in laboratory tasks in older adults, they can still perform daily life very well. Compared to the damages to their brain structure, older adults' performance is generally relatively good. Specifically most healthy aging people do some tasks as good as younger adults, such as world knowledge memory (Salthouse, 2010b), self-relevant memory (Glisky & Marquine, 2009; Gutchess et al., 2007) and several social cognitive functions (Keightley et al., 2006; Ruby et al., 2009). Empirically there are still many older adults who have substantial cognitive reserve such as Profs. Jan Koenderink[2] and Andrea J. van Doorn[3], who are in their seventies but visit several labs every year and published about 10 first-author peer-reviewed papers every year on average in recent 3 years.

Corroborating with these impressions, some distinct patterns have been found in older adults' brain activity (Eyler et al., 2011; Sugiura, 2016; Spreng, Wojtowicz & Grady, 2010). Some of them are associated with better performance suggesting their functional role as compensations rather than impairments. When it comes to the nature of these compensations, they could be interpreted as passive changes to countact the impairments in older adults' brain structure (Park & Reuter-Lorenz, 2009) or active adaptive responses to their more narrow and central environments (Sugiura, 2016).

Posterior-Anterior Shift

Comparing to young adults, older adults' brain during various tasks seems to involve much stronger activity in frontal cortex whereas weaker activity in sensory processing cortex (Eyler et

al., 2011; Davis et al., 2008; Dennis & Cabeza, 2008; Grady et al., 1994; Cabeza et al., 2004). For example, Grady and colleagues (1994) used PET to measure subjects' regional cerebral blood flow (rCBF) activities during location matching tasks and found that comparing to young adults, older adults show weaker activations in prestriate cortex whereas surprising stronger activations in prefrontal cortex, occipitotemporal cortex, inferior and medial parietal cortex. These weaker activations in sensory processing cortex and stronger activations in prefrontal cortex in older adults were replicated in studies with different tasks and materials (Cabeza, 2001; Cabeza et al., 1997; Reuter-Lorenz et al., 2000). Similarly Cabeza and colleagues (2004) used fMRI to measure subjects' Blood-oxygen-level dependent (BOLD) activities during working memory, visual attention and episodic retrieval tasks and found that older adults show weaker activations in occipital cortex and hippocampus in all the tasks whereas they show stronger activities in prefrontal and parietal cortex.

The more widespread prefrontal activations in older adults was speculated to be compensated for the impaired structure in PFC (Persson et al., 2006) and / or for their reduced processing efficiency of occipital cortex (Daselaar et al., 2006; Davis et al., 2008; Reuter-Lorenz & Lusitig, 2005) because of the found correlation between the enhanced activations in PCF and the impaired structure or the reduced activations in posterior brain area.

Dedifferential PFC activity

Older adults are also found to show more general bilateral prefrontal activity compared to left or right lateralized prefrontal activity in young adults (Cabeza, 2002; Cabeza & Dennis, 2012). For example, Grady and colleagues (1994) found that young adults showed activations in right prefrontal cortex during facing matching task whereas older adults in both prefrontal cortex. This right PFC in younger and both sides of PFC in older adults pattern was replicated in different tasks, such as episodic memory retrieval task (Cabeza et al., 1997), word-pair cued-recall task (Bäckman et al., 1997), and word recognition task (Madden et al., 1999). Furthermore this pattern was not limited to the aforementioned verbal materials, but was extended to nonverbal materials (Grady et al., 2002). In addition to the bilateral PFC activities in older adults when it is right lateralized in young adults, older adults also show bilateral PFC activities when it is left lateralized in young adults. For example, the left PFC of younger adults is always activated stronger than the right PFC during episodic memory encoding and semantic memory retrieval

(Cabeza et al., 1997; Tulving et al., 1994). However, older adults still show bilateral PFC activity through reducing left PFC activity during these tasks (Stebbins et al., 2002).

Some studies found the associations between these bilateral changes and better performance (Bergerbest et al., 2009; Cabeza, 2002). For example, Reuter-Lorenz and colleagues (2000) found that older adults with a more bilateral activation pattern performed more quickly in a verbal working memory task. Cabeza et al. (2002) found bilateral PFC recruitment in high- but not in low-performing older adults. Performance of older adults in recognition memory task was impaired by TMS to either PFC hemisphere whereas that of young adults was impaired by TMS to only one side (Rossi et al, 2005).

The benefits of this compensation might be through the recruitments of contralateral regions, which were also found in patients with brain injury (Butefisch et al. 2005; Saur, Ronneberger, et al. 2010; Tyler et al. 2011).

Scaffolding hypothesis

To integrate all these evidences in aging and cognition, Park & Reuter- Lorenz (2009) proposed the scaffolding theory of aging and cognition (STAC). In the theory, as illustrated in Fig. 7, on one hand, they posited that level of cognitive functioning declines due to age-related neural challenges (such as shrinkage, white matter changes, cortical thinning and dopamine depletion, poses neural changes) and functional deterioration (dedifferentiation of ventral visual area, decreased medial temporal recruitment, increased default activity); on the other hand, these declines could be reduced by compensatory scaffolding through more frontal recruitment, neurogenesis, distributed processing and bilaterality. In this STAC theory, the brain is assumed to be adaptive and it would increase or active the scaffolding once it is fronted by challenges, such as novel skill acquisition in young adults, aging so on and so forth.
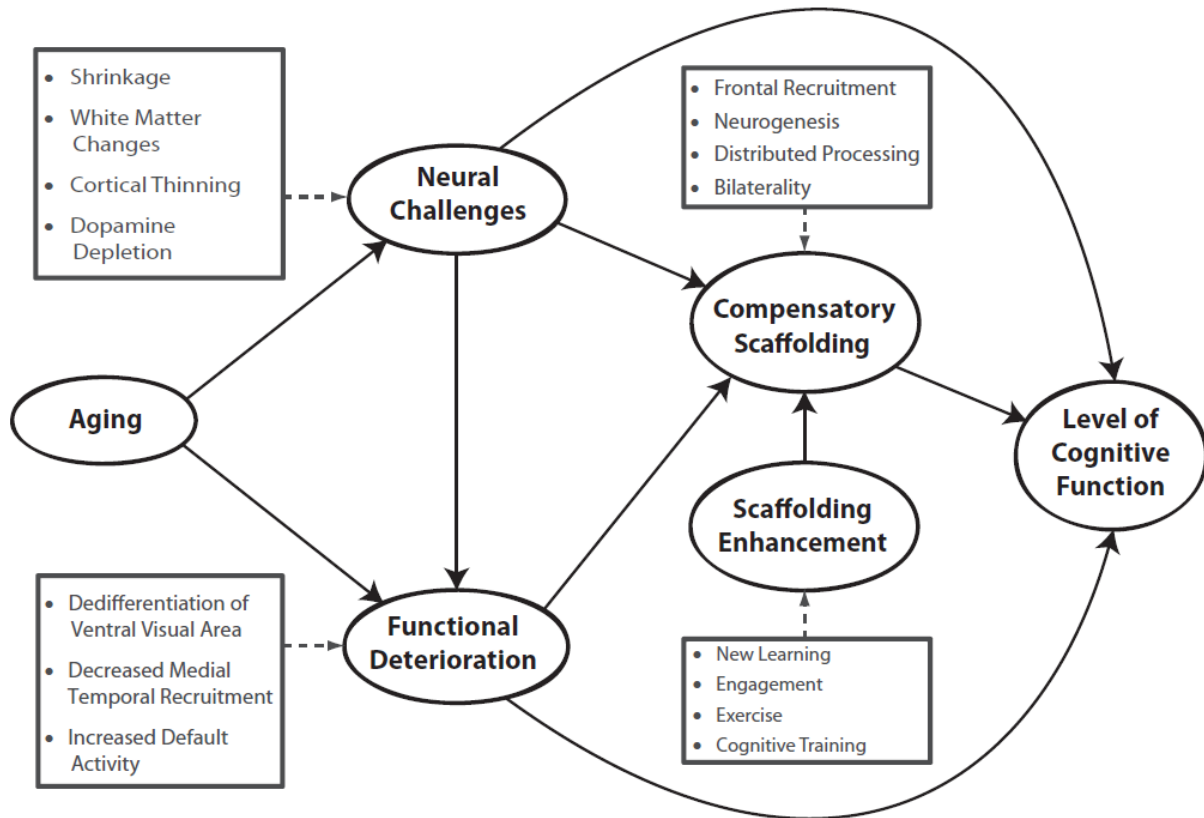
Figure 7. A conceptual model of the scaffolding theory of aging and cognition (STAC). From Park & Reuter- Lorenz (2009).

Adaptation interpretations

However, the compensation interpretation could not explain everything. For example, for the posterior-anterior shift, if the structure of the posterior area is not impaired, such as primary visual cortex (Raz et al., 2005), why does its activations become weaker and need to be compensated by additional PFC activations. The adaptive interpretation is it is a cognitive strategy change from a proactive to a reactive control ((Davis & Cabeza, 2015; Jimura & Braver, 2010; Martins et al., 2012; Paxton et al., 2008). For example, Jimura and Braver (2010) used a task switching task, in which stimuli could be judged from two dimensions (small / large or manmade / nature) and which dimension should be judged was indicated by a preceding cue, and found that older adults showed less cue-related sustain activities in PFC whereas stronger stimuli-related transient activities in PFC. Only the transient activity could predict behavioral performance.

For the compensation of the dedifferentiaonal PFC activity, it is beneficial when one hemisphere is impaired. However, if there is no damage, bilateral activity would be less efficient and that is why young adults do in unilateral way. Then the problem is why older adults even want to keep this bilateral activity with reducing left PFC activity (Stebbins et al., 2002). The adaptive interpretation is that this is a general strategy and that it is more efficient for older adults. Firstly, this bilateral pattern could be more general because it is not limited to PFC but also extended to some other areas (Cabeza, 2002), such as temporal and parietal regions (Grady et al., 2000), temporoparietal regions (Grady et al., 2002). And this general way might be more efficient for older adults (Davis & Cabeza, 2015). Davis and Cabeza (2015) found that cross-hemispheric functional connectivity in young adults increased in domain-general frontal cortex but decreased in domain-specific ventral temporal cortex when the task was more difficult.

The strategy change from a proactive to reactive control and change from specific area to general area might be related to older adults' narrow and more central environments (Sugiura, 2016). For example, older adults tend to have less growth-oriented goals (Ebner et al., 2006; Heckhause, 1997), narrow intimate personal relationships (Carstensen, 1992) and a focused positive self-concept (Riediger & Freund, 2006; Staudinger et al., 1999). This tendency is considered as an adaptive attitude change in response to the altered perception of the social environment, in terms of the increased awareness of the limited time left in life (Carstensen et al., 1999).

Certainly, the compensation hypothesis and the adaptation hypothesis are not exclusive to each other and the integration of them could provide a more unified picture of brain and aging. Sugiura (2016) mentions that one potential way to reconstruct them is investigations on sensorimotor control because the peripheral nerve system of sensorimotor control is like the external environment to the brain and there are strong connections between sensorimotor control and cognition.

The main task of sensorimotor system is to integrate information from multiple sensory channels about the world, and to use them to plan and execute meaningful motor responses. Sensorimotor system is highly interacted with cognitive system. For example, sensory is the antecedent of perception and cognition and it controls which kind of information is put into the brain. For example, fixation is the sampling of information (Toscani, Valsecchi & Gegenfurtner, 2013a; 2013b). Moving fixation distributes attention sources before moving (Chen, Valsecchi &

Gegenfurtner, 2017). Sole vision and hearing acuity of older adults could account for 97% variance of age-related performance in cognition and intelligence (Baltes & Lindenberger, 1997). Older adults who regularly participate in physical activity have faster psychomotor speed on simple and choice reaction-time tests comparing to their sedentary peers (Pierson & Montoye, 1958). Several studies found that cognitive performance could be improved through physical excise (Hillman, Erikson & Kramer, 2008), such as Tao chi (Wayne et al., 2014).

However, sensorimotor control has rather been ignored and less explored in older adults.

General introduction to visuomotor Control

The basic visuomotor control system consists of extrinsic coordinate system and intrinsic coordinate system. For example, in real life, if we want to move your eyes to an object, firstly the visual location of the object should be transformed to our-eyes-referenced position, such as how much degree (extent) it is far from our eyes and in which orientation (direction) of our eyes it is. The system serving to these functions is called extrinsic coordinate system. After receiving this visuomotor transformation, the motor command specifies our eye muscle forces to make the action. In this processing, the command system should consider the current biomechanical properties of our eye muscles. For example, if we have watched a movie for 2 hours and our eyes are tied (muscle fatigue), the command at this moment should be different from the command when we just wake up in the morning. The system serving to these functions is called intrinsic coordinate system. Similarly if we want to move our hand to an object, firstly the visual location of the object should be transformed to body- and hand-referenced position. After receiving this transformation the motor command specifies muscle forces and joint motions after considering current biomechanical properties of the moving arm, such as musculoskeletal dynamics and other forces acting on the limb.

Visuomotor control system is extensively explored through investigating saccadic eye movements, pointing movements and reaching movements with many different tasks, such as visuomotor adaptation, visuomotor sequence learning, visually-guided motor decision making so on and so forth. Saccadic eye movements and reaching movements have their own special characteristics. For example, comparing to pointing and reaching movements, saccadic eye movements are extremely faster (saccade duration is about 40 ms) and more precise. Therefore these different movements are investigated from different respects with different tasks although

they point to similar scientific questions. Investigations from these different movements provide complementary knowledge about the visuomotor control. This thesis mainly focuses on saccadic eye movement and reaching movement.

Visuomotor plasticity is an important ability and is an important form to predict the future state both of the environment and of ourselves and then to compensate for noise, delays and errors. The most important questions in visuomotor adaptation studies are how subjects learn the internal models and how they remember these internal models. To answer these questions, most investigations focused on 1) what factors could induce adaptation; 2) whether adaptation to one factor could be transferred to another or influence another factor; 3) computational models to account for behavioral results; 4) neural mechanisms underlying the adaptation. In the next two sections, I would introduce what has been found on these aspects in saccade adaptation and reaching adaptation.

Saccade adaptation

Saccadic eye movement is the rapid shift of gaze direction. It is so brief that information from online visual or proprioceptive feedback cannot be used to correct its trajectory (Gaveau et al., 2003; Guthrie et al., 1983; Zee et al., 1976). Therefore the initiation of saccades depends critically on a continuous recalibration of the oculomotor system which means there must be a system to guarantee it. This control system is called forward model.

The plasticity capacity of saccade system is widely found in patients with eye lesions and has been well explored with laboratory double-step paradigm. The mechanisms of saccade adaptation have been extensively investigated through the factors driving adaptation, the transfer between saccade adaptations to different factors and neural studies with monkeys and patients. Evidence from different lines suggests distinct mechanisms of saccade adaptation.

Forward model to guarantee saccade accuracy

The saccade system is not perfect. It has inevitable internal noise and variation cause by mechanical properties of the oculomotor plant, such as muscle fatigue so on and so forth. But the saccade is highly correct. The saccade gain (the ration of saccade amplitude to target eccentricity) is stick to 0.9 to 0.95 (Becker, 1989). How the movement is executed with so high accuracy despite of the imperfect of its system? There must be some error-correcting mechanisms to make

it. Robinson (1975) proposed the internal model in which the motor command is speculated to be copied to the motor controller (so-called efference copy) so that the output of command can be predicted without external sensory feedback and this prediction is speculated to be calculated in cerebellum. The hypothesis was confirmed by Xu-Wilson and colleagues (2009), in whose study they found that the decreased acceleration of saccade velocity caused by repetition of saccade is compensated with later decreased deceleration in healthy subjects so that they still keep the accuracy of saccade whereas patients with lesion in cerebellum do not show this compensation resulting in dysmetric saccade.
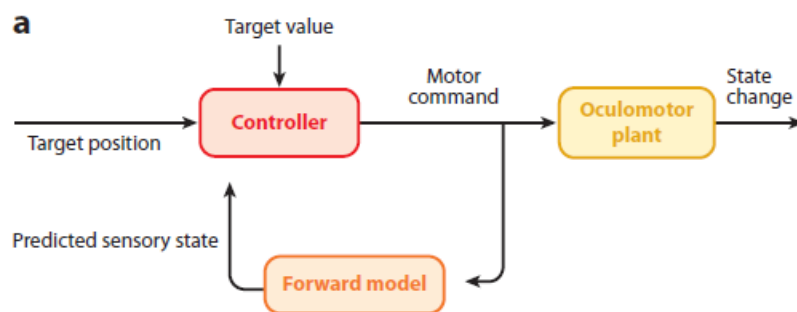

Figure 8. Forward model in motor control system. From Xu-Wilson et al., (2009).

Categories of saccade adaptation

Natural adaptation caused by eye lesions

The saccade accuracy is highly maintained despite of weakening of the extraocular muscles. For example, Kommerell and colleagues (1976) found that a patient with weakened lateral rectus muscle of his dominant eye, which results in problem with rotating the eye laterally, show large hypermetric saccade of his normal eye naturally. However, saccade of his normal eye became normetric after his dominant eye was patched for 3 days. Similar saccade adaptation was confirmed by Abel et al. (1978) in another patient and confirmed in monkeys with resection of the tendons of the horizontal recti of one eye (Optican & Robinson, 1980; Snow et al., 1985).

Laboratory adaptation induced by intransaccadic step

Saccade adaptation has been extensively investigated in laboratory with a double-step paradigm firstly reported by McLaughlin (1967). In the paradigm, as illustrated in Fig. 9, subject experienced an error between saccade landing position and the target due of the imperceptible

displacement of the target during saccade execution. At the beginning of the adaptation, subject made a second automatically corrective saccade because of the post-saccadic retina error. This correction makes the saccade system recalibration the visual position and motor position to reduce the experienced error which is reflected by the amplitude change of the primary saccade. Therefore, amplitude of primary saccade changes to the displaced target position gradually. After the adaptation, amplitude of primary saccade changes back to the initial target position gradually, which is always called recovery.
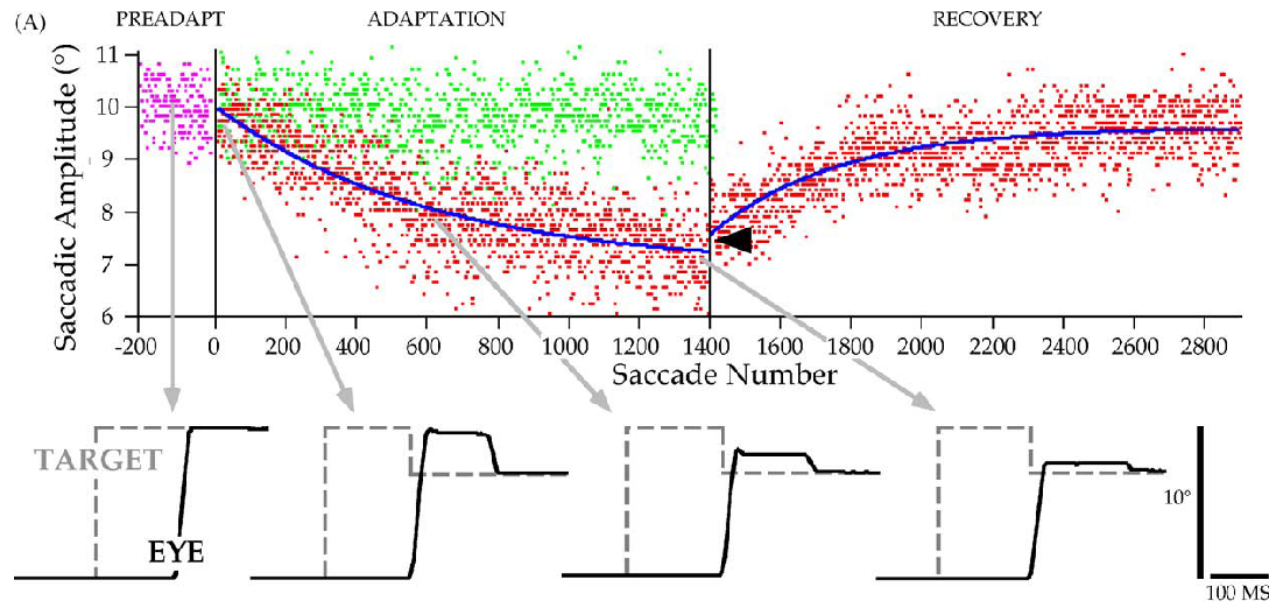

Figure 9. Courses of representative saccadic amplitude adaptations for monkeys. Top:Adaptation and recovery of saccades made to 10◦ horizontal target steps with a 30% backward adaptation step. Saccadic amplitude is plotted as a function of the number of the trial in each direction. Magenta points, data from preadaptation trials. Red points, data from trials in the adapted direction. Green points, data from interleaved trials in the non-adapted direction. Adaptation and recovery data are fit by exponential function blue. Arrow indicates initial rapid recovery phase. Bottom: Representative examples of target (gray dashed lines) and eye (black lines) position for different trials during preadaptation and adaptation. From Hopp & Fuchs, 2004.

During the first several trials of the beginning of the adaptation, there is a relative fast change of the primary saccade amplitude (so-called fast adaptation) and followed by gradual slower adaptation. The adaptation and recovery could be well fitted with an exponential function (as the blue line in Fig. 9). Correspondingly, there is always a fast recovery at the beginning of the post-adaptation phase (black arrow in Fig. 9) and followed by a gradual slower recovery.

Mechanisms of Saccade adaptation

Considerable studies have been done to investigate the mechanisms of saccade adaptation. Distinct mechanisms underlying the adaptation have been confirmed from different lines of studies, such as what drives the laboratory adaptation, how adaptation to different vectors influence each other, differences between natural and laboratory saccade adaptation so on and so forth.

Drivers: error signal, reinforcement, perceptual task

What drives the adaptation can tell something about the mechanisms of adaptation. Apparently the adaptation in double-step paradigm is driven by the mismatch between the primary saccade and displaced target (error-driven). However, what is the nature of the error? The visual hypothesis posits that given the forward model this driver error could be prediction error, i.e., the visual estimate of the spatial separation between target position and saccade endpoint. But the motor hypothesis thinks that this adaptation is due to the corrective saccade so that the error is retinal error, i.e., the motor commands of the corrective saccades generated toward the target. The prediction error or visual hypothesis was confirmed by findings that the adaptation happened even with the post-saccadic error minimized or eliminated (Bonnetblanc & Baraduc, 2007; Gegenfurtner et al., 2008; Noto & Robinson, 2001; Wallman & Fuchs, 1998;). For example, Gegenfurtner and colleagues (2000) found that amplitude of saccade to a stationary target filled with a drifting sine-wave grating which changed its motion direction during the saccade and thus creates a visual illusion of target displacement could also be changed by this illusion, suggesting that saccade adaptation can also be elicited without any physical change of target position, i.e., no retinal error. Collins and Wallman (2012) even elicited backward saccade adaptation (amplitude decrease) with selectively giving feedback of the landing position of saccades with larger-than-median amplitude and forward adaptation (amplitude increase) with giving feedback of the landing position of saccades with smaller-than-median amplitude. In this case, there is no retinal error at all and this adaptation is just elicited by the reinforcement of some saccades. Schütz, Kerzel and Souto (2014) further elicited saccade adaptation with a perceptual task. As illustrated in Fig. 10, subjects were asked to make a saccade to the peripheral array with 7 characters and then to report the content of the black character. During the baseline trials (Fig. 10A), the target character letter was in the middle (4th position) of the array whereas in the far-away position (6th

position, forward adaptation, Fig. 10B) or the closer position (2nd position, backward adaptation, Fig. 10C) during the adaptation trials. They found clear forward adaptation and backward adaptation. The adaptation of vertical saccade was also determined when the characters were vertically aligned whereas no adaptation was found when subjects were only asked to make the saccade without reporting the character. Therefore, the adaptation is mainly induced by the perceptual task but not the displacement of the black character. Meanwhile, they also compared the adaptation induced by this perceptual task with that induced by ISS and found that the fast adaptation is much larger in the perceptual task whereas the slower adaptation is equivalent.

Figure 10. Perceptual tasks paradigm. Subjects were asked to make a saccade to the peripheral array with 7 characters and then to report the content of the black character. (A) During baseline trials, the black target was placed in the middle (4th position) of the array; (B) During forward adaptation trials, the target was placed in the far-away position (6th position); (C) During backward adaptation trials, the target was placed in the closer position (2th position). From Schütz, Kerzel & Souto (2014).

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Taken together, saccade adaptation could be induced by different factors, from prediction error to reinforcement to perceptual task. The differential differences in faster and slower adaptation between different paradigms suggest distinct mechanisms of saccade adaptation.

Adaptation is specific to saccade vector

The distinct mechanisms hypothesis is also implicated by studies on adaptation transfer. On one hand, saccade adaptation is specific to saccade vector (saccade direction and amplitude) and the adaptation of one saccade vector could be not fully transferred to saccade with different amplitude or direction (Alahyan & Pélisson, 2004; Frens & van Opstal, 1997; Deubel, 1987; 1989; Noto, Watanabe & Fuchs, 1999; Straube et al., 1997; Alahyan & Pélisson, 2004) which suggests the low-level mechanism of saccade adaptation.

On the other hand, the adaptation can be elicited by high-level processing, such as aforementioned reinforcement and perceptual task which suggests the high-level mechanism of saccade adaptation (Collins & Wallman, 2012; Wong & Shelhamer, 2012; Schütz, Kerzel & Souto, 2014; Schütz & Souto, 2015).

Timecourse of adaptation: multiple states

The timecourse of saccade adaptation could tell something about its mechanisms. The different timecourse of natural saccade adaptation and laboratory saccade adaptation suggest there might be distinct mechanisms: patients with damage of the eye muscles or their innervations need several days to compensate for the abnormal saccades caused by this lesion (Abel et al., 1978; Kommerell et al., 1976; Optican & Robinson, 1980; Snow et al., 1985;) whereas it just takes tens of minuses for human or hours for monkeys to adapt to the laboratory double-step manipulates (McLaughlin, 1967; Miller et al., 1981; Straube et al., 1997; Scudder et al., 1998). Although the slower adaptation in patients could be explained by specificity of adaptation to saccade vector so that they need more time to adapt to saccades with different directions and amplitude (Miller et al., 1981; Scudder et al., 1998; Robinson et al., 2002), different components of adaptation were still be proposed because 1) of the incomplete adaptation, i.e., the magnitude of adaptation is smaller than the step size (Miller et al., 1981; Robinson et al., 2002); 2) the rapid adaptation at the first several trials of adaptation but slower adaptation at the late adaptation phase (Scudder et al., 1998).

This distinct mechanisms hypothesis is further suggested by facilitations for relearning (Kojima, Iwamoto & Yoshida, 2004). In their study, Kojima and colleagues found that re-adapting to the previous adaptation after the recovery is faster than the initial adaptation (this facilitation is called savings), suggesting the facilitation from history of adaptation. Although re-adaptation is faster at the beginning, it achieved to the similar level as the initial adaptation which might be due to the slower adaptation at the late phase. These differential effects imply distinct mechanisms underpinned the adaptation.

Neural mechanisms

All the studies from the factors inducing adaptation, transfer of adaptation and the timecourse of adaptation suggest distinct mechanisms of adaptation. This is also supported by neural studies which found different areas responsible for the adaptation.

Firstly superior colliculus has been found to involve in the adaptation. As mentioned above, saccade adaptation is specific to saccade vector and adaptation of specific direction and amplitude is partly or not transferred to saccade with other directions and amplitudes. This adaptation field (the transfer relation of the adapted saccade vector and other vectors) is very similar with SC movement field, i.e., the relation between SC neuron response to preferred saccade vector and to other vectors (Deubel, 1987, 1989; Noto et al., 1999). This similarity suggests that the adaptation occurs at or upstream of the SC or at collicular descending pathways where the saccade is represented as a vector and thus are supposed to involve low-level processing mechanisms.

Secondly cerebellum has also been confirmed to involve the adaptation and different parts of cerebellum are involved in adaptation of reactive and voluntary saccades separately. Human patients with cerebellar lesions show saccadic dysmetria which could not be resolved with time suggesting the role of cerebellum in establishing normal saccades (Zee et al., 1976; Straube et al., 1995). Desmeurget and colleagues (1998) found the correlation between the magnitude of adaptation induced by double-step paradigm and PET signal in subjects' medio-posterior cerebellum. Specifically patient with lesion in medio-posterior cerebellum only has problem with adaptation of reactive saccades whereas patient with lesion in latero-anterior cerebellum only has problem with adaptation of voluntary saccades (Alahyane et al., 2008). Similar results were

found in monkeys with lesions in cerebellum (Goldberg et al., 1993; Optican & Robinson, 1980; Robinson et al., 2002).

Finally cortical areas, such as thalamus and basal ganglia might also involve in the adaptation (Alahyane et al., 2007; Gaymard et al., 2001).

Aging effects on saccade adaptation

Some studies have explored aging effects on saccade control. It seems different processing is impacted by aging differentially. For details please seen "aging effects on saccade control" in the saccadic decision making section.

There has been no study investigating how ageing influence saccade adaptation. Therefore, to further explore how aging impacts different parts of saccade system, the first study of this thesis investigated the low-level and high-level mechanism of saccade adaptation in younger and older adults with double-step paradigm and perceptual tasks paradigm respectively.

Reaching adaptation

Reaching control system differs from saccade control system in target representation and trajectory formation. When representing the targeting object, extra-retinal information and head-trunk information should be added into the motor command in addition to the retina information. After this visuomotor transformation (extrinsic coordinate system), motor commands specify muscle forces and joint motions to move the hand to the desired location (intrinsic coordinate system). This transformation needs to take account of the biomechanical properties of the moving arm, such as musculoskeletal dynamics and other forces acting on the limb.

Reaching movements are with longer duration and less precision so that the two coordinate systems could be more easily and separately manipulated. The mechanisms of reaching adaptation have also been investigated through comparing adaptations of these two systems. Similar as investigating saccade adaptation with double-step paradigm, the learning of extrinsic coordinate system of reaching system has also been investigated by visuomotor rotation paradigm; instead of using lesions to study intrinsic coordinate system of saccade system, the intrinsic coordinate system of reaching system has been investigated by lateral force fields paradigm.

Comparing to the imperceptible manipulations or adaptations in saccade adaptation tasks, manipulations are more noticeable to subjects in reaching adaptation so that explicit processing is more profound in reaching adaptation. Mechanisms of reaching adaptation have also been investigated through the interactions between implicit processing and explicit processing.

Given these difference between saccade system and reaching system, reinforcement learning has been relatively more investigated in reaching adaptation.

Categories of reaching adaptation

Most of reaching adaptation studies use error-based paradigm, such as prisms, visuomotor rotations, or lateral force fields. In these paradigms, an error between the movement execution and the targeting movement was made through the lateral displacement by prisms, rotation of movement direction, or lateral forces applied by a robot arm. These paradigms could be categorized into two types: learning of kinematics (visuomotor-rotation-based adaptation induced by prisms or screen-cursor rotation) and learning of dynamics (lateral-force-based adaptation induced by lateral force imposed to the arm).

The left of Fig.11 is a typical adaptation induced by cursor-screen rotation (learning of kinematics). In the experiment, subjects are asked to reach to the target (vertical position in this example) but cannot see their hand and movement at all so that there would be a cursor indicating the position of their hand. During the adaptation, the cursor is always rotated in certain degree to the exact movement (45° counter-clock wised in Fig.11 left). The error between reaching direction of subjects and target direction is very similar with the results illustrated in Fig. 12A, in which the rotation is 30°. At the beginning of the adaptation, subjects have no idea about the rotation so that the error is close to the rotation 45°. Then the error reduces gradually.

The right of Fig.11 is a typical adaptation induced by lateral force field (learning of dynamics). During the adaptation, a lateral force induced by extra mass placed laterally to the forearm on an outrigger attached to an airsled. The adaptation induced by this lateral force is very similar with the results illustrated in Fig. 12C and it is very similar with that induced by screen-cursor rotation.

However, in spite of the similarity between the two learning, they have been found to involve in different systems.
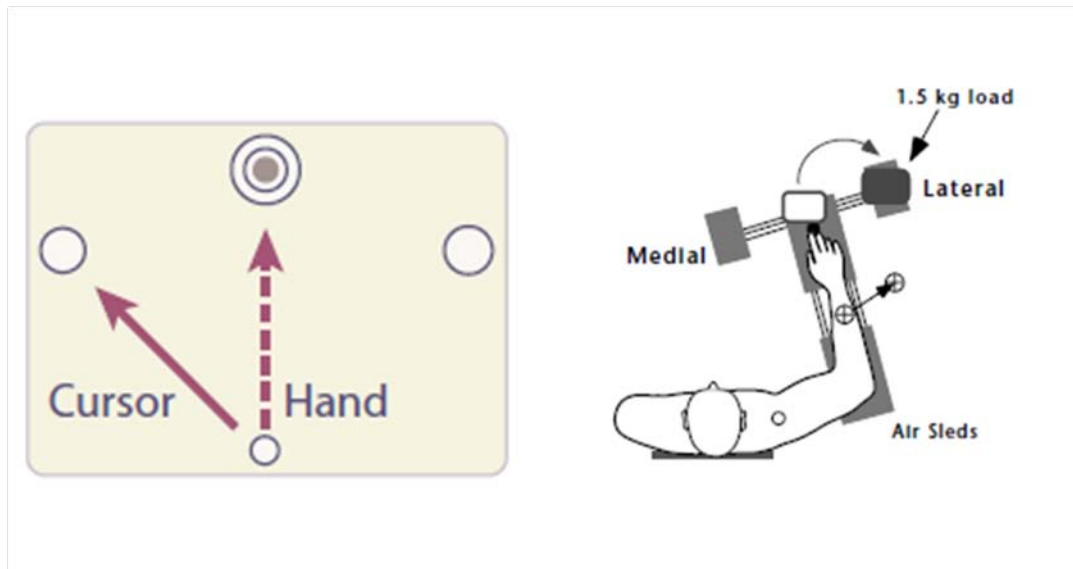
Figure 11. visuomotor rotation paradigm (left) and force field paradigm (right). From Krakauer, Ghilardi &Ghez (1999)

Characteristics of reaching adaptation: Aftereffect, savings, consolidation

As similar as what found in saccade adaptation, adaptation of reaching movement is limited to adapted vector (Cunningham, 1989; Krakauer et al., 2000) and have large aftereffects (Caithness et al., 2004; Wigmore, Tong & Flanagan, 2002), i.e., subjects continuously made the compensation even when the visuomotor rotation or lateral force was removed. When exposed to the same visuomotor rotation or lateral force again on subsequent days, contrast to no savings at all in saccade adaptation with ISS (Straube et al., 1997), Savings in reaching adaptation is larger and longer, and can be as long as a week, if not longer (Krakauer, Ghez & Ghilardi, 2005). This savings is supposed to be caused by recall of the off-line consolidation.

Mechanisms of reaching adaptation

Mechanisms of reaching adaptation have been explored through investigating the differences and interactions between the two coordinal systems with the two categories of adaptation tasks, and through investigating the distinct acquisition and retention processing and neural studies with PET, fMRI, tDCS, TMS and patients with lesions.

Drivers: Errors in extrinsic coordinate system and intrinsic coordinate system

The reaching kinematics (reaching position and direction) are supposed to be learned from errors in extrinsic coordinate system whereas dynamics are supposed to be learned from proprioceptive errors in intrinsic coordinate system (Flanders, Tillery & Soechting, 1992; Desmurget et al., 1998).

Krakauer, Ghez and Ghilardi (1999) further investigated these two systems through the consolidations and interferences of these two types of adaptation. In their study, as illustrated in Table 1, the learning of the two systems were separately investigated by reaching adaptation induced by visuomotor rotation (Group 1), and by mass force (Group 3). Consolidation of the adaptation was tested by the same second adaptation tested on the successive day. The interference from the same system was investigated by testing how adaptation on the second day is impacted by another different adaptation with the same type on the first day (Group 2 and Group 4). The interactions between the two systems were tested by interfering the consolidation of rotation adaptation by doing later-force adaptation on the first day (Group 5) and by doing the two adaptations simultaneously (Group 6).

Table 1. Experimental Conditions

Group	Day 1 Training	Day 2 Training
Group 1	30° CCW rotation	30° CCW rotation
Group 2	30° CCW rotation → 30° CW rotation	30° CCW rotation
Group 3	Lateral mass*	Lateral mass*
Group 4	Lateral mass* → medial mass*	Lateral mass*
Group 5	30° CCW rotation → lateral mass*	30° CCW rotation
Group 6	30° CCW rotation plus lateral mass	30° CCW rotation plus lateral mass

* No visual feedback

As illustrated in Fig. 12, subjects in all the groups showed clear adaptation on both of the two days. However, although Group 1 showed clear consolidation (smaller error at the beginning of the next day comparing to the error at the beginning of the first day), the consolidation is not complete (Fig.12A, error at the beginning of the next day is larger than the error at the end of the first day). Besides, the consolidation is removed by adaptation of an opposite rotation: there is no difference (consolidation) between adaptations on the two days in Group 2 (Fig12. B).
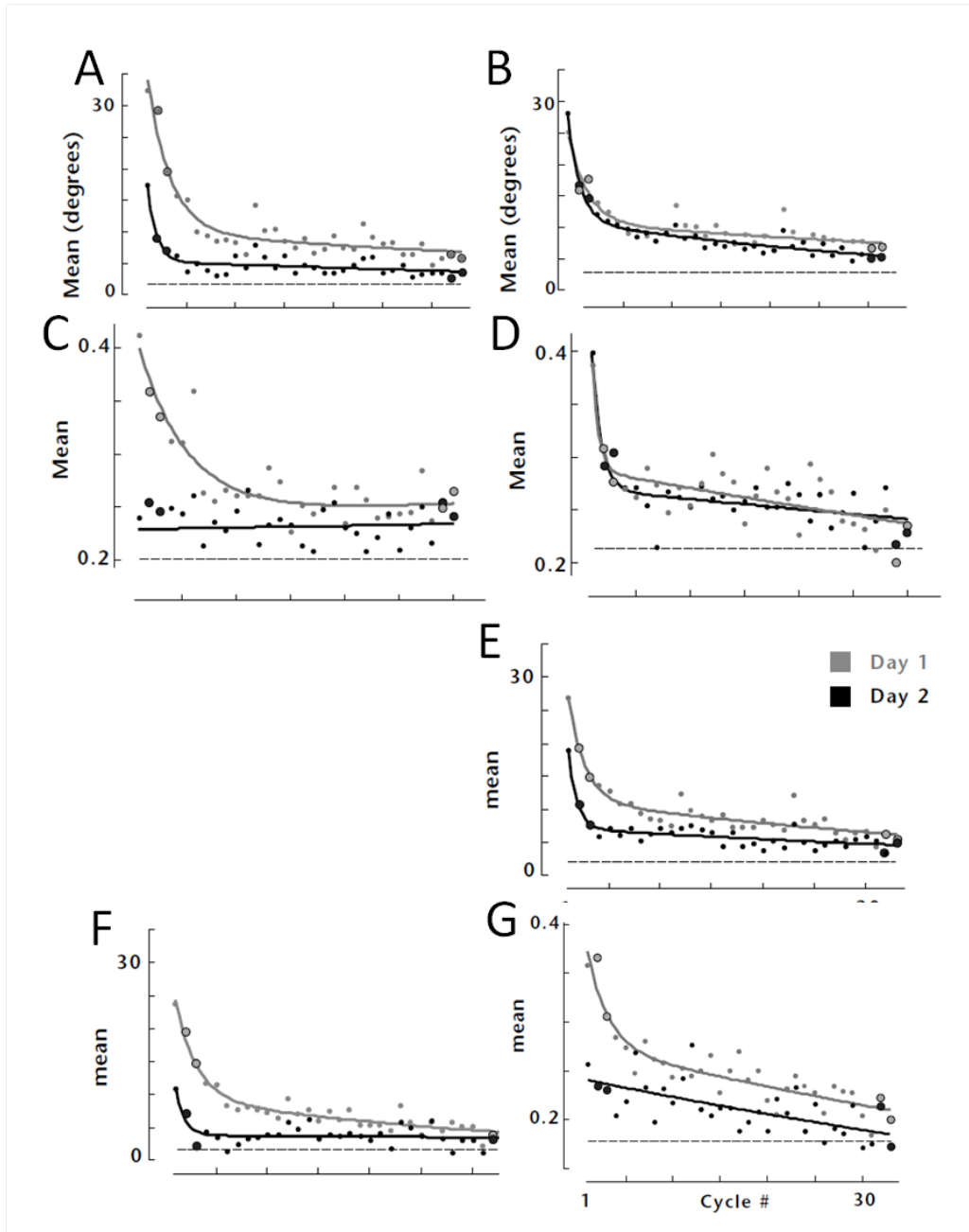
34

Figure 12. Learning and consolidation of reaching adaptation on the first day (gray lines) and the successive day (black lines) induced by visuomotor rotation (A), by visuomotor rotation with opposite adaptation interference during the two days (B), by lateral mass (C), by lateral mass with medial mass interference during the two days (D), by visuomotor rotation with lateral mass interference during the two days (E), rotation plus lateral mass (F, results for rotation and G, results for lateral mass). X axis is the cycle (set of trials) number; y axis is error between reaching movement and desired target. Grey lines represent adaptation on the first; black lines represent that on the second day; dash line represents the movement of the baseline trials on first day.

Subjects in Group 3 showed complete consolidation: adaptation at the beginning of second is similar with that at the end of the first day (Fig.12C). This consolidation is also removed by adaptation of another adaptation of medial force (Fig.12D).

No interference of the mass-force was found on adaptation of rotation: adaptation on the second in Group 5 is similar with that in Group 1(Fig.12E). Neither difference is found between Group 6 (Fig.12 F/G) and Group 1(Fig.12A) or Group 3(Fig.12C).

These findings suggest that learning of the two systems do not interfere with each other and they are constructed and consolidated in parallel.

However, the lack of interference across two kinds of learning might also result from the fact that the context was sufficiently different to put them in distinct working memory system. Then the problems came out: When an error occurred in a reaching movement, how the system figures out what is the source of the error and how to adjust the movement in the following movement. Before answering this question, we should firstly figure out its inverse question how the motor command integrates these two stream information to make the movement. It is found that the two streams of information are integrated through Bayesian model, i.e., the weight of each stream is inversely related to the variance of each system (Körding & Wolpert, 2004; Körding, Ku & Wolpert, 2004; Izawa & Shadmehr, 2008). Similarly how much of the error would be corrected is also found to depend on the internal noise of movement system and the quality of visual feedback signal. For example, Wei and Kording (2010) found that the error during a reaching adaptation with visuomotor rotation is less corrected every trial when the visual feedback of the movement trajectory is uncertain through being artificially blurred.

Consistently the Bayesian causal inference is found to solve the problem how the system figures out the source of the experienced error (Berniker & Kording, 2008). In this source-estimation casual inference model, the nervous system constantly updates its parameter estimates and its uncertainty about those estimates through an application of Bayesian inference and uses the probability to source the error. Wei and Kording (2009) extended this hypothesis that the nervous system estimates the relevance of observed error and only adapts to relevant errors. The relevance of the error could also be estimated through context (wearing a prism goggle or not), cues, or cognitive strategies.

Implicit processing could not be overridden by explicit strategies

Contexture cues could help identify the source of experienced error and help to recall learning of specific internal model in the end. These cues might also bring cognitive strategies into adaptation and then impact adaptation. For example, in the study of Mazzoni & Krakauer (2006)', they told subjects explicitly about the visuomotor rotation (45° CCW) and asked subjects to cancel it by aiming 45° CW the target. At the beginning, subjects successfully used the strategy and made an abrupt stepwise cancelling the rotation resulting in near zero error. However, as subjects continued to make movements, a CW error increased gradually which was very similar with the adaptation when subjects did not know the rotation at all (normal adaptation). These results suggest that subjects still adapted their internal models under explicit strategies and that the learning of the internal model could not be eliminated by the explicit awareness of the rotation and explicit strategies. Therefore, the adaptation of the internal model is also called implicit processing because it is non-intentional and automatic. Other processing is called explicit processing.

Christou and colleagues (2006) further found that individual difference in working memory would make a contribution to individual difference in xx adaptation but this contribution is through the explicit strategy so that its contribution is eliminated once the strategy is restricted by the task.

Multiple states: Acquisition, retention and reward

The reaching adaptation induced by visuomotor rotation is similar with saccade adaptation induced by ISS; the reaching adaptation induced by lateral force is similar with saccade adaptation induced by eye lesion. Similar with the rapid and slow two-state in saccade adaptation, multiple states are also found in reaching adaptation. For example, Smith, Ghazizadeh and Shadmehr (2006) found that a two-rate state-space model can fit the reaching adaptation very well. In their model, it is posited that there are two states in the adaptation: The fast state responds strongly to error but has poor retention whereas the slow state responds weakly to error but retains information well. This two-rate state model does not fit the adaptation data very well but also predicts that the saving comes from the fast decay of the fast state, which is the same direction of subsequent initial rotation.

From the two-rate two-state space model, two distinct processing during the adaptation are identified: Acquisition and retention. Acquisition refers to learning of the internal models through trial-by-trial error reduction; retention refers to the memory of the learned internal models.

In addition to explicit knowledge, reward and punishment are also found to impact reaching adaptation but the results are rather mixed. Firstly, using implicit procedural learning, Wächter and colleagues (2009) found enhanced learning by monetary reward but no punishment effect on learning. Abe and colleagues (2011) found improved long-term retention by reward whereas limited impairment by punishment. Izawa and Shadmehr (2011) found that performance-based reward auditory feedback (a sound of explosion in successful performance) could only induce reaching adaptation when the visual feedback of the end moving position is presented but not without visual feedback. Nikooyan and Ahmed (2015) found reward feedback could induce reaching adaptation alone and reward plus visual feedback could accelerate reaching adaptation. But Gelea and colleagues (2015) found the dissociable effects of monetary reward and punishment during reaching adaptation: punishment speeds up acquisition of adaptation but does not impact retention whereas reward does not impact acquisition but increases retention. Despite these inconsistency, they appear to support the distinct function of reward-based learning and implicit learning of internal models.

Neural mechanisms of reaching adaptation

Numerous Studies have explored the neural structures underlying reaching adaptation using PET, fMRI, transcranial magnetic stimulation (TMS), transcranial direct current stimulation (tDCS) and neurological populations. Comparing the brain activity during normal movement and reaching adaptation with PET, a network including cerebellum, posterior parietal cortex, primary motor cortex (M1), dorsolateral prefrontal cortex, and striatum is engaged specifically in reaching adaptation not just to reaching movement (Krakauer et al., 2004; Krebs et al., 1998; Nezafat et al., 2001; Shadmehr & Holcomb, 1997). The function of cerebellum and PPC in acquisition and M1 in retention and consolidation has been confirmed by studies with TMS and tDCS.

As similar as patients with lesion in cerebellum showed problems in saccadic adaptation, they also showed problems in pointing adaptation with prism (Weiner, Hallett & Funkenstein, 1983; Martin et al. 1996) and in reaching adaptation (Smith & Shadmehr, 2005; Maschke et al., 2004). Rabe and colleagues (2009) even found atrophy of the intermediate and lateral zone of the

anterior lobe correlated with impairment in adaptation with force field whereas atrophy of the intermediate zone of the posterior lobe correlated with adaptation deficits in adaptation with visuomotor rotation. Galea and colleagues (2011) found that when anodal tDCS was applied to subjects' cerebellum while they performance visuomotor rotation reaching adaptation, their adaptation much faster whereas the aftereffect of adaptation is not impacted at all.

Although substantial studies support the role of PPC in visuomotor transformations and its function in motor planning, studies from patients with Optic ataxia also suggest its role in adjustment in on-line reaching movement. Optic ataxia is a disorder that results from damage to the posterior parietal cortex (PPC) leading to deficits in reaching and grasping objects presented in the visual field opposite to the damaged hemisphere (Perenin & Vighetto, 1988; Battaglia-Mayer and Caminiti, 2002; Pisella, Rossetti & Rode, 2017), suggesting the role of PPC in reaching adaptation. For example, Pisella and colleagues (2000) found that normal subjects could automatically correct their hand path when the reaching target was displaced whereas the patient with optic ataxia cause by bilateral damage to the PPC could not. Similarly with this study, Desmurget and colleagues (1999) used similar task and found that the application of single pulses of TMS over PPC at the onset of movement disrupts the adjustment of hand paths to displaced target but not to stationary targets. The direct evidence of the role of PPC in reaching adaptation is Della-Maggiore and colleagues' study (2004). Their study found that single pulses of TMS stimulation over the left PPC 40ms after the onset of movement during lateral-force adaptation does not impact the early stages of adaptation but decrease the later stages of adaptation. But it has no effect on aftereffect.

Initially M1 is found to be involved in movement execution (Li et al., 2001), but its specific role in movement adaptation is unknown. Accumulating evidence from monkey studies and TMS studies suggests its role in consolidation of reaching adaptation (Baraduc et al., 2004; Hadipur-Niktarash et al., 2007; Li, Padoa-Schioppa & Bizzi, 2001; Paz et al., 2003). For example, Richardson and colleagues (2006) stimulated subjects' M1 with repetitive transcranial magnetic stimulation (rTMS) for 15mins before they performance the force lateral reaching adaptation. They found that this before stimulation does not impact subjects' following adaptation at all. However, subjects received rTMS stimulation showed less adaptation in the re-adaptation on the following day. When anodal transcranial direct current stimulation (tDCS) was applied to subjects' M1 when they performance visuomotor rotation or the force field reaching adaptation,

their adaptation was not impacted at all whereas they show larger aftereffect (Gelea et al., 2011; Hunter et al., 2009).

Aging effects on reaching adaptation

One decade ago aging effects on reaching adaptation have been explored by numerous studies whereas the results are still not very clear (Boch & Schneider, 2002; Seidler 2006). For example, Fernandez-Ruiz and colleagues (2000) found that older adults showed slower adaptation rate and larger aftereffect. But using similar task, Roller and colleagues (2002) found adaptation in older adults is preserved. With more and more knowledge about motor adaptation from studies in young adults, through well-designed experiments these discrepant results could be reconciled by the preserved implicit learning but declined explicit learning (Bock, 2005; Heuer &Hegele, 2008; Hegele & Heuer, 2013; McNay & Willingham, 1998). Therefore when different tasks involves in different extent of different processing, the aging effects on these tasks would be different. For example, found older adults show deficit in awareness of the nature of the task. For example, Hegele and Heuer (2013) found stronger age effects in younger and older adults who have high explicit knowledge whereas this difference is missing in younger and older adults who have poor explicit knowledge.

From the limited studies in young adults, there seems to be positive influence of monetary reward and punishment on reaching adaptation. Their influence on reaching adaptation in older adults has never been explored although their influence on behaviors has between explored, the second study of thesis aimed to figure out whether monetary reward and punishment helps to reduce aging declines in reaching adaptation.

Saccadic decision making

Visuomotor control has also been explored by motor decision making: how the motor landing positions are influenced by different factors. As a window of cognition, decision making is an action based on information and values related to potential outcomes (Shadlen & Kiani, 2013). Saccade landing position is impacted by several factors, including physical properties of object and value of the outcome so that saccade-making has been investigated as decision making recently. This decision making processing has been explored mainly with reward.

Factors influencing saccade-making

Saccade landing position is found to be influenced by different factors (Schutz, Braun & Gegenfurtner, 2011), from salience of object, to object recognition, to value and plans (illustrated in Fig. 13). For example, when viewing a static scene, our eyes are firstly attracted by the salient parts of the scene (Itti, Koch & Niebure, 1998) and this landing position could be predicted by a salience map model (Betz et al., 2010; Itti, Koch & Niebure, 1998; Talter & Vincent, 2009). Subjects tended to fixate faces in scenes even when there they were not instructed to search for them (Cerf, Frady & Koch, 2009). Saccades were made to target with reward (Sohn & Lee, 2006). However, how these different information are combined and finally determine the landing position is still not clear.
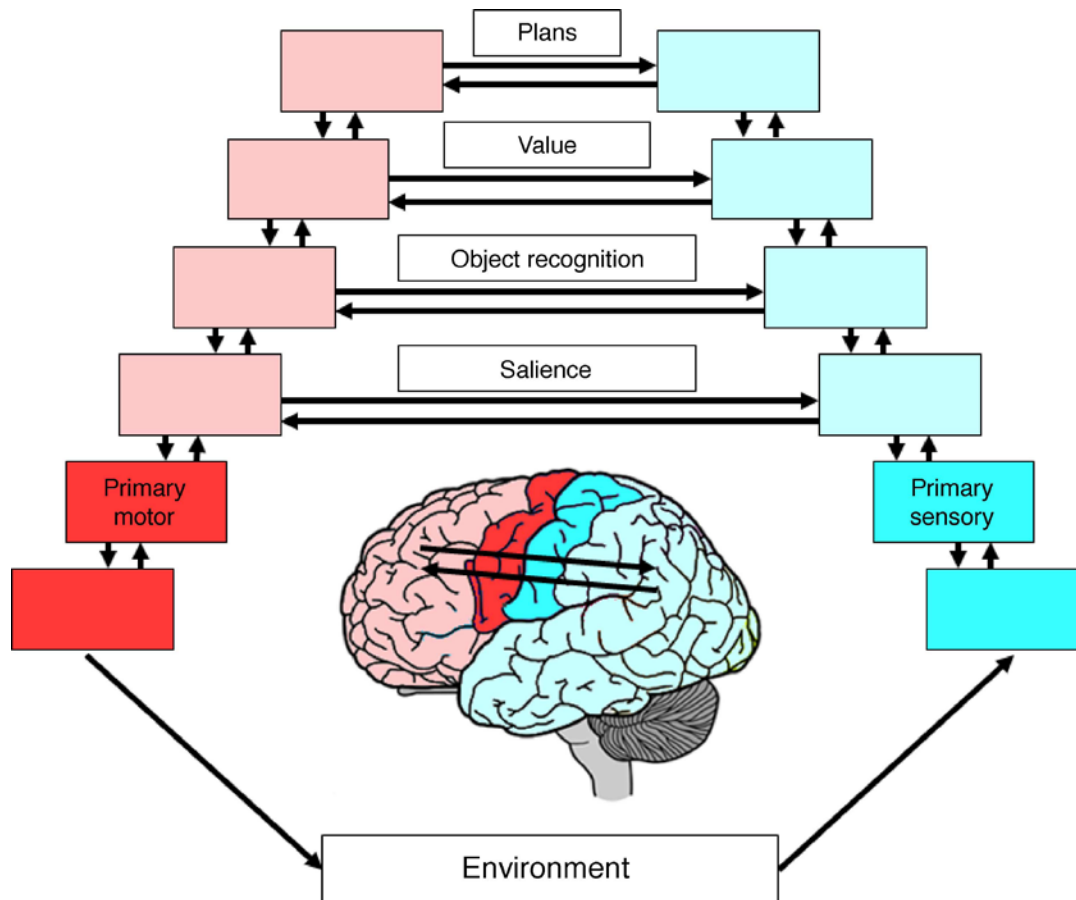

Figure 13. Framework for the control of saccadic eye movements. There are several interacting layers of control that influence saccadic target selection and landing position. From Schutz, Braun & Gegenfurtner, 2011.

Saccade latency is also influenced by some of the factors. For example, reactive saccade, such as making gazes shift to an immediately disappeared target, is much faster than voluntary saccade, such as saccading to a target in memory (Hopp & Fuchs, 2004). Saccades to faces are faster (Crouzet, Kirchner & Thorpe, 2010).

Reward influences on saccade-making

Firstly although both amplitude and probability of reward impact saccade landing position, it is the expected reward (product of them) which determines the landing position (Navalpakkam et al., 2010). However, only information available before saccade execution is taken into account (Caspi, Beutter & Eckstein, 2004). As such, when top-down processing, such as reward competes with bottom-up processing, such as salience, saccades go to which object or which part of one single object depends on saccade latency, i.e., when saccades are executed. For example, Markowitz and colleagues (2011) found that saccade ending positions of monkey observers are dominated by salience if they are made before the switch time (140-180 ms after target onset); they are dominated by value if they are made after the switch period. Furthermore, with varying luminance of different parts of one single object we found that the integration of salience and value information is dynamic and most observers could learn to use strategies to make optical saccades to position with expected reward (Schütz, Trommershäuser, & Gegenfurtner, 2012).

Not only saccade landing position is influenced by reward, but also is saccade latency (Bucker et al., 2015; Stankevich & Geng, 2015). On one hand, this influence could be executed through low-level processing (Dunne, Ellison, & Smith, 2015; Watanabe, Lauwereyns, & Hikosaka, 2003). For example, Dunne, Ellison and Smith (2015) found that saccades to the rewarded hemisphere are faster than that to the unrewarded hemisphere in a simple stimulus-driven saccade task. This reward speeding up effect is specific to rewarded hemisphere and does not transfer to unrewarded hemisphere in saccadic peripheral cuing task and oculomotor inhibition of return task, suggesting it is executed through reducing the distance between baseline and execution threshold rather than evidence accumulating rate. On the other hand, this influence could also be executed through top-down control (Heuer et al., 2017; Milstein & Dorris, 2007; Theeuwes & Belopolsky, 2012; Wolf et al., 2017). For example, Milstein and Dorris (2007) found that saccade latency does not simply decrease with the increase of magnitude and probability of reward, but rather decreases with expected reward. Furthermore, Wolf and colleagues (2017) found that reward effects on saccade

latency are influenced by the necessity, uncertainty of outcome and task difficulty. The integration of low-level influence and top-down influence could yield no overall changes in average saccade latency (Leon & Shadlen, 1999; Platt & Glimcher, 1999) and the integration can also be dynamic (Schütz, Trommershäuser, & Gegenfurtner, 2012). For example, reward speeds up the salience-dominated short-latency saccades overall while slows down the value-dominated long-latency saccades overall (Schütz, Trommershäuser, & Gegenfurtner, 2012).

Neural system of generation of saccadic eye movements

The neural structures and pathways involved in generating saccade are illustrated in Fig. 14. The centers of saccade system are in the brainstem and cerebellum and they are similarly involved in generating all kinds of saccades and their pathway is illustrated in black lines (Leigh and Zee, 2015; Scudder et al., 2002). Posterior cortical areas (visual, parietal) show larger involvement for reactive saccades and the pathway is illustrated in white line; frontal areas and basal ganglia are more recruited for voluntary saccades and the pathway is illustrated in grey lines (McDowell et al., 2008; Munoz & Everling, 2004; Pierrot-Deseilligny et al., 2003).
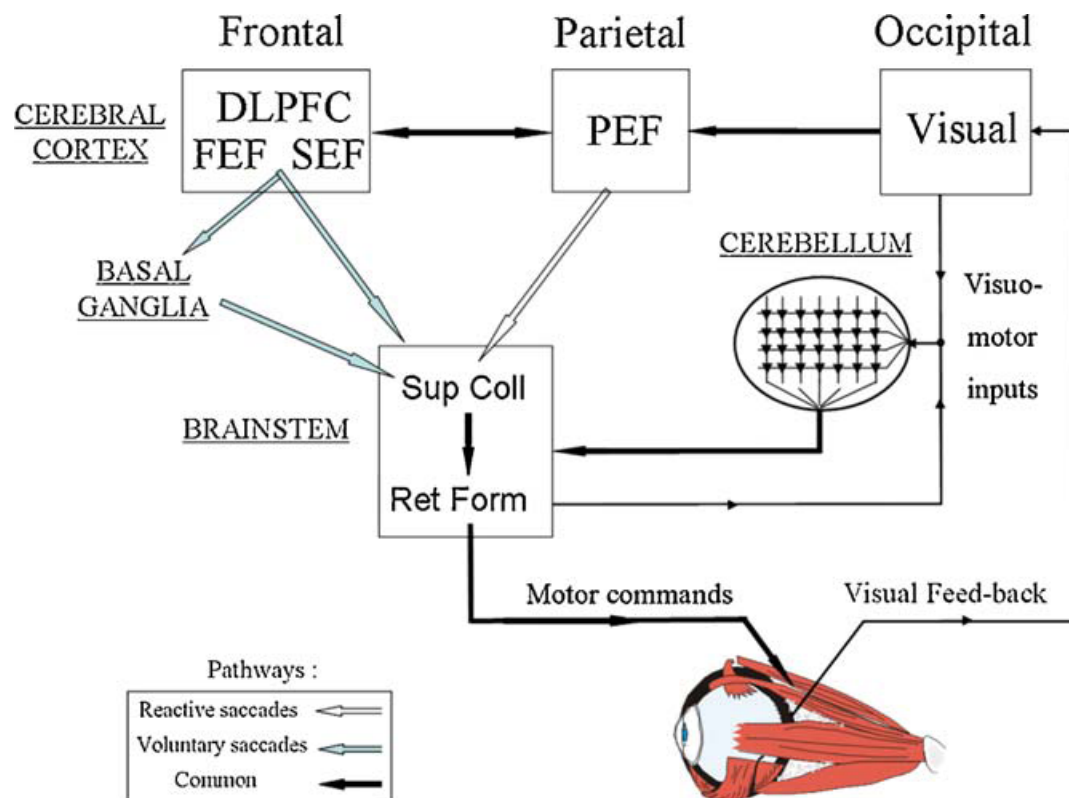
Figure 14. Schematics of neural network involved in the generation of saccadic eye movements. FEF: frontal eye fields, SEF: supplementary eye fields, DLPFC: dorso-lateral prefrontal cortex, PEF: parietal eye fields, Sup Coll: superior colliculus, Ret Form: reticular formation

Aging effects on saccade control

Age-related changes in saccadic control have been investigated by numerous studies. On one hand, saccade latency of older adults has been consistently found to be slower in different kinds of saccades (Abel & Douglas, 2007; Goldring & Armstrong, 1998; Peltsch et al., 2011; Warabi, Kase, & Kato, 1984;) suggesting that there might be age-related declines in older adults' saccade system. At least some parts of the circuitry saccade system were found to be damaged, such as frontal and parietal lobes, and cerebellum (Raz et al., 2005). On the other hand, older adults, even at the age of 80, could make saccades to a target as accurately as young adults (Munoz et al., 1998; Warabi, Kase & Kato, 1984) suggesting that there might be some compensations in their system. Furthermore, differential age-related changes were found in different categories of saccades (Peltsch et al., 2011). For example, Peltsch and colleagues (2011) found that the proportion of express saccade during pro-saccade is similar among different age groups whereas all the measurements of anti-saccade changes with age, suggesting more impaired age effects in voluntary saccades.

Outline

Aging effects have been investigated for decades, ranging from the initial studies with behavioral cognitive tasks to recent more neuroimaging studies. The theories accounting for these effects changed from the initial general decline hypotheses to recent compensative and / or adaptive aging brain hypothesis. Discrepancies between these studies and theories underlie the differential aging effects and the potential role of environments in them. To reconcile these discrepancies, investigations on aging effects on distinct processing should be especially helpful.

Visuomotor control is naturally connected to external environment and is also tightly connected to cognition. Besides, it is well modeled with distinct subcomponents, making it a pretty good way to investigate aging processing.

Visuomotor control system consists of extrinsic coordinate system transforming visual information into motor-based information and intrinsic coordinate system specifying the motor

information into motor forces and motions, as well as their interactions with other factors, such as cognitive strategies, reward, so on and so forth.

This control system has been extensively explored with visuomotor adaptation tasks, in which subjects learn to reduce the error from the internal models and remember and consolidate the learned internal models. Explicit knowledge about the nature of the tasks and strategies to cancel the errors could also impact the adaptation. But they could not override the learning of the internal models during the tasks so that the learning of internal models is implicit. The processing underlying this implicit learning is called implicit processing. Although several labs have explored ageing effects on visuomotor adaptation through reaching adaptation tasks, the results started to become clear from last decade. It seems that the implicit processing is preserved in older adults. Aging effects on saccade adaptation had not been explored yet. The first study of this thesis explored it through two saccade adaptation tasks, in one of which the double step task was used and the implicit processing is dominant, and in the other of which the perceptual task was used and the explicit processing is dominant so that aging effect on the processing, if there is, will be much easier to detect.

The distinct mechanisms of visuomotor adaptation are suggested by the differences between natural and behavioral saccade adaptation and the differences between reaching adaptation of extrinsic coordinate system and intrinsic coordinate system. Multiple states space models account for these differences really well and two distinct processing are identified by these models: learning and retention.

Given the substantial importance of motivation in behaviors and actions, reward effects have captured considerable attention in many disciplines in recent decades. Reward and punishment effects on visuomotor control have also been investigated through reaching adaptation by several studies although the results are inconsistent. Despite the inconsistency, it seems that they impact learning and retention of adaptation positively, if there is any impact, and distinctively. Aging effects on reaching adaptation have been explored before and it seems like the learning is impaired by aging whereas the retention is preserved. Whether these differential aging effects could be impacted by reward and punishment has never been explored. The second study of this thesis investigated this issue with a screen-cursor rotation task, in which performance-based

monetary reward and punishment were administered during the initial adaptation trials between different groups of subject.

Reward and punishment effects on visuomotor control have also been explored with saccadic decision making. Although different tasks have been used, it seems that they impact several saccade kinematics, such as saccade landing position (direction), saccade latency, saccade peak velocity so on and so forth. Besides, some impacts seem to be are interacted. For example, impact on saccade direction depends on saccade latency. Given differential aging effects on saccade accuracy (position or amplitude) and saccade latency, the third study of this thesis investigated how reward and punishment impact this kinematics of older adults and their interaction.

Chapter 2: Age effects on saccadic adaptation

Age effects on saccadic adaptation: Evidence from different paradigms reveals specific vulnerabilities

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Abstract

Saccadic eye movements provide an opportunity to study closely interwoven perceptual, motor, and cognitive changes during aging. Here, we investigated age effects on different mechanisms of saccadic plasticity. We compared age effects in two different adaptation paradigms that tap into low- and high-level adaptation processes. A total of 27 senior adults and 25 young adults participated in our experiments. In our first experiment, we elicited adaptation by a double-step paradigm, which is designed to trigger primarily low-level, gradual motor adaptation. Age groups showed equivalent adaptation of saccadic gain. In our second experiment, adaptation was induced by a perceptual task that emphasizes high-level, fast processes. We consistently found no evidence for age-related differences in low-level adaptation, however, the fast, strategic adaptation response was significantly more pronounced in the young adult group. We conclude that low-level motor adaptation is robust during healthy aging, but that high-level contributions, presumably involving executive strategies, are subject to age-related decline. Our findings emphasize the need to differentiate between specific aging processes in order to understand functional decline and stability across the adult lifespan.

Keywords: healthy aging, saccadic eye movements, visuomotor adaptation, plasticity, visual error, executive control

Introduction

Increased life expectancy and decreased birth rates contribute to massive demographic changes in most developed societies. The mean age of the population is continuously shifting toward the senior range so that it appears imperative to acquire a detailed understanding of functional resources across the adult lifespan. Whereas cognitive changes have been extensively studied over the last decades (for reviews see Baltes, Staudinger, & Lindenberger, 1999; Cabeza, Nyberg, & Park, 2005b; Craik & Byrd, 1982; Hasher & Zacks, 1988; Park & Reuter-Lorenz, 2009; Salthouse, 1996), age effects on sensorimotor capacities have been rather neglected. In particular, age-related changes in plasticity of sensorimotor behavior, which is highly relevant in a continuously changing environment, are not well understood.

Previous studies concerned with age-related differences in sensorimotor plasticity have almost exclusively focused on adaptation of hand and arm movements, i.e. reaching movements. Although findings from cognitive studies consistently indicated a plasticity decline with increasing age, results for reaching adaptation have been ambiguous (e.g. Bock, 2005; Bock & Schneider, 2001; Buch, Young, & Contreras-Vidal, 2003; Heuer & Hegele, 2008a). Overall, only a minor decline of sensorimotor plasticity has been reported, however, the detrimental impact of reduced cognitive strategies during adaptation has been emphasized (Bock & Girgenrath, 2006; Heuer & Hegele, 2008b; Heuer, Hegele, & Sulzenbruck, 2011). We suggest that the investigation of saccadic adaptation is particularly well suited to disentangle age-related vulnerabilities that contribute to plasticity changes.

Saccadic eye movements provide a fundamental possibility to explore our visual environment and offer the opportunity to investigate basic mechanisms of sensorimotor control (Krauzlis, 2005). Indeed, age-related changes in saccadic control have been explored by numerous studies. Results consistently support a pronounced increase of latencies with age, but stability of saccade dynamics (Abel & Douglas, 2007; Munoz, Broughton, Goldring, & Armstrong, 1998; Peltsch, Hemraj, Garcia, & Munoz, 2011). A further robust finding is an age-related increase of directional error rates in saccade tasks that require inhibitory control processes, e.g. in the antisaccade task (Gottlob, Fillmore, & Abroms, 2007; Olk & Jin, 2011; Peltsch et al., 2011; Sweeney, Rosano, Berman, & Luna, 2001). In particular saccade accuracy seems to be maintained stable across the adult lifespan, even up to an age of 80 years (Munoz et al., 1998).

This suggests preserved capacities to compensate for possible age-related changes of ocular muscles or neuronal circuitries that might challenge saccadic accuracy. However, only a single study so far has been dedicated to age effects on saccadic adaptation and has provided evidence of similar capacities in different adult age groups (Bock, Ilieva, & Grigorova, 2014).

Adaptation of saccadic eye movements is well described and can be considered as a very basic model of sensorimotor plasticity (Hopp & Fuchs, 2004; Pelisson, Alahyane, Panouilleres, & Tilikete, 2010). Saccades allow for bringing relevant visual information rapidly to the fovea, which enables detailed analysis. If inaccuracies are experienced, e.g. due to fluctuations in the oculomotor system, accuracy of saccades is re-established by adjusting their amplitude. Adaptive adjustments can be robustly induced in the laboratory by an unnoticed target shift during the saccade that results in a post-saccadic error. This manipulation elicits adaptive amplitude changes that compensate for the experienced error and maintain accuracy of saccades. The retinal error was identified to be the dominant or even exclusive error signal driving this adaptation process (e.g. Wallman & Fuchs, 1998). Given this focus on bottom-up error signals, saccadic adaptation was understood as a low-level mechanism that compensates for accuracy deviations.

More recent findings from a variety of adaptation paradigms, though, have challenged this classical view on saccadic adaptation (for review see Herman, Blangero, Madelain, Khan, & Harwood, 2013). In several studies saccadic gain changes were reliably elicited without visual errors. Dissociating retinal error from prediction error, i.e. the discrepancy between predicted and actual movement outcome, there has been evidence that saccadic adaptation might be primarily driven by prediction errors (Collins & Wallman, 2012; Wong & Shelhamer, 2012). Moreover, it has been shown that saccadic adaptation can be induced even in the absence of any error signal. Amplitude-dependent reinforcement has proved to be sufficient to trigger appropriate gain changes (Madelain, Paeye, & Darcheville, 2011; Madelain, Paeye, & Wallman, 2011). Congruently, saccadic adaptation has been successfully induced using a perceptual task without manipulation of the visual target (Schütz, Kerzel, & Souto, 2014; Schütz & Souto, 2015). Thus, plasticity can be also driven by behavioral goals. In summary, these recent results question that saccadic adaptation exclusively represents a low-level mechanism that compensates for systematic errors in the oculomotor system. They rather suggest that saccades can as well be adapted based on high-level mechanisms involving top-down behavioral goals and strategies.

We aimed to investigate how age affects different mechanisms of saccadic adaptation. Since age-related cognitive decline, in particular decline of executive functioning, is well-documented (Park & Reuter-Lorenz, 2009), we hypothesize that high-level adaptation mechanisms might be especially prone to age-related decline, while low-level mechanisms might tend to be preserved. We chose two established saccadic adaptation paradigms that are supposed to tap into different mechanisms. For each paradigm we compared saccadic plasticity between young adult and healthy, community-dwelling senior adults.

Experiment 1: Evidence from the double-step paradigm

In our first experiment we chose the well-known double-step paradigm (McLaughlin, 1967) to induce saccadic adaptation. The typical procedure demands a saccade to a visual target, which is displaced during saccade execution. The target step results in a post-saccadic error and repeated experience triggers adaptive changes of saccade amplitude within few trials. Notably, this adaptation process occurs without conscious perception of the target manipulation (Bridgeman, Hendry, & Stark, 1975). Efficient stabilization of movement accuracy is driven by post-saccadic errors. Thus, saccadic adaptation in the double-step paradigm is generally considered to reflect a low-level mechanism that enables compensation for systematic errors and maintains accuracy of the oculomotor system (for review see Hopp & Fuchs, 2004; Pelisson et al., 2010).

Methods

Participants

A total of 18 young adults (12 females) and 19 senior adults (13 females) participated in the experiment. Age ranged from 22 to 38 years with a mean age of 27.9 years ($SD = 4.7$) in the young adult group, and from 52 to 76 years with a mean age of 66.6 years ($SD = 6.0$) in the senior adult group. Recruitment of subjects was managed by calls for participation at the University of Giessen and in local newspapers. All subjects were paid for participation. Any history of ophthalmologic, neurologic, or psychiatric disorders as well as medications presumed to interfere with oculomotor functioning were screened out by a detailed interview protocol. Visual acuity was measured binocularly confirming normal or corrected-to- for all participants. In addition, we ran a battery of standard cognitive tasks in order to exclude pathological age-related decline. Moreover, measures of executive functioning were of particular interest for our study.

The battery included several standard executive tasks, i.e. span measures of verbal and visual working memory, task switching, and problem solving (Berch, Krikorian, & Huha, 1998; Horn, 1983; Kessels, van den Berg, Ruis, & Brands, 2008; Kortte, Horner, & Windham, 2002). Methods and procedures agreed with the Declaration of Helsinki (World Medical Association, 2013) and were approved by the local ethics committee. Informed consent was obtained by all participants and protection of data privacy was provided.

Task and procedure

We applied a standard double-step paradigm to elicit backward saccadic adaptation. Subjects were asked to fixate a black cross (0.5° x 0.5°) presented on a mean gray background. Location of the fixation cross was randomly jittered within an area around the centre of the screen extending -5° to 0° horizontally and -3° to 3° vertically. Subjects initiated each trial by pressing the space bar. Given stable fixation the cross turned red and jumped 10° rightward after a delay that varied uniformly between 300 and 400 ms. Subjects were instructed to follow the cross with their eyes. Saccade onset was determined online. The experiment consisted of three phases, i.e. 50 pre-adaptation trials, 300 adaptation trials, and 50 post-adaptation trials. In the pre- and post-adaptation trials the target cross disappeared as soon as saccade onset was detected. In the adaptation trials the cross was displaced backwards by 2.5° during the saccade and maintained visible at the new location for 600 to 700 ms, uniformly jittered. The experiment was divided into a total of 7 blocks, a pre-adaptation block, 5 adaptation blocks with 60 trials each, and finally a post-adaptation block.

Eye tracking equipment

Stimuli were generated using Matlab with the Psychophysics Toolbox (Brainard, 1997). They were displayed on a 22-inch Samsung SynMaster 2233BW monitor driven by an Nvidia GeForce 9800 graphics board with a refresh rate of 120 Hz. The spatial resolution was set to 1680 x 1050 pixels. Subjects were seated in a darkened room at a distance of 90 cm in front of the monitor. Eye position was recorded by an SR Research Eyelink 1000 Desktop Mount system (SR Research Ltd., Missisauga, Ontario, Canada) at a sampling rate of 1000 Hz. Viewing was binocular and subjects' heads were stabilized by a chin- and headrest. A standard 9-point calibration covering the whole screen was applied before each block and accuracy was accepted if the validation procedure yielded values of average error not larger than 0.4 deg and worst error

not larger than 0.7 deg. Each trial started with a drift correction in order to guarantee calibration across data collection. Subjects were instructed to keep their sitting position as stable as possible. The experimenter continuously monitored the subjects and restarted the calibration procedure when an accidental change in position occurred.

Data analysis

Saccade onset during each trial was determined on-line using a combined velocity criterion. Onset was defined by the time when eye velocity of two consecutive samples exceeded 50°/s and 100°/s, respectively. Subsequently eye position data was analyzed off-line using the Eyelink built-in algorithms. We excluded trials from further analyses if saccades had latencies < 80 ms or > 500 ms, if they had a duration of < 10 ms or > 100 ms, or if they had an amplitude < 5° or >15°. We excluded on average 25.5% of trials ($SD = 10.1\%$) in the young adult group and 31.4% of trials ($SD = 10.8\%$) in the senior adult group. Data of five observers (two young adults) were discarded because more than 50% of their trials had to be excluded based on our criteria.

We first analyzed saccade gain for four defined trial intervals. The average across all pre-adaptation trials was used as baseline performance. For the adaptation phase we derived two parameters. Initial adaptation performance was derived by averaging across the first 10 adaptation trials; final adaptation performance was derived by averaging across the last 10 adaptation trials. The average across all post-adaptation trials was used as measure of post-adaptation performance. Gain differences between intervals were considered to be indicative for specific adaptation components. We supposed that the difference between baseline and initial adaptation reflects immediate adjustment, while the difference between initial and final adaptation indicates gradual adjustment. The difference between final adaptation and post-adaptation performance was taken as a measure of recovery from adaptation.

Furthermore, we fitted an exponential model to the gain data in all adaptation trials for each subject. We applied a model with three free parameters (Souto, Gegenfurtner, & Schütz, 2016):
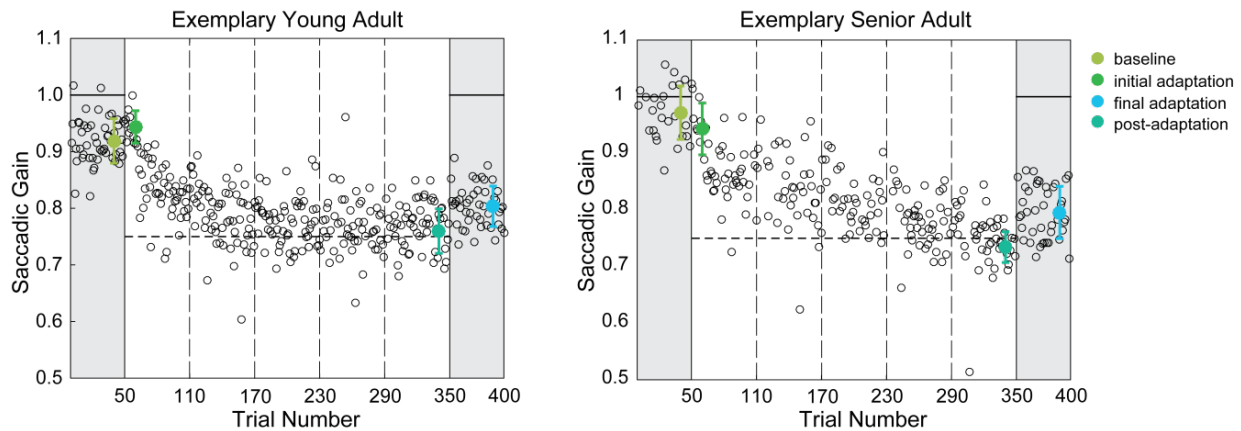
$$S(t) = \alpha + \beta e^{-\lambda t} \quad (1)$$

S(t) gives the fitted saccadic gain for a given trial t. The three free parameters used are the asymptotic level α, the amplitude of adaptation β, and the adaptation rate λ; 1/λ corresponds to the exponential rate constant, i.e. the number of trials it takes the function to reach about a third

of the initial value. Given the definition of parameters (for illustration see Figure 3A) the difference between α and β provides a measure for immediate adjustment and β directly reflects gradual adjustment. After removing baseline gain in adaptation trials was fitted iteratively until best solution was found using a nonlinear least-squares fitting procedure provided by the OPTI toolbox for Matlab (Currie & Wilson, 2012). In order to obtain robust fits we constrained α and β to a range of -0.5 to 0.5, and λ to a range of 0.001 to 1.
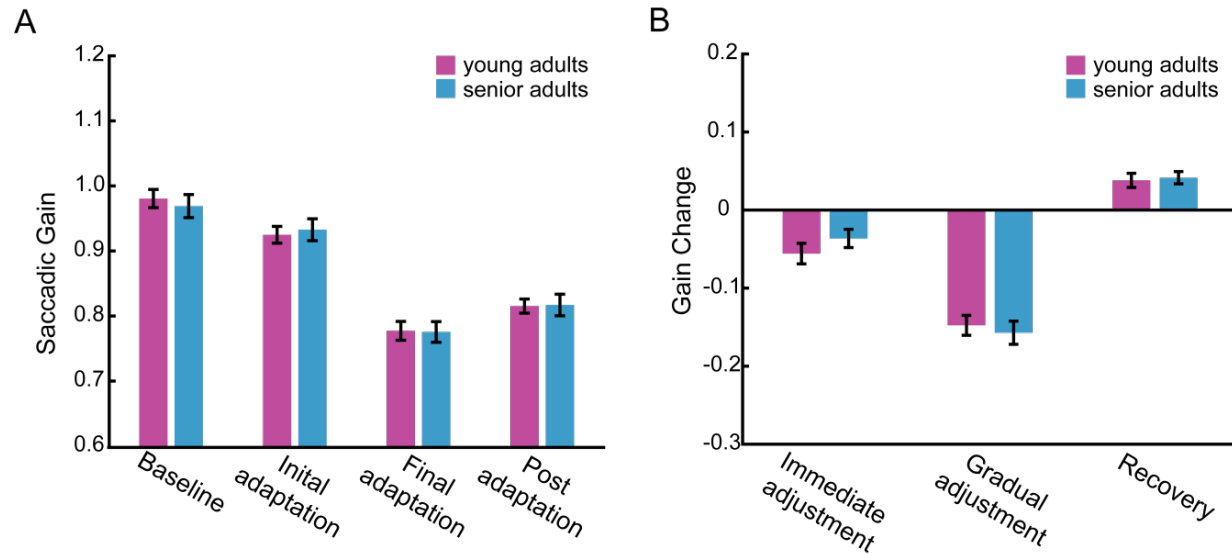
Results

The applied double-step paradigm robustly elicited backward saccadic adaptation in both age groups. Figure 1 shows exemplary saccadic gain data across trials for a single young and senior subject, respectively. Data overall appeared similar across both subjects. For the young adult we determined an average gain of 0.92 in the baseline trial interval; by the end of the adaptation phase the gain was reduced to 0.76. The senior subject showed a gain of 0.97 in the baseline trial interval and reduced it to 0.73 across the adaptation trials. Note that gain did not increase to baseline in the post-adaptation phase because the target was extinguished after saccade onset and did not reappear. Thus, the gain shift reflects retention, rather than the extent of re-adaptation to baseline.

Figure 1. Single-subject data of an exemplary young adult, left panel, and an exemplary senior adult, right panel. Saccadic gain is given as a function of trial number. Black open dots: individual trials; green filled dots: average data across specified intervals; error bars: SD. Gray-shaded areas indicate pre-adaptation phase and post-adaptation phase, respectively; vertical lines: trial blocks; horizontal lines: perfect gain, i.e. eye and target positions match perfectly after the saccade.

We analyzed age group differences across the specified trial intervals by a mixed ANOVA with the within-subject factor trial interval (baseline, initial adaptation, final adaptation, and post-adaptation), and the between-subject factor age group (young adults and senior adults). If appropriate we used the Greenhouse-Geisser correction. Figure 2A illustrates saccadic gain

results for both age groups and shows saccadic plasticity across the experiment in both age groups. Congruently, the ANOVA yielded a significant main effect of trial interval, $F(3, 90) = 215.83$, $p < .001$, $\eta^2 = .88$. However, we found neither a main effect of age group, $F(1, 30) < 0.01$, $p = .995$, $\eta^2 < .01$, nor an interaction effect of both factors, $F(3, 90) = 0.41$, $p = .696$, $\eta^2 = .01$.

Figure 2. Saccadic gain in the double-step paradigm. (A) Average gain in the specified trial intervals for young adults and senior adults. (B) Changes in gain indicating immediate adjustment, gradual adjustment, and recovery for young adults and senior adults. Error bars: SEM.
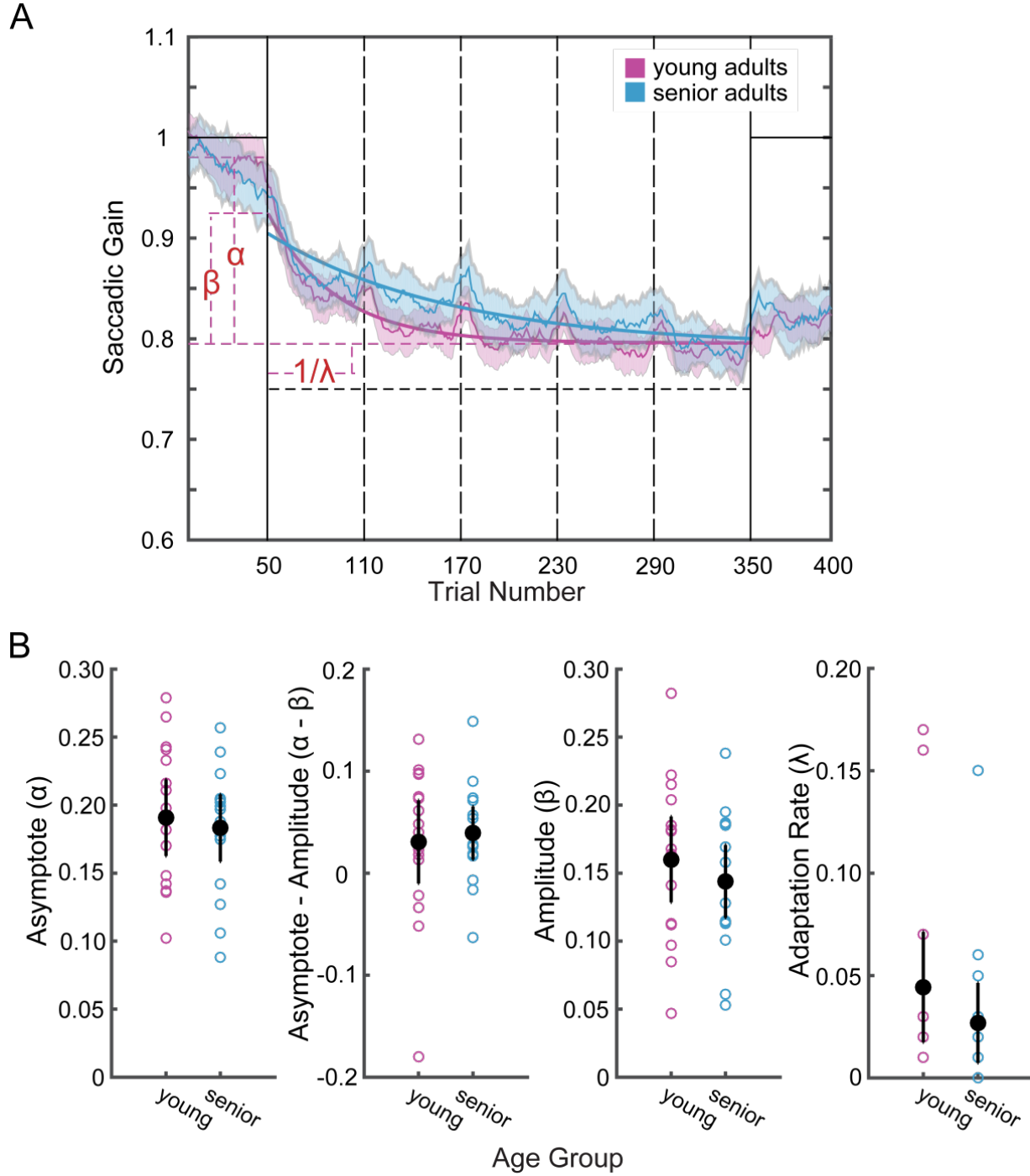
The main effect of trial interval was followed up by post hoc paired comparisons with Bonferroni correction. Results indicated that average gain differed significantly between all specified intervals (all $p < .001$). Highest gain was found in the baseline trials ($M = 0.98$, $SD = 0.06$). A significant decrease was already found at the beginning ($M = 0.93$, $SD = 0.06$) and also at the end ($M = 0.78$, $SD = 0.06$) of the learning phase. After removal of the target manipulation gain increased again, but did not reach the baseline level within the post-adaptation phase ($M = 0.82$, $SD = 0.05$).

We also explored adaptation across the experiment by directly considering gain differences between the specified trial intervals. Change data are shown in Figure 2B. Additional analyses overall confirmed the results from the initial ANOVA. We used one-sample t tests to evaluate whether changes differed significantly from zero. In both age groups we observed significant immediate adjustment at the beginning of the learning phase, significant gradual adjustment across the learning phase, and finally significant recovery from adaptation (all $p < .005$). This further supports that the paradigm robustly elicited learning processes in both age groups. We used one-tailed t tests in order to clarify whether young adults show more pronounced plasticity than senior adults. Neither immediate adjustment, $t(30) = -1.14$, $p = .132$, $d = 0.40$, nor gradual adjustment, $t(30) = 0.50$, $p = .309$, $d = -0.20$, nor recovery from adaptation, $t(30) = -0.29$, $p = .386$, $d = -0.10$, were found to be significantly more pronounced in young adults.

Fitting of the data with the three-parameter model yielded consistent results. Figure 3A illustrates saccadic gain as a function of trial number averaged across young adults and senior adults, respectively.

The model fits for the averaged data suggests only minor differences between both age groups. Parameters of the individual fits are provided in Figure 3B. Using one-tailed t tests we analyzed whether parameters reveal more pronounced adaptation processes in young adults than in senior adults. Results yielded no significant differences between both age groups, asymptotic level α: $t(30) = -0.43$, $p = .334$, $d = -0.15$, difference between asymptotic level and adaptation amplitude α-β: $t(30) = 0.38$, $p = .335$, $d = 0.13$, adaptation amplitude β: $t(30) = -0.83$, $p = .206$, $d = -0.29$, and adaptation rate λ: $t(30) = -1.08$, $p = .146$, $d = -0.38$. Consistency across the applied analysis approaches was supported by significant correlations between immediate adjustment of saccadic gain and the parameter difference score α – β, $r(31) = 0.75$, $p < 0.001$), as well as between gradual adjustment of saccadic gain and the parameter β, $r(31) = 0.62$, $p < 0.001$). In summary, fitting results confirmed that young and senior adults show similar adaptation capacities immediately at the beginning of the learning phase and gradually across the learning phase. Furthermore, they provided evidence that the adaptation rate was not affected by age.

Figure 3. Fitting results for the double-step paradigm. (A) Saccadic gain as a function of trial number. The thin pink and blue lines represent the averaged gain across young and senior adults, respectively. Data are smoothed by a running average with a bin size of 10 trials. Shaded areas: 95% confidence intervals; vertical lines: trial blocks; horizontal lines: perfect gain, i.e. eye and target positions match perfectly after the saccade. The thick pink and blue lines represent the three-parameter model fit for young and senior adults, respectively. Meaning of parameters is

illustrated within the plot for young adults' data; the parameter α gives the asymptote of the function starting from the average baseline gain level; the parameter β gives the overall amplitude of adaptation from beginning of the adaptation phase to its end; the parameter λ gives the adaptation rate and $1/\lambda$ corresponds to the number of trials it takes the function to reach about a third of the initial value. (B) Estimated model parameters for young adults and senior adults. Panels form left to right: asymptotic level α, difference between asymptotic level and adaptation amplitude α - β, adaptation amplitude β, adaptation rate λ. Error bars: 95% confidence intervals.

We finally explored saccadic latencies in the double-step paradigm by an additional ANOVA. Figure 4 illustrates average latencies for each age group. Increased saccadic latencies represent the most consistently reported age effect on oculomotor control. As expected age groups differed substantially in saccadic latencies across all trial intervals, younger adults showing lower latencies, $F(1, 30) = 23.11$, $p < .001$, $\eta^2 = .44$. Latencies decreased across trial intervals, $F(3, 90) = 4.64$, $p = .011$, $\eta^2 = .13$. There was no significant interaction between both main effects, $F(3, 90) = 0.11$, $p = 0.957$, $\eta^2 < .01$. Furthermore, latencies did not correlate with any parameter derived from fitting accuracy data with the exponential model. Thus, exploration of latencies yielded support for expected age differences, but also showed that these differences do not affect saccadic plasticity.

Figure 4. Average saccadic latencies in the specified trial intervals of the double-step paradigm for young adults and senior adults. Error bars: SEM.

Discussion

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In our first experiment we studied saccadic adaptation in the established double-step paradigm. We explored whether sensorimotor plasticity differs between young and senior adults. When adaptation was induced by systematic post-saccadic errors, we found robust plasticity in young and senior adults. Both age groups showed similar adaptive changes of saccadic gain at the beginning as well as at the end of the adaptation phase and they did not differ in adaptation rate, i.e. after how many trials they reached a given change criterion. In addition, there was no evidence for age differences in recovery from adaptation when error information was abolished.

It is well known that aging challenges behavioral and neuronal plasticity (Jones et al., 2006; Lustig, Shah, Seidler, & Reuter-Lorenz, 2009). Thus, the question arises which mechanisms contribute to preserved saccadic plasticity we observed in the double-step paradigm. Most basically, we can exclude that our senior age group represented a positively biased sample saved from age-related functional decline. Saccadic latencies in the senior adult group were found significantly increased, consistent with seminal studies on aging of saccadic control (Munoz et al., 1998; Peltsch et al., 2011) and indicating typical age-related slowing of processing speed (Salthouse, 1996). Similar adaptive capacities despite distinctive latency differences moreover corroborate results showing that saccade latencies per se do not influence the magnitude of adaptation (e.g. Schütz & Souto, 2015).

Our findings contribute to the understanding of age-related changes in visuomotor plasticity. Notably, they are consistent with evidence provided by the only previous study concerned with saccadic adaptation, suggesting preserved plasticity across adult lifespan (Bock et al., 2014). This is in contrast to the heterogeneous pattern of results for reaching adaptation. Several studies have documented an age-related decline of reaching plasticity induced by visuomotor rotations (e.g. Bock, 2005; Bock & Girgenrath, 2006; Buch et al., 2003; Heuer & Hegele, 2008a), but vulnerabilities have been primarily attributed to reduced explicit, strategic adjustments. When dissociating explicit and implicit components of reaching adaptation by appropriate paradigms, age effects have been shown to be limited to less efficient use of explicit strategies while sparing implicit adjustments (Hegele & Heuer, 2010b, 2013; Heuer et al., 2011; McNay & Willingham, 1998; Roller, Cohen, Kimball, & Bloomberg, 2002). These results indicate resiliency of low-level adaptation mechanisms, which might contribute to robust saccadic plasticity in the double-step paradigm. Reaching movements and saccadic movements differ fundamentally. Saccades represent extremely fast, ballistic movements that cannot be corrected online after initiation. In

addition, due to perceptual suppression during the saccade the observer usually remains unaware of the target manipulation inducing post-saccadic errors. These characteristics exclude or at least minimize the use of explicit strategies during adaptation. Thus, in particular in the double-step paradigm in which adaptive changes are considered to rely on low-level mechanisms, the absence of age effects can be reconciled with differential results for reaching adaptation. They further support that fundamental components of visuomotor plasticity are not affected by healthy aging.

This interpretation also agrees with our detailed results on different components contributing to adaptive shifts in saccade amplitude. In our analysis, we distinguished between immediate, strategic adjustments after the onset of target manipulation and gradual adjustments that develop over the adaptation phase. In the typical double-step paradigm this distinction can be considered as redundant since strategic processes require awareness of the target manipulation. Intra-saccadic target displacement usually prevents awareness due to perceptual suppression. Thus, immediate adjustments can be expected to contribute only minimally to overall adaptation induced by the double-step paradigm. We indeed observed less than 5% immediate adjustment, but about 16% gradual adjustment across the adaptation course (compare also Schütz et al., 2014). Thus, adaptation primarily relied on gradual, automatic processes, whereas strategic, high-level processes, which are assumed to be more vulnerable to aging, played only a minor role. We suggest that the still significant immediate adjustments at the beginning of the adaptation phase are most likely based on incomplete intra-saccadic suppression of target displacement (see Bridgeman et al., 1975). Thus, awareness was clearly minimized, but probably not completely abolished, allowing for some strategic contributions to adaptation. However, these contributions were not reliable enough to indicate age-related differences. In summary, our findings corroborate that adaptation in the double-step task is dominated by gradual processes and that these processes remain efficient across the adult lifespan.

Although our results for immediate and gradual adjustments cannot be directly mapped onto the distinction between fast and slow adaptation processes proposed by Körding, Tenenbaum, and Shadmer (2007), some plausible links can be presumed. Sensorimotor adaptation has been modeled as a combination of fast and slow processes. Whereas fast processes drive rapid adaptive changes which are prone to rapid decay, slow processes contribute gradually over a prolonged timescale to adaptation and decay only slowly (Ethier, Zee, & Shadmehr, 2008). In our paradigm, immediate adjustments are presumably linked to fast processes. Gradual adjustments might

involve both fast and slow processes, but we suppose that they predominantly rely on slow processes. Thus, recovery from adaptation after removal of the visual error can be expected to be rather slow. In the post-adaptation phase, when the target was extinguished during the saccade and did not reappear, we congruently determined a re-increase of saccadic amplitude of about 5%, showing a rather slow decay or in other words strong retention in both age groups. This pattern tentatively indicates that slow adaptation processes are preserved during aging.

To conclude, stable saccadic adaptation in the double-step paradigm across the adult age range suggests robust low-level visuomotor plasticity that compensates primarily for visual errors. Since our data does not allow to dissociate the contributions of prediction errors and visual errors to adaptation in the double-step paradigm (compare Collins & Wallman, 2012), the particular role of prediction errors cannot be specified.

Expperiment2: Evidence from a perceptual task

In our second experiment we induced saccadic adaptation by a perceptual task recently introduced by Schütz and colleagues (Schütz et al., 2014; Schütz & Souto, 2015). While in the double-step paradigm visual errors drive adaptation, the applied perceptual task triggers adaptive changes of saccade amplitude by a behavioral goal. This task specifically allows studying high-level mechanisms that contribute to saccadic plasticity because amplitude is shaped by top-down goals, not by bottom-up visual errors. Efficient goal-directed behavior relies substantially on executive functions which are particularly prone to age-related decline (Park & Reuter-Lorenz, 2009; West, 1996). Thus saccadic adaptation induced by a perceptual task might be particularly attenuated with increasing age.

Methods

Participants

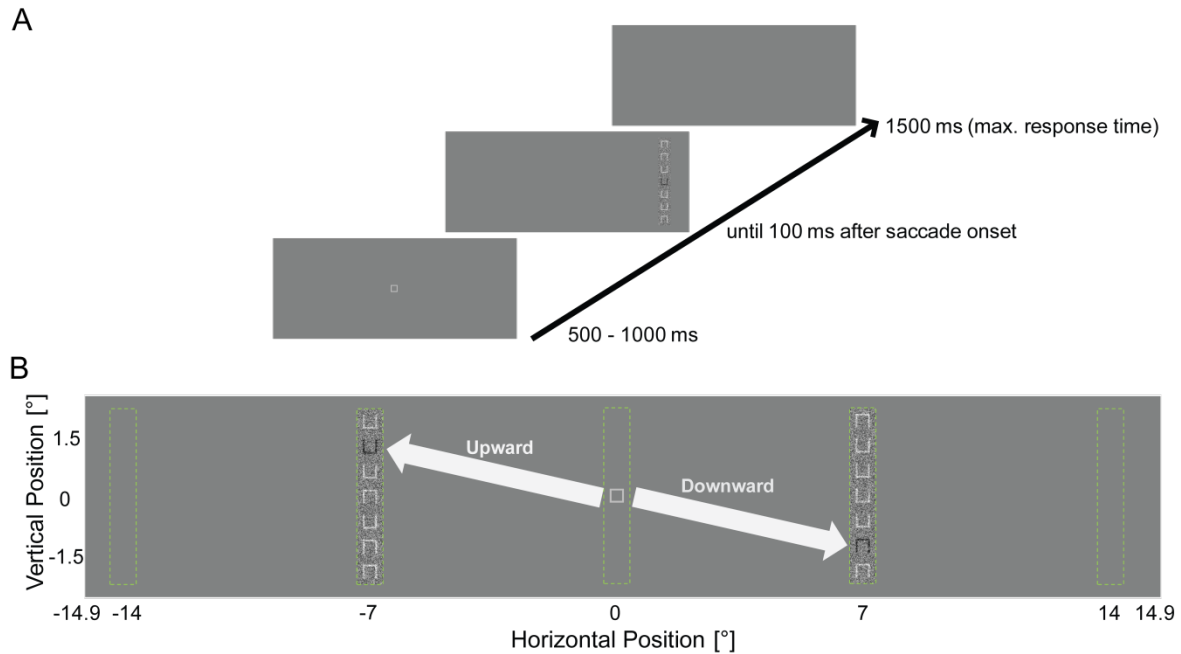A total of 17 young adults (11 females) and 16 senior adults (5 females) participated in the experiment. Age ranged from 22 to 37 years with a mean of 26.4 years ($SD = 4.6$) in the young adult group, and from 64 to 83 years with a mean age of 71.3 years ($SD = 4.8$) in the senior adult group. The recruitment procedure and screening protocol were equivalent to experiment 1.

Task and Procedure

We applied a perceptual task to induce vertical adaptation saccade amplitude. The general task procedure is illustrated in Figure 5A.

Figure 5. Perceptual task inducing adaptation. (A) General task procedure. After a variable fixation period a vertical stimulus compound was shown at an eccentricity of 7° either to the left or the right of the fixation square. The fixation square was always shown at the vertical center of the screen; horizontal position was determined by the position of the compound in the previous trial. The discrimination target was a black square within the compound. It had a gap either at the bottom or at the top and participants had to indicate its location. In baseline trials the discrimination target was always placed in the center of the compound. (B) Adaptation procedure. In adaptation trials the position of the discrimination target within the compound was shifted upward or downward in the case of leftward or rightward saccades, respectively. The coupling of shift direction and saccade direction was counterbalanced across participants. Dotted rectangles illustrate possible locations of the stimulus compound.

Subjects had to fixate a fixation square (0.36° x 0.36°) presented on a mean gray background. The fixation period was uniformly varied between 500 and 1000 ms. Subsequently the fixation square was extinguished and a compound stimulus appeared at an eccentricity of 7°, randomly either to the right or to the left. The compound consisted of seven vertically aligned squares (0.36° x 0.36°) with a line width of 0.05°. Squares were displayed on a random noise background that extended 0.16° beyond them. Contrast of squares and noise background were set to 50%. The compound had a total height of 5.52° and a total width of 0.68°. Position of the fixation square

and the stimulus compound followed a random walk across five horizontal positions shown in Figure 5B. The fixation square was always shown at the vertical center of the screen; the horizontal position was determined by the position of the compound in the previous trial.

Subjects were asked to accomplish a discrimination task. The stimulus compound included always six white squares and a unique black square, representing the target. All squares had a gap either at the bottom or at the top. Subjects had to decide whether the gap of the target square was at the bottom or at the top. The task was designed to require foveal acuity so that subjects had to saccade to the compound in order to solve the task successfully. The compound was displayed for 100 ms after saccade onset, which was determined online. Subjects had to indicate their decision within 1500 ms after saccade onset by a key press. If the perceptual judgment was incorrect, negative feedback was provided by a beep.

The experiment consisted of three phases, i.e. 50 pre-adaptation trials, 200 adaptation trials, and 200 post-adaptation trials. In pre-adaptation and post-adaption trials the target square was always centered in the compound (compare Figure 4A). In adaptation trials the target was shifted two positions, corresponding to 1.47°, either upward or downward within the compound (compare Figure 4B). The direction of the target shift depended on the saccade direction. For half of the subjects rightward saccades were coupled with downward shifted targets and leftward saccades were coupled with upward shifted targets, whereas for the other subjects coupling was the other way around. The specific coupling was counterbalanced across subjects within each age group. Notably, the manipulation in the adaptation trials did not induce bottom-up visual errors since the position of the stimulus compound remained stable. Adaptive changes in saccade direction, i.e. rotation upward or downward, were exclusively driven by the demands of the discrimination task. The experiment was divided into a total of 5 blocks, a pre-adaptation block, 2 adaptation and 2 post-adaptation blocks with 100 trials each. Between blocks there were breaks of 30 s in which subjects were advised to close their eyes.

Eye tracking equipment

We used exactly the same setup as in experiment 1 and applied the same calibration procedure.

Data analysis

Saccades were analyzed using the same procedures as in experiment 1. Criteria for exclusion of trials were also consistent, except for the saccade amplitude criterion. Given the stimulus layout we classified saccades with a horizontal amplitude $< 3.5°$ or $> 10.5°$ as invalid. We excluded on average 9.1% of trials ($SD = 5.2\%$) in the young adult group and 20.7% of trials ($SD = 8.5\%$) in the senior adult group. Data of three senior observers were discarded because more than 40% of their trials had to be excluded based on our criteria.
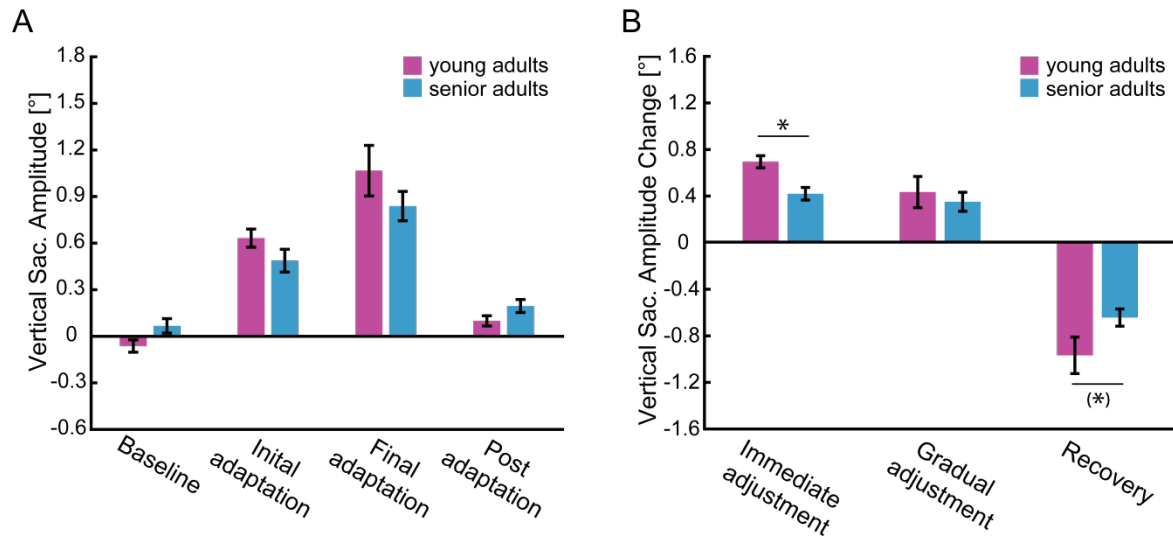
Discrimination performance in the behavioral task was measured across all trial intervals. Young adults performed at ceiling with an average accuracy rate of 98.2% ($SD = 1.1\%$). Senior adults showed a slightly lower accuracy rate of 93.7% ($SD = 3.2\%$), but performed the task appropriately. We discarded data of one senior observer because his performance was at chance level (48.4%) and thus we assumed that he misunderstood task instructions.

The critical parameter of interest for our analyses was vertical saccade amplitude. Since adaptation was found to be similar in upward and downward conditions, we collapsed data in order to increase the trial number for our analyses. We derived vertical amplitude for baseline, initial adaptation, final adaptation, and post-adaptation trial intervals according to the methods used in experiment 1. We again calculated defined change scores. Amplitude data was further analyzed by fitting the three-parameter exponential model (see Formula 1). We first removed baseline amplitude from all trials and then we fitted amplitude in adaptation and post-adaptation trials with the model until the best solution was found. We constrained α and β to a range of -5 to 5, and λ to 0.001 to 0.2.

Results

Both age groups showed substantial adaptive changes in vertical saccade amplitude induced by the perceptual task. In the baseline trial interval vertical saccade amplitude was close to zero, on average-0.06° and 0.07° for young and senior adults, respectively. The young adults increased the amplitude to 1.06° by the end of the adaptation phase; the senior adults reached on average an amplitude of 0.84°. Figure 6A summarizes vertical amplitudes in the different trial intervals for both age groups.
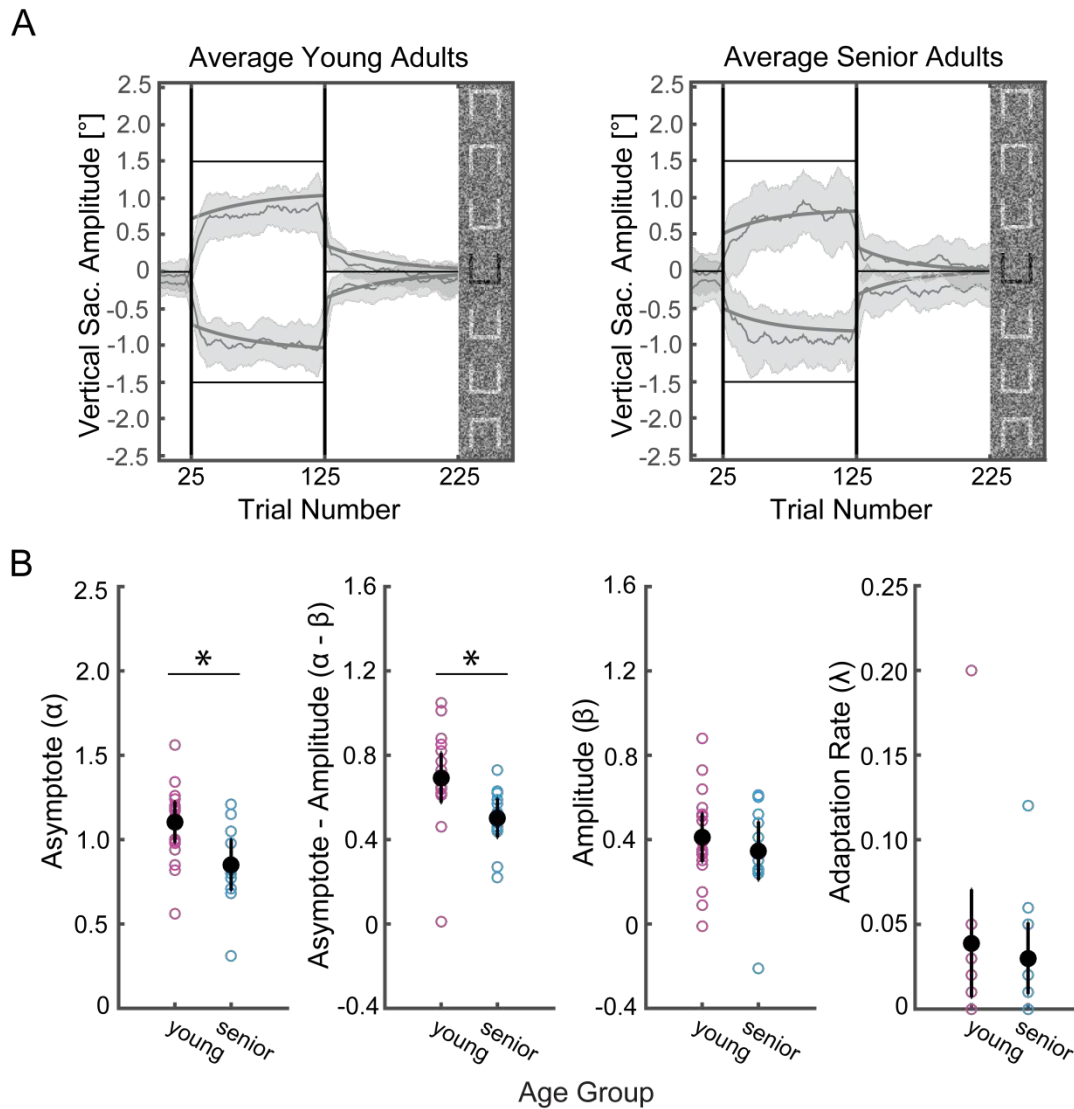
Figure 6. Vertical saccade amplitude in the perceptual task. (A) Average amplitudes in the specified trial intervals for young adults and senior adults. (B) Changes in amplitude indicating immediate adjustment, gradual adjustment, and recovery for young adults and senior adults. Error bars: SEM.

We analyzed amplitude data equivalent to the procedure applied for experiment 1. ANOVA results showed a main effect of trial interval, $F(3, 81) = 74.74$, $p < .001$, $\eta^2 = .74$, whereas there was no main effect of age group, $F(1, 27) < 0.21$, $p = .650$, $\eta^2 < .01$. The interaction effect of both factors just failed to reach significance, $F(3, 81) = 3.17$, $p = .068$, $\eta^2 = .11$.

We explored adaptive changes further by considering amplitude differences between specified trial intervals. Change data is provided in Figure 6B. For both age groups all change scores, i.e. immediate adjustment, gradual adjustment and recovery from adaptation, differed significantly from zero (all $p < .001$). Thus, data consistently supported saccadic plasticity across the perceptual task. However, one-tailed t tests yielded specific plasticity advantages for young adults. Senior adults showed less pronounced immediate adjustment, $t(27) = -3.71$, $p < .001$, $d = -1.42$, and a trend towards attenuated recovery from adaptation $t(27) = 1.69$, $p = .051$, $d = 0.68$. In contrast, age groups did not differ in gradual adjustment, $t(27) = -0.49$, $p = .313$, $d = -0.20$.

Results from fitting of the amplitude data corroborated age-related differences. Figure 7A illustrates vertical saccade amplitude as a function of trial number averaged across young adults and the senior adults. Note that for purpose of illustration, the data for upward and downward conditions are plotted separately here, but analyses are based on collapsed data as described

above. Inspection of model fits indicates that the adaptation process differs between young and senior adults. Individual fit parameters are shown in Figure 7B.

Figure 7. Fitting results for the perceptual task. (A) Averaged vertical saccade amplitude as a function of trial number of young (left panel) and senior (right panel) group. Please note that data for upward and downward conditions are plotted separately for the purpose of illustration, but analyses are based on collapsed data as described in the methods. The solid vertical lines indicate onset and offset of adaptation phase, the horizontal line indicates target position. The thin color lines represent averaged amplitude across participants. Data are smoothed by averaging across a bin size of 10 trials for display. The shaded regions represent 95% confidence intervals. The thick gray lines represent the three-parameter model fits. For interpretation of parameters, please see Figure 3A. (B) Estimated model parameters for young adults and senior adults. Panels form left

to right: asymptotic level α, difference between asymptotic level and adaptation amplitude α- β, adaptation amplitude β, adaptation rate λ. Error bars: 95% confidence intervals.

We again ran one-tailed t tests in order to explore age group differences. Asymptotic level α, $t(27)$ = -2.80, p = .005, d = -1.06, as well as the difference between asymptotic level and adaptation amplitude α-β, $t(27)$ = -2.51, p = .009, d = -0.98, differed significantly between young and senior adults. Adaptation amplitude β, $t(27)$ = -0.74, p = .231, d = -0.28, and adaptation rate λ, $t(27)$ = -0.50, p = .310, d = -0.20, were not affected by age. Consistency across analysis methods was confirmed by significant correlations between immediate adjustment of saccade amplitude and the parameter difference score α – β, $r(28)$ = 0.63, p < 0.001), as well as between gradual adjustment of saccade amplitude and the parameter β, $r(28)$ = 0.57, p = 0.002). Overall, model fits provided evidence that young adults show more pronounced immediate adjustment at the beginning of the adaptation phase than senior adults. Gradual adjustment and adaptation rate were found equivalent in both age groups.

Since we considered in particular immediate adaptive changes in the perceptual task as driven by top-down goals, we aimed to explore their association with standard measures of executive functioning. Multiple regression analysis was used to test whether immediate adjustment can be predicted by individuals' performance in standard executive tasks included in our battery of cognitive tasks, i.e. span measures of verbal and visual working memory, task switching, and problem solving. Results indicated that the four predictor model explained 47.4% of the variance in the magnitude of immediate adjustment, R = .69, $F(4, 23)$ = 5.18, p = .004. This result further validates that saccadic plasticity in the perceptual task is substantially triggered by high level mechanisms.

Consistent with our findings in the double-step paradigm, we found a pronounced saccadic latency difference between age groups, $F(1, 27)$ = 17.34, p < .001, η^2 = .39, and a latency decrease across trial intervals, $F(3, 81)$ = 3.98, p = .011, η^2 = .13. The interaction between both main effects was not significant, $F(3, 81)$ = 0.65, p = 0.585, η^2 = .02. Figure 8 illustrates average latencies for each age group. Latencies did not correlate with any parameter derived from fitting vertical amplitude data with the exponential model. This replicates the finding of Experiment 1 that saccadic plasticity is not modulated by latency differences.

Figure 8. Average saccadic latencies in the specified trial intervals of the perceptual task for young adults and senior adults. Error bars: SEM.

Discussion

In our second experiment we studied saccadic adaptation in a perceptual task (Schütz et al., 2014; Schütz & Souto, 2015). In this task, adaptive changes of saccade amplitude are triggered by a behavioral goal, i.e. accomplishing a discrimination task, while low-level visual errors are not manipulated. We thus explored age differences in sensorimotor plasticity when high-level mechanisms are emphasized. Although young as well as senior adults showed efficient amplitude shifts, they substantially differed in the contributions of immediate and gradual adjustments to overall adaptation in this perceptual task. Whereas immediate, strategic adjustments were found to be significantly stronger in young adults than in senior adults, gradual adjustments were not affected by age. Similar as in the double-step paradigm age groups showed equivalent adaptation rates. In the post-adaptation phase, more pronounced recovery from adaptive amplitude shifts was observed in younger adults.

Differential age effects on immediate and gradual adjustments across the adaptation process suggest a specific decline of underlying mechanisms. In particular, immediate adjustments reflect high-level strategic capacities, which are applied to meet the demands of the suddenly manipulated task at the beginning of the adaptation phase. Notably, task manipulation is completely transparent and thus fully accessible to awareness. Accordingly, in contrast to

adaptation dynamics in the double-step paradigm immediate adjustments in the perceptual task contribute crucially to overall adaptation. In senior adults, immediate adjustments contributed to 50% of the final amplitude change at the end of the adaptation phase, however, in young adults this contribution reached 65%. This difference indicates that visuomotor adaptation in younger adults relies more on strategic shifts than in senior adults. Gradual adjustments across the adaptation course were equivalent in both age groups. The advantage of young adults in immediate adjustments was perpetuated at the end of the adaptation phase when young and senior groups had compensated 73% and 57% of the target amplitude manipulation, respectively. Less pronounced amplitude shifts presumably also contributed lower discrimination accuracy we observed in senior adults because their saccades were not sufficiently optimized for the behavioral task.

Consistent with our findings in the double-step paradigm saccadic latencies were not associated with adaptive changes. We observed the typical age-related differences in saccadic latencies (Munoz et al., 1998; Peltsch et al., 2011), but these did not explain adjustment differences. However, we were able to predict immediate adjustment by standard measures of executive functioning. This further emphasizes that fast adaptive changes of saccade amplitude reflect high-level, strategic adjustments. Age-related vulnerability of these strategic adjustments agrees with evidence from reaching adaptation indicating that reduced sensorimotor plasticity is due to less efficient explicit strategy use while low-level mechanisms are preserved (Hegele & Heuer, 2010a, 2013; Heuer & Hegele, 2011; McNay & Willingham, 1998; Roller et al., 2002). In addition, particular decline of executive behavior control is consistently supported by findings on cognitive aging (Hasher & Zacks, 1988; Park & Reuter-Lorenz, 2009; Span, Ridderinkhof, & van der Molen, 2004; West, 1996). Executive functioning is widely accepted as psychological core primitive of functional changes with increasing age. Our findings show that this impact is also valid for visuomotor control. Age-related decline of saccadic plasticity is primarily based on less efficient high-level mechanisms.

Interpretation of more pronounced recovery from adaptation in young adults appears ambiguous. We speculate that young adults' plasticity relies more on immediate, strategic changes which are most likely linked to proposed fast adaptation processes that decay rapidly (Ethier et al., 2008; Körding et al., 2007). In contrast, given less efficient use of executive functions senior adults might rely more on gradual changes which are dominated by slow adaptation processes that

decay slowly. This pattern could contribute to faster recovery from adaptation in young adults than in senior adults. However, modeling of two adaptation components that differ in build-up and decay considers pure retention without sensory feedback. Since visual feedback was available in the post-adaptation phase of the perceptual task, the model might not apply to our data directly. Thus, the link between differences in recovery and dominance of specific adaptation components has to remain tentative.

The observed age-related vulnerabilities of saccadic adaptation are functionally based on age effects on involved neuronal substrates. Candidate structures are in particular the cerebellum and the brainstem (Robinson, Fuchs, & Noto, 2002). However, more recently also cortical areas, especially frontal and parietal areas, have been found to be involved in saccadic adaptation (Blurton, Raabe, & Greenlee, 2012; Gerardin, Miquée, Urquizar, & Pélisson, 2012; Panouilleres et al., 2014). Different areas might contribute to specific adaptation components. Whereas subcortical structures can be assumed to be functionally relevant rather for low-level mechanisms of sensorimotor plasticity, cortical areas might specifically fuel high-level mechanisms. Age-related detrimental changes have been described in all functionally involved regions *(Jernigan et al., 2001; Raz et al., 2005; Sowell et al., 2003), but subcortical decline occurs later than decline in cortical areas. Thus, our finding* of preserved low-level visuomotor plasticity, but impaired high-level processes in senior adults might reflect differential time courses of regional decline.

In summary, age effects on saccadic adaptation in a perceptual task show that in particular fast, strategic changes that reflect high-level mechanisms are attenuated with increasing age. In contrast, slower, gradual changes that are primarily driven by low-level mechanisms seem robust across the adult lifespan, at least across the age range covered in our study.

General Conclusions

Our results provide evidence of differential aging processes in saccadic adaptation. Current theories of age-related functional changes assume a general reduction in processing resources and global decline with increasing age (Salthouse, 1996). Our data highlight that differentiation between specific vulnerabilities and preserved resources is needed. Differential age effects emphasize the often ignored complexity of aging processes and call for comprehensive investigation of subprocesses in order to improve our understanding of decline and stability (Cabeza, Nyberg, & Park, 2005a).

Resiliency of low-level mechanisms and specific vulnerability of high-level mechanisms in saccadic adaptation moreover provide a link between cognitive and sensorimotor aging. Our findings indicate that psychological core primitives identified for cognitive decline, i.e. executive functioning, apply also to age-related changes in sensorimotor capacities. Saccadic plasticity was not affected by age-related slowing and there was no evidence for reduced compensation for visual errors, however, we found age-related decline of strategic adaptive adjustments. Thus, not sensorimotor plasticity per se might be reduced in senior adults, but rather executive contributions to efficient resource control (compare also Chang, Shibata, Andersen, Sasaki, & Watanabe, 2014).

References

Abel, L. A., & Douglas, J. (2007). Effects of age on latency and error generation in internally mediated saccades. *Neurobiology of Aging*, *28*(4), 627–637. doi:10.1016/j.neurobiolaging.2006.02.003

Baltes, P. B., Staudinger, U. M., & Lindenberger, U. (1999). Lifespan psychology: theory and application to intellectual functioning. *Annual Review of Psychology*, *50*, 471–507. doi:10.1146/annurev.psych.50.1.471

Berch, D. B., Krikorian, R., & Huha, E. M. (1998). The Corsi block-tapping task: methodological and theoretical considerations. *Brain and Cognition*, *38*(3), 317–338. doi:10.1006/brcg.1998.1039

Blurton, S. P., Raabe, M., & Greenlee, M. W. (2012). Differential cortical activation during saccadic adaptation. *Journal of Neurophysiology*, *107*(6), 1738–1747. doi:10.1152/jn.00682.2011

Bock, O., & Schneider, S. (2001). Acquisition of a sensorimotor skill in younger and older adults. *Acta Physiologica et Pharmacologica Bulgarica*, *26*(1-2), 89–92.

Bock, O. (2005). Components of sensorimotor adaptation in young and elderly subjects. *Experimental Brain Research*, *160*(2), 259–263. doi:10.1007/s00221-004-2133-5

Bock, O., & Girgenrath, M. (2006). Relationship between sensorimotor adaptation and cognitive functions in younger and older subjects. *Experimental Brain Research*, *169*(3), 400–406. doi:10.1007/s00221-005-0153-4

Bock, O., Ilieva, M., & Grigorova, V. (2014). Effects of old age and resource demand on double-step adaptation of saccadic eye movements. *Experimental Brain Research*, *232*(9), 2821–2826. doi:10.1007/s00221-014-3969-y

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436. doi:10.1163/156856897X00357

Bridgeman, B., Hendry, D., & Stark, L. (1975). Failure to detect displacement of the visual world during saccadic eye movements. *Vision Research*, *15*(6), 719–722.

Buch, E. R., Young, S., & Contreras-Vidal, J. L. (2003). Visuomotor adaptation in normal aging. *Learning & Memory*, *10*(1), 55–63. doi:10.1101/lm.50303

Cabeza, R., Nyberg, L., & Park, D. C. (2005a). Cognitive neuroscience of aging: Emergence of a new discipline. In R. Cabeza, L. Nyberg, & D. C. Park (Eds.), *Cognitive neuroscience of aging. Linking cognitive and cerebral aging* (pp. 3–15). Oxford: Oxford University Press.

Cabeza, R., Nyberg, L., & Park, D. C. (Eds.). (2005b). *Cognitive neuroscience of aging: Linking cognitive and cerebral aging*. Oxford: Oxford University Press.

Chang, L.-H., Shibata, K., Andersen, G. J., Sasaki, Y., & Watanabe, T. (2014). Age-related declines of stability in visual perceptual learning. *Current Biology*, *24*(24), 2926–2929. doi:10.1016/j.cub.2014.10.041

Collins, T., & Wallman, J. (2012). The relative importance of retinal error and prediction in saccadic adaptation. *Journal of Neurophysiology*, *107*(12), 3342–3348. doi:10.1152/jn.00746.2011

Craik, F. I. M., & Byrd, M. (1982). Aging and cognitive deficits. In F. I. M. Craik & S. Trehub (Eds.), *Advances in the study of communication and affect: Vol. 8. Aging and cognitive processes* (pp. 191–211). Boston, MA: Springer US. doi:10.1007/978-1-4684-4178-9_11

Currie, J., & Wilson, D. I. (2012). OPTI: Lowering the barrier between open source optimizers and the industrial MATLAB user. *Foundations of Computer-Aided Process Operations*, 8–11.

Ethier, V., Zee, D. S., & Shadmehr, R. (2008). Spontaneous recovery of motor memory during saccade adaptation. *Journal of Neurophysiology*, *99*(5), 2577–2583. doi:10.1152/jn.00015.2008

Gerardin, P., Miquée, A., Urquizar, C., & Pélisson, D. (2012). Functional activation of the cerebral cortex related to sensorimotor adaptation of reactive and voluntary saccades. *NeuroImage*, *61*(4), 1100–1112. doi:10.1016/j.neuroimage.2012.03.037

Gottlob, L. R., Fillmore, M. T., & Abroms, B. D. (2007). Age-group differences in inhibiting an oculomotor response. *Neuropsychology, Development, and Cognition. Section B, Aging, Neuropsychology, and Cognition*, *14*(6), 586–593. doi:10.1080/13825580600878752

Hasher, L., & Zacks, R. T. (1988). Working memory, comprehension, and aging: A review and a new view. In G. H. Bower (Ed.), *Psychology of learning and motivation* (pp. 193–225). Academic Press. doi:10.1016/S0079-7421(08)60041-9

Hegele, M., & Heuer, H. (2010a). Implicit and explicit components of dual adaptation to visuomotor rotations. *Consciousness and Cognition*, *19*(4), 906–917. doi:10.1016/j.concog.2010.05.005

Hegele, M., & Heuer, H. (2010b). Adaptation to a direction-dependent visuomotor gain in the young and elderly. *Psychological Research*, *74*(1), 21–34. doi:10.1007/s00426-008-0221-z

Hegele, M., & Heuer, H. (2013). Age-related variations of visuomotor adaptation result from both the acquisition and the application of explicit knowledge. *Psychology and Aging*, *28*(2), 333–339. doi:10.1037/a0031914

Herman, J. P., Blangero, A., Madelain, L., Khan, A., & Harwood, M. R. (2013). Saccade adaptation as a model of flexible and general motor learning. *Experimental Eye Research*, *114*, 6–15. doi:10.1016/j.exer.2013.04.001

Heuer, H., & Hegele, M. (2008a). Adaptation to visuomotor rotations in younger and older adults. *Psychology and Aging*, *23*(1), 190–202. doi:10.1037/0882-7974.23.1.190

Heuer, H., & Hegele, M. (2008b). Adaptation to direction-dependent visuo-motor rotations and its decay in younger and older adults. *Acta Psychologica*, *127*(2), 369–381. doi:10.1016/j.actpsy.2007.07.006

Heuer, H., & Hegele, M. (2011). Generalization of implicit and explicit adjustments to visuomotor rotations across the workspace in younger and older adults. *Journal of Neurophysiology*, *106*(4), 2078–2085. doi:10.1152/jn.00043.2011

Heuer, H., Hegele, M., & Sulzenbruck, S. (2011). Implicit and explicit adjustments to extrinsic visuo-motor transformations and their age-related changes. *Human Movement Science*, *30*(5), 916–930. doi:10.1016/j.humov.2010.07.004

Hopp, J. J., & Fuchs, A. F. (2004). The characteristics and neuronal substrate of saccadic eye movement plasticity. *Progress in Neurobiology*, *72*(1), 27–53. doi:10.1016/j.pneurobio.2003.12.002

Horn, W. (1983). *Leistungsprüfsystem L-P-S*. Göttingen: Hogrefe.

Jernigan, T. L., Archibald, S. L., Fennema-Notestine, C., Gamst, A. C., Stout, J. C., Bonner, J., & Hesselink, J. R. (2001). Effects of age on tissues and regions of the cerebrum and cerebellum. *Neurobiology of Aging*, *22*(4), 581–594. doi:10.1016/S0197-4580(01)00217-2

Jones, S., Nyberg, L., Sandblom, J., Stigsdotter Neely, A., Ingvar, M., Magnus Petersson, K., & Backman, L. (2006). Cognitive and neural plasticity in aging: general and task-specific limitations. *Neuroscience and Biobehavioral Reviews*, *30*(6), 864–871. doi:10.1016/j.neubiorev.2006.06.012

Kessels, R. P. C., van den Berg, E., Ruis, C., & Brands, A. M. A. (2008). The backward span of the Corsi Block-Tapping Task and its association with the WAIS-III Digit Span. *Assessment*, *15*(4), 426–434. doi:10.1177/1073191108315611

Körding, K. P., Tenenbaum, J. B., & Shadmehr, R. (2007). The dynamics of memory as a consequence of optimal adaptation to a changing body. *Nature Neuroscience*, *10*(6), 779–786. doi:10.1038/nn1901

Kortte, K. B., Horner, M. D., & Windham, W. K. (2002). The trail making test, part B: cognitive flexibility or ability to maintain set? *Applied Neuropsychology*, *9*(2), 106–109. doi:10.1207/S15324826AN0902_5

Krauzlis, R. J. (2005). The control of voluntary eye movements: new perspectives. *Neuroscientist*, *11*(2), 124–137. doi:10.1177/1073858404271196

Lustig, C., Shah, P., Seidler, R., & Reuter-Lorenz, P. A. (2009). Aging, training, and the brain: a review and future directions. *Neuropsychology Review*, *19*(4), 504–522. doi:10.1007/s11065-009-9119-9

Madelain, L., Paeye, C., & Darcheville, J.-C. (2011). Operant control of human eye movements. *Behavioural Processes*, *87*(1), 142–148. doi:10.1016/j.beproc.2011.02.009

Madelain, L., Paeye, C., & Wallman, J. (2011). Modification of saccadic gain by reinforcement. *Journal of Neurophysiology*, *106*(1), 219–232. doi:10.1152/jn.01094.2009

McLaughlin, S. C. (1967). Parametric adjustment in saccadic eye movements. *Perception & Psychophysics*, *2*(8), 359–362. doi:10.3758/BF03210071

McNay, E. C., & Willingham, D. B. (1998). Deficit in learning of a motor skill requiring strategy, but not of perceptuomotor recalibration, with aging. *Learning & Memory*, *4*(5), 411–420. doi:10.1101/lm.4.5.411

Munoz, D. P., Broughton, J. R., Goldring, J. E., & Armstrong, I. T. (1998). Age-related performance of human subjects on saccadic eye movement tasks. *Experimental Brain Research*, *121*(4), 391–400. doi:10.1007/s002210050473

Olk, B., & Jin, Y. (2011). Effects of aging on switching the response direction of pro- and antisaccades. *Experimental Brain Research*, *208*(1), 139–150. doi:10.1007/s00221-010-2466-1

Panouilleres, M., Habchi, O., Gerardin, P., Salemme, R., Urquizar, C., Farne, A., & Pelisson, D. (2014). A role for the parietal cortex in sensorimotor adaptation of saccades. *Cerebral Cortex*, *24*(2), 304–314. doi:10.1093/cercor/bhs312

Park, D. C., & Reuter-Lorenz, P. (2009). The adaptive brain: aging and neurocognitive scaffolding. *Annual Review of Psychology*, *60*, 173–196. doi:10.1146/annurev.psych.59.103006.093656

Pelisson, D., Alahyane, N., Panouilleres, M., & Tilikete, C. (2010). Sensorimotor adaptation of saccadic eye movements. *Neuroscience and Biobehavioral Reviews*, *34*(8), 1103–1120. doi:10.1016/j.neubiorev.2009.12.010

Peltsch, A., Hemraj, A., Garcia, A., & Munoz, D. P. (2011). Age-related trends in saccade characteristics among the elderly. *Neurobiology of Aging*, *32*(4), 669–679. doi:10.1016/j.neurobiolaging.2009.04.001

Raz, N., Lindenberger, U., Rodrigue, K. M., Kennedy, K. M., Head, D., Williamson, A.,. . . Acker, J. D. (2005). Regional brain changes in aging healthy adults: general trends, individual differences and modifiers. *Cerebral Cortex*, *15*(11), 1676–1689. doi:10.1093/cercor/bhi044

Robinson, F. R., Fuchs, A. F., & Noto, C. T. (2002). Cerebellar Influences on Saccade Plasticity. *Annals of the New York Academy of Sciences*, *956*(1), 155–163. doi:10.1111/j.1749-6632.2002.tb02816.x

Roller, C. A., Cohen, H. S., Kimball, K. T., & Bloomberg, J. J. (2002). Effects of normal aging on visuo-motor plasticity. *Neurobiology of Aging*, *23*(1), 117–123.

Salthouse, T. A. (1996). The processing-speed theory of adult age differences in cognition. *Psychological Review*, *103*(3), 403–428. doi:10.1037/0033-295X.103.3.403

Schütz, A. C., Kerzel, D., & Souto, D. (2014). Saccadic adaptation induced by a perceptual task. *Journal of Vision*, *14*(5), 4. doi:10.1167/14.5.4

Schütz, A. C., & Souto, D. (2015). Perceptual task induces saccadic adaptation by target selection. *Frontiers in Human Neuroscience*, *9*, 566. doi:10.3389/fnhum.2015.00566

Souto, D., Gegenfurtner, K. R., & Schütz, A. C. (2016). Saccade Adaptation and Visual Uncertainty. *Frontiers in Human Neuroscience*, *10*, 227. doi:10.3389/fnhum.2016.00227

Sowell, E. R., Peterson, B. S., Thompson, P. M., Welcome, S. E., Henkenius, A. L., & Toga, A. W. (2003). Mapping cortical change across the human life span. *Nature Neuroscience*, *6*(3), 309–315. doi:10.1038/nn1008

Span, M. M., Ridderinkhof, K. R., & van der Molen, M. W. (2004). Age-related changes in the efficiency of cognitive processing across the life span. *Acta Psychologica*, *117*(2), 155–183. doi:10.1016/j.actpsy.2004.05.005

Sweeney, J. A., Rosano, C., Berman, R. A., & Luna, B. (2001). Inhibitory control of attention declines more than working memory during normal aging. *Neurobiology of Aging*, *22*(1), 39–47.

Wallman, J., & Fuchs, A. F. (1998). Saccadic Gain Modification: Visual Error Drives Motor Adaptation. *Journal of Neurophysiology*, *80*(5), 2405–2416. Retrieved from http://jn.physiology.org/content/jn/80/5/2405.full.pdf

West, R. L. (1996). An application of prefrontal cortex function theory to cognitive aging. *Psychological Bulletin*, *120*(2), 272–292. doi:10.1037/0033-2909.120.2.272

Wong, A. L., & Shelhamer, M. (2012). Using prediction errors to drive saccade adaptation: the implicit double-step task. *Experimental Brain Research*, *222*(1-2), 55–64. doi:10.1007/s00221-012-3195-4

World Medical Association. (2013). Declaration of Helsinki: ethical principles for medical research involving human subjects. *JAMA*, *310*(20), 2191–2194. doi:10.1001/jama.2013.281053

Chapter 3: Motivational modulations of age-related effects on reaching adaptation

Motivational modulation of age-related effects on reaching adaptation

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Abstract

Previous studies have provided consistent evidence that adaptation to visuomotor rotations during reaching declines with age. Since it has been recently shown that learning and retention components of motor adaptation are modulated by reward and punishment, we were interested in how motivational feedback affects age-related decline in reaching adaptation. We studied 35 young and 32 older adults in a reaching task which required fast shooting movements towards visual targets with their right hand. A robotic manipulandum (vBOT system) allowed measuring reaching trajectories. Targets and visual feedback on hand position were presented using a setup that prevented direct vision of the hand and projected a virtual image by a semi-silvered mirror. After a baseline block with veridical visual feedback we introduced a 30° counterclockwise visuomotor rotation. After this adaptation block we also measured retention of adaptation without visual feedback and finally readaptation for the previously experienced rotation. In the adaptation block participants were assigned to one of three motivational feedback conditions, i.e. neutral, reward, or punishment. Reward and punishment feedback was based on reaching endpoint error. Our results consistently corroborated reduced motor learning capacities in older adults ($p < .001$, $\eta 2 = .56$). However, motivational feedback modulated learning rates equivalently in both age groups ($p =.028$, $\eta 2 = .14$). Rewarding feedback induced faster learning, though punishing feedback had no effect. For retention we determined a significant interaction effect between motivational feedback and age group ($p =.032$, $\eta 2 = .13$). Previously provided motivational feedback was detrimental for young adults, but not for older adults. We did not observe robust effects of motivational feedback on readaptation ($p =.167$, $\eta 2 = .07$). Our findings support that motor learning is subject to modulation by motivational feedback. Whereas learning is boosted across both age groups, retention is vulnerable to previously experienced motivational incentives in young adults. In summary, in particular older adults benefit from motivational feedback during reaching adaptation so that age-related differences in visuomotor plasticity, though persisting, can be attenuated. We suggest that the use of motivational information provides a potentially compensatory mechanism during functional aging.

Keywords: motor learning, visuomotor adaptation, reaching, healthy aging, motivation

Introduction

The current understanding of functional aging processes is dominated by a strong focus on cognitive capacities (for reviews see Baltes, Staudinger, & Lindenberger, 1999; Hasher & Zacks, 1988; Park & Reuter-Lorenz, 2009; West, 1996). Whereas sophisticated models for cognitive decline and the underlying neural mechanisms have been developed, visuomotor changes across the adult lifespan are still not well understood. However, they provide a unique opportunity to investigate the complexity of functional aging in which sensory, motor, cognitive, and also motivational processes interact. Although most cognitive theories share the general assumption of a core primitive of aging that ultimately results in global decline, there is emerging evidence that emphasizes the need to investigate developmental changes considering the complexity of interwoven functional subprocesses that ultimately shape behavioral capacities (van den Bos & Eppinger, 2016). This comprehensive approach might contribute to improving ageing models in order to differentiate between decline and stability across the lifespan.

Plasticity of visuomotor behavior represents a crucial capacity in a continuously changing environment and a number of studies have explored age-related changes. Previous studies were in particular concerned with motor adaptation, i.e. the recalibration of well-trained movements to changes in the environment. Motor adaptation thus represents a basic type of motor learning that is generally distinguished from skill acquisition which refers to learning of novel movement patterns (Diedrichsen & Kornysheva, 2015; Wolpert, Diedrichsen, & Flanagan, 2011). Note that in the context of motor adaptation learning is frequently inferred from both changes in performance during adaptation as well as subsequent retention and transfer tests. In contrast, skill acquisition, characterized as a peristent change in the behavioral capabilities of the learner, has typically been assessed in retention and transfer tests in order to obtain purer measures of the newly acquired skill independent of practice-related variables (Schmidt & Lee, 2011; Sternad, 2018). This distinction should be kept in mind to avoid confusions. Typical motor adaptation paradigms elicit gradual changes in eye or reaching movements in order to compensate for manipulated visual feedback on movement outcome or disturbing force fields during movement execution. Age effects on motor adaptation have been primarily investigated in reaching paradigms introducing a visuomotor rotation (for review see Bock & Schneider, 2002).

Congruent with knowledge on cognitive plasticity decline with increasing age (for review see Jones et al., 2006), numerous studies on reaching adaptation in different age groups have provided overall support for an age-related vulnerability (e.g. Bock, 2005; Buch, Young, & Contreras-Vidal, 2003; Heuer & Hegele, 2008a; Seidler, 2006). However, it has remained ambiguous which processes contribute to the observed deterioration and which processes are robust to decline, thus potentially stabilizing adaptation capacities. Indeed several findings have suggested that reaching adaptation might be subject to only minor decline or can be even preserved across the lifespan depending on specific experimental conditions (Bock & Schneider, 2001; Cressman, Salomonczyk, & Henriques, 2010; Heuer & Hegele, 2008b). These results suggest that adaptation can be driven by a variety of processes that differ in vulnerability during aging. Consequently, vivid efforts have emerged aimed at identifying critical modulators of age-related decline in motor plasticity.

A particularly important distinction has been made between implicit and explicit knowledge fuelling visuomotor adaptation. Implicit knowledge eludes consciousness and builds up gradually across adaptation. In contrast, explicit knowledge of visuomotor perturbations triggers intentional, conscious movement corrections in order to compensate for the experienced error. The availability and efficiency of this adaptation component is closely linked to executive resources and cognitive strategies. Using paradigms that allowed dissociating both components, consistent evidence has been provided that aging is detrimental to explicit adaptation processes, whereas implicit adaptation processes remain remarkably stable across the lifespan (Bock & Girgenrath, 2006; Hegele & Heuer, 2010c, 2010b, 2013; Heuer & Hegele, 2009; Heuer, Hegele, & Sülzenbrück, 2011; Huang, Gegenfurtner, Schütz, & Billino, 2017). Another candidate modulator of age-related effects on motor adaptation has been suggested recently by a study on the role of reinforcement mechanisms during adaptation (Heuer & Hegele, 2014). Findings indicated that a reduced efficiency of motivational mechanisms might add to the decline in adaptive capacities.

This evidence for the impact of motivational factors on age-related changes in motor adaptation appears intriguing because there is a coincidence with accumulating recent work on the effects of reward and punishment during motor adaptation. In the traditional understanding of motor adaptation as a most basic mechanism of motor control, the effects of motivational feedback on plasticity were assumed to be negligible (e.g. Mazzoni & Krakauer, 2006; Wolpert et al., 2011). However, this assumption has been questioned by several findings. A number of studies have

supported beneficial effects of motivational feedback, in particular reward, on motor adaptation (Kojima & Soetedjo, 2017; Nikooyan & Ahmed, 2015; Quattrocchi, Greenwood, Rothwell, Galea, & Bestmann, 2017; but see van der Kooij & Overvliet, 2016). In addition, Galea, Mallia, Rothwell, and Diedrichsen (2015) disentangled differential contributions of reward and punishment to learning and retention during adaptation. Their results showed that punishment was associated with faster learning, but reward boosted retention when visual feedback on movement outcomes was withdrawn. In summary, motivational feedback qualifies for a substantial modulator of motor adaptation. The question arises how this functional link is affected by increasing age.

The impact of motivational processing on behavioral control during aging has been intensively investigated over the last years, however almost exclusively in cognitive learning or decision paradigms. Findings suggested a reduced sensitivity to reward and punishment with increasing age, resulting in an attenuation of motivational feedback effects on behavior (e.g. Bauer et al., 2013; Brown & Ridderinkhof, 2009; Eppinger, Hämmerer, & Li, 2011; Eppinger, Schuck, Nystrom, & Cohen, 2013; Mata, Josef, Samanez-Larkin, & Hertwig, 2011). Heterogeneity of results, though, points to a strong dependence on task characteristics and the critical role of cognitive control processes. It remains to be clarified whether age-related changes in motivational mechanisms also challenge motor control. Neural correlates of motivational processing in particular include dopaminergic neuromodulation and connectivity between brain networks (Ernst & Fudge, 2009; Montague, Hyman, & Cohen, 2004). These are known to be subject to pronounced age-related decline (Bäckman, Lindenberger, Li, & Nyberg, 2010; Sala-Llonch, Bartrés-Faz, & Junqué, 2015; Samanez-Larkin & Knutson, 2015). Thus, the effects of motivational manipulations on motor performance might differ between age groups.

We aimed to investigate how motivational incentives modulate age-related differences in motor learning. Using an established visuomotor rotation paradigm that is known to robustly induce adaption in reaching movements, we compared motor plasticity between young adults and healthy, community-dwelling older adults. In addition, within each age group we provided neutral, rewarding, or punishing feedback when adapting for reaching endpoint errors. We expected to observe age-related decline in reaching adaptation, but hypothesized that the age-related differences are modulated by motivational feedback.
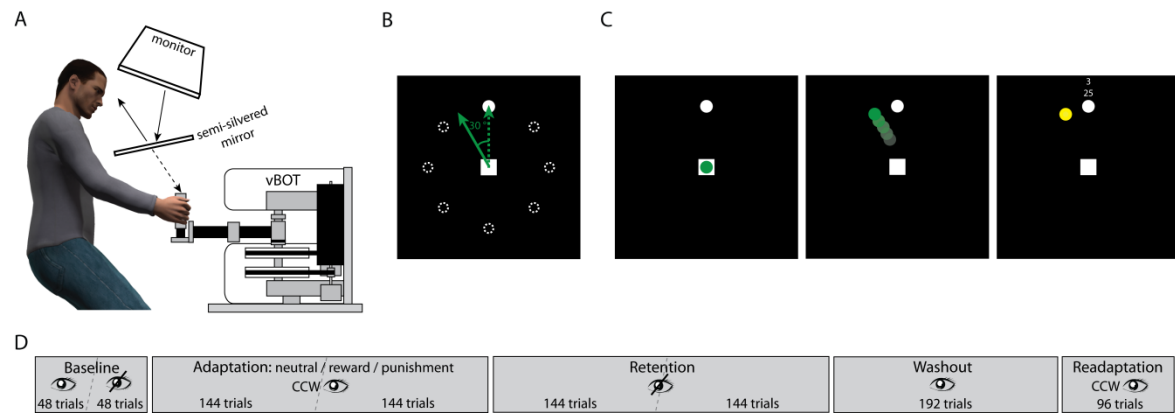
Methods

Participants

A total of 35 young adults (22 females) and 32 older adults (18 females) participated in our study. In the young adult group age ranged from 18 to 37 years with a mean age of 25.3 years (*SD* = 4.3). In the senior adult group age ranged from 60 to 77 years with a mean age of 68.4 years (*SD* = 5.0). Recruitment of subjects was managed by calls for participation at the University of Giessen and in local newspapers. All participants were naive with respect to the purpose of the study and were paid for participating. Any history of ophthalmologic, neurologic, or psychiatric disorders as well as medications presumed to interfere with perceptual capacities were screened out by a detailed interview protocol. In addition, we ran a battery of standard cognitive tasks in order to exclude pathological age-related decline. Visual acuity was measured binocularly confirming normal or corrected-to-normal for all participants. Assessment by the Edinburgh Inventory (Oldfield, 1971) showed right-handedness for the majority of participants. We identified three left-handed young adults and three ambidextrous adults, one in the young adult group and two in the older adult group, respectively. Methods and procedures agreed with the Declaration of Helsinki (World Medical Association, 2013) and were approved by the local ethics committee of the Faculty of Psychology and Sports Science, Justus-Liebig-Universität Gießen. Informed consent was obtained by all participants and protection of data privacy was provided.

Setup and stimuli

Figure 1A illustrates the setup of our study. We used a two-dimensional planar manipulandum, a vBOT system (Howard, Ingram, & Wolpert, 2009), to investigate reaching movements in our participants. Position of the manipulandum handle was recorded at a sampling rate of 1000 Hz. The vBOT system was integrated in a virtual-reality setup consisting of a monitor/mirror projection system. Stimuli were generated using Matlab with the Psychophysics Toolbox (Brainard, 1997) and displayed on the monitor. The monitor image was projected onto a semi-silvered mirror which produced a virtual image of the display. Participants were seated on a height-adjustable chair so that they were able to take a comfortable position in order to look at the semi-silvered mirror and to grasp the manipulandum handle that was occluded by the mirror. Head position was supported by a chin and a head rest. Distances and angles between monitor,

mirror, and the handle plane under the mirror were calibrated such that the virtual image was perceived being at the same plane as the handle.

Figure 1. Illustration of setup and stimuli. (A) Side view showing the participant in front of the vBOT and looking at the semi-silvered mirror that reflects the image of the monitor. (B) Layout of reaching targets; note that only one target was shown at a time, the dotted circles here just illustrate defined positions; the green dotted arrow shows a veridical handle trajectory, the green solid arrow shows the corresponding displayed trajectory in an adaptation trial, i.e. a trajectory rotated counterclockwise by 30°. (C) Example adaptation trial, reward condition; at trial start the handle position was indicated by a green dot; the reaching trajectory was displayed online by a moving green dot with a 30° counterclockwise rotation; the reaching endpoint was indicated by a yellow dot and was accompanied by feedback on points based on endpoint error. (D) Sequence of experimental blocks, for details see text.

The layout of possible reaching targets is shown in Figure 1B. At the center of a black background a white square with edge length of 1 cm indicated the starting position of the reaching movement. The reaching target was a white dot with a diameter of 0.3 cm. There were eight possible target positions arranged circularly around the start square at a distance of 8 cm and separated by 45° each.

Procedure

Before each trial a white square appeared at the center of the display. As soon as the participant encompassed the handle the vBOT system guided it to the square, i.e. the starting position. The square then disappeared and reappeared after 200 ms indicating the trial start. At the same time the reaching target was shown at one of the eight possible positions. In a sequence of eight trials each position occurred once and the order of positions was randomized. All participants used their right hand for steering the handle and were asked to reach to the target as fast and accurately

as possible. Response time was defined as the time between the trial start and the handle leaving the starting square, giving the movement onset. Movement time was defined by the time between movement onset and the handle hitting the virtual circle around the starting square on which the target positions were arranged. Visual feedback on the handle position could be provided by a green dot with a diameter of 0.3 cm. An example adaptation trial is shown in Figure 1C.

The complete reaching adaptation procedure consisted of five blocks and is illustrated in Figure 1D. The participants started with a baseline block with 96 trials overall. While in the first half of this block veridical visual feedback on the handle position was provided, no visual feedback was given in the second half. Both halves were separated by a short rest period that was limited to one minute. In the baseline block participants were supposed to get used to the task under conditions with and without visual feedback. Movement accuracy differences between both feedback conditions were not observed since participants were instructed to reach fast and directly to the targets.

Following the baseline trials, the adaptation block started in which visual feedback on the handle trajectory was provided, but introducing a counterclockwise rotation by 30°. There were a total of 288 adaptation trials split in two halves by a short rest period limited to one minute. At the end of each trial the final handle position was indicated by a yellow dot with a diameter of 0.3 cm and displayed for 500 ms. Additional motivational feedback was simultaneously displayed next to the reaching target (see Figure 1C). There were three different motivation conditions, i.e. neutral, reward, and punishment. In the neutral condition, two uninformative horizontal lines were displayed. In the reward and the punishment conditions, participants were told in advance that they could earn additional points in some phases of the experiment that would be finally converted to money, i.e. two points yielding one cent. In the reward condition, participants started with zero points and their gain added up across the trials; in the punishment condition participants were given an initial credit of 1200 points that was reduced by negative points. As motivational feedback both points earned or lost in each trial and totally accumulated points were displayed. Points were based on endpoint error. In the reward condition and the punishment condition, respectively, hitting the target gave 4 points and 0 points, an error $< 10°$ gave 3 points and -1 point, an error $< 20°$ gave 2 points and -2 points, an error $< 30°$ gave 1 point and -3 points, an error $> 30°$ gave 0 points and -4 points. In order to avoid strategic slowing in the adaptation block, a warning signal was shown in trials in which movement time exceeded the 90th percentile of the

baseline block. The starting square then turned to red indicating that the reaching movement was too slow. In those trials 0 points and -4 points were given in the reward condition and in the punishment condition, respectively. Assignment of participants to one of the three motivation conditions was done according to the order in which they participated in the study. For every three consecutive young and older adults, respectively, each condition was applied once and was randomly assigned. In the young adult group, there were 13 participants in the neutral condition, 10 participants in the reward condition, and 12 participants in the punishment condition. In the older adult group, there were 10 participants in the neutral condition, 10 participants in the reward condition, and 12 participants in the punishment condition.

The adaptation block was followed by a retention block that comprised 288 trials again split in two halves by a short rest period limited to one minute. Similar to the second half of the baseline block, here no visual feedback on the handle position was provided. Thus, participants did not receive any performance information that could drive further motor learning processes. This block allowed for investigating retention without feedback on movement errors, i.e. errorless retention. The gradual decay of the adaptive shift in reaching direction specifically characterizes retention.

After retention a washout block with a total of 192 trials was supposed to return the reaching error to the baseline level. Veridical visual feedback of the handle trajectory was given. Finally, relearning was investigated in a readaptation block. There were 96 trials in which the visual feedback was manipulated equivalently to the adaptation block. However, no motivational feedback was provided.

After the last block participants received 8 €per hour plus their additional gain if they were assigned either to the reward or to the punishment condition. Overall the procedure took about 60 to 90 minutes and thus the duration was still appropriate for the older participants.

Data analysis

Analyses of time measures, i.e. response times and movement times, were based on average data across defined blocks including all trials. Since the washout block was not critical for the investigation of learning parameters, time measures from this block were not considered in detail.

Angular reaching direction was calculated as the difference between the angular target position and the angular handle position at the end of each trial. Thus, in trials without visuomotor rotation reaching directions closer to 0° indicated smaller deviations between the final handle position and the target. In contrast, in adaption trials reaching directions closer to 30° indicated the more accurate movements since feedback on the handle position was rotated counterclockwise by 30°. We excluded trials with extreme reaching directions exceeding 50° or -20°. In addition, trials with response times larger than 1500 ms were discarded because initiation of the reaching movement was considered as overly delayed putatively due to high-level cognitive processes. Based on these criteria on average 4.4% ($SD = 2.7\%$) of all trials had to be discarded. Data from four participants, i.e. one young adult and the three older adults, who showed exclusion rates > 10% were excluded from further analyses.

Furthermore, we examined overall time needed for reaching movements in the baseline block in order to identify participants who did not accomplish the task appropriately. We determined within each age group outlier data by inspection of boxplots and considered time measures deviating more than 1.5 times the interquartile range from the range borders as outliers. We identified outlier data for two young adults and two older adults. They were also excluded from further analyses.

Reaching direction data was analyzed using angular measure circular statistics (Berens, 2009). For each participant the average of reaching directions across all trials in the baseline block was removed from the following trials in order to adjust for individual biases in reaching movements. We then derived different parameters that characterize motor learning. As model-free parameters for adaptation and retention we considered the reaching direction shown by the end of the adaptation block and the retention block, respectively. We were here specifically interested in the finally achieved adaptive shift and the persisting retention status. In order to obtain robust measures, we averaged reaching direction across the last third of trials in both the adaptation and the retention block, i.e. across 96 trials each. In addition, we derived model-based parameters using a single-state state-space model to quantify learning and retention parameters (Smith, Ghazizadeh, & Shadmehr, 2006). For the adaptation block, the retention block, and the readaptation block we fitted reaching direction data trial-by-trial based on the following model equations.

$$\hat{y}_n = -z_n^t \quad \text{and} \quad z_{n+1}^t = Az_n^t + B(r_n - z_n^t) \quad (1)$$

$\hat{y}_n$ gives the angular reaching direction on trial n. The current estimated visuomotor rotation associated with the target t is given by z_n^t. r_n represents the visuomotor rotation on trial n. Thus, $r_n - z_n^t$ gives the reaching error on trial n. Given the model equation, the parameter A provides a measure for retention rate, i.e. persistence of the previous learning state. For the adaptation and readaptation blocks this parameter was not further followed up since in each trial consistent rotated feedback was given excluding substantial forgetting. The parameter B provides a measure for adaptation for the experienced reaching error on the previous trial, i.e. the learning rate. Since no visual feedback on the reaching error was provided in the retention block, we set $B = 0$ for fitting. A measure for the learning benefit based on repeated exposure to the visuomotor rotation was given by the difference between the learning rates in the readaptation block and the adaptation block, i.e. savings.

By evaluating boxplots for the different learning parameters and applying the same criteria as described above we determined further outlier data for each age group. Extreme parameters suggested that the corresponding participants showed insufficient compliance with the task instructions, applied specific strategies for accomplishing the task, or were affected early by fatigue. In the adaptation block, two young participants showed an extremely high or low learning performance, respectively. For another young participant we determined almost complete persistence of adaptation in the retention block. Finally, an older adult showed extremely low savings, i.e. benefit from repeated learning, in the readaptation block suggesting pronounced fatigue across the experiment. In order to reduce noise in our data we excluded the identified participants from further analyses.

The exploratory data analysis and the corresponding exclusion of participants reduced our dataset to 29 young adults and 26 older adults. We tested whether exclusion of participants was related to age group or motivational condition. There was no significant bias in exclusion that could complicate analyses of the final dataset, $\Phi = .63$, $p = .091$.

If not stated otherwise, data were analyzed using two-way factorial ANOVAs with the between-subjects factor *age group* (young adults vs. older adults) and the between-subjects factor *motivation condition* (neutral vs. reward vs. punishment). Significant main effects were followed up by planned simple contrasts comparing both the reward and the punishment condition to the

neutral condition, respectively. Significant interaction effects were scrutinized by one-way ANOVAs for each age group with the factor *motivation condition*. Post-hoc contrasts were Bonferroni-Holm corrected for multiple comparisons. A significance level of $\alpha = .05$ was used for all statistical analyses. Descriptive values are given as means ± SEMs.
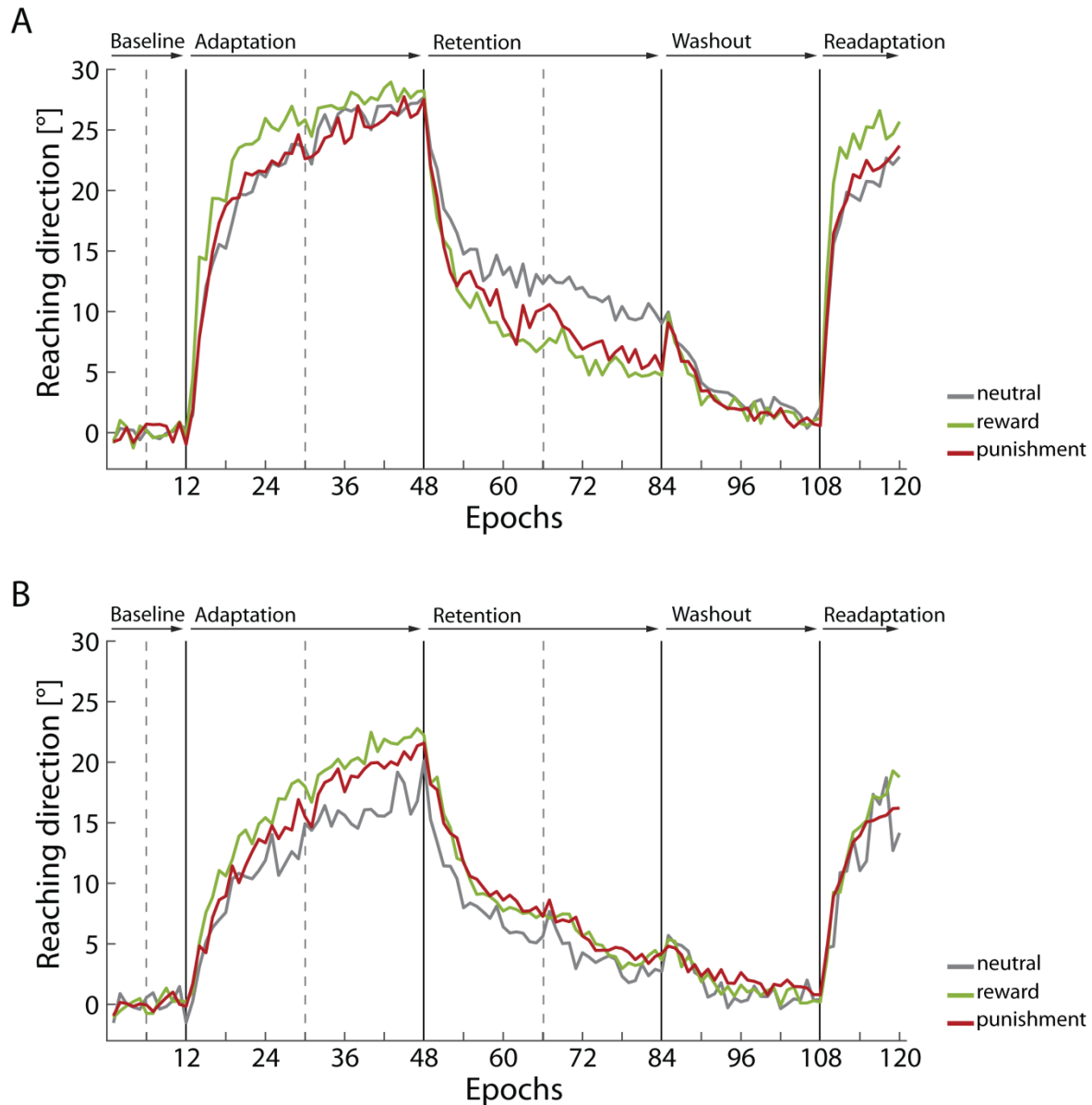
Results

We aimed to investigate how motivational incentives modulate age-related differences in motor learning. Performance of a young adult group and an older adult group was assessed in a reaching task that required fast shooting movements towards visual targets.

Adaptive processes were triggered by manipulation of visual feedback on the individual reaching trajectories. The applied visuomotor rotation paradigm robustly elicited adaptation of reaching direction in both age groups. Figure 2 shows the averaged angular reaching direction across the experimental blocks for young adults (panel A) and older adults (panel B). Reaching direction is plotted epochs that give the average across eight reaching movements.

The illustration shows an overall similar pattern in both age groups. In the baseline block, reaching direction fluctuated around 0°, i.e. a perfect match between final handle position and the target. Considering the complete sample, we indeed determined a counterclockwise bias, -0.91 ± 0.18°, that significantly deviated from 0°, $t(54) = -5.11$, $p < .001$, $d = -1.39$. This bias was most likely due to our procedure requiring that the right hand was used for the reaching movements. A one-way ANOVA with the factor *motivation condition* yielded no evidence that this bias was affected by the motivation condition participants were assigned to, $F(2, 52) = 0.47$, $p = .631$, $\eta^2 = .02$. As described above in the Methods section we adjusted reaching direction data for the bias by removing the average across the baseline block from the following trials.

In the adaptation block, in which visual feedback on reaching trajectories was systematically rotated counterclockwise by 30°, reaching direction shifted across the epochs so that the angular error between the final handle position and the target was reduced. In the retention block without visual feedback the adaptive shift in reaching direction declined, but was not completely abolished. The washout block with veridical visual feedback on reaching trajectories finally brought the reaching direction back close to 0°. Picking up rotated visual feedback in the readaptation block again elicited adaptive shifts of reaching direction. In summary, young and older adults showed the expected pattern of shifts in reaching direction that were supposed to be

triggered by the experimental procedure. However, the comparison between panels A, i.e. young adults, and B, i.e. older adults, in Figure 2 points to substantial differences in magnitude of shifts observed in both age groups and in particular to specific effects of motivational feedback provided in the adaptation. In the following, detailed results for motor learning parameters in the adaptation block, the retention block, and the readaptation block are presented.
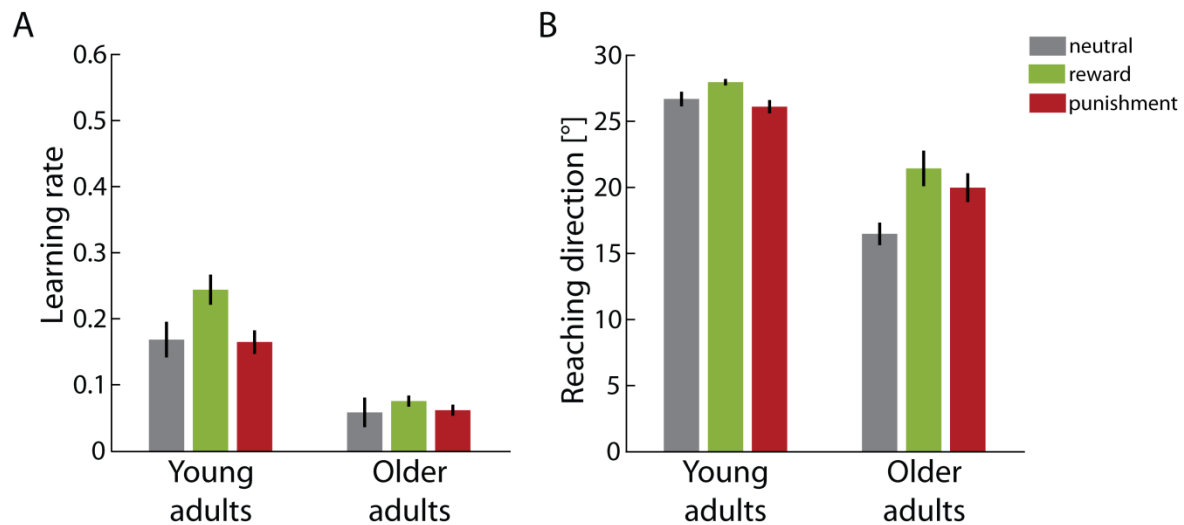

Figure 2. Averaged reaching direction across the experimental blocks for (A) the young adult group and (B) the older adult group, respectively. Epoch data, i.e. average across eight trials, is used for plotting reaching direction. Data is given in gray for neutral condition groups, in green for the reward condition groups, and in red for the punishment condition groups.

Visuomotor learning

In the adaptation block, participants who were assigned to either the reward or the punishment condition had the opportunity to earn points based on endpoint error of their reaching movements (see Methods section). Thus, better motor learning yielded more points in the reward condition and reduced lost points in the punishment condition, respectively. For both conditions we determined significant age effects on the point outcome. In the reward condition, young adults won on average 2.72 ± 0.04 points per trial, but older adults won only 1.90 ± 0.12 points per trial *(t(11.1) = 6.33, p < .001, d = 2.79). In the punishment condition,* young adults lost on average -1.55 ± 0.07 points per trial whereas older adults lost -2.30 ± 0.12 points per trial *(t(18) = 5.46, p < .001, d = 2.57). These differences indicated an age-related disadvantage in motor learning that was corroborated by analysis of the specified learning parameters in the adaptation block.*

Figure 3A illustrates the learning rate for both adult groups in the different motivational feedback conditions. We determined significant main effects of *age group*, $F(1, 49) = 66.19$, $p < .001$, $\eta^2 = .56$, and *motivation condition*, $F(2, 49) = 3.84$, $p = .028$, $\eta^2 = .14$. The interaction effect of both factors did not reach significance, $F(2, 49) = 1.74$, $p = .185$, $\eta^2 = .07$. Older adults showed lower learning rates than young adults in all motivational feedback conditions.

Figure 3. Learning results in the adaptation block. (A) Average learning rates in the different motivation condition groups for young and older adults. (B) Average final reaching direction in the different motivation condition groups for young and older adults. Error bars depict $\pm$ 1 SEM.

The main effect of motivation condition was followed up by two planned contrasts comparing the neutral condition to the reward and the punishment condition, respectively. Whereas the learning rate was significantly higher in the reward condition than in the neutral condition, contrast estimate 0.05 ± 0.02, p = .046, punishment did not affect the learning rate, contrast estimate < 0.01 ± 0.02, p = .991.
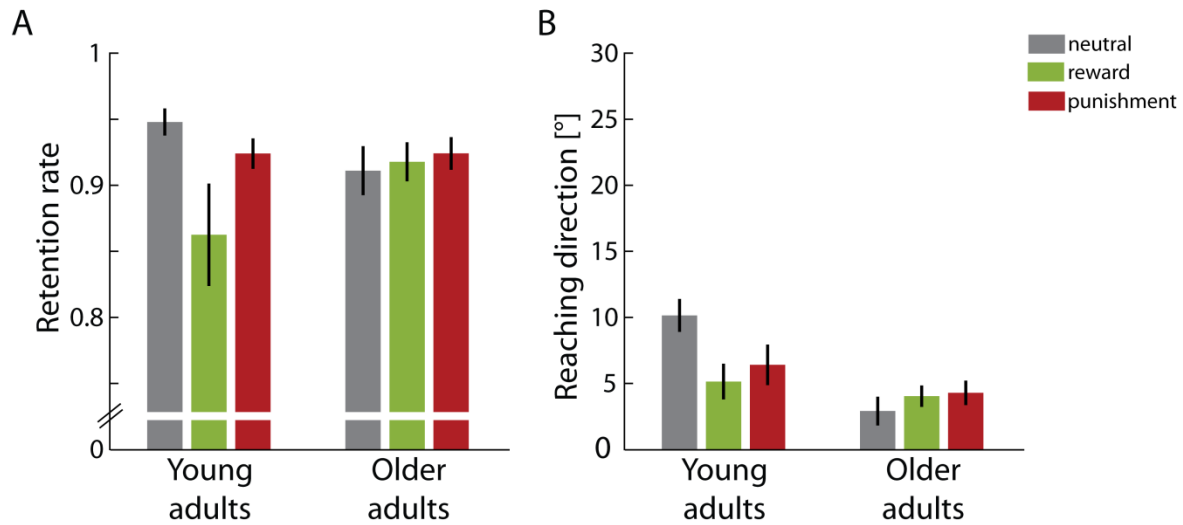
The final adaptive state at the end of the adaptation block is shown in Figure 3B. Reaching direction in the last third of trials was significantly affected by age group, $F(1, 49) = 115.63$, p <.001, $\eta^2 = .70$, and motivation condition, $F(2, 49) = 6.05$, p =.005, $\eta^2 = .20$. However the main effects were qualified by a significant interaction of both factors, $F(2, 49) = 3.27$, p =.046, $\eta^2 = .12$. As post-hoc analyses we ran separate one-way ANOVAs with the factor motivation condition for both age groups. For young adults, the effect motivation condition just failed to reach significance, $F(2, 26) = 3.18$, p =.058, $\eta^2 = .20$. In contrast, in the older adult group significant differences between the motivational feedback groups were supported, $F(2, 23) = 4.10$, p =.030, $\eta^2 = .26$. Planned contrasts showed a more pronounced adaptive shift in the reward condition than in the neutral condition, contrast estimate $4.95 \pm 1.74°$, p = .018. The comparison between the punishment condition and the neutral condition neared significance, contrast estimate $3.50 \pm 1.74°$, p = .056.

In summary, our findings in the adaptation block consistently corroborated expected reduced motor learning capacities in older adults when compared with young adults. In addition, analyses yielded evidence that motivational feedback modulates motor adaptation in both age groups. Results from model-based and model-free analyses did not overlap completely, but overall supported a similar pattern. Faster learning was induced by rewarding feedback. Punishing feedback was less efficient and did not boost learning significantly relative to neutral feedback. This pattern was observed for young adults as well as for older adults. However, at the end of the adaptation block it only neared significance for younger adults. Since the adaptive shift in reaching direction then was close to complete for young adults, the attenuation of the motivational effect might be due to a ceiling effect.

Visuomotor retention

In the retention block no visual feedback was provided and thus it allowed for investigating errorless retention. Figure 4A shows the retention rate for both adult groups in the different

motivational feedback conditions. The lower the retention rate was, the faster the reaching direction shift built up across the adaptation block decayed in the absence of performance feedback. The two-factorial ANOVA yielded a significant main effect for *motivation condition*, $F(2, 49) = 3.20$, $p = .049$, $\eta^2 = .12$, but not for *age group*, $F(1, 49) = 0.21$, $p = .650$, $\eta^2 < .01$. In addition, a significant interaction effect of both factors was found, $F(2, 49) = 3.70$, $p = .032$, $\eta^2 = .13$. Post-hoc one-way ANOVAs for each age group showed that retention rate significantly varied across motivational feedback conditions in young adults, $F(2, 26) = 5.47$, $p = .010$, $\eta^2 = .30$, but not in older adults, $F(2, 23) = 0.20$, $p = .825$, $\eta^2 = .02$. For the young adults, we further clarified that the retention rate was significantly lower in the reward condition than in the neutral condition, contrast estimate -0.09 ± 0.03, $p = .006$. However, retention rates in the punishment condition and in the neutral condition were equivalent, contrast estimate -0.02 ± 0.02, $p = .317$.

Figure 4. Retention results. (A) Average retention rates in the different motivation condition groups for young and older adults. (B) Average final reaching direction in the different motivation condition groups for young and older adults. Error bars depict ± 1 SEM.

Figure 4B gives the final reaching direction in the last third of the retention block. For this parameter we determined a significant main effect of age group, $F(1, 49) = 13.02$, $p = .001$, $\eta^2 = .21$, but not for motivation condition, $F(2, 49) = 1.28$, $p = .287$, $\eta^2 = .05$. Again a significant interaction effect of both factors, $F(2, 49) = 3.66$, $p = .033$, $\eta^2 = .13$, qualified main effect results. Post-hoc one-way ANOVAs again yielded a significant effect of motivation condition for young adults, $F(2, 26) = 3.95$, $p = .032$, $\eta^2 = .23$, but not for older adults, $F(2, 23) = 0.57$, $p = .572$, $\eta^2 = .05$. Young adults showed a significantly lower retention rate in both the reward condition, -

$5.01 \pm 1.96°$, p = .034, and in the punishment condition, $-0.02 \pm 0.02°$, p = .044, when compared to the neutral condition.
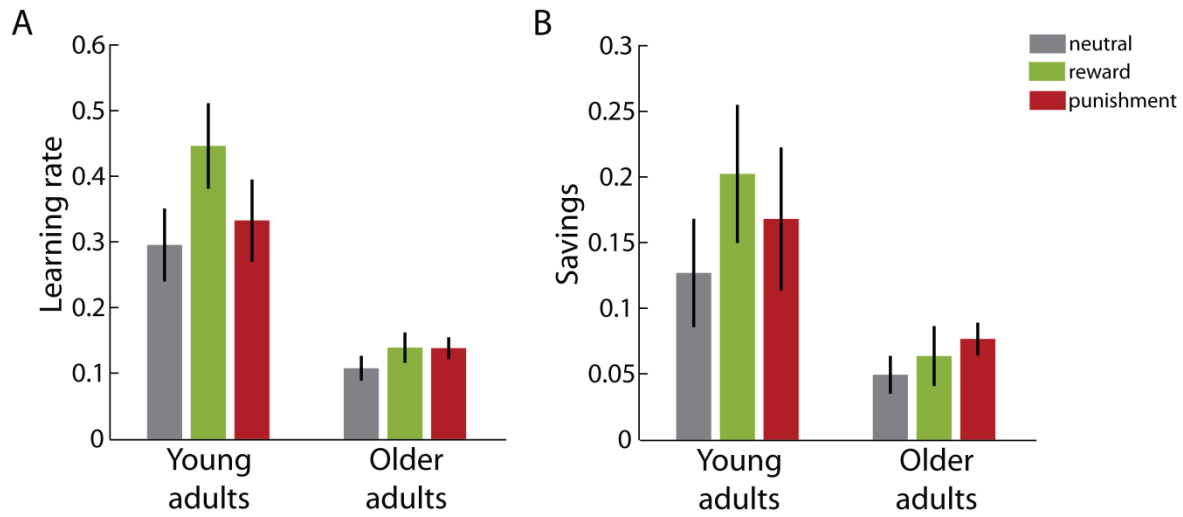
Overall results in the retention block pointed to an interaction effect between motivational feedback and age group. For young adults motivational feedback during initial learning was detrimental for retention performance. In particular, rewarding feedback induced significantly faster forgetting and was associated with a smaller persisting adaptive shift at the end of the retention block. Punishing feedback, though not triggering performance differences during initial learning, similarly was associated with a smaller persisting adaptive shift. In contrast to these finding for younger adults, older adults' retention performance was not affected by the motivational condition during initial learning.

Visuomotor relearning

We investigated relearning rates in the readaptation block in order to clarify how motivational effects on adaptation and retention affect relearning in the different age groups. By the end of the washout block reaching direction was close to 0° in all experimental groups (compare Figure 2). Using the last 16 trials of the washout block as reference, we however found a persisting shift in reaching direction for the complete sample, $0.80 \pm 0.23°$, $t(54) = 3.56$, $p = .001$, $d = 0.97$. This means that no complete washout was accomplished by the 192 trials with veridical visual feedback. The persisting shift, though, did not correlate with learning rate in the following readaptation block, $r(55) = .05$, $p = .729$. Furthermore, factorial analysis yielded no evidence for significant main effects of *age group*, $F(1, 49) = 2.10$, $p = .153$, $\eta^2 = .04$, or *motivation condition*, $F(2, 49) = 0.11$, $p = .897$, $\eta^2 = .01$, on the reaching direction by the end of the washout block. In addition, the interaction effect was also not significant, $F(2, 49) = 0.82$, $p = .446$, $\eta^2 = .03$. Thus we suggest that any differences in relearning are rather unlikely to be induced by incomplete washout, but can be linked to differences in previous adaptation and retention.

Figure 5A illustrates the learning rate in the readaptation block for each age group in the different motivational feedback conditions. Please note that during readaptation no additional motivational feedback was provided. We determined a significant main effect of *age group*, $F(1, 49) = 36.71$, $p < .001$, $\eta^2 = .43$. Older adults showed lower learning rates during readaptation than young adults in all motivational feedback conditions. Neither the main effect of *motivation condition*, $F(2, 49)$

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= 1.86, $p = .167$, $\eta^2 = .07$, nor the interaction effect, $F(2, 49) = 1.02$, $p = .369$, $\eta^2 = .04$, reached significance.

Figure 5. Learning in the readaptation block. (A) Average learning rates in the different motivation condition groups for young and older adults. (B) Average savings, i.e. the difference between the learning rates in the readaptation block and the adaptation block, in the different motivation condition groups for young and older adults. Error bars depict ± 1 SEM.

In Figure 5B savings, i.e. the difference between the learning rate in the readaptation block and the learning rate in the adaptation block, are shown. Savings represent the learning benefit when participants adapt to a visuomotor manipulation that they have already experienced before. In all age groups and motivational feedback condition, respectively, savings were significantly larger than zero (all $ps \leq .017$). We found a significant main effect of age group, $F(1, 49) = 11.06$, $p = .002$, $\eta^2 = .18$, but neither a significant main effect of *motivation condition*, $F(2, 49) = 0.73$, $p = .489$, $\eta^2 = .03$, nor a significant interaction effect, $F(2, 49) = 0.35$, $p = .710$, $\eta^2 = .01$. Older adults benefitted less from the previous learning experience than young adults.

In summary, congruent with our findings in the adaptation block learning rate in the readaptation block was significantly lower in older than in young adults. In addition, older adults showed smaller benefits from repeated learning indicated by savings. However, there was no significant evidence that motivational feedback during initial learning affected learning performance during readaptation. Although visual inspection of Figure 5 suggests an overall beneficial effect of motivational feedback on learning rate and savings across both age groups, differences did not reach significance given pronounced variability of parameters in this last experimental block.

Response and movement times

Finally we analyzed response and movement times in order to clarify whether the effects of motivation condition during reaching adaptation are linked to differential movement strategies. Table 1 summarizes the data for young and older adults.

Time measures were specifically of interest in the adaptation block, the retention block, and the readaptation block since the learning parameters were derived from these blocks. Data from the baseline block was used for checking systematic differences between our participant groups that were not due to the specific motivational manipulations. For each block we ran 2 (*age group*) x 3 (*motivation condition*) ANOVAs on both response times and movement times, respectively.

In the baseline block we only determined a significant main effect of *age group* on response times, $F(1, 49) = 28.1$, $p < .001$, $\eta_p^2 = .36$. Older adults started their movements significantly slower than young adults. Most importantly, response times were affected neither by a main effect of *motivation condition* nor an interaction effect between both factors ($ps \geq .292$). Analysis of movement times yielded no significant effects. Thus, we found no evidence for systematic biases in the baseline block that could limit interpretation of our results in the later blocks.

ANOVAs for the main experimental blocks consistently showed significant main effects of *age group* on response times (adaptation block: $F(1, 49) = 24.0$, $p < .001$, $\eta_p^2 = .33$; retention block: $F(1, 49) = 19.2$, $p < .001$, $\eta_p^2 = .28$; readaptation block: $F(1, 49) = 16.2$, $p < .001$, $\eta_p^2 = .25$). However, reaction times were not affected by main or interaction effects of *motivation condition* (all $ps \geq .463$). Analysis of movement times again yielded no significant effects across all considered blocks. In summary, these results indicated that motivational effects on the different learning parameters could not be explained by specific strategies for movement initiation or execution that would have affected time measures. Congruently, in neither age group we found significant correlations between the time measures and the relevant learning parameters in the specific experimental blocks (all $ps \geq .10$).

Table 1. Response times (RT) and movement times (MT) in the different motivation condition groups for young and older adults; data is given for the baseline block and the main experimental blocks.

	Younger adults		Older adults	
	RT [ms]	MT [ms]	RT [ms]	MT [ms]
Baseline				
Neutral	403 ± 10	123 ± 6	481 ± 11	144 ± 8
Reward	413 ± 19	131 ± 14	514 ± 18	137 ± 10
Punishment	424 ± 10	144 ± 13	529 ± 38	140 ± 11
Adaptation				
Neutral	441 ± 20	121 ± 9	542 ± 10	142 ± 16
Reward	415 ± 34	120 ± 13	523 ± 22	143 ± 9
Punishment	439 ± 19	137 ± 13	567 ± 41	138 ± 7
Retention				
Neutral	408 ± 16	109 ± 5	484 ± 19	125 ± 7
Reward	396 ± 22	117 ± 12	519 ± 36	134 ± 8
Punishment	432 ± 22	116 ± 9	523 ± 31	123 ± 6
Readaptation				
Neutral	421 ± 18	117 ± 6	557 ± 34	142 ± 18
Reward	419 ± 30	130 ± 16	554 ± 66	140 ± 10
Punishment	431 ± 22	137 ± 12	550 ± 35	150 ± 16

Discussion

This study was concerned with motivational modulation of motor learning. We investigated reaching adaptation in a well-established visuomotor rotation paradigm that is known to robustly induce adaptive movement shifts (e.g. Krakauer, 2009; Krakauer, Pine, Ghilardi, & Ghez, 2000). We coupled movement endpoint error experienced during adaptation to neutral, rewarding, or punishing feedback. Comparing reaching performance in a group of young adults and a group of healthy older adults, we explored whether motivational incentives modulate age-related decline in motor learning.

Visuomotor perturbations in our paradigm triggered consistent recalibration of reaching direction across all participants. However, motor plasticity was found significantly reduced in older adults. This result corroborated findings from previous studies using similar reaching adaptation procedures (e.g. Bock, 2005; Buch et al., 2003; Heuer & Hegele, 2008a, 2009). It has been suggested that in particular an age-related vulnerability of explicit, strategic components contributing to adaptation drive these age effects; in contrast implicit components have found to be preserved across the lifespan and putatively stabilize motor learning (Heuer et al., 2011; Heuer & Hegele, 2009; Huang et al., 2017). Although both implicit and explicit components were supposed to be involved in the observed recalibration of reaching direction (see Taylor, Krakauer, & Ivry, 2014), our procedure putatively favored the flexible application of explicit strategies. The visuomotor perturbation was introduced abruptly and no supporting instructions were given. In addition, we used varying target directions for which explicit, but not implicit components generalize (Heuer & Hegele, 2011). Given the particular vulnerability of explicit adaptation components, we suggest that the age-related attenuation of reaching adaption primarily reflects reduced availability or use of explicit strategies.

Although we determined an overall detrimental age effect on reaching adaptation, motivational modulation of motor learning was found to be stable across both age groups. In particular error-based reward boosted learning during acquisition, while punishment was less efficient. Young and older adults equivalently showed faster learning rates with rewarding feedback than with neutral feedback. The final adaptive state as measured by reaching direction at the end of the adaptation block varied between the feedback conditions in older adults, but not in young adults. Older adults showed larger adaptive shifts with rewarding feedback. Also punishing feedback

tended to have a positive effect, though significance was failed. We speculate that in young adults motivational modulation was obscured at the end of the adaptation block because their adaptive shifts in reaching direction then were close to complete, resulting in a ceiling phenomenon. Indeed, our paradigm seemed to trigger especially high learning rates in young adults when compared with previous studies using similar visuomotor rotations by 30°. In the neutral condition we determined an average learning rate of 0.16 for young adults, whereas e.g. in the study of Galea and colleagues (2015) a learning rate of about 0.06 was described. Thus, by the end of the adaptation block the additional beneficial impact of motivational feedback was probably limited. In summary, our findings supported a significant boost of motor learning induced by rewarding feedback. This motivational modulation is preserved across the adult life span and qualifies as a potentially compensating mechanism for age-related functional decline.

Beneficial effects of reward on motor learning are congruent with recently accumulating evidence showing increased learning rates when rewarding feedback is provided (Kojima & Soetedjo, 2017; Nikooyan & Ahmed, 2015). Even in participant groups with presumably reduced processing resources, i.e. stroke patients, reward was found to enhance adaptive processes (Quattrocchi et al., 2017). However, our findings on punishment effects on reaching adaptation deviate from previous reports. Galea and colleagues (2015) as well as Quatttrocchi and colleagues (2017) determined significant beneficial effects of punishing feedback during adaptation in a reaching task. The absence of an equivalent effect in our study might be explained by procedural details. It has been speculated that the observed punishment effects were driven by loss avoidance. However, actual loss avoidance is strongly shaped by contextual parameters (Palminteri, Khamassi, Joffily, & Coricelli, 2015; Sternad & Körding, 2015). In our procedure, participants assigned to the punishment condition started with an initial credit of 1200 points which was reduced by losses and converted to money only by the end of the experiment. Either the magnitude of the initial credit or the rather abstract concept of points might have buffered loss avoidance. In the previous studies, initial credit was immediately provided in concrete units of money, i.e. 12 and 50 £, respectively. Thus, we tentatively assume that the operationalization of punishment feedback constrained its functional efficiency.

In our experimental procedure, the adaptation block was followed by a block in which participants did not receive any feedback on their reaching trajectories. Thus, we were able to explore errorless retention in both adult age groups and in particular in the different motivational

feedback conditions. Our data showed an intriguing interaction effect between age group and motivational feedback. Corroborating previous results we found no main effect of age group on retention rates (e.g Bock, 2005; Hegele & Heuer, 2013; Heuer & Hegele, 2008b, 2008a). However, while motivational feedback during learning was detrimental to retention in young adults, *older adults' retention performance did not vary across motivational conditions.*

The results for the young adults provided further support that beneficial effects of motivational feedback during adaptation do not necessarily transfer to retention (compare Galea at al., 2015; Steel, Silson, Stagg, & Baker, 2016). In addition, a detrimental effect on performance might be triggered by withdrawal of extrinsic incentives so that intrinsic motivation is reduced (for review see Deci, Koestner, & Ryan, 1999). Galea and colleagues (2015) indeed found that a beneficial effect of punishment during adaptation disappeared during following retention, whereas reward only became efficient for retention. They interpreted this pattern as evidence for independent mechanisms driving learning and retention in reaching adaptation. *We did not replicate the positive effect of reward on retention; in contrast our results showed that in particular reward was detrimental to retention rates. However, since efficiency of reward and punishment we found during adaptation substantially deviated from the previous study, we refrain from direct comparison and suggest that a more elaborated clarification is needed.*

Discrepant effects of motivational feedback for both age groups might indicate that motivational feedback modulates differential adaptation components in young and older adults. Körding, Tenenbaum, and Shadmer (2007) proposed that sensorimotor adaptation can be modeled as a combination of fast and slow processes. Fast processes are supposed to drive rapid adaptive changes which are prone to rapid decay when visuomotor feedback is withdrawn. Slow processes, in contrast, contribute to adaptation and decay only slowly (Ethier, Zee, & Shadmehr, 2008). We suggest that the distinction between explicit and implicit components involved in adaptation can be linked to the distinction between fast and slow processes, respectively (compare Huang et al., 2017). It can be supposed that adaptation primarily driven by explicit strategies decays faster, whereas contributions of implicit components result in movement shifts more robust to decay. Given this pattern we speculate that motivational feedback in particular boosts explicit adaptation components in young adults, resulting in more pronounced decay. In contrast, in older adults the availability and use of explicit strategies during reaching adaptation have been shown to be reduced (Hegele & Heuer, 2010a; Heuer et al., 2011). Thus, in this age group motivational

feedback might primarily act on implicit adaptation components that decay slowly and stabilize retention. Since we did not assess the differential contributions of explicit and implicit components directly in our study, this link has to remain speculative, but points to a highly relevant dissociation that could underlie observed age effects.

Readaptation to the previously experienced visuomotor rotation was subject to significant age effects, but modulation by motivational feedback failed to reach significance. Older adults showed again lower learning rates and benefitted less from repeated learning as indicated by savings. Savings represent the ability of initial learning to enhance later relearning (Smith et al., 2006). Although both implicit and explicit processes are involved in readaptation, explicit processes, e.g. recognition of the previously experienced rotation, can be assumed to play a dominant role. Thus, our results for readaptation appear consistent with the age-related vulnerability of explicit, strategic mechanisms contributing to adaptation. Descriptive inspection of our data supported persistence of the beneficial effects of reward on learning in both age groups. Also punishment absolutely enhanced learning rates and savings during readaptation. Even though these observed effects were not statistically significant and therefore elude authoritative conclusions, overall the beneficial trend of motivational feedback agrees with previous findings (Galea et al., 2015; Quattrocchi et al., 2017).

There was no evidence that within each age group motivational feedback affected response or movement times. It has been recently suggested that the use of explicit strategies during adaptation is associated with increasing latencies (Benson, Anguera, & Seidler, 2011; Fernandez-Ruiz, Wong, Armstrong, & Flanagan, 2011; Sülzenbrück & Heuer, 2012). Thus, varying latencies across the different feedback conditions could indicate differential contributions of implicit and explicit adaptation components. Since slowing represents a core primitive of functional changes with increasing age (Salthouse, 1996), a comparison of latency differences between age groups did not allow for specific conclusions. Most importantly, neither in the young nor in the older adult group motivational effects on learning parameters were linked to motivational feedback. We propose that motivational feedback does not substantially shift the balance between explicit and implicit components contributing to adaptation, but affects the components that are particularly efficient in the specific age group, i.e. explicit components in young adults and implicit components in older adults.

Several neuronal substrates have been suggested to functionally contribute to motor learning. Candidate structures in particular include the cerebellum and the motor cortex (see e.g. Krakauer et al., 2004; Li, Padoa-Schioppa, & Bizzi, 2001). There is evidence that the cerebellum contributes to error-based learning, whereas cortical areas are crucial for retention of motor adaptation (Galea, Vazquez, Pasricha, Orban de Xivry, & Celnik, 2011; Hadipour-Niktarash, Lee, Desmond, & Shadmehr, 2007; Orban de Xivry, Criscimagna-Hemminger, & Shadmehr, 2011). Aging is supposed to negatively affect both processes since cortical as well as cerebellar structures are subject to pronounced age-related decline (Jernigan et al., 2001; Raz et al., 2005; Sowell et al., 2003). However, differential contributions to reduced motor learning capacities during aging appear far from conclusive. For example, impaired use of explicit learning strategies has been identified as characteristic of age effects on motor learning. At the same time, this capacity has been found preserved in cerebellar patients (Taylor, Klemfuss, & Ivry, 2010). Consistent with previous findings, our results indicate detrimental age effects on learning as well as retention during reaching adaptation, but specific underlying neuronal substrates remain ambiguous. Motivational modulation of motor learning is critically conveyed by dopamine (Hosp & Luft, 2013; Montague et al., 2004). Although dopaminergic transmission is known to decline with increasing age (for review see Bäckman et al., 2010), our results provided evidence for preserved motivational modulation of reaching adaptation. They further emphasized that robust behavioral resources can be available despite significant physiological changes during healthy aging. Age-related pathological processes, though, might challenge these resources.

To conclude, our study provides evidence that motivational modulation of reaching adaptation is preserved during healthy aging. Although older adults showed reduced motor learning capacities and typical slowing effects, they substantially benefitted from motivational incentives during learning. Most importantly, this benefit applied to learning as well as retention of adaptive shifts. We suggest that motivational feedback can be used as a potentially compensatory mechanism during functional aging. Although our data corroborate a persistent age-related decline in visuomotor plasticity, motivational feedback attenuates performance differences. Our findings further emphasize the complexity of processes that contribute to motor adaptation (compare also Krakauer & Mazzoni, 2011). There is a need to disentangle these processes in order to evaluate their behavioral significance, in particular in populations that face functional challenges.

References

Bäckman, L., Lindenberger, U., Li, S.-C., & Nyberg, L. (2010). Linking cognitive aging to alterations in dopamine neurotransmitter functioning: recent data and future avenues. *Neuroscience and Biobehavioral Reviews*, *34*(5), 670–677. https://doi.org/10.1016/j.neubiorev.2009.12.008

Baltes, P. B., Staudinger, U. M., & Lindenberger, U. (1999). Lifespan psychology: theory and application to intellectual functioning. *Annual Review of Psychology*, *50*, 471–507. https://doi.org/10.1146/annurev.psych.50.1.471

Bauer, A. S., Timpe, J., Edmonds, E. C., Bechara, A., Tranel, D., & Denburg, N. L. (2013). Myopia for the future or hypersensitivity to reward? Age-related changes in decision making on the Iowa Gambling Task. *Emotion*, *13*(1), 19–24. https://doi.org/10.1037/a0029970

Benson, B. L., Anguera, J. A., & Seidler, R. D. (2011). A spatial explicit strategy reduces error but interferes with sensorimotor adaptation. *Journal of Neurophysiology*, *105*(6), 2843–2851. https://doi.org/10.1152/jn.00002.2011

Berens, P. (2009). CircSat: A MATLAB Toolbox for circular statistics. *Journal of Statistical Software*, *31*(10).

Bock, O., & Schneider, S. (2001). Acquisition of a sensorimotor skill in younger and older adults. *Acta Physiologica Et Pharmacologica Bulgarica*, *26*(1-2), 89–92.

Bock, O. (2005). Components of sensorimotor adaptation in young and elderly subjects. *Experimental Brain Research*, *160*(2), 259–263. https://doi.org/10.1007/s00221-004-2133-5

Bock, O., & Girgenrath, M. (2006). Relationship between sensorimotor adaptation and cognitive functions in younger and older subjects. *Experimental Brain Research*, *169*(3), 400–406. https://doi.org/10.1007/s00221-005-0153-4

Bock, O., & Schneider, S. (2002). Sensorimotor adaptation in young and elderly humans. *Neuroscience and Biobehavioral Reviews*, *26*(7), 761–767.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436. https://doi.org/10.1163/156856897X00357

Brown, S. B. R. E., & Ridderinkhof, K. R. (2009). Aging and the neuroeconomics of decision making: A review. *Cognitive, Affective & Behavioral Neuroscience*, *9*(4), 365–379. https://doi.org/10.3758/CABN.9.4.365

Buch, E. R., Young, S., & Contreras-Vidal, J. L. (2003). Visuomotor adaptation in normal aging. *Learning & Memory*, *10*(1), 55–63. https://doi.org/10.1101/lm.50303

Cressman, E. K., Salomonczyk, D., & Henriques, D.Y.P. (2010). Visuomotor adaptation and proprioceptive recalibration in older adults. *Experimental Brain Research*, *205*(4), 533–544. https://doi.org/10.1007/s00221-010-2392-2

Deci, E. L., Koestner, R., & Ryan, R. M. (1999). A meta-analytic review of experiments examining the effects of extrinsic rewards on intrinsic motivation. *Psychological Bulletin*, *125*(6), 627–668. https://doi.org/10.1037//0033-2909.125.6.627

Diedrichsen, J., & Kornysheva, K. (2015). Motor skill learning between selection and execution. *Trends in Cognitive Sciences*, *19*(4), 227–233. https://doi.org/10.1016/j.tics.2015.02.003

Eppinger, B., Hämmerer, D., & Li, S.-C. (2011). Neuromodulation of reward-based learning and decision making in human aging. *Annals of the New York Academy of Sciences*, *1235*, 1–17. https://doi.org/10.1111/j.1749-6632.2011.06230.x

Eppinger, B., Schuck, N. W., Nystrom, L. E., & Cohen, J. D. (2013). Reduced striatal responses to reward prediction errors in older compared with younger adults. *Journal of Neuroscience*, *33*(24), 9905–9912. https://doi.org/10.1523/JNEUROSCI.2942-12.2013

Ernst, M., & Fudge, J. L. (2009). A developmental neurobiological model of motivated behavior: Anatomy, connectivity and ontogeny of the triadic nodes. *Neuroscience and Biobehavioral Reviews*, *33*(3), 367–382. https://doi.org/10.1016/j.neubiorev.2008.10.009

Ethier, V., Zee, D. S., & Shadmehr, R. (2008). Spontaneous recovery of motor memory during saccade adaptation. *Journal of Neurophysiology*, *99*(5), 2577–2583. https://doi.org/10.1152/jn.00015.2008

Fernandez-Ruiz, J., Wong, W., Armstrong, I. T., & Flanagan, J. R. (2011). Relation between reaction time and reach errors during visuomotor adaptation. *Behavioural Brain Research*, *219*(1), 8–14. https://doi.org/10.1016/j.bbr.2010.11.060

Galea, J. M., Mallia, E., Rothwell, J., & Diedrichsen, J. (2015). The dissociable effects of punishment and reward on motor learning. *Nature Neuroscience*, *18*(4), 597–602. https://doi.org/10.1038/nn.3956

Galea, J. M., Vazquez, A., Pasricha, N., Orban de Xivry, J.-J., & Celnik, P. (2011). Dissociating the roles of the cerebellum and motor cortex during adaptive learning: The motor cortex retains what the cerebellum learns. *Cerebral Cortex*, *21*(8), 1761–1770. https://doi.org/10.1093/cercor/bhq246

Hadipour-Niktarash, A., Lee, C. K., Desmond, J. E., & Shadmehr, R. (2007). Impairment of retention but not acquisition of a visuomotor skill through time-dependent disruption of primary motor cortex. *Journal of Neuroscience*, *27*(49), 13413–13419. https://doi.org/10.1523/JNEUROSCI.2570-07.2007

Hasher, L., & Zacks, R. T. (1988). Working memory, comprehension, and aging: A review and a new view. In G. H. Bower (Ed.), *Psychology of learning and motivation* (pp. 193–225). Academic Press. https://doi.org/10.1016/S0079-7421(08)60041-9

Hegele, M., & Heuer, H. (2010a). The impact of augmented information on visuo-motor adaptation in younger and older adults. *PloS One*, *5*(8), e12071. https://doi.org/10.1371/journal.pone.0012071

Hegele, M., & Heuer, H. (2010b). Implicit and explicit components of dual adaptation to visuomotor rotations. *Consciousness and Cognition*, *19*(4), 906–917. https://doi.org/10.1016/j.concog.2010.05.005

Hegele, M., & Heuer, H. (2010c). Adaptation to a direction-dependent visuomotor gain in the young and elderly. *Psychological Research*, *74*(1), 21–34. https://doi.org/10.1007/s00426-008-0221-z

Hegele, M., & Heuer, H. (2013). Age-related variations of visuomotor adaptation result from both the acquisition and the application of explicit knowledge. *Psychology and Aging*, *28*(2), 333–339. https://doi.org/10.1037/a0031914

Heuer, H., & Hegele, M. (2008a). Adaptation to visuomotor rotations in younger and older adults. *Psychology and Aging*, *23*(1), 190–202. https://doi.org/10.1037/0882-7974.23.1.190

Heuer, H., & Hegele, M. (2008b). Adaptation to direction-dependent visuo-motor rotations and its decay in younger and older adults. *Acta Psychologica*, *127*(2), 369–381. https://doi.org/10.1016/j.actpsy.2007.07.006

Heuer, H., & Hegele, M. (2009). Adjustment to a complex visuo-motor transformation at early and late working age. *Ergonomics*, *52*(9), 1039–1054. https://doi.org/10.1080/00140130902912795

Heuer, H., & Hegele, M. (2011). Generalization of implicit and explicit adjustments to visuomotor rotations across the workspace in younger and older adults. *Journal of Neurophysiology*, *106*(4), 2078–2085. https://doi.org/10.1152/jn.00043.2011

Heuer, H., & Hegele, M. (2014). Age-related variations of visuo-motor adaptation beyond explicit knowledge. *Frontiers in Aging Neuroscience*, *6*, 152. https://doi.org/10.3389/fnagi.2014.00152

Heuer, H., Hegele, M., & Sülzenbrück, S. (2011). Implicit and explicit adjustments to extrinsic visuo-motor transformations and their age-related changes. *Human Movement Science*, *30*(5), 916–930. https://doi.org/10.1016/j.humov.2010.07.004

Hosp, J. A., & Luft, A. R. (2013). Dopaminergic meso-cortical projections to m1: Role in motor learning and motor cortex plasticity. *Frontiers in Neurology*, *4*, 145. https://doi.org/10.3389/fneur.2013.00145

Howard, I. S., Ingram, J. N., & Wolpert, D. M. (2009). A modular planar robotic manipulandum with end-point torque control. *Journal of Neuroscience Methods*, *181*(2), 199–211. https://doi.org/10.1016/j.jneumeth.2009.05.005

Huang, J., Gegenfurtner, K. R., Schütz, A. C., & Billino, J. (2017). Age effects on saccadic adaptation: Evidence from different paradigms reveals specific vulnerabilities. *Journal of Vision*, *17*(6), 9. https://doi.org/10.1167/17.6.9

Jernigan, T. L., Archibald, S. L., Fennema-Notestine, C., Gamst, A. C., Stout, J. C., Bonner, J., & Hesselink, J. R. (2001). Effects of age on tissues and regions of the cerebrum and cerebellum. *Neurobiology of Aging*, *22*(4), 581–594. https://doi.org/10.1016/S0197-4580(01)00217-2

Jones, S., Nyberg, L., Sandblom, J., Stigsdotter Neely, A., Ingvar, M., Magnus Petersson, K., & Backman, L. (2006). Cognitive and neural plasticity in aging: general and task-specific limitations. *Neuroscience and Biobehavioral Reviews*, *30*(6), 864–871. https://doi.org/10.1016/j.neubiorev.2006.06.012

Kojima, Y., & Soetedjo, R. (2017). Selective reward affects the rate of saccade adaptation. *Neuroscience*, *355*, 113–125. https://doi.org/10.1016/j.neuroscience.2017.04.048

Körding, K. P., Tenenbaum, J. B., & Shadmehr, R. (2007). The dynamics of memory as a consequence of optimal adaptation to a changing body. *Nature Neuroscience*, *10*(6), 779–786. https://doi.org/10.1038/nn1901

Krakauer, J. W. (2009). Motor learning and consolidation: the case of visuomotor rotation. *Advances in Experimental Medicine and Biology*, *629*.

Krakauer, J. W., Ghilardi, M.-F., Mentis, M., Barnes, A., Veytsman, M., Eidelberg, D., & Ghez, C. (2004). Differential cortical and subcortical activations in learning rotations and gains for reaching: A PET study. *Journal of Neurophysiology*, *91*(2), 924–933. https://doi.org/10.1152/jn.00675.2003

Krakauer, J. W., & Mazzoni, P. (2011). Human sensorimotor learning: Adaptation, skill, and beyond. *Current Opinion in Neurobiology*, *21*(4), 636–644. https://doi.org/10.1016/j.conb.2011.06.012

Krakauer, J. W., Pine, Z. M., Ghilardi, M.-F., & Ghez, C. (2000). Learning of Visuomotor Transformations for Vectorial Planning of Reaching Trajectories. *Journal of Neuroscience*, *20*(23), 8916–8924. https://doi.org/10.1523/JNEUROSCI.20-23-08916.2000

Li, C.-S. R., Padoa-Schioppa, C., & Bizzi, E. (2001). Neuronal Correlates of Motor Performance and Motor Learning in the Primary Motor Cortex of Monkeys Adapting to an External Force Field. *Neuron*, *30*(2), 593–607. https://doi.org/10.1016/S0896-6273(01)00301-4

Mata, R., Josef, A. K., Samanez-Larkin, G. R., & Hertwig, R. (2011). Age differences in risky choice: A meta-analysis. *Annals of the New York Academy of Sciences*, *1235*, 18–29. https://doi.org/10.1111/j.1749-6632.2011.06200.x

Mazzoni, P., & Krakauer, J. W. (2006). An implicit plan overrides an explicit strategy during visuomotor adaptation. *Journal of Neuroscience*, *26*(14), 3642–3645. https://doi.org/10.1523/JNEUROSCI.5317-05.2006

Montague, P. R., Hyman, S. E., & Cohen, J. D. (2004). Computational roles for dopamine in behavioural control. *Nature*, *431*, 760–767.

Nikooyan, A. A., & Ahmed, A. A. (2015). Reward feedback accelerates motor learning. *Journal of Neurophysiology*, *113*(2), 633–646. https://doi.org/10.1152/jn.00032.2014

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*(1), 97–113. https://doi.org/10.1016/0028-3932(71)90067-4

Orban de Xivry, J.-J., Criscimagna-Hemminger, S. E., & Shadmehr, R. (2011). Contributions of the motor cortex to adaptive control of reaching depend on the perturbation schedule. *Cerebral Cortex*, *21*(7), 1475–1484. https://doi.org/10.1093/cercor/bhq192

Palminteri, S., Khamassi, M., Joffily, M., & Coricelli, G. (2015). Contextual modulation of value signals in reward and punishment learning. *Nature Communications*, *6*, 8096. https://doi.org/10.1038/ncomms9096

Park, D. C., & Reuter-Lorenz, P. (2009). The adaptive brain: aging and neurocognitive scaffolding. *Annual Review of Psychology*, *60*, 173–196. https://doi.org/10.1146/annurev.psych.59.103006.093656

Quattrocchi, G., Greenwood, R., Rothwell, J. C., Galea, J. M., & Bestmann, S. (2017). Reward and punishment enhance motor adaptation in stroke. *Journal of Neurology, Neurosurgery, and Psychiatry*, *88*(9), 730–736. https://doi.org/10.1136/jnnp-2016-314728

Raz, N., Lindenberger, U., Rodrigue, K. M., Kennedy, K. M., Head, D., Williamson, A., . . . Acker, J. D. (2005). Regional brain changes in aging healthy adults: general trends, individual differences and modifiers. *Cerebral Cortex*, *15*(11), 1676–1689. https://doi.org/10.1093/cercor/bhi044

Sala-Llonch, R., Bartrés-Faz, D., & Junqué, C. (2015). Reorganization of brain networks in aging: A review of functional connectivity studies. *Frontiers in Psychology*, *6*, 663. https://doi.org/10.3389/fpsyg.2015.00663

Salthouse, T. A. (1996). The processing-speed theory of adult age differences in cognition. *Psychological Review*, *103*(3), 403–428. https://doi.org/10.1037/0033-295X.103.3.403

Samanez-Larkin, G. R., & Knutson, B. (2015). Decision making in the ageing brain: Changes in affective and motivational circuits. *Nature Reviews Neuroscience*, *16*(5), 278–289. https://doi.org/10.1038/nrn3917

Schmidt, R. A., & Lee, T. D. (2011). *Motor control and learning: A behavioral emphasis* (5th ed.). Champaign, Ill., Leeds: Human Kinetics.

Seidler, R. D. (2006). Differential effects of age on sequence learning and sensorimotor adaptation. *Brain Research Bulletin*, *70*(4-6), 337–346. https://doi.org/10.1016/j.brainresbull.2006.06.008

Smith, M. A., Ghazizadeh, A., & Shadmehr, R. (2006). Interacting adaptive processes with different timescales underlie short-term motor learning. *PLoS Biology*, *4*(6), e179. https://doi.org/10.1371/journal.pbio.0040179

Sowell, E. R., Peterson, B. S., Thompson, P. M., Welcome, S. E., Henkenius, A. L., & Toga, A. W. (2003). Mapping cortical change across the human life span. *Nature Neuroscience*, *6*(3), 309–315. https://doi.org/10.1038/nn1008

Sternad, D. (2018). It's Not (Only) the Mean that Matters: Variability, Noise and Exploration in Skill Learning. *Current Opinion in Behavioral Sciences*, *20*, 183–195. https://doi.org/10.1016/j.cobeha.2018.01.004

Sternad, D., & Körding, K. P. (2015). Carrot or stick in motor learning. *Nature Neuroscience*, *18*(4), 480–481.

Sülzenbrück, S., & Heuer, H. (2012). Enhanced mechanical transparency during practice impedes open-loop control of a complex tool. *Experimental Brain Research*, *218*(2), 283–294. https://doi.org/10.1007/s00221-012-3011-1

Taylor, J. A., Klemfuss, N. M., & Ivry, R. B. (2010). An explicit strategy prevails when the cerebellum fails to compute movement errors. *Cerebellum (London, England)*, *9*(4), 580–586. https://doi.org/10.1007/s12311-010-0201-x

Taylor, J. A., Krakauer, J. W., & Ivry, R. B. (2014). Explicit and implicit contributions to learning in a sensorimotor adaptation task. *Journal of Neuroscience*, *34*(8), 3023–3032. https://doi.org/10.1523/JNEUROSCI.3619-13.2014

Van den Bos, W., & Eppinger, B. (2016). Developing developmental cognitive neuroscience: From agenda setting to hypothesis testing. *Developmental Cognitive Neuroscience*, *17*, 138–144. https://doi.org/10.1016/j.dcn.2015.12.011

Van der Kooij, K., & Overvliet, K. E. (2016). Rewarding imperfect motor performance reduces adaptive changes. *Experimental Brain Research*, *234*(6), 1441–1450. https://doi.org/10.1007/s00221-015-4540-1

West, R. L. (1996). An application of prefrontal cortex function theory to cognitive aging. *Psychological Bulletin*, *120*(2), 272–292. https://doi.org/10.1037/0033-2909.120.2.272

Wolpert, D. M., Diedrichsen, J., & Flanagan, J. R. (2011). Principles of sensorimotor learning. *Nature Reviews Neuroscience*, *12*(12), 739–751. https://doi.org/10.1038/nrn3112

World Medical Association. (2013). Declaration of Helsinki: ethical principles for medical research involving human subjects. *JAMA*, *310*(20), 2191–2194. https://doi.org/10.1001/jama.2013.281053

Chapter 4: Age effects on integration of salience and value in saccadic control

Manuscript is in preparation

Abstract

Saccadic control has been shown to depend on both salience and value and the integration of them is dynamic. Saccades with long latency are more remarkably influenced by value whereas saccades with short latency are mainly determined by target salience. This integration could be challenged by healthy aging because of its well-documented association with slower saccade latency as well as declines in value representation. To investigate how these processes impact the integration, we explored the trade-off between salience and expected value in young and senior adults by asking them to make saccades to target patches with subregions differing in salience and associated reward. We determined a significant interaction between value manipulation and age group on saccade direction with equivalent reward effects in two groups but weaker penalty effects in senior group. When respecting with saccade latency, reward triggers an average latency decrease in senior adults but not in young adults. These differential reward effects on saccade direction and latency are also reflected by the less dependence of saccade direction on latency although the dependence exists in both groups. We suggest that the less dependency might result from the facilitated top-down modulation by the general slower response in senior adults.

Key words: neuroeconomics, decision-making, cue combination, visual perception, aging

Introduction

As a window of cognition, decision making is an action based on information and values related to potential outcomes (Shadlen & Kiani, 2013), accuracy of which is challenged by age-related declines in cognitive abilities (for review see Mata, Josef, & Lemaire, 2015). However, results of how ageing influences decision making vary substantially depending largely on tasks and mythologies (McGovern et al., 2017), calling more studies to tap into specific processes to elucidate its influences.

As a kind of motor decision making, saccadic eye movement has been studied for decades and is a good way to investigate decision making (Glimcher, 2003; Gold & Shadlen, 2007). It is found to be determined not only by visual-stimulus-based bottom-up processing, such as luminance (Schütz, Braun, & Gegenfurtner, 2011), but also by top-down processing, such as task demands (Johansson et al., 2001; Jovancevic-Misic & Hayhoe, 2009; Land, 2006; Schütz, Kerzel, & Souto, 2014; Schütz & Souto, 2015; Williams, 1996) and reward (Ikeda & Hikosaka, 2003, McCoy & Theeuwes, 2016). We tapped into implicit processing and explicit processing with different paradigms for saccadic eye movements and found specific stability and vulnerability associated with aging (Huang et al., 2017).

The weighting of different information can to some degree predict saccadic eye movements (Itti & Koch, 2001; Tatler et al., 2011). Navalpakkam and colleagues (2010) even found that this integration of information is to reach the goal of expected reward but not the most valuable or the easiest achievable goal. However, only information available before saccade execution is taken into account (Caspi, Beutter & Eckstein, 2004). As such, when top-down processing, such as reward competes with bottom-up processing, such as salience, saccades go to which object or which part of one single object depends on saccade latency, i.e., when saccades are executed. For example, Markowitz and colleagues (2011) found that saccade ending positions of monkey observers are dominated by salience if they are made before the switch time (140-180 ms after target onset); they are dominated by value if they are made after the switch period. Furthermore, with varying luminance of different parts of one single object we found that the integration of salience and value information is dynamic and most observers could learn to use strategies to make optical saccades to position with expected reward (Schütz, Trommershäuser, & Gegenfurtner, 2012).

Not only saccade ending-position is influenced by reward, but also is saccade latency (Bucker et al., 2015; Stankevich & Geng, 2015). On one hand, this influence could be executed through low-level processing (Dunne, Ellison, & Smith, 2015; Watanabe, Lauwereyns, & Hikosaka, 2003). For example, Dunne, Ellison and Smith (2015) found that saccades to the rewarded hemisphere are faster than that to the unrewarded hemisphere in a simple stimulus-driven saccade task. This reward speeding up effect is specific to rewarded hemisphere and dose not transfer to unrewarded hemisphere in saccadic peripheral cuing task and oculomotor inhibition of return task, suggesting it is executed through reducing the distance between baseline and execution threshold rather than evidence accumulating rate. On the other hand, this influence could also be executed through top-down control (Heuer et al., 2017; Milstein & Dorris, 2007; Theeuwes & Belopolsky, 2012; Wolf et al., 2017). For example, Milstein and Dorris (2007) found that saccade latency does not simply decrease with the increase of magnitude and probability of reward, but rather decreases with expected reward, i.e., the combination of magnitude and probability. Furthermore, Wolf and colleagues (2017) found that reward effects on saccade latency are influenced by the necessity, uncertainty of outcome and task difficulty. The integration of low-level influence and top-down influence could yield no overall changes in average saccade latency (Leon & Shadlen, 1999; Platt & Glimcher, 1999) and the integration can also be dynamic (Schütz, Trommershäuser, & Gegenfurtner, 2012). For example, reward speeds up the salience-dominated short-latency saccades overall while slows down the value-dominated long-latency saccades overall (Schütz, Trommershäuser, & Gegenfurtner, 2012).

The dynamic integration of information of salience and value could be changed by healthy aging. On one hand, this integration would be less influential by value since senior adults are found to have impairments in representation of expected reward value (Eppinger, Hämmerer, & Li, 2011; Chowdhury et al., 2013). Since the optical saccades towards positions with expected reward needs strategies (Schütz, Trommershäuser, & Gegenfurtner, 2012), they would also be challenged by aging because senior's performance is always found to be worse in cognitive tasks or strategy demanding tasks (Mata, von Helversen, & Rieskamp, 2010). Even their performance is as suboptimal as to young adults, their strategies are different (Valsecchi, Billino, & Gegenfurtner, 2018), which might also change the integration or saccade making. On the other hand, the integration in senior adults could be facilitated in nature saccades because they have general

slower response and longer saccade latency (Huang et al., 2017; Munoz et al., 1998; Peltsch et al., 2011) so that more top-down information is available when their saccades are executed.

Taken together, how aging changes these processes is unknown and has not been explored together before. In current study, to investigate this question we used the paradigm we created before (Schütz, Trommershäuser, & Gegenfurtner, 2012), in which salience was manipulated by varying contrasts of different regions of target and value was manipulated in different blocks through administering nothing, reward and reward and penalty.

Methods

Participants

Twenty-one young adults aging from 22 to 39 years old (mean = 30.0; SD = 4.6; Female = 13) and 20 senior adults aging from 62 to 81 years old (mean = 69.7; SD = 4.7; Female = 7) participated in our experiment. As the same as participants in our other studies (Huang et al, 2017; Huang, Hegele, & Billino, submitted ; Valsecchi, Billino, & Gegenfurtner, 2018), all participants in this study were naïve to the purpose of the study and were paid volunteers from our battery database, in which all the participants were recruited from local residence by calls or in local newspapers. They were screened by a battery of standard cognitive tasks and a detailed interview protocol to make sure they did not have any history of ophthalmologic, neurologic, psychiatric disorders or medications interfering with perceptual capacities. Visual acuity was measured binocularly confirming normal or corrected-to-normal for all participants. Agreeing with the Declaration of Helsinki (World Medical Association, 2013), methods and procedures were approved by the local ethics committee. All participants gave their informed consent and their data was protected by privacy.

Stimuli and procedure

Participants were seated in a dimly lit room with their forehead rested on a chin in front of a 22-inch monitor with a resolution of 1680 x 1050 at a refreshing rate of 120 Hz. For each trial, they were asked to fixated at the center bull's eye first (0.15 deg v.a. x 0.3deg v.a.) for 500 ms and then make a saccade to the target which appeared 200 ms after the bull offset and was presented for 500 ms. The saccade targets were patches with a generalized Gaussian envelope with a power
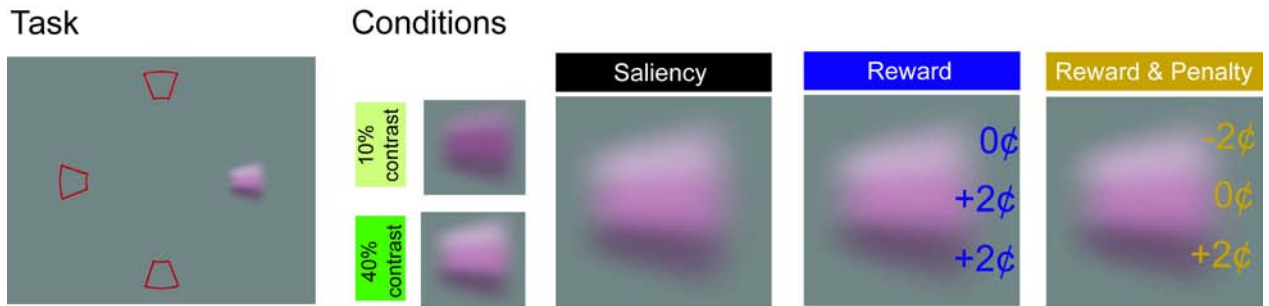
of 4 in the radial (r) and angular (α) dimension (Eq. 1)

$$Luminiance(r, \alpha) = \frac{1}{2\pi\sigma_r\sigma_\alpha e^{-0.5\left[\left(\frac{r-\mu_r}{\sigma_r}\right)^4 + \left(\frac{\alpha-\mu_\alpha}{\sigma_\alpha}\right)^4\right]}}$$ [1]

in which the mean radial $\mu_r = 6.5$ deg v.a ; standard deviation of radial $\sigma_r = 2$ deg v.a.; mean angular $\mu_\alpha = \pm 8°$; standard deviation of angular $\sigma_\alpha = 8°$. The contrast of each patch was either 10% (low contrast) or 40% (high contrast). The center of the configured patches could be presented at one of the four cardinal axes, and the clockwise or counterclockwise arrangement of dark and light patches was randomized (Fig.1).

To manipulate the value effect, the experiment was divided into 3 value conditions, Salience (192 trials), Reward (288 trials), and Reward & Penalty (288 trials). A break was following every 96 trials. In trials of Salience condition, luminance of the target could be homogeneous (only one luminance was used) or heterogeneous (two luminance were used yielding the contrast 10% or 40%). Participants were asked to make a saccade from the central fixation to the peripheral target. In trials of Reward condition, all the targets were heterogeneous and participants were told that they would earn 2 cents in each trial if their saccade landed in the dark patch (Fig. 1). In trials of Reward & Penalty condition, all the things were as same as that in Reward trials except participants would lose 2 cents if their saccade landed in the light patch (Fig. 1). All the participants did Salience condition first, then Reward and Reward & Penalty finally. The experiment took about 80 minutes in young and 90 minutes in old adults.

Figure 1. Stimuli and experiment design. A compound patches consisting of 2 different luminance was presented at one of the four cardinal positions. The contrast of the patches could be 10% or 40%. Each participant did Saliency condition first in which saccades were neither rewarded nor penalized; then they did Reward condition in which saccades landing on the dark patch would gain 2 cents each trial; finally they did Reward & Penalty condition in which

saccades landing on the dark patch would gain 2 cents, on the light patch would lose 2 cents each trial.

Eye movements recording and data analysis

During the experiment, participants viewed the display binocularly and movements of their right eye were recording at a sampling rate of 1000 Hz with SR Research Eyelink 1000. Starting and ending of saccade was identified with Eyelink saccade detector.

Primary saccade of each trial was analyzed and all the saccades were rotated as that all the targets were presented at the right size of horizontal axis with the light patch on the top and dark patch on the bottom. As such, positive saccade direction means saccade towards the light region of target; negative saccade direction means saccade towards the dark region of target. Trials were excluded for further analysis if their saccades latency was beyond 80 to 500 ms, if their saccade amplitude was beyond 0.5 to 1.5 target amplitude (6°), if their saccade direction was beyond -30 to 30° or if their fixation was 2° outside horizontal position of presenting fixation or 1° outside vertical position. Since there were no practice trials at the beginning of Reward and Reward & Penalty condition, only trials in the last 2 blocks of these conditions were used for analysis. One young participant was excluded because he had less than 64 trials (one third of total trials) in Salience condition, which made his data noisy. We excluded 24.0 ± 18.86 % of trials on average in young adults and 32.7 ± 14.29 % in senior adults.

Cents each participant earned per trial in Reward and Reward & Penalty condition were calculated by dividing the total number of valid trials from the sum cents they earned in these trials. Two senior adults did not performance appropriately and were excluded because they earned less than 0.58 cents per trial in Reward condition, which were more than 2.09 S.D. away from the group mean (1.18 ± 0.288).

For saccade latency analysis, median mean was used for average across all trials in each condition. To look into the dependence of saccade direction on latency, firstly saccades were split into 6 bins based on their latency for each contrast, each value condition and each individual separately; then trials in each bin were averaged.

To quantify the extent to which saccade direction is dependent on saccade latency and to which it is influenced by contrast, we used multiple regression to fit saccade direction of each trial with 3 dependent variables for Reward and Reward & Penalty condition and each individual separately:

$$Saccade\ direction = \beta_0 + \beta_1 * contrast + \beta_2 * saccade\ latency$$

in which contrast is a virtual variable with setting 0 for trials with 10% contrast and 1 for trials with 40% so that positive estimated β_1 means saccade direction is larger in trials with 40% contrast, i.e., more further to the lighter region of target, which is expected, and negative estimated β_1 means saccade direction is smaller in trials with 40%, i.e., more further to the dark region of target. In the equation, saccade latency is a continuous variable (in ms) and estimated β_2 means how many degrees saccade direction changes when saccade latency changes by 1 ms. Positive estimated β_2 means saccade direction increases (shifting towards the light region of target) when saccade latency increases and negative estimated β_2 means saccade direction decreases (shifting towards the dark region of target) when saccade latency increases. Therefore negative estimated β_2 is expected. Estimated betas were compared with 0 by student T-test to see whether variables predict saccade direction statistically significantly.

For other statistic analysis, data were analyzed using ANOVAs with between-subject factor Age (young, senior) and potential with-in-subject factor Latency (6 bins), Contrast (10%, 40%), Value (Salience, Reward, Reward & penalty). Reward effects were always measured by the difference between Salience condition and Reward condition (Salience VS. Reward); penalty effects were always measured by difference between Reward condition and Reward & Penalty condition (Reward VS. Reward & Penalty). A significance level of α = .05 was used for all statistical analyses.
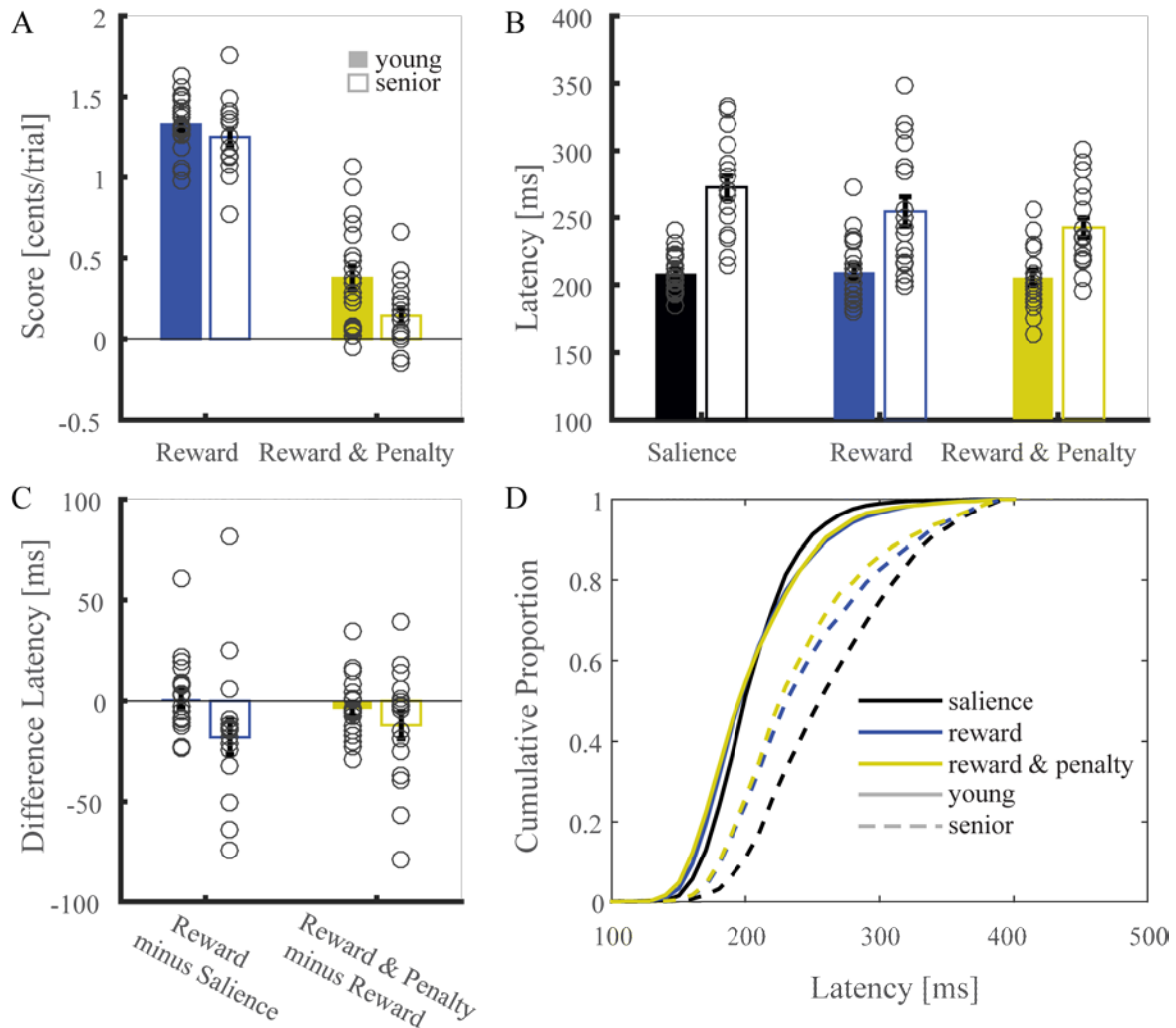
Results

Score

To investigate the influence of reward on saccadic eye movements, we told participants that they would gain 2 cents if their primary saccade landed on the rewarded dark region of target in each trial in Reward condition (Fig.1). We found that this manipulation is significantly and equivalently effective in two age groups: senior adults earned 1.25 ± 0.214 cents per trial on average comparing to 1.33 ± 0.173 gained by young adults (see Fig.2A). These earnings are both

significantly larger than zero (ts > 24.87, ps < .001, ds > 12.06) but do not sig nificantly differ from each other (t(36) = 1.24, p = .224, d = 0.40).

To investigate the influence of penalty on saccadic eye movements, in Reward & Penalty condition we told participants that they would gain 2 cents if their primary saccade landed on the rewarded dark region of target and that they would lose 2 cents if their primary saccade landed on the penalized light region of target (Fig.1). As similar as what we found in the Reward condition, the penalty manipulation is also significantly and equivalently effective in two age groups, supported by a significant main Value effect (F(1, 36) = 504.21, p < .001, η^2 = .93) and nonsignificant Value X Age interaction (F(1, 36) = 2.80, p = .103, η^2 = .07) in the ANOVA analysis with Value (Reward, Reward & Penalty) and Age (Young, Senior) . However, the overall combination of reward and penalty was significantly different between two groups (young: 0.37 ± 0.318; senior: 0.14 ± 0.201; t (36) = 2.64, p = .012, d = 0.87 ; see Fig.2A), yielding a significant Age main effect (F(1, 36) = 6.46, p = .016 , η^2 = .15) in the ANOVA analysis.

Figure 2. Score and saccade latency results. (A) Cents participants earned per trial on average in Reward (blue bars) and Reward & Penalty (yellow bars) condition. Filled bars represent young group and empty bars represent senior group. Error bars represent ±1SEM and dots represent individuals. (B) Saccade latency in Salience (black bars), Reward and Reward & Penalty condition. (C) Difference latency measuring reward (calculated by subtracting latency in Salience from that in Reward condition) and penalty (calculated by subtracting latency in Reward from that in Reward & Penalty condition) effects on saccade latency. (D) Cumulative saccade latency for all the participants of young (solid lines) and senior group (dash lines).

Saccade latency

As illustrated in Fig.2B, senior adults made their primary saccade 256 ± 32.6 ms on average after target appeared, forty-eight ms significantly longer than young adults (208 ± 19.50), supported by the main Age effect ($F(1, 36) = 32.03$, $p < .001$, $\eta^2 = .47$) in the ANOVA analysis with Value

(Salience, Reward, Reward & Penalty) and Age. Reward and penalty impacts latency significantly (main Value effect: $F(2, 72) = 8.15$, $p = .001$, $\eta^2 = .19$) and these impacts differ between two age groups (Value X Age interaction: $F(2, 72) = 5.74$, $p = .005$, $\eta^2 = .14$). This interaction is shown more obviously by difference latency calculated by subtracting latency in Salience and Reward condition from that in Reward and Reward & Penalty condition (see Fig.2C): Latency of senior adults decreases by 18 ± 35.3 ms in Reward condition comparing to that in Salience condition, which is significantly different from zero($t(17) = 2.17$, $p = .04$, $d = 1.05$), and decreases further by 12 ± 28.0 ms in Reward & Penalty condition, which tends to be different from zero ($t(17) = 1.81$, $p = .088$, $d = 0.88$) whereas latency of young adults does not change in Reward condition (1 ± 19.1ms, $t(19) = 0.23$, $p = 0.817$, $d = 0.11$) and decreases slightly in Reward & Penalty (-4 ± 14.8 ms, $t(19) = 1.21$, $p = 0.240$, $d = 0.56$).
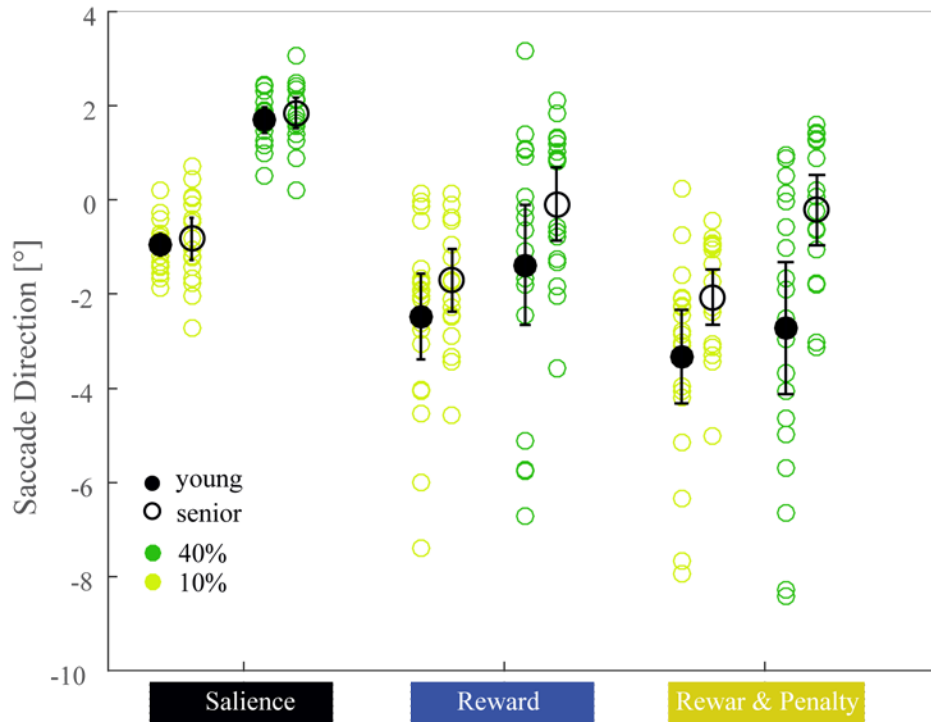
Since it is found that the distribution of saccade latency is more sensitive to reward than average latency (Wolf et al., 2017), we also looked into saccade latency distribution of all the participants together. We found that the decreased average latency in Reward and Reward & Penalty in senior adults is due to a general left-shift of latency (dash lines in Fig. 2D); the slightly or not changed latency in young adults is due to cancellation of increasing frequencies before and after the latency 209 ms in Reward condition (solid blue line in Fig. 2D) and before and after the latency 212 ms in Reward & Penalty condition (solid yellow line in Fig. 2D).

Saccade direction

When participants were asked to make a saccade from a central fixation to the peripheral target without any reward or penalty involved in Salience condition, saccade directions are impacted significantly by contrast (Contrast main effect in the ANOVA analysis with Contrast (10%, 40%) and Age: $F(1,36) = 283.50$, $p < .001$, $\eta^2 = .89$; see Fig.3). However, it is not impacted by age at all: Neither Age main effect nor Age X Contrast interaction is significant (Fs < 0.86, ps $> .361$, η^2s $< .03$).

When the darker region of target was rewarded in Reward condition, saccade ending position shifts towards it substantially, supporting by significant Value main effect ($F(1,36) = 36.62$, $p < .001$, $\eta^2 = .50$) in the ANOVA analysis with Value (Salience, Reward), Contrast and Age. This shift does not differ between two age groups (Value X Age interaction: $F(1,36) = 2.13$, $p = .153$, $\eta^2 = .06$) but it is more pronounced in trials of high contrast (Value X Contrast interaction: $F(1,36)$

= 18.61, p <.001 , η^2 = .34) although the shift is still significant in trials of low contrast (Value main effect in the post-hoc analysis for low contrast condition: F(1,36) = 18.18, p <.001 , η^2 = .34). The interaction between Value and Contrast is similar in two groups (Value X Contrast X Age interaction: F(1,36) = 0.68, p = .417, η^2s = .02).
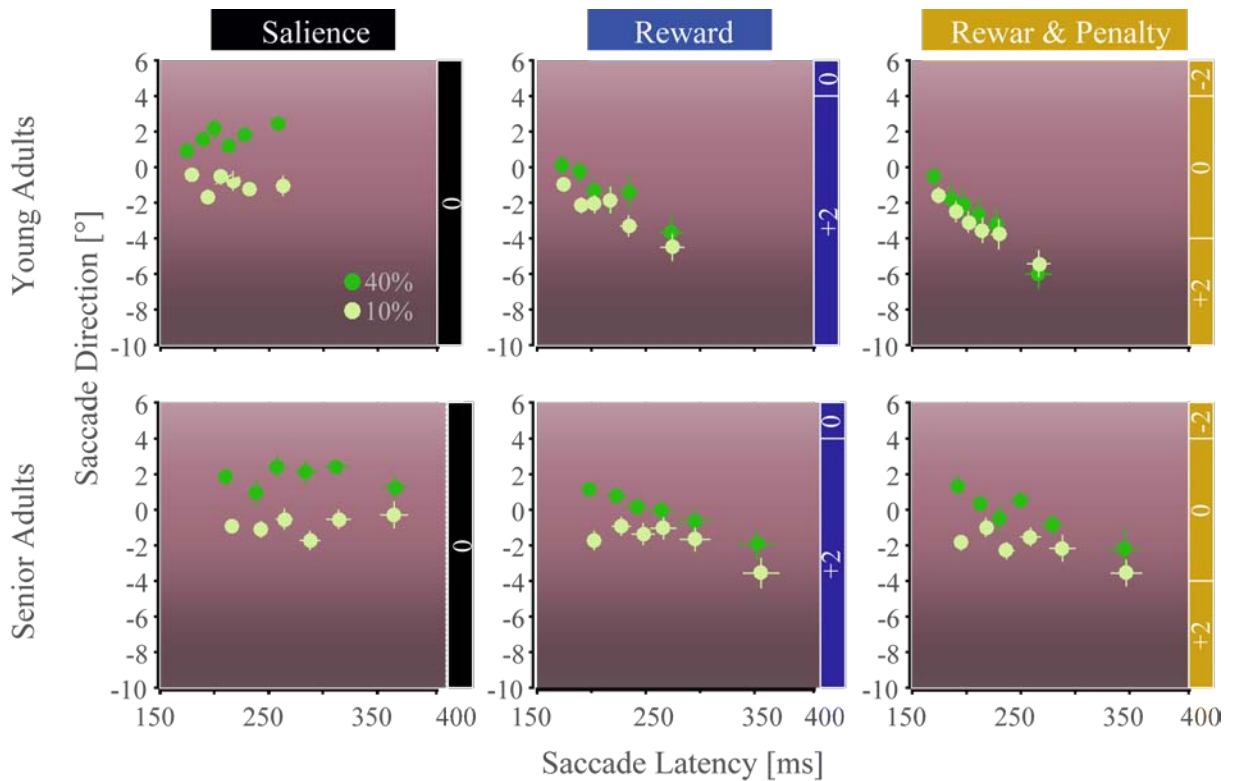

Figure 3. Average saccade direction as a function of value and contrast. Big black dots and error bars represent mean and 95% confidence interval with filled dots representing young group and empty dots senior group. All the small dots represent individuals with dark green representing contrast with 40% and light green contrast of 10%.

When not only the darker region of target was rewarded but also was the lighter region of target was penalized in Reward & Penalty condition, The penalty influences saccade direction significantly (main Value effect in the ANOVA analysis with Value (Reward, Reward & Penalty), Contrast and Age: F(1,36) = 13.65, p =.001 , $\eta2$ = .28). This penalty influence is not impacted by contrast (Value X Contrast interaction: F(1,36) = .15, p = .701 , $\eta2$ < .01), although the difference between 2 contrasts still exists (main Contrast effect: F(1,36) = 42.38, p < .001 , $\eta2$ = .54). However, it is impacted by age (Value X Age interaction: F(1,36) = 5.51, p = .025 , $\eta2$ = .13). Follow-up post-hoc analysis found that the penalty influence is not significant in senior adults (main Value effect: F(1,17) = 1.22, p =.285 , $\eta2$ = .07). The diminishing penalty effect in

senior adults is similar in two contrasts conditions (Value X Age X Contrast interaction (F(1,36) = 1.11, p = .299 , η2 = .03), yielding a significant main Age effect(F(1,36) = 6.25, p = .017 , η2 = .15).

Dependence of saccade direction on saccade latency

Previously we found that effects of value on saccade direction are dependent on saccade latency: long-latency saccades are much more influenced by value whereas short-latency saccades are more determined by salience (Schütz, Trommershäuser & Gegenfurtner, 2012). To investigate this dynamic integration of salience and value, we split trials into 6 bins based on their latency for each individual. Four –way ANOVA with Latency, Value, Contrast and Age found significant Latency main effect (F(5, 360) = 19.87, p < .001 , η^2 = .36; see Fig.4) and Latency X Value interaction (F(10, 360) = 8.72, p < .001 , η^2 = .20).

Figure 4. Saccade direction as a function of saccade latency in young adults (top panel) and senior adults (bottom panel) for Salience (left panel), Reward (middle) and Reward & Penalty condition (right), respectively. Dots and error bars represent mean and ± 1 SEM. Dark green dots represent contrast with 40% and light green contrast of 10%.

Follow-up 3-way ANOVA with Latency, Contrast and Age in Salience condition found that Latency main effect is not significant ($F(5,180) = 1.85$, $p = .105$, $\eta^2 = .05$; see left panel of Fig. 4), suggesting independence of saccade direction on saccade latency. This independence is not influenced by either contrast or age (interactions: Fs < 0.49, ps > .784, η^2s < .02). Confirming what were found in average direction (Fig.3), Contrast main effect is significant ($F(1,180) = 252.73$, $p < .001$, $\eta^2 = .88$) but neither Age main effect ($F(1,36) = 0.69$, $p = .413$, $\eta^2 = .02$) nor Age X Contrast interaction ($F(1,180) = 0.01$, $p = .911$, $\eta^2 < .01$).

On the contrary, Latency main effect is significant in Reward condition ($F(5,180) = 16.53$, $p < .001$, $\eta^2 = .32$; see middle panel of Fig.4), suggesting dependence of saccade direction on saccade latency. This dependence is not influenced by either contrast (interaction: $F(5,180) = 1.62$, $p = .158$, $\eta^2 = .04$) or age (interaction: $F(5,180) = 0.70$, $p = .621$, $\eta^2 = .02$). Confirming what were found in average direction(Fig.3), Contrast main effect was significant ($F(1,180) = 24.62$, $p < .001$, $\eta^2 = .41$) but neither Age main effect ($F(1,36) = 3.11$, $p = .086$, $\eta^2 = .08$) nor Age X Contrast interaction ($F(1,180) = 1.03$, $p = .318$, $\eta^2 = .03$).
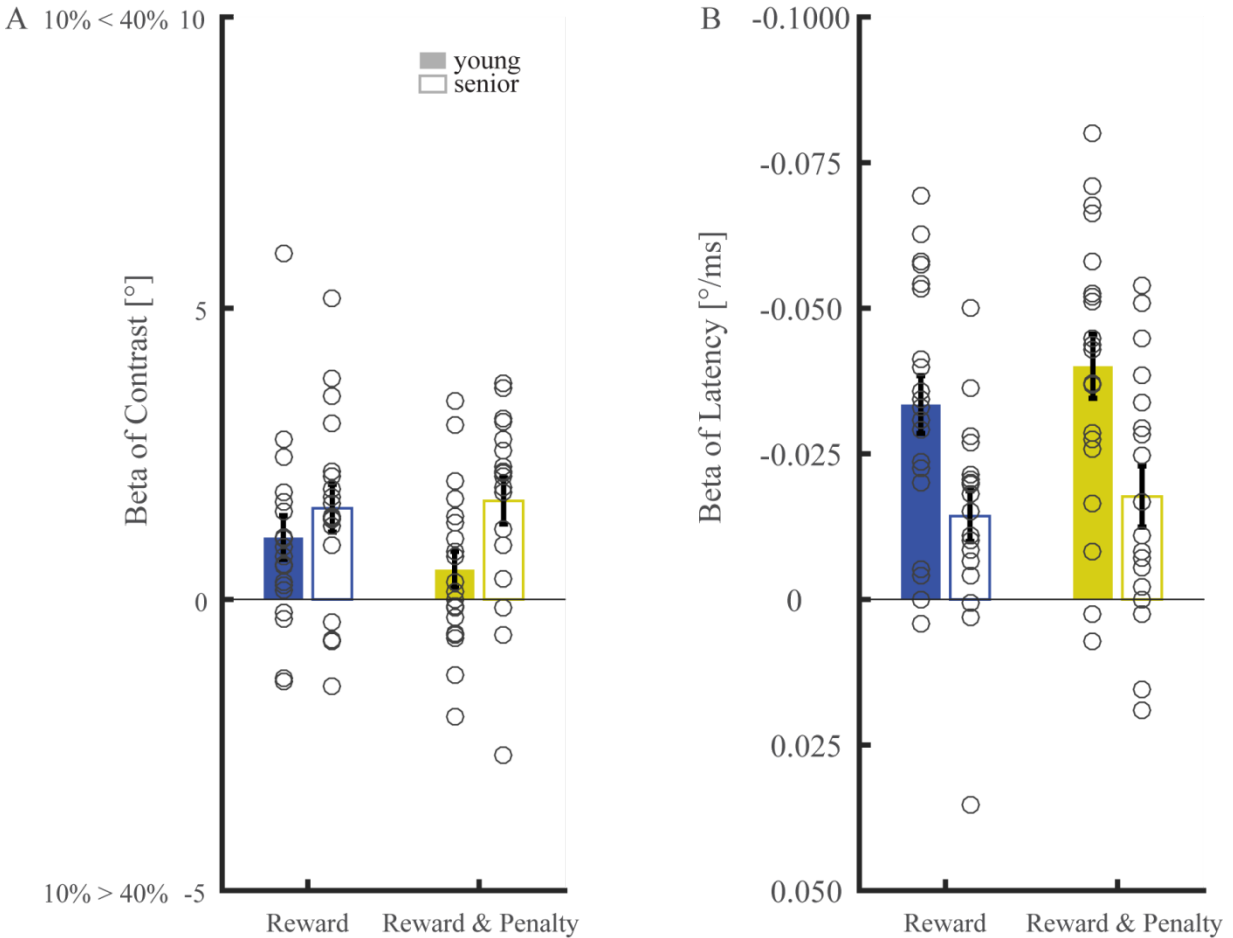
As similar as what were found in Reward condition, Latency main effect is significant ($F(5,180) = 16.74$, $p < .001$, $\eta^2 = .32$; see right panel of Fig.4) in Reward & Penalty condition. Its interaction with Contrast and Age are neither significant (Fs < 1.62, ps > .158, η^2s < .05). Confirming what were found in average direction, Contrast main effect was significant ($F(1,180) = 23.64$, $p < .001$, $\eta^2 = .40$) as well as Age main effect ($F(1,36) = 8.77$, $p = .005$, $\eta^2 = .20$) and their interaction ($F(1,180) = 6.12$, $p = .018$, $\eta^2 = .15$).

Separation of contrast and value effects on saccade direction

To further quantify the extent to which saccade direction is dependent on saccade latency and to which it is influenced by contrast in value conditions, general linear model was used to fit saccade direction with predictors Contrast and Latency. We found that in Reward condition both contrast and latency predict saccade direction significantly in both groups (T-test against zero: ts > 4.82, ps < .001, ds > 1.58; see blue bars in Fig.5). Besides, the dependence on saccade latency is smaller in senior adults ($t(36) = 2.96$, $p = .006$, $d = 0.97$; see blue bars in Fig.5B) whereas the influence of contrast is similar ($t(36) = 0.93$, $p = .359$, $d = 0.30$; see blue bars in Fig.5A).

In Reward & Penalty condition, betas of predictors are different from zero in both groups (ts > 4.13, ps < .001, ds > 1.36; yellow bars of Fig.5). Comparing to saccade direction of young adults,

saccade direction of senior adults is more strongly influenced by contrast (t(36) = 2.43, p = .020, d = 0.78; yellow bars of Fig.5A) whereas it is less dependent on saccade latency (t(36) = 3.01, p = .005, d = 0.98; yellow bars of Fig.5B). The influence of contrast and the dependence of saccade latency are equivalent in Reward and Reward & Penalty conditions (Fs < 1.18, ps > .284 , η2s < .04; see Fig.5).
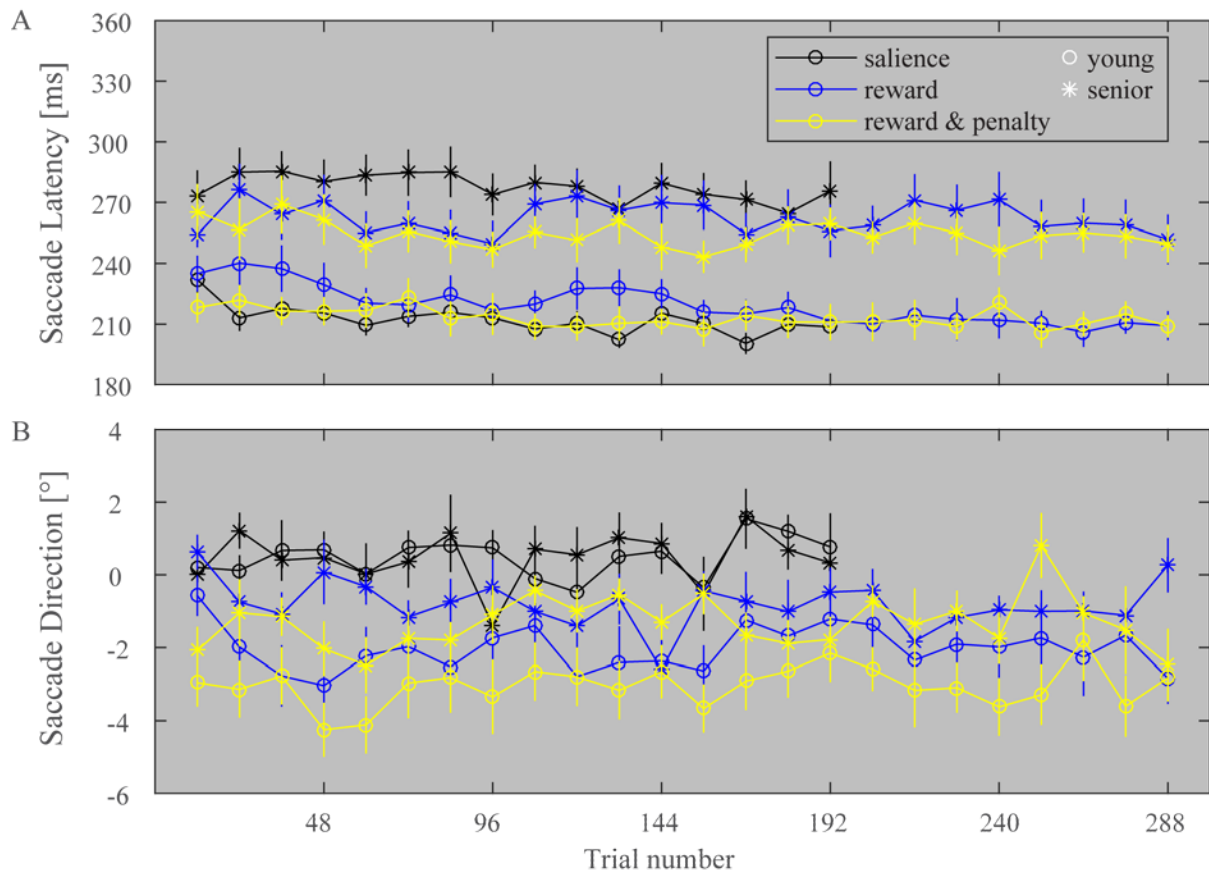

Figure 5. Estimated beta of contrast (A) and saccade latency (B) in multiple regression of saccade direction in Reward (in blue color) and Reward & Penalty condition (in yellow color), respectively. (A) Positive beta of contrast means direction in trials with 40% contrast is larger than that with 10% (i.e., more further to the light region of target); negative beta means the opposite, namely, direction in trials with 40% contrast goes more further to the dark region of target. (B) Negative beta of latency means direction decreases (going toward the darker region of target) when saccade latency increases; positive beta means direction increases (going toward the lighter region of target) when saccade latency increases. Bars and error bars represent mean and ±1 SEM. Dots represent individuals.

Learning effect

To check whether there is any learning effect on saccade latency and saccade direction in Reward and Reward & Penalty condition, we compared them across successive trials as a function of trial number. As illustrated in Fig.6A (blue lines), average saccade latency is 235 ms in young adults and 254 ms in senior adults at the first bin of Reward condition and ends with 209 ms in young adults and 252 ms in senior adults, with a significant decrease in young adults ($F(23, 414) = 3.66$, $p < .001$, $\eta^2 = .17$; see blue line with circles in Fig.6A) but without in senior adults ($F(23, 391) = 1.30$, $p = .165$, $\eta^2 = .07$; see blue line with asterisks in Fig.6A). However, these are no changes in saccade latency in Reward & Penalty condition (main Bin effect: $F(23, 805) = 1.12$, $p = .319$, $\eta^2 = .03$; see yellow lines in Fig.6A) in both groups (Bin X Age interaction: $F(23, 805) = 0.70$, $p = .547$, $\eta^2 = .02$).

There are no significant changes in saccade direction in either Reward condition ($F(23, 805) = 1.53$, $p = .054$, $\eta^2 = .04$; see blue lines in Fig.6B) or Reward & Penalty condition ($F(23, 805) = 1.27$, $p = .177$, $\eta^2 = .04$; see yellow lines in Fig.6B). Neither any interaction with Age is found ($Fs < 1.10$, $ps > .342$, $\eta^2s < .03$).

Figure 6. Saccade latency (A) and Saccade direction (B) changes over trials. Black, blue and yellow color represents salience, reward and reward & penalty condition with dots and asterisks representing young and senior, respectively. Bin size is 12 trials. Error bars represent ±1 SEM.

Discussion

To investigate how aging impacts the integration of salience and value for saccadic eye movements, we traded off salience against expected value of target patches whilst recording eyemovements of young and senior adults. We found that reward and penalty makes no changes to saccade latency of young adults whereas makes decreases to that of senior adults. Reward encourages saccade direction towards rewarded darker region in both young and senior adults; Penalty discourages saccade direction towards penalized lighter region in young adults but not in senior adults.

Lacking of learning effect in young adults

Confirmed what we found previously reward-related influences on saccade direction in young adults are latency-dependent: Ending position of saccade shifts to rewarded darker region further as saccade latency increases. This may be because the value information takes time to reach to the saccadic system (Caspi, Beutter & Eckstein, 2004; Schütz, Trommershäuser, & Gegenfurtner, 2012). However, we did not replicate the previous finding that optimal saccades are made towards the position with expected value. This might be due to the much smaller amount of trials in current study (288 trials VS. 576 trials in the previous study) so that there is little learning to use strategies - lengthening saccade latency to wait until value information available to make the optimal saccades. There is strong learning effect in the previous study (see Fig.4A of the paper), i.e. substantial increases in saccade latency and decreases in saccade direction, and most of the optical saccades are made after the 192th trial. However, there is no learning in current study (see Fig. 6). This failed optimal control makes the relationship between saccade direction and saccade latency more like linear so that we used general linear model to analyze it instead of the previous MEGaMove (Maximum Expected Gain). Besides, Milstein and Dorris (2007) also found the linear relationship between expected reward value and saccade latency, which suggests saccade latency as a good proxy of immediate value influence when value information reaching to the saccadic system fluctuate along with saccade latency.

Equivalent reward effect on saccade direction in senior adults

Surprisingly, we found equivalent reward-related effects on monetary score and saccade direction in senior adults. These results are also kind of unsurprising. Firstly, we previously found that implicit low-level processes are immune to aging ((Huang et al., 2017) as well as reward influences on them (Huang, Hegele & Billino, submitted). In current study there is almost no learning or strategies involved in Reward condition, as discussed in last paragraph, so that what reward impacts is almost implicit processing. Besides, some studies also suggest that the reason why senior adults perform worse in reward-related tasks is because of the complexity of the tasks but not of reward itself . Supporting this speculation we found that senior adults need more trials to adapt to the task by showing age differences at the first block of Reward condition (see Fig.5B). But the difference disappears at the first bin after the first block (96 trials is one block). To note, there were no practice trials for Reward and Reward & Penalty condition.

Weaker dependence on saccade latency in senior adults

Although the reward influence on saccade direction in senior adults is as strong as that in young adults, their influence and dependence on saccade latency are substantially different. Saccade latency is generally slower and is generally speeded up by reward in senior adults whereas it is both speeded up and slowed down by reward in young adults. Besides, the amount of change in saccade direction caused by 1 ms increase in saccade latency is smaller in senior adults. Consistent with our results, studies with the diffusion model found that senior adults have an about 50 ms longer nondecision time (Fisher & Glaser, 1996; Ratcliff, Thapar, & McKoon, 2001; 2003). Reward influence on saccade latency is content-dependent. For example, Wolf and colleagues (2017) found that this influence is impacted by the necessity. Besides, they also found that even when saccades are faster in choices with high reward, it is because of the reduced baseline level in choices with low reward. The longer nondecision time in senior adults would make their latency long enough to receive the value information so that it is unnecessary to reducing the baseline level of decision. As such, there is only seeding up effect in senior adults but no slowing down effect. Taken together, this means nature saccades in senior adults receive relatively more top-down control because of their general slower response.

Penalty effects in young and senior adults

In addition to reward, we also found penalty effective in influencing saccade direction of young adults in Reward & Penalty condition with more profound effects in trials with high contrast. However, failure of learning also happens in this condition. In the previous study (Schütz, Trommershäuser & Gegenfurtner, 2012), saccade latency increases at the 192nd trial obviously and maintains after that (see Fig.4A of the paper); similarly saccade direction reaches to the optimal direction at that trial and also maintains after that (see Fig.4B of the paper). However, saccade latency does not change in current study or decreases slightly and saccade direction just has a general decrease which looks as similar as that in the first 192 trials in the previous study (the first 4 yellow bins of Fig.4B of the paper).

In contrast, penalty does not impact saccade direction at all in senior adults. Two reasons may be account for these results. Firstly, reward and penalty is found to involve activities in different brain area with reward involving more in vmPFC whereas penalty more in cognitive control areas such as the dlPFC, the dACC and the inferior parietal lobule (Eppinger et al., 2013;Hämmerer & Eppinger, 2012). Secondly, the combination of reward and loss signals mostly occurs in the

prefrontal cortex (Basten et al., 2010; Hare et al., 2011). The cognitive control and prefrontal cortex might be more impaired by aging.

In conclusion, we found that when people get old reward effects on their decision making are stable when strategies and learning not involve in whereas penalty effects always decline. Although senior adults have general slower response, it facilitates top-down influence naturally.

Reference

Basten, U., Biele, G., Heekeren, H. R., & Fiebach, C. J. (2010). How the brain integrates costs and benefits during decision making. Proceedings of the National Academy of Sciences, 107(50), 21767-21772.

Bucker, B., Silvis, J. D., Donk, M., & Theeuwes, J. (2015). Reward modulates oculomotor competition between differently valued stimuli. Vision Research, 108, 103–112. doi: 10.1016/j.visres.2015.01.020

Caspi, A., Beutter, B. R., & Eckstein, M. P. (2004). The time course of visual information accrual guiding eye movement decisions. Proceedings of the National Academy of Sciences, 101(35), 13086-13090.

Chowdhury, R., Guitart-Masip, M., Lambert, C., Dayan, P., Huys, Q., Düzel, E., & Dolan, R. J. (2013). Dopamine restores reward prediction errors in old age. Nature neuroscience, 16(5), 648.

Dunne, S., Ellison, A., & Smith, D. T. (2015). Rewards modulate saccade latency but not exogenous spatial attention. Frontiers in psychology, 6, 1080.

Eppinger, B., Hämmerer, D., & Li, S. C. (2011). Neuromodulation of reward‐based learning and decision making in human aging. Annals of the New York Academy of Sciences, 1235(1), 1-17.

Eppinger, B., Schuck, N. W., Nystrom, L. E., & Cohen, J. D. (2013). Reduced striatal responses to reward prediction errors in older compared with younger adults. Journal of Neuroscience, 33(24), 9905-9912.

Eppinger, B., Walter, M., Heekeren, H. R., & Li, S. C. (2013). Of goals and habits: age-related and individual differences in goal-directed decision-making. Frontiers in neuroscience, 7, 253.

Fisher, D. L., & Glaser, R. A. (1996). Molar and latent models of cognitive slowing: Implications for aging, dementia, depression, development, and intelligence. Psychonomic Bulletin & Review, 3(4), 458-480.

Glimcher, P. W. (2003). The neurobiology of visual-saccadic decision making. Annual review of neuroscience, 26(1), 133-179.

Gold, J. I., & Shadlen, M. N. (2007). The neural basis of decision making. Annual review of neuroscience, 30.

Hämmerer D. & Eppinger B. (2012). Dopaminergic and prefrontal contributions to reward-based learning and outcome monitoring during child development and aging. Developmental Psychology, 48, 862– 874.

Hare, T. A., Schultz, W., Camerer, C. F., O'Doherty, J. P., & Rangel, A. (2011). Transformation of stimulus value signals into motor commands during simple choice. Proceedings of the National Academy of Sciences, 201109322.

Heuer, A., Wolf, C., Schütz, A. C., & Schubö, A. (2017). The necessity to choose causes reward-related anticipatory biasing: Parieto-occipital alpha-band oscillations reveal suppression of low-value targets. Scientific reports, 7(1), 14318.

Huang, J., Gegenfurtner, K. R., Schütz, A. C., & Billino, J. (2017). Age effects on saccadic adaptation: evidence from different paradigms reveals specific vulnerabilities. Journal of vision, 17(6), 9-9.

Huang, J., Hegele, M., & Billino, J. (2017). Motivational effects on reaching adaptation in young and senior adults. Submitted.

Ikeda, T., and Hikosaka, O. (2003). Reward-dependent gain and bias of visual responses in primate superior colliculus. Neuron 39, 693–700. doi: 10.1016/S0896-6273(03)00464-1

Itti, L., & Koch, C. (2001) Computational modelling of visual attention. Nat Rev Neurosci 2: 194–203.

Johansson, R. S., Westling, G., Bäckström, A., & Flanagan, J. R. (2001). Eye–hand coordination in object manipulation. Journal of Neuroscience, 21(17), 6917-6932.

Jovancevic-Misic, J., & Hayhoe, M. (2009). Adaptive gaze control in natural environments. Journal of Neuroscience, 29(19), 6234-6238.

Land, M. F. (2006). Eye movements and the control of actions in everyday life. Progress in retinal and eye research, 25(3), 296-324.

Leon, M. I., & Shadlen, M. N. (1999). Effect of expected reward magnitude on the response of neurons in the dorsolateral prefrontal cortex of the macaque. Neuron, 24(2), 415-425.

Markowitz, D. A., Shewcraft, R. A., Wong, Y. T., & Pesaran, B. (2011). Competition for visual selection in the oculomotor system. Journal of Neuroscience, 31(25), 9298-9306.

Mata, R., Josef, A. K., & Lemaire, P. (2015). Adaptive decision making and aging. In Aging and Decision Making (pp. 105-126).

Mata, R., von Helversen, B., & Rieskamp, J. (2010). Learning to choose: Cognitive aging and strategy selection learning in decision making. Psychology and aging, 25(2), 299.

McCoy, B., & Theeuwes, J. (2016). Effects of reward on oculomotor control. Journal of Neurophysiology, 116(5), 2453-2466.

McGovern, D. P., Hayes, A., Kelly, S. P., & O'Connell, R. (2017). Reconciling age-related changes in behavioural and neural indices of human perceptual decision making. bioRxiv, 228965.

Milstein, D. M., & Dorris, M. C. (2007). The influence of expected value on saccadic preparation. Journal of Neuroscience, 27(18), 4810-4818.

Munoz, D. P., Broughton, J. R., Goldring, J. E., & Armstrong, I. T. (1998). Age-related performance of human subjects on saccadic eye movement tasks. Experimental Brain Research, 121(4), 391–400. doi:10.1007/s002210050473

Navalpakkam, V., Koch, C., Rangel, A., & Perona, P. (2010). Optimal reward harvesting in complex perceptual environments. Proceedings of the National Academy of Sciences, 107(11), 5232-5237.

Peltsch, A., Hemraj, A., Garcia, A., & Munoz, D. P. (2011). Age-related trends in saccade characteristics among the elderly. Neurobiology of aging, 32(4), 669-679.

Platt, M. L., & Glimcher, P. W. (1999). Neural correlates of decision variables in parietal cortex. Nature, 400(6741), 233.

Ratcliff, R., Thapar, A., & McKoon, G. (2001). The effects of aging on reaction time in a signal detection task. Psychology and aging, 16(2), 323.

Ratcliff, R., Thapar, A., & Mckoon, G. (2003). A diffusion model analysis of the effects of aging on brightness discrimination. Perception & psychophysics, 65(4), 523-535.

Salthouse, T. A. (1996). The processing-speed theory of adult age differences in cognition. Psychological review, 103(3), 403.

Schütz, A. C., Braun, D. I., & Gegenfurtner, K. R. (2011). Eye movements and perception: A selective review. Journal of vision, 11(5), 9-9.

Schütz, A. C., Kerzel, D., & Souto, D. (2014). Saccadic adaptation induced by a perceptual task. Journal of vision, 14(5), 4-4.

Schütz, A. C., & Souto, D. (2015). Perceptual task induces saccadic adaptation by target selection. Frontiers in human neuroscience, 9, 566.

Schütz, A. C., Trommershäuser, J., & Gegenfurtner, K. R. (2012). Dynamic integration of information about salience and value for saccadic eye movements. Proceedings of the National Academy of Sciences, 201115638.

Shadlen, M. N., & Kiani, R. (2013). Decision making as a window on cognition. Neuron, 80(3), 791-806.

Stankevich, B. A., & Geng, J. J. (2015). The modulation of reward priority by top-down knowledge. Visual Cognition, 23(1-2), 206-228. doi: 10.1080/13506285.2014.981626

Tatler, B. W., Hayhoe, M. M., Land, M. F., & Ballard, D. H. (2011). Eye guidance in natural vision: Reinterpreting salience. Journal of vision, 11(5), 5-5.

Theeuwes, J., & Belopolsky, A. V. (2012). Reward grabs the eye: oculomotor capture by rewarding stimuli. Vision research, 74, 80-85. doi: 10.1016/j.visres.2012.07.024

Valsecchi, M., Billino, J., & Gegenfurtner, K. R. (2018). Healthy aging is associated with decreased risk-taking in motor decision-making. Journal of Experimental Psychology: Human Perception and Performance, 44(1), 154-167.

Watanabe, K., Lauwereyns, J., & Hikosaka, O. (2003). Neural correlates of rewarded and unrewarded eye movements in the primate caudate nucleus. Journal of Neuroscience, 23(31), 10052-10057.

Williams, L. G. (1966). The effect of target specification on objects fixated during visual search. Perception & Psychophysics, 1(5), 315-318.

Wolf, C., Heuer, A., Schubö, A., & Schütz, A. C. (2017). The necessity to choose causes the effects of reward on saccade preparation. Scientific reports, 7(1), 16966.

World Medical Association. (2013). World Medical Association Declaration of Helsinki: Ethical principles for medical research involving human subjects. Journal of the American Medical Association, 310, 2191–2194.

Discussion

In this thesis, firstly with a double-step paradigm and a perceptual tasks paradigm, the first study found preserved low-level saccade adaptation capacity in older adults but impaired high-level saccade capacity. With a screen-cursor reaching adaptation task, the second study found preserved retention rate in older adults but impaired learning rate. However, the impaired learning rate could be reduced by reward. With a saccade making task, the third study found equivalent salience and reward influence on the saccade landing position. Taken together, this thesis found reserved low-level processing in older adults but impaired the high-level processing which are both consistent what found in cognitive tasks.

Although the results are consistent with the dominant impressions of the literature, it contributes substantially to the literature.

Consistency and Extensions

Although previous literature found either age-related vulnerability or stability, this thesis found both stability and vulnerability of one task through teasing different processes. Consistent with the common cause theories, these differential aging effects could result from the different extents to which the high-level and the low-level processing the tasks involve. For example, in tasks which involve almost low-level processing, performance of old adults would be similar with that of young adults, such as situations like the saccade adaptation with intrasaccadic step of the first study, the salience condition in the third study). In tasks which involve more high-level processing, performance of old adults would show impairments, such as situations like saccade adaptation with perceptual tasks, reaching adaptation with large visuomotor rotation.

This thesis could also extend how we think about aging, for example in a circuitry. Initially, researchers thought that the aging effects were based on the structure of the tasks, such as short-term memory, long-term memory (Tulving, 1984). Then it evolved to be based on functions, operations or processing (Craik, 1986; Hasher and Zacks, 1988; Salthouse, 1996), such as working memory, attention, inhibition so on and so forth. However, this thesis extends that to a circuitry system, such as low-level system. This extension is consistent with all kinds of preserved capacity in the implicit tasks and the reorganized aging brain system. The aging brain does not change locally, but from proactive processing to reactive processing, from specific processing to general processing.

Adaptive way to interpret declines

Supports of the adaptive hypothesis of aging also come from the alternative interpretation of the aging decline results in this thesis, strategy change.

One declining but also puzzling result is that the aging declines in saccade adaptation with the perceptual task. Schütz and colleagues found that the closer the saccade landing position is to the target, the better their perceptual discrimination performance would be (Schütz, Kerzel, & Souto, 2014). This is also confirmed in my study. However, if it helps, why do older adults not do it? After all, saccades are very cheap. Maybe the reason is they do not need / want to instead of they could not do, i.e., change in strategy.

During reading, older adults are found to have larger saccade length, which means their eyes are more far away from the reading characters, and this could be explained by their risky guess strategies to predict next characters (Rayner et al., 2006; Rayner, Castelhano & Yang, 2009). Despite this difference, the comprehension performance in two groups is the same. Therefore, this truth seems to be that older adults have more knowledge to predict what the next several characters would be so that they do not need short-amplitude saccade to check them. Since this reading pattern does not result in any problems with comprehension, it becomes the reaching habit.

This reading habit might be automatically used in any reading or reading similar task, such as character discrimination tasks in the Experiment 2 of the first study. This prediction is confirmed by the reduced horizontal saccade amplitude during the baseline trials in which the target character is placed horizontally to the fixation.

This strategy change could be in the saccade making study. In the study, to get the reward money, young adults lengthen their saccade latency so that the saccade system could receive the reward information. Therefore there is no change in the average saccade latency. But older adults do not lengthen their saccade latency that could be: their saccade latency is longer enough to get the reward information. After all, even they do not do it, they still can get similar amount of money.

Familiarity and strategy effects on Reward

Previously some studies found equivalent rewards effects in old adults whereas some studies found reduced effects in old adults. This thesis consistently found positive reward effects on performance indicating its potential function in reducing aging declines.

Some studies speculated that the factor is involved in the discrepancy of these results could be task complexity. Older adults always need more time to understand the tasks and use strategies. Two results of the saccade making study support this speculation.

In the saccade making study, there were no practice trials before the reward condition. As illustrated in the Fig. 6, young adults changed their saccade latency at the beginning of the reward condition so that their saccade landing position also shifted to the rewarded parts of the target. Whereas older adults only started to do that from the second block so that there were relatively larger group difference at the first block of reward. This practice effect was also found in cognitive tasks. Salthouse (2010a) found that even the second time measurement in longitude study is better than the first time measurement in cross-section study.

As discussed before, the reward effect on saccade latency in older adults could be a strategy change. Therefore strategy also changes the reward effects.

Future

Results from this thesis emphasize the future investigations on circuitry processing, familiarity and strategy. They are highly related. Since older adults seem to use reactive processing strategies so that familiarity of the tasks are especially important for them or familiarity contributes substantially to observed aging declines. This might also explain differential age-related changes in behavioral and neural performance in perceptual decision making (McGovern et al. 2018). Given that sensorimotor control tasks could be pretty good for aging research because it is more natural and could be more natural with the advances in movement recording devices.

Taken together, this thesis found both stability and vulnerability in older adults whereas the vulnerability could result from strategy change suggesting the adaptive brain.

Footnotes

[1] The population of Germany in 2016: https://www.statista.com/statistics/454349/population-by-age-group-germany/

[2] Google Scholar profile of Prof. Jan Koenderink who are even more productive after his retirement: https://scholar.google.de/citations?user=lxW3wvMAAAAJ&hl=en

[3] Google Scholar profile of Prof. Andrea J. van Doorn, who are even more productive after his retirement: https://scholar.google.de/citations?user=_6VnqIwAAAAJ&hl=en&oi=sra

References

Abe, M., Schambra, H., Wassermann, E. M., Luckenbaugh, D., Schweighofer, N., & Cohen, L. G. (2011). Reward improves long-term retention of a motor memory through induction of offline memory gains. Current Biology, 21(7), 557-562.

Abel, L. A., & Douglas, J. (2007). Effects of age on latency and error generation in internally mediated saccades. Neurobiology of Aging, 28(4), 627-637.

Abel, L. A., & Douglas, J. (2007). Effects of age on latency and error generation in internally mediated saccades. Neurobiology of Aging, 28(4), 627-637.

Abel, L. A., Schmidt, D., Dell'Osso, L. F., & Daroff, R. B. (1978). Saccadic system plasticity in humans. Annals of Neurology: Official Journal of the American Neurological Association and the Child Neurology Society, 4(4), 313-318.

Alahyane, N., & Pélisson, D. (2004). Eye position specificity of saccadic adaptation. Investigative Ophthalmology & Visual Science, 45(1), 123-130.

Alahyane, N., Fonteille, V., Urquizar, C., Salemme, R., Nighoghossian, N., Pelisson, D., & Tilikete, C. (2008). Separate neural substrates in the human cerebellum for sensory-motor adaptation of reactive and of scanning voluntary saccades. The Cerebellum, 7(4), 595-601.

Alahyane, N., Salemme, R., Urquizar, C., Cotti, J., Guillaume, A., Vercher, J. L., & Pélisson, D. (2007). Oculomotor plasticity: are mechanisms of adaptation for reactive and voluntary saccades separate?. Brain research, 1135, 107-121.

Bäckman, L., Almkvist, O., Andersson, J., Nordberg, A., Winblad, B., Reineck, R., & Långström, B. (1997). Brain activation in young and older adults during implicit and explicit retrieval. Journal of Cognitive neuroscience, 9(3), 378-391.

Balint, R. (1909). Seelenhammung des 'Schauens', optische Ataxie, raümliche Störungen des Aufmersamkeit. Monastchrift für Psychiatrie und Neurologie 25, 51–81.

Baltes, P. B., & Lindenberger, U. (1997). Emergence of a powerful connection between sensory and cognitive functions across the adult life span: a new window to the study of cognitive aging?. Psychology and aging, 12(1), 12.

Baltes, P. B., Staudinger, U. M., & Lindenberger, U. (1999). Lifespan psychology: Theory and application to intellectual functioning. Annual review of psychology, 50(1), 471-507.

Baraduc, P., Lang, N., Rothwell, J. C., & Wolpert, D. M. (2004). Consolidation of dynamic motor learning is not disrupted by rTMS of primary motor cortex. Current Biology, 14(3), 252-256.

Battaglia‐Mayer, A., & Caminiti, R. (2002). Optic ataxia as a result of the breakdown of the global tuning fields of parietal neurones. Brain, 125(2), 225-237.

Beck, S. M., Locke, H. S., Savine, A. C., Jimura, K., & Braver, T. S. (2010). Primary and secondary rewards differentially modulate neural activity dynamics during working memory. PloS one, 5(2), e9251.

Becker, W. (1989). The neurobiology of saccadic eye movements. Metrics. Reviews of oculomotor research, 3, 13.

Bergerbest, D., Gabrieli, J. D., Whitfield-Gabrieli, S., Kim, H., Stebbins, G. T., Bennett, D. A., & Fleischman, D. A. (2009). Age-associated reduction of asymmetry in prefrontal function and preservation of conceptual repetition priming. Neuroimage, 45(1), 237-246.

Bergerbest, D., Gabrieli, J.D., Whitfield-Gabrieli, S., Kim, H., Stebbins, G.T., Bennett,D.A., Fleischman, D.A., 2009. Age-associated reduction of asymmetry inprefrontal function and preservation of conceptual repetition priming.Neuroimage 45, 237–246.

Berniker, M., & Kording, K. (2008). Estimating the sources of motor errors for adaptation and generalization. Nature neuroscience, 11(12), 1454.

Betz, T., Kietzmann, T. C., Wilming, N., & König, P. (2010). Investigating task-dependent top-down effects on overt visual attention. Journal of vision, 10(3), 15-15.

Bock, O. (2005). Components of sensorimotor adaptation in young and elderly subjects. Experimental Brain Research, 160(2), 259-263.

Bock, O., & Schneider, S. (2002). Sensorimotor adaptation in young and elderly humans. Neuroscience & Biobehavioral Reviews, 26(7), 761-767.

Bonnetblanc, F., & Baraduc, P. (2007). Saccadic adaptation without retinal postsaccadic error. Neuroreport, 18(13), 1399-1402.

Bucker, B., Silvis, J. D., Donk, M., & Theeuwes, J. (2015). Reward modulates oculomotor competition between differently valued stimuli. Vision Research, 108, 103–112. doi: 10.1016/j.visres.2015.01.020

Butefisch CM, Kleiser R, Korber B, Muller K, Wittsack HJ, Homberg V, Seitz RJ. 2005. Recruitment of contralesional motor cortex in stroke patients with recovery of hand function. Neurology. 64:1067—1069

Cabeza, R. (2001). Functional neuroimaging of cognitive aging. In HANDBOOK OF FUNCTIONAL NEUROIMAGING OF COGNITION.

Cabeza, R., & Dennis, N. A. (2012). Frontal lobes and aging. Principles of frontal lobe function. 2d ed. New York: Oxford University Press. p, 628-652.

Cabeza, R., Daselaar, S. M., Dolcos, F., Prince, S. E., Budde, M., & Nyberg, L. (2004). Task-independent and task-specific age effects on brain activity during working memory, visual attention and episodic retrieval. Cerebral cortex, 14(4), 364-375.

Cabeza, R., Dolcos, F., Graham, R., & Nyberg, L. (2002). Similarities and differences in the neural correlates of episodic memory retrieval and working memory. Neuroimage, 16(2), 317-330.

Cabeza, R., Grady, C. L., Nyberg, L., McIntosh, A. R., Tulving, E., Kapur, S., ... & Craik, F. I. (1997). Age-related differences in neural activity during memory encoding and retrieval: a positron emission tomography study. Journal of neuroscience, 17(1), 391-400.

Cabeza, R., Grady, C. L., Nyberg, L., McIntosh, A. R., Tulving, E., Kapur, S., ... & Craik, F. I. (1997). Age-related differences in neural activity during memory encoding and retrieval: a positron emission tomography study. Journal of neuroscience, 17(1), 391-400.

Cabeza, R., Nyberg, L., & Park, D. C. (Eds.). (2016). Cognitive neuroscience of aging: Linking cognitive and cerebral aging. Oxford University Press.

Caithness G, et al. Failure to consolidate the consolidation theory of learning for sensorimotor adaptation tasks. J Neurosci 2004;24(40):8662–71.

Caithness, G., Osu, R., Bays, P., Chase, H., Klassen, J., Kawato, M., ... & Flanagan, J. R. (2004). Failure to consolidate the consolidation theory of learning for sensorimotor adaptation tasks. Journal of Neuroscience, 24(40), 8662-8671.

Carstensen, L. L. (1992). Social and emotional patterns in adulthood: support for socioemotional selectivity theory. Psychology and aging, 7(3), 331.

Caspi, A., Beutter, B. R., & Eckstein, M. P. (2004). The time course of visual information accrual guiding eye movement decisions. Proceedings of the National Academy of Sciences, 101(35), 13086-13090.

Cerf, M., Frady, E. P., & Koch, C. (2009). Faces and text attract gaze independent of the task: Experimental data and computer model. Journal of vision, 9(12), 10-10.

Chen, J., Valsecchi, M., & Gegenfurtner, K. R. (2017). Attention is allocated closely ahead of the target during smooth pursuit eye movements: evidence from EEG frequency tagging. Neuropsychologia, 102, 206-216.

Christou, A. I., Miall, R. C., McNab, F., & Galea, J. M. (2016). Individual differences in explicit and implicit visuomotor learning and working memory capacity. Scientific reports, 6, 36633.

Cohen, G., & Faulkner, D. (1984). MEMORY IN OLD-AGE-GOOD IN PARTS. New Scientist, 104(1425), 49-51.

Collins, T., & Wallman, J. (2012). The relative importance of retinal error and prediction in saccadic adaptation. Journal of Neurophysiology, 107(12), 3342-3348.

Craik, F. I. (1977). Similarities between the effects of aging and alcoholic intoxication on memory performance, construed within a "levels of processing" framework. Alcohol and human memory, 9-21.

Craik, F. I. (1986). A functional account of age differences in memory. In Memory, Attention, and Aging (pp. 409-422).

Craik, F. I. M. (1983). On the transfer of information from temporary to permanent memory. Phil. Trans. R. Soc. Lond. B, 302(1110), 341-359.

Craik, F. I. M. (1984). Age differences in remembering. Neuropsychology of memory, 3-12.

Craik, F. I., & Byrd, M. (1982). Aging and cognitive deficits. In Aging and cognitive processes (pp. 191-211). Springer, Boston, MA.

Cunningham, H. A. (1989). Aiming error under transformed spatial mappings suggests a structure for visual-motor maps. Journal of Experimental Psychology: Human Perception and Performance, 15(3), 493.

Daselaar, S., Fleck, Dobbins, I., Madden, D., & Cabeza, R. (2006). Effects of healthy aging on hippocampal and rhinal memory functions: An event-related fMRI study. Cerebral Cortex, 16, 1771–1782.

Davis, S. W., & Cabeza, R. (2015). Cross-hemispheric collaboration and segregation associated with task difficulty as revealed by structural and functional connectivity. Journal of Neuroscience, 35(21), 8191-8200.

Davis, S. W., Kragel, J. E., Madden, D. J., & Cabeza, R. (2011). The architecture of cross-hemispheric communication in the aging brain: linking behavior to functional and structural connectivity. Cerebral cortex, 22(1), 232-242.

Della-Maggiore, V., Malfait, N., Ostry, D. J., & Paus, T. (2004). Stimulation of the posterior parietal cortex interferes with arm trajectory adjustments during the learning of new dynamics. Journal of Neuroscience, 24(44), 9971-9976.

Dennis NA, Cabeza R (2008): Neuroimaging of healthy cognitive aging. In: Craik FIM, Salthouse TA, editors. The Handbook of Aging and Cognition, 3rd ed. New York: Psychology Press, 1–54.

Dennis, N. A., & Cabeza, R. (2008). Neuroimaging of healthy cognitive aging. The handbook of aging and cognition, 3, 1-54.

Desmurget, M., Epstein, C. M., Turner, R. S., Prablanc, C., Alexander, G. E., & Grafton, S. T. (1999). Role of the posterior parietal cortex in updating reaching movements to a visual target. Nature neuroscience, 2(6), 563.

Desmurget, M., Pélisson, D., Rossetti, Y., & Prablanc, C. (1998). From eye to hand: planning goal-directed movements. Neuroscience & Biobehavioral Reviews, 22(6), 761-788.

Desmurget, M., Pelisson, D., Urquizar, C., Prablanc, C., Alexander, G. E., & Grafton, S. T. (1998). Functional anatomy of saccadic adaptation in humans. Nature neuroscience, 1(6), 524.

Desmurget, M., Pelisson, D., Urquizar, C., Prablanc, C., Alexander, G. E., & Grafton, S. T. (1998). Functional anatomy of saccadic adaptation in humans. Nature neuroscience, 1(6), 524.

Deubel, H. (1987). Adaptivity of gain and direction in oblique saccades. In Eye movements from physiology to cognition (pp. 181-190).

Deubel, H. (1989). Sensory and motor aspects of saccade control. European archives of psychiatry and neurological sciences, 239(1), 17-22.

Nyberg , L. , & Backman , L. (Eds.). (2004). New frontiers in cognitive aging . New York : Oxford University Press .

Doyon, J., & Benali, H. (2005). Reorganization and plasticity in the adult brain during learning of motor skills. Current opinion in neurobiology, 15(2), 161-167.

Dunne, S., Ellison, A., & Smith, D. T. (2015). Rewards modulate saccade latency but not exogenous spatial attention. Frontiers in psychology, 6, 1080.

Ebner, N. C., Freund, A. M., & Baltes, P. B. (2006). Developmental changes in personal goal orientation from young to late adulthood: from striving for gains to maintenance and prevention of losses. Psychology and aging, 21(4), 664.

Eyler, L. T., Sherzai, A., Kaup, A. R., & Jeste, D. V. (2011). A review of functional brain imaging correlates of successful cognitive aging. Biological psychiatry, 70(2), 115-122.

Fernández-Ruiz, J., Hall, C., Vergara, P., & Dıaz, R. (2000). Prism adaptation in normal aging: slower adaptation rate and larger aftereffect. Cognitive Brain Research, 9(3), 223-226.

Fernandez-Ruiz, J., Wong, W., Armstrong, I. T., & Flanagan, J. R. (2011). Relation between reaction time and reach errors during visuomotor adaptation. Behavioural brain research, 219(1), 8-14.

Flanders, M., Tillery, S. I. H., & Soechting, J. F. (1992). Early stages in a sensorimotor transformation. Behavioral and Brain Sciences, 15(2), 309-320.

Frens, M. A., & Van Opstal, A. J. (1994). Transfer of short-term adaptation in human saccadic eye movements. Experimental Brain Research, 100(2), 293-306.

Galea, J. M., Mallia, E., Rothwell, J., & Diedrichsen, J. (2015). The dissociable effects of punishment and reward on motor learning. Nature neuroscience, 18(4), 597.

Galea, J. M., Vazquez, A., Pasricha, N., Orban de Xivry, J. J., & Celnik, P. (2010). Dissociating the roles of the cerebellum and motor cortex during adaptive learning: the motor cortex retains what the cerebellum learns. Cerebral cortex, 21(8), 1761-1770.

Gaveau, V., Martin, O., Prablanc, C., Pélisson, D., Urquizar, C., & Desmurget, M. (2003). On-line modification of saccadic eye movements by retinal signals. Neuroreport, 14(6), 875-878.

Gaymard, B., Rivaud‑Péchoux, S., Yelnik, J., Pidoux, B., & Ploner, C. J. (2001). Involvement of the cerebellar thalamus in human saccade adaptation. European Journal of Neuroscience, 14(3), 554-560.

Gegenfurtner, K., Schütz, A., & Schneider, M. (2008). Saccadic gain adaptation follows perceived position. Journal of Vision, 8(6), 917-917a.

Glisky, E. L., & Marquine, M. J. (2009). Semantic and self-referential processing of positive and negative trait adjectives in older adults. Memory, 17(2), 144-157.

Goldberg, M. (1993). The role of the cerebellum in the control of saccadic eye movements. Role of the cerebellum and basal ganglia in voluntary movement, 203-211.

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. Trends in neurosciences, 15(1), 20-25.

Grady, C. (2012). The cognitive neuroscience of ageing. Nature Reviews Neuroscience, 13(7),

Grady, C. L., Bernstein, L. J., Beig, S., & Siegenthaler, A. L. (2002). The effects of encoding task on age-related differences in the functional neuroanatomy of face memory. Psychology and aging, 17(1), 7.

Grady, C. L., Maisog, J. M., Horwitz, B., Ungerleider, L. G., Mentis, M. J., Salerno, J. A., ... & Haxby, J. V. (1994). Age-related changes in cortical blood flow activation during visual processing of faces and location. Journal of Neuroscience, 14(3), 1450-1462.

Gutchess, A. H., Kensinger, E. A., Yoon, C., & Schacter, D. L. (2007). Ageing and the self-reference effect in memory. Memory, 15(8), 822-837.

Guthrie, B. L., Porter, J. D., & Sparks, D. L. (1983). Corollary discharge provides accurate eye position information to the oculomotor system. Science, 221(4616), 1193-1195.

Hadipour-Niktarash, A., Lee, C. K., Desmond, J. E., & Shadmehr, R. (2007). Impairment of retention but not acquisition of a visuomotor skill through time-dependent disruption of primary motor cortex. Journal of Neuroscience, 27(49), 13413-13419.

Harper, S. (2014). Economic and social implications of aging societies. Science, 346(6209), 587-591.

Harvey, M. (2005). Translation of 'Psychic paralysis of gaze, optic ataxia, and spatial disorder of attention' by Rudolph Bálint. Cogn. Neuropsychol. 12, 261–282. doi: 10.1080/02643299508251998

Hasher, L., & Zacks, R. T. (1984). Automatic processing of fundamental information: the case of frequency of occurrence. American Psychologist, 39(12), 1372.

Hasher, L., & Zacks, R. T. (1988). Working memory, comprehension, and aging: A review and a new view. In Psychology of learning and motivation (Vol. 22, pp. 193-225). Academic Press.

Haug, H., & Eggers, R. (1991). Morphometry of the human cortex cerebri and corpus striatum during aging. Neurobiology of aging, 12(4), 336-338.

Haug, H., & Eggers, R. (1991). Morphometry of the human cortex cerebri and corpus striatum during aging. Neurobiology of Aging, 12, 336-338.

Head, D., Buckner, R. L., Shimony, J. S., Williams, L. E., Akbudak, E., Conturo, T. E., ... & Snyder, A. Z. (2004). Differential vulnerability of anterior white matter in nondemented aging with minimal acceleration in dementia of the Alzheimer type: evidence from diffusion tensor imaging. Cerebral cortex, 14(4), 410-423.

Hebert, L. E., Weuve, J., Scherr, P. A., & Evans, D. A. (2013). Alzheimer disease in the United States (2010–2050) estimated using the 2010 census. Neurology, 80(19), 1778-1783.

Heckhausen, J. (1997). Developmental regulation across adulthood: Primary and secondary control of age-related challenges. Developmental psychology, 33(1), 176.

Hegele, M., & Heuer, H. (2013). Age-related variations of visuomotor adaptation result from both the acquisition and the application of explicit knowledge. Psychology and aging, 28(2), 333.

Heuer, A., Wolf, C., Schütz, A. C., & Schubö, A. (2017). The necessity to choose causes reward-related anticipatory biasing: Parieto-occipital alpha-band oscillations reveal suppression of low-value targets. Scientific reports, 7(1), 14318.

Heuer, H., & Hegele, M. (2008). Adaptation to visuomotor rotations in younger and older adults. Psychology and aging, 23(1), 190.

Hillman, C. H., Erickson, K. I., & Kramer, A. F. (2008). Be smart, exercise your heart: exercise effects on brain and cognition. Nature reviews neuroscience, 9(1), 58.

Hopp, J. J., & Fuchs, A. F. (2004). The characteristics and neuronal substrate of saccadic eye movement plasticity. Progress in neurobiology, 72(1), 27-53.

Huberdeau, D. M., Krakauer, J. W., & Haith, A. M. (2015). Dual-process decomposition in human sensorimotor adaptation. Current Opinion in Neurobiology, 33, 71-77.

Hultsch, D. F., Hertzog, C., Dixon, R. A., & Small, B. J. (1998). Memory change in the aged. Cambridge University Press.

Hunter, T., Sacco, P., Nitsche, M. A., & Turner, D. L. (2009). Modulation of internal model formation during force field‐induced motor learning by anodal transcranial direct current stimulation of primary motor cortex. The Journal of physiology, 587(12), 2949-2961.

Itti, L., Koch, C., & Niebur, E. (1998). A model of saliency-based visual attention for rapid scene analysis. IEEE Transactions on pattern analysis and machine intelligence, 20(11), 1254-1259.

Izawa, J., & Shadmehr, R. (2008). On-line processing of uncertain information in visuomotor control. Journal of Neuroscience, 28(44), 11360-11368.

Izawa, J., & Shadmehr, R. (2011). Learning from sensory and reward prediction errors during motor adaptation. PLoS computational biology, 7(3), e1002012.

Jimura, K., Locke, H. S., & Braver, T. S. (2010). Prefrontal cortex mediation of cognitive enhancement in rewarding motivational contexts. Proceedings of the National Academy of Sciences, 201002007.

Keightley, M. L., Winocur, G., Burianova, H., Hongwanishkul, D., & Grady, C. L. (2006). Age effects on social cognition: faces tell a different story. Psychology and Aging, 21(3), 558.

Kim, S., Ogawa, K., Lv, J., Schweighofer, N., & Imamizu, H. (2015). Neural substrates related to motor memory with multiple timescales in sensorimotor adaptation. PLoS biology, 13(12), e1002312.

Kojima, Y., Iwamoto, Y., & Yoshida, K. (2004). Memory of learning facilitates saccadic adaptation in the monkey. Journal of Neuroscience, 24(34), 7531-7539.

Kommerell, G., Olivier, D., & Theopold, H. (1976). Adaptive programming of phasic and tonic components in saccadic eye movements. Investigations of patients with abducens palsy. Investigative Ophthalmology & Visual Science, 15(8), 657-660.

Körding, K. P., & Wolpert, D. M. (2004). Bayesian integration in sensorimotor learning. Nature, 427(6971), 244.

Körding, K. P., Ku, S. P., & Wolpert, D. M. (2004). Bayesian integration in force estimation. Journal of neurophysiology, 92(5), 3161-3165.

Krakauer, J. W., & Shadmehr, R. (2006). Consolidation of motor memory. Trends in neurosciences, 29(1), 58-64.

Krakauer, J. W., Ghez, C., & Ghilardi, M. F. (2005). Adaptation to visuomotor transformations: consolidation, interference, and forgetting. Journal of Neuroscience, 25(2), 473-478.

Krakauer, J. W., Ghilardi, M. F., & Ghez, C. (1999). Independent learning of internal models for kinematic and dynamic control of reaching. Nature neuroscience, 2(11), 1026.

Krakauer, J. W., Ghilardi, M. F., Mentis, M., Barnes, A., Veytsman, M., Eidelberg, D., & Ghez, C. (2004). Differential cortical and subcortical activations in learning rotations and gains for reaching: a PET study. Journal of neurophysiology, 91(2), 924-933.

Krakauer, J. W., Pine, Z. M., Ghilardi, M. F., & Ghez, C. (2000). Learning of visuomotor transformations for vectorial planning of reaching trajectories. Journal of Neuroscience, 20(23), 8916-8924.

Krebs, H. I., Brashers‐Krug, T., Rauch, S. L., Savage, C. R., Hogan, N., Rubin, R. H., ... & Alpert, N. M. (1998). Robot‐aided functional imaging: Application to a motor learning study. Human brain mapping, 6(1), 59-72.

Leigh, R. J., & Zee, D. S. (2015). The neurology of eye movements. Oxford University Press, USA.

Leon, M. I., & Shadlen, M. N. (1999). Effect of expected reward magnitude on the response of neurons in the dorsolateral prefrontal cortex of the macaque. Neuron, 24(2), 415-425.

Li, C. S. R., Padoa-Schioppa, C., & Bizzi, E. (2001). Neuronal correlates of motor performance and motor learning in the primary motor cortex of monkeys adapting to an external force field. Neuron, 30(2), 593-607.

Lindenberger, U., & Baltes, P. B. (1994). Sensory functioning and intelligence in old age: a strong connection. Psychology and aging, 9(3), 339.

Lindenberger, U., Mayr, U., & Kliegl, R. (1993). Speed and intelligence in old age. Psychology and aging, 8(2), 207.

Lindenberger, U., Scherer, H., & Baltes, P. B. (2001). The strong connection between sensory and cognitive performance in old age: not due to sensory acuity reductions operating during cognitive assessment. Psychology and aging, 16(2), 196.

Madden, D. J., Turkington, T. G., Provenzale, J. M., Denny, L. L., Hawk, T. C., Gottlob, L. R., & Coleman, R. E. (1999). Adult age differences in the functional neuroanatomy of verbal recognition memory. Human brain mapping, 7(2), 115-135.

Marik, P. E. (2015). The cost of inappropriate care at the end of life: implications for an aging population. American Journal of Hospice and Palliative Medicine®, 32(7), 703-708.

Markowitz, D. A., Shewcraft, R. A., Wong, Y. T., & Pesaran, B. (2011). Competition for visual selection in the oculomotor system. Journal of Neuroscience, 31(25), 9298-9306.

Martin, T. A., Keating, J. G., Goodkin, H. P., Bastian, A. J., & Thach, W. T. (1996). Throwing while looking through prisms: I. Focal olivocerebellar lesions impair adaptation. Brain, 119(4), 1183-1198.

Martins, R., Simard, F., Provost, J. S., & Monchi, O. (2012). Changes in regional and temporal patterns of activity associated with aging during the performance of a lexical set-shifting task. Cerebral Cortex, 22(6), 1395-1406.

Maschke, M., Gomez, C. M., Ebner, T. J., & Konczak, J. (2004). Hereditary cerebellar ataxia progressively impairs force adaptation during goal-directed arm movements. Journal of neurophysiology, 91(1), 230-238.

Mazzoni, P., & Krakauer, J. W. (2006). An implicit plan overrides an explicit strategy during visuomotor adaptation. Journal of neuroscience, 26(14), 3642-3645.

McDougle, S. D., Bond, K. M., & Taylor, J. A. (2015). Explicit and implicit processes constitute the fast and slow processes of sensorimotor learning. Journal of Neuroscience, 35(26), 9568-9579.

McDowell, J. E., Dyckman, K. A., Austin, B. P., & Clementz, B. A. (2008). Neurophysiology and neuroanatomy of reflexive and volitional saccades: evidence from studies of humans. Brain and cognition, 68(3), 255-270.

McGovern, D. P., Hayes, A., Kelly, S. P., & O'Connell, R. (2017). Reconciling age-related changes in behavioural and neural indices of human perceptual decision making. bioRxiv, 228965.

McLaughlin, S. C. (1967). Parametric adjustment in saccadic eye movements. Perception & Psychophysics, 2(8), 359-362.

McNay EC, Willingham DB. Deficit in learning of a motor skill requiring strategy, but not of perceptualmotor recalibration, with aging. Learn Mem 1998;4:411–20.

McNay, E. C., & Willingham, D. B. (1998). Deficit in learning of a motor skill requiring strategy, but not of perceptuomotor recalibration, with aging. Learning & Memory, 4(5), 411-420.

Miller, J. M., Anstis, T., & Templeton, W. B. (1981). Saccadic plasticity: parametric adaptive control by retinal feedback. Journal of Experimental Psychology: Human Perception and Performance, 7(2), 356.

Milstein, D. M., & Dorris, M. C. (2007). The influence of expected value on saccadic preparation. Journal of Neuroscience, 27(18), 4810-4818.

Moses, H., Matheson, D. H., Dorsey, E. R., George, B. P., Sadoff, D., & Yoshimura, S. (2013). The anatomy of health care in the United States. Jama, 310(18), 1947-1964.

Munoz, D. P., & Everling, S. (2004). Look away: the anti-saccade task and the voluntary control of eye movement. Nature Reviews Neuroscience, 5(3), 218.

Munoz, D. P., Broughton, J. R., Goldring, J. E., & Armstrong, I. T. (1998). Age-related performance of human subjects on saccadic eye movement tasks. Experimental brain research, 121(4), 391-400.

Navalpakkam, V., Koch, C., Rangel, A., & Perona, P. (2010). Optimal reward harvesting in complex perceptual environments. Proceedings of the National Academy of Sciences, 107(11), 5232-5237.

Neumann, O. (1987). Beyond capacity: A functional view of attention. Perspectives on perception and action, 14, 361-394.

Nezafat, R., Shadmehr, R., & Holcomb, H. H. (2001). Long-term adaptation to dynamics of reaching movements: a PET study. Experimental Brain Research, 140(1), 66-76.

Nikooyan, A. A., & Ahmed, A. A. (2014). Reward feedback accelerates motor learning. Journal of neurophysiology, 113(2), 633-646.

Noto, C. T., & Robinson, F. R. (2001). Visual error is the stimulus for saccade gain adaptation. Cognitive brain research, 12(2), 301-305.

Noto, C. T., Watanabe, S., & Fuchs, A. F. (1999). Characteristics of simian adaptation fields produced by behavioral changes in saccade size and direction. Journal of Neurophysiology, 81(6), 2798-2813.

Nyberg, L., & Bäckman, L. (2004). Cognitive aging: a view from brain imaging. New frontiers in cognitive aging, 135-160.

Optican, L. M., & Robinson, D. A. (1980). Cerebellar-dependent adaptive control of primate saccadic system. Journal of Neurophysiology, 44(6), 1058-1076.

O'Regan, J. K., & Noë, A. (2001). A sensorimotor account of vision and visual consciousness. Behavioral and brain sciences, 24(5), 939-973.

Park, D. C., & Reuter-Lorenz, P. (2009). The adaptive brain: aging and neurocognitive scaffolding. Annual review of psychology, 60, 173-196.

Park, D. C., Lautenschlager, G., Hedden, T., Davidson, N. S., Smith, A. D., & Smith, P. K. (2002). Models of visuospatial and verbal memory across the adult life span. Psychology and aging, 17(2), 299.

Paxton, J. L., Barch, D. M., Racine, C. A., & Braver, T. S. (2007). Cognitive control, goal maintenance, and prefrontal function in healthy aging. Cerebral cortex, 18(5), 1010-1028.

Paz, R., Boraud, T., Natan, C., Bergman, H., & Vaadia, E. (2003). Preparatory activity in motor cortex reflects learning of local visuomotor skills. Nature neuroscience, 6(8), 882.

Peltsch, A., Hemraj, A., Garcia, A., & Munoz, D. P. (2011). Age-related trends in saccade characteristics among the elderly. Neurobiology of aging, 32(4), 669-679.

Pélisson, D., Alahyane, N., Panouilleres, M., & Tilikete, C. (2010). Sensorimotor adaptation of saccadic eye movements. Neuroscience & Biobehavioral Reviews, 34(8), 1103-1120.

Perenin, M. T., & Vighetto, A. (1988). Optic ataxia: A specific disruption in visuomotor mechanisms: I. Different aspects of the deficit in reaching for objects. Brain, 111(3), 643-674.

Perlmutter, M. (1978). What is memory aging the aging of?. Developmental Psychology, 14(4), 330.

Persson, J., Nyberg, L., Lind, J., Larsson, A., Nilsson, L.G., Ingvar, M., &Buckner, R.L. (2006). Structure–function correlates of cognitive decline in aging. Cerebral Cortex, 16, 907–915.

Pierrot-Deseilligny, C., Müri, R. M., Ploner, C. J., Gaymard, B., & Rivaud-Péchoux, S. (2003). Cortical control of ocular saccades in humans: a model for motricity. In Progress in brain research (Vol. 142, pp. 3-17). Elsevier.

Pierson, W. R., & Montoye, H. J. (1958). Movement time, reaction time and age. Journal of Gerontology, 13(4), 418-421.

Pisella, L., Grea, H., Tilikete, C., Vighetto, A., Desmurget, M., Rode, G., ... & Rossetti, Y. (2000). An 'automatic pilot'for the hand in human posterior parietal cortex: toward reinterpreting optic ataxia. Nature neuroscience, 3(7), 729.

Pisella, L., Rossetti, Y., & Rode, G. (2017). Optic ataxia in Bálint-Holmes syndrome. Annals of physical and rehabilitation medicine, 60(3), 148-154.

Platt, M. L., & Glimcher, P. W. (1999). Neural correlates of decision variables in parietal cortex. Nature, 400(6741), 233.

Quattrocchi, G., Greenwood, R., Rothwell, J. C., Galea, J. M., & Bestmann, S. (2017). Reward and punishment enhance motor adaptation in stroke. J Neurol Neurosurg Psychiatry, 88(9), 730-736.

Que´ PASA? The Posterior--Anterior Shift in Aging. Simon W. Davis, Nancy A. Dennis, Sander M. Daselaar, Mathias S. Fleck1,2 and Roberto Cabeza1,2 2008

Rabe, K., Livne, O., Gizewski, E. R., Aurich, V., Beck, A., Timmann, D., & Donchin, O. (2009). Adaptation to visuomotor rotation and force field perturbation is correlated to different brain areas in patients with cerebellar degeneration. Journal of neurophysiology, 101(4), 1961-1971.

Rayner, K., Castelhano, M. S., & Yang, J. (2009). Eye movements and the perceptual span in older and younger readers. Psychology and aging, 24(3), 755.

Rayner, K., Reichle, E. D., Stroud, M. J., Williams, C. C., & Pollatsek, A. (2006). The effect of word frequency, word predictability, and font difficulty on the eye movements of young and older readers. Psychology and aging, 21(3), 448.

Raz, N. (2000). Aging of the brain and its impact on cognitive performance: Integration of structural and functional findings.

Raz, N., Ghisletta, P., Rodrigue, K. M., Kennedy, K. M., & Lindenberger, U. (2010). Trajectories of brain aging in middle-aged and older adults: regional and individual differences. Neuroimage, 51(2), 501-511.

Raz, N., Lindenberger, U., Rodrigue, K. M., Kennedy, K. M., Head, D., Williamson, A., ... & Acker, J. D. (2005). Regional brain changes in aging healthy adults: general trends, individual differences and modifiers. Cerebral cortex, 15(11), 1676-1689.

Reuter-Lorenz PA, Jonides J, Smith EE, Hartley A, Miller A, Marshuetz C, Koeppe RA (2000): Age differences in the frontal lateralization of verbal and spatial working memory revealed by PET. J Cogn Neurosci 12:174–187

Richardson, A. G., Overduin, S. A., Valero-Cabré, A., Padoa-Schioppa, C., Pascual-Leone, A., Bizzi, E., & Press, D. Z. (2006). Disruption of primary motor cortex before learning impairs memory of movement dynamics. Journal of Neuroscience, 26(48), 12466-12470.

Riediger, M., & Freund, A. M. (2006). Focusing and restricting: Two aspects of motivational selectivity in adulthood. Psychology and Aging, 21(1), 173.

Robinson DA. 1975. Oculomotor control signals. In Basic Mechanisms of Ocular Motility and Their Clinical Implications, ed. P Bachyrita, G Lennerstrand, pp. 337–74. Oxford, UK: Pergamon

Robinson, F. R., Fuchs, A. F., & Noto, C. T. (2002). Cerebellar influences on saccade plasticity. Annals of the New York Academy of Sciences, 956(1), 155-163.

Roller C, Cohen H, Kimball K, Bloomberg J. Effects of normal aging on visuo-motor plasticity. Neurobiol Aging 2002;23:117–23.

Roller, C. A., Cohen, H. S., Kimball, K. T., & Bloomberg, J. J. (2002). Effects of normal aging on visuo-motor plasticity. Neurobiology of aging, 23(1), 117-123.

Rosen, A. C., Prull, M. W., Gabrieli, J. D., Stoub, T., O'hara, R., Friedman, L., ... & deToledo-Morrell, L. (2003). Differential associations between entorhinal and hippocampal volumes and memory performance in older adults. Behavioral neuroscience, 117(6), 1150.

Rossetti, Y., Revol, P., McIntosh, R., Pisella, L., Rode, G., Danckert, J., ... & Michel, F. (2005). Visually guided reaching: bilateral posterior parietal lesions cause a switch from fast visuomotor to slow cognitive control. Neuropsychologia, 43(2), 162-177.

Rossi, S., Miniussi, C., Pasqualetti, P., Babiloni, C., Rossini, P.M., & Cappa, S.F. (2004). Age-related functional changes of prefrontal cortex in long-term memory: A repetitive transcranial magnetic stimulation study. Journal of Neuroscience, 24, 7939–7944.

Salat, D. H., Kaye, J. A., & Janowsky, J. S. (2002). Greater orbital prefrontal volume selectively predicts worse working memory performance in older adults. Cerebral Cortex, 12(5), 494-505.

Salthouse , T.A. (2010a). Major issues in cognitive aging. New York: Oxford University Press .

Salthouse, T. A. (1993). Speed and knowledge as determinants of adult age differences in verbal tasks. Journal of Gerontology, 48(1), P29-P36.

Salthouse, T. A. (1994). The nature of the influence of speed on adult age differences in cognition. Developmental Psychology, 30(2), 240.

Salthouse, T. A. (1996). The processing-speed theory of adult age differences in cognition. Psychological review, 103(3), 403.

Salthouse, T. A. (2010a). Influence of age on practice effects in longitudinal neurocognitive change. Neuropsychology, 24(5), 563.

Salthouse, T. A. (2010b). Selective review of cognitive aging. Journal of the International neuropsychological Society, 16(5), 754-760.

Saur D, Ronneberger O, Kummerer D, Mader I, Weiller C, Kloppel S. 2010. Early functional magnetic resonance imaging activations predict language outcome after stroke. Brain. 133:1252--1264.

Schütz, A. C., & Souto, D. (2015). Perceptual task induces saccadic adaptation by target selection. Frontiers in human neuroscience, 9, 566.

Schütz, A. C., Braun, D. I., & Gegenfurtner, K. R. (2011). Eye movements and perception: A selective review. Journal of vision, 11(5), 9-9.

Schütz, A. C., Kerzel, D., & Souto, D. (2014). Saccadic adaptation induced by a perceptual task. Journal of vision, 14(5), 4-4.

Scudder, C. A., Batourina, E. Y., & Tunder, G. S. (1998). Comparison of two methods of producing adaptation of saccade size and implications for the site of plasticity. Journal of Neurophysiology, 79(2), 704-715.

Scudder, C. A., Kaneko, C. R., & Fuchs, A. F. (2002). The brainstem burst generator for saccadic eye movements. Experimental brain research, 142(4), 439-462.

Seidler, R. D. (2006). Differential effects of age on sequence learning and sensorimotor adaptation. Brain research bulletin, 70(4-6), 337-346.

Shadlen, M. N., & Kiani, R. (2013). Decision making as a window on cognition. Neuron, 80(3), 791-806.

Shadmehr, R., & Holcomb, H. H. (1997). Neural correlates of motor memory consolidation. Science, 277(5327), 821-825.

Shadmehr, R., Smith, M. A., & Krakauer, J. W. (2010). Error correction, sensory prediction, and adaptation in motor control. Annual review of neuroscience, 33, 89-108.

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Smith, M. A., & Shadmehr, R. (2005). Intact ability to learn internal models of arm dynamics in Huntington's disease but not cerebellar degeneration. Journal of Neurophysiology, 93(5), 2809-2821.

Smith, M. A., Ghazizadeh, A., & Shadmehr, R. (2006). Interacting adaptive processes with different timescales underlie short-term motor learning. PLoS biology, 4(6), e179.

Snow, R., Hore, J., & Vilis, T. (1985). Adaptation of saccadic and vestibulo-ocular systems after extraocular muscle tenectomy. Investigative ophthalmology & visual science, 26(7), 924-931.

Sohn, J. W., & Lee, D. (2006). Effects of reward expectancy on sequential eye movements in monkeys. Neural networks, 19(8), 1181-1191.

Spilich, G. J. (1983). Life-span components of text processing: Structural and procedural differences. Journal of Memory and Language, 22(2), 231.

Spreng, R. N., Wojtowicz, M., & Grady, C. L. (2010). Reliable differences in brain activity between young and old adults: a quantitative meta-analysis across multiple cognitive domains. Neuroscience & Biobehavioral Reviews, 34(8), 1178-1194.

Spreng, R.N., Schacter, D.L., 2012. Default network modulation and large-scalenetwork interactivity in healthy young and old adults. Cereb. Cortex 22, 2610–2621.

Stankevich, B. A., & Geng, J. J. (2015). The modulation of reward priority by top-down knowledge. Visual Cognition, 23(1-2), 206-228. doi: 10.1080/13506285.2014.981626

Staudinger, U. M., Freund, A. M., Linden, M., & Maas, I. (1999). Self, personality, and life regulation: Facets of psychological resilience in old age. Staudinger, U.M., Freund, A.M., Linden, M., Maas, I., 1999. Self, personality, and liferegulation: facets of psychological resilience in old age. In: Baltes, P.B., Mayer,K.U. (Eds.), The Berlin Aging Study: Aging from 70 to 100. CambridgeUniversity Press, New York, pp. 302–328.

Stebbins, G. T., Carrillo, M. C., Dorfman, J., Dirksen, C., Desmond, J. E., Turner, D. A., ... & Gabrieli, J. D. (2002). Aging effects on memory encoding in the frontal lobes. Psychology and aging, 17(1), 44.

Straube, A., Fuchs, A. F., Usher, S., & Robinson, F. R. (1997). Characteristics of saccadic gain adaptation in rhesus macaques. Journal of neurophysiology, 77(2), 874-895.

Sugiura, M. (2016). Functional neuroimaging of normal aging: declining brain, adapting brain. Ageing Research Reviews, 30, 61-72.

Tatler, B. W., & Vincent, B. T. (2009). The prominence of behavioural biases in eye guidance. Visual Cognition, 17(6-7), 1029-1054.

Theeuwes, J., & Belopolsky, A. V. (2012). Reward grabs the eye: oculomotor capture by rewarding stimuli. Vision research, 74, 80-85. doi: 10.1016/j.visres.2012.07.024

Therrien, A. S., Wolpert, D. M., & Bastian, A. J. (2015). Effective reinforcement learning following cerebellar damage requires a balance between exploration and motor noise. Brain, 139(1), 101-114.

Toscani, M., Valsecchi, M., & Gegenfurtner, K. R. (2013a). Optimal sampling of visual information for lightness judgments. Proceedings of the National Academy of Sciences, 110(27), 11163-11168.

Toscani, M., Valsecchi, M., & Gegenfurtner, K. R. (2013b). Selection of visual information for lightness judgements by eye movements. Phil. Trans. R. Soc. B, 368(1628), 20130056.

Tulving, E. (1984). Multiple learning and memory systems. In Advances in Psychology, 18, 163-184.

Tulving, E., Kapur, S., Craik, F. I., Moscovitch, M., & Houle, S. (1994). Hemispheric encoding/retrieval asymmetry in episodic memory: positron emission tomography findings. Proceedings of the National Academy of Sciences, 91(6), 2016-2020.

Tyler LK, Marslen-Wilson WD, Randall B, Wright P, Devereux BJ, Zhuang J, Papoutsi M, Stamatakis EA. 2011. Left inferior frontal cortex and syntax: function, structure and behaviour in patients with left hemisphere damage. Brain. 134:415--431.

van der Kooij, K., & Overvliet, K. E. (2016). Rewarding imperfect motor performance reduces adaptive changes. Experimental brain research, 234(6), 1441-1450.

Wächter, T., Lungu, O. V., Liu, T., Willingham, D. T., & Ashe, J. (2009). Differential effect of reward and punishment on procedural learning. Journal of Neuroscience, 29(2), 436-443.

Wallman, J., & Fuchs, A. F. (1998). Saccadic gain modification: visual error drives motor adaptation. Journal of neurophysiology, 80(5), 2405-2416.

Warabi, T., Kase, M., & Kato, T. (1984). Effect of aging on the accuracy of visually guided saccadic eye movement. Annals of Neurology: Official Journal of the American Neurological Association and the Child Neurology Society, 16(4), 449-454.

Watanabe, K., Lauwereyns, J., & Hikosaka, O. (2003). Neural correlates of rewarded and unrewarded eye movements in the primate caudate nucleus. Journal of Neuroscience, 23(31), 10052-10057.

Wayne, P. M., Walsh, J. N., Taylor‑Piliae, R. E., Wells, R. E., Papp, K. V., Donovan, N. J., & Yeh, G. Y. (2014). Effect of Tai Chi on cognitive performance in older adults: Systematic review and meta‑Analysis. Journal of the American Geriatrics Society, 62(1), 25-39.

Wei, K., & Kording, K. (2009). Relevance of error: what drives motor adaptation?. Journal of neurophysiology, 101(2), 655-664.

Wei, K., & Körding, K. (2010). Uncertainty of feedback and state estimation determines the speed of motor adaptation. Frontiers in computational neuroscience, 4, 11.

Weiner, M. J., Hallett, M., & Funkenstein, H. H. (1983). Adaptation to lateral displacement of vision in patients with lesions of the central nervous system. Neurology, 33(6), 766-766.

West, R. L. (1996). An application of prefrontal cortex function theory to cognitive aging. Psychological bulletin, 120(2), 272.

Wigmore, V., Tong, C., & Flanagan, J. R. (2002). Visuomotor rotations of varying size and direction compete for a single internal model in a motor working memory. Journal of Experimental Psychology: Human Perception and Performance, 28(2), 447-457.

Wolf, C., Heuer, A., Schubö, A., & Schütz, A. C. (2017). The necessity to choose causes the effects of reward on saccade preparation. Scientific reports, 7(1), 16966.

Wolpert, D. M., & Flanagan, J. R. (2016). Computations underlying sensorimotor learning. Current opinion in neurobiology, 37, 7-11.

Wong, A. L., & Shelhamer, M. (2012). Using prediction errors to drive saccade adaptation: the implicit double-step task. Experimental brain research, 222(1-2), 55-64.

Wright, R. E. (1981). Aging, divided attention, and processing capacity. Journal of Gerontology, 36(5), 605-614.

Xu-Wilson, M., Chen-Harris, H., Zee, D. S., & Shadmehr, R. (2009). Cerebellar contributions to adaptive control of saccades in humans. Journal of Neuroscience, 29(41), 12930-12939.

Zacks, R. T. (1982). Encoding Strategies Used by Young and Elderly Adults in a Keeping Track Ta. Journal of Gerontology, 37(2), 203-211.

Zee, D. S., Optican, L. M., Cook, J. D., Robinson, D. A., & Engel, W. K. (1976). Slow saccades in spinocerebellar degeneration. Archives of neurology, 33(4), 243-251.

Publications

Huang, J., Hegele, M., & Billino, J. (2018). Motivational modulation of age-related effects on reaching adaptation. *Frontiers in Psychology*, , 9, 2285, 1-13.

Huang, J., Gegenfurtner, K. R., Schütz, A. C., & Billino, J. (2017). Age effects on saccadic adaptation: evidence from different paradigms reveals specific vulnerabilities. *Journal of vision*, 17(6), 9-9.

Huang, J., …, & Billino, J. Age-related changes in modulation of saccadic control by salience and value. *In preparation*.

Declaration

"I hereby declare that I have prepared the thesis at hand independently and without undue aid or the use of any resources other than indicated within the thesis. All parts of my thesis taken either verbatim or analogously from the published or unpublished works of or based on oral communications with others are indicated as such. Regarding all aspects of my scientific enquiries as they appear in my thesis, I have upheld the tenets of good scientific practice as laid out in the "Satzung der Justus-Liebig-Universität Gießen zur Sicherung guter wissenschaftlicher Praxis" and complied with the precept of ethics, data protection and animal welfare. I declare that I have neither directly nor indirectly given monetary or any other valuable considerations to others in connection with the thesis at hand. I declare that I have not presented the thesis at hand, either in an identical or similar form, to an examination office or agency in Germany or any other country as part of any examination or degree. All materials from other sources as well as all works performed by others used or directly referenced within the thesis at hand have been indicated as such. In particular, all persons involved directly or indirectly in the development of the thesis at hand have been named. I agree with the screening of my thesis for plagiarism via offline or online detection-software."

Jing Huang