Nadine Diersch: Action Prediction in the Aging Mind. Leipzig: Max Planck Institute for Human Cognitive and Brain Sciences, 2013 (MPI Series in Human Cognitive and Brain Sciences; 151)

ACTION PREDICTION IN THE AGING MIND

Impressum

Max Planck Institute for Human Cognitive and Brain Sciences, 2013

Druck: Sächsisches Druck- und Verlagshaus Direct World, Dresden
Titelbild: © Felix Schneeweiß „No. 73", 2013

ISBN 978-3-941504-35-6

ACTION PREDICTION IN THE AGING MIND

Von der Fakultät für Biowissenschaften, Pharmazie und Psychologie

der Universität Leipzig

genehmigte

DISSERTATION

zur Erlangung des akademischen Grades

Doctor rerum naturalium
(Dr. rer. nat.)

vorgelegt von

Diplom-Psychologin Nadine Diersch,

geboren am 13. März 1981 in Zwickau, Deutschland.

Dekan:	Prof. Dr. Andrea A. Robitzki
Gutachter:	Prof. Dr. Sonja A. Kotz
	Prof. Dr. Joachim Hermsdörfer
	Prof. Dr. Ute Kunzmann
Tag der Verteidigung:	02. Mai 2013

BIBLIOGRAPHIC DETAILS

Dipl. – Psych. Nadine Diersch

Action Prediction in the Aging Mind

Fakultät für Biowissenschaften, Pharmazie und Psychologie
Universität Leipzig
Dissertation
184 Seiten, 269 Literaturangaben, 12 Abbildungen, 7 Tabellen

One of the most essential abilities that enables us to navigate successfully through our social environment and interact with others is the prediction of actions that are performed by other individuals. Based on the widely held assumption of a shared representation between action execution and action observation, the crucial feature for effective prediction is that an observed action is part of the observer's motor repertoire. This assumption is supported by a vast amount of neuroimaging studies that provide evidence for a remarkable overlap between brain regions recruited during action execution and action observation. At present, however, it is still poorly understood whether and how predictive abilities and their underlying neural mechanisms change over the lifespan due to age-related changes in the brain and body. Therefore, this dissertation investigated how action prediction changes with advancing age and the observers' level of sensorimotor experience. In two behavioral experiments, evidence was found that there might be a specific age-related decline in the ability to predict observed actions, possibly based on less precise internal action representations. The results further showed that extensive amounts of sensorimotor experience seem to enable experts to predict actions from their domain of expertise more precisely even in older age. In a follow-up fMRI experiment, age-related changes in neural activation patterns during action prediction were examined. The results showed that this task engages a distributed network in the brain that is modulated by the content of the observed actions and the age and experience of the observer. Compared to younger adults, older adults seemed to create a visual image of the observed actions and evaluated its features instead of effectively exploiting their sensorimotor system. Taken together, this dissertation provides new and important insights into the way older adults predict observed actions, as well as the first evidence demonstrating how aging impacts the neural underpinnings of this process.

ACKNOWLEDGEMENTS

First of all, I want to thank my supervisors, Martina Rieger and Simone Schütz-Bosbach, for all the feedback and support you offered throughout my PhD. I have benefited very much from our discussions and your way of guiding me without setting limits to my ideas. I am also thankful to my collaborators Emily S. Cross, Karsten Müller, and Waltraud Stadler for providing methodological but also general support at different stages of the PhD. I am more than grateful to have had the opportunity to work with you.

Special thanks go to Wolfgang Prinz and the members of the former Department of Psychology and the Research Group "Body and Self" at the MPI for Human Cognitive and Brain Sciences. It has been a wonderful experience to conduct my research in this exceptional working environment. In particular, I would like to thank my colleagues Miriam Beisert, Esther Kühn, Derek Ott, Peggy Sparenberg, Andrea Walter, Carmen Weiss and Norbert Zmyj for creating a productive and friendly working atmosphere in Leipzig. Further, I wish to acknowledge the great assistance of Juliane Eberth, Franziska Ritschel, Silke Straube, and especially Tanja Schorch in realizing the experiments and recruiting the participants.

I was also privileged to be part of the interdisciplinary MaxNetAging Research School (MNARS). The initial period of my PhD at the MPI for Demographic Research in Rostock was extremely stimulating and helped me to gain invaluable skills for conducting my research without losing track of the big picture. I wish to thank my fellow PhD students, particularly Friederike Heinze, Fanny Kluge, Franziska Kunz, and Susanne Passow, for fruitful discussions and collegial support. Thanks also to Rainer Heuer, Annett Döpke, and Mirko Sporket for great organizational support.

Ingeburg Böhm and the athletes from the USG Chemnitz e. V., Olivia Dittrich and Martin Rappe, deserve special thanks for their participation in developing the stimulus material for the figure skating experiments. In addition, I thank Anne Heusinger and Siegfried Gauggel from the Zentrum für Psychotherapie gGmbH in Chemnitz, who provided office space that enabled me to collect data close to the figure skaters' area of residence.

I am also grateful to Luise Albrecht, Hans-Joachim Gehre, Michaela Kermer Bettina Schnabel, and Felix Schneeweiß who devoted their time to act in the different video sets. To my family and friends, thanks for always believing in me and encouraging me to master all the challenges I was facing during my PhD. In particular, I wish to thank Nils Ehlers for all your patience and loving support.

Last but not least, I would like to thank MaxNetAging and the MPI for Human Cognitive and Brain Sciences for funding support.

TABLE OF CONTENTS

I. INTRODUCTION

In daily life, we frequently encounter the situation where we must navigate our way through a busy street, bustling with people hurrying in a multitude of directions. In order to successfully manage such situations without bumping into someone else all the time, we must monitor other people's actions so that our own actions do not interfere with those made by them. Usually we do reasonably well in flexibly reacting and adapting to such changes in our social environment. Empirical evidence suggests that we, as observers, not only rely on what we see but also generate predictions about the potential course of others' actions (cf., Schütz-Bosbach & Prinz, 2007). Based on the widely held assumption of a shared representation between action execution and action observation, the crucial feature for effective prediction is that the observed action is part of the observer's motor repertoire. This enables him or her to "slip into another's shoes". This assumption is further supported by a vast amount of neuroimaging studies that provide evidence for a remarkable overlap between brain regions recruited during action execution and action observation. Overall, prediction is considered to play a fundamental role in cognitive and neural processing for guiding goal-directed and adaptive behavior (cf., Brown & Brüne, 2012; Bubic, Von Cramon, & Schubotz, 2010).

At present, however, it is still poorly understood whether and how our predictive abilities and their underlying neural mechanisms change over the lifespan due to age-related changes in the brain and body. Only very few studies addressed these questions from a lifespan perspective, despite the growing number of older people in our society. Today already one out of nine people all over the world is aged 60 and over and this proportion is expected to increase up to 22% by the year 2050 (United Nations, 2010). The main reasons for this increase are lower fertility rates and rising life expectancies that result in growing numbers of individuals reaching ages well beyond 80 (Christensen, Doblhammer, Rau, & Vaupel, 2009). In the light of this demographic change, it is essential to include older adults as part of the scientific study for a better understanding of changes in action prediction over the lifespan. New insights into the way these processes operate in older age groups may have important applications for the development of prevention and intervention programs that help older adults to maintain an active and independent lifestyle in the community over many years.

Therefore, this dissertation aimed to investigate how the ability to predict observed actions changes with advancing age and the observers' level of sensorimotor experience. More specifically, the accuracy and timing in action prediction and its neural correlates were examined in different groups of healthy older and younger adults during the observation of temporarily occluded action sequences. In the following, it will be outlined what is known so far about action prediction and its implementation in the human brain based on the assumption that action execution and action observation share a common representational domain. In addition, age-related changes in action perception and general changes in the aging brain will be reviewed. Finally, the aim of the dissertation and its experimental approach will be formulated based on the consideration of these two lines of research. The action occlusion paradigm will be introduced as a measure for action prediction. Before summarizing the main results and discussing their implications and caveats, the empirical findings will be presented in the form of two manuscripts. The first manuscript has been published in the journal *Psychological Research* and the second manuscript is currently under review in a peer-reviewed journal:

II. Representing others' actions: The role of expertise in the aging mind (Diersch, Cross, Stadler, Schütz-Bosbach, & Rieger, 2012) [see page 23],

III. Action prediction in younger versus older adults: Neural correlates of motor familiarity (Diersch et al., submitted) [see page 55].

SHARED REPRESENTATIONS IN ACTION AND PERCEPTION

How do we perceive, understand, and anticipate the actions of other individuals? According to the traditional information processing view of human cognition, cognition is defined as an abstract computation on amodal symbols that are created based on representations in modal systems for action, perception, and introspection (cf., Barsalou, 2008; Niedenthal, Barsalou, Winkielman, Krauth-Gruber, & Ric, 2005). However, it remains unclear how these symbols are implemented in the human brain and there is a large body of empirical evidence arguing for a wide variety of interactions between these seemingly different entities (see Barsalou, 2008; Hommel, Muesseler, Aschersleben, & Prinz, 2001 for reviews). As a consequence, embodied approaches to cognition, which emphasize sensorimotor processing in cognition, are receiving increasing attention in the cognitive (neuro)sciences (cf., Prinz, 2012). Although single embodied conceptualizations may differ in some aspects depending on their particular focus (e.g., motor cognition, cognitive linguistics, social cognition), they all share the assumption that mechanisms such as reenactment, simulation, situated action, and bodily states are central to cognition (Barsalou, 2008; Wilson, 2002). In the following, prominent conceptualizations of motor cognition will be outlined that offer an explanation as to how observed actions may be anticipated based on a common representational basis for both action and perception.

According to the simulation hypothesis of motor cognition proposed by Jeannerod (2006; 2001), the observation of another person performing an action automatically activates an internal action representation or motor program of how the observer's body would perform that particular action. This action representation is anticipatory and includes the goal of the observed action, the way to reach the goal, and its consequences. Within this framework, the covert representation and the actual execution of an action are assumed to represent a continuum in which the former forms the hidden part of the latter. Thus, a covertly represented action does not necessarily result in overt movement. An executed action, on the contrary, implies the existence of an internal action representation. One frequently observed phenomenon in favor for this assumption is that it takes approximately the same time to imagine (i.e., to covertly represent) and to execute a given action (cf., Decety, 2002; Jeannerod, 2001).

Another influential approach on the link between action and perception is the common coding principle proposed by Prinz (1997). According to this approach, action execution and action observation share a common representational domain. In contrast to the simulation hypothesis, it assumes that planned actions are coded in terms of the perceivable effects they should generate (i.e., the action goal). Thus, the representation of an action effect has an essential impact on the planning and the control of that action. Prinz and colleagues further elaborated this principle in their Theory of Event Coding (TEC; Hommel et al., 2001). This theory posits that late perceptual processing and early action planning are functionally equivalent processes that are represented in networks of so-called event codes. These event codes consist of feature codes representing abstract (distal) attributes of the perceived or produced event (e.g., orientation, speed, location, color). For example, the observation of a cat crossing the street might activate feature codes that represent attributes such as “left”, “black”, and “fast”. The authors further argued that the activation of feature codes facilitates other events that share some of the same features. The observation of the cat would consequently facilitate events such as running fast to the left as compared to walking slowly to the right. After being activated, these feature codes are integrated into a coherent event-code and are not available anymore for the representation of other events. This results in interference with the coding of other, feature-overlapping events. In accordance with these assumptions, numerous studies have shown that action execution is modulated by concurrent action observation and vice versa (e.g., Jacobs & Shiffrar, 2005; Springer et al., 2011; see also Prinz, 2005 for an overview of empricial evidence).

Already these two conceptualizations show that there are different possible levels of abstraction in the shared representation of an observed and executed action ranging from the corresponding motor program to its sensory consequences (cf., De Vignemont & Haggard, 2008). The observers' body most likely differs in some aspects from the body of the observed individual and certain action effects might be achieved by means of different movements. In addition, actions may not always serve a certain goal in the sense that they are directed towards an object. In the case of athletic movement sequences, for example, the action itself might be considered the goal. De Vignemont and Haggard (2008) therefore suggested that actions are most likely neither represented in all their bodily parameters nor in their disembodied abstract goals. Instead, they proposed that the dynamic sequence of specific movements is shared in a common representational domain, that is, the intention in action following the terminology of Searle (1983). In his theory of intentionality, Searle (1983) differentiated between "prior intentions" that represent conscious, complex goals (e.g., having lunch in the cafeteria) and "intentions in action", that is, the intentional, implicit content of the action itself (e.g., going to the cafeteria, choosing one meal, taking it to the table, etc.). It follows that all intentional actions have intentions in action but not necessarily any prior intention.

With respect to the functional role of shared representations between action execution and action observation, a number of hypotheses have been put forth in the literature. It has been suggested that they might not only support action planning and the control of self-intended actions but also the understanding of others' actions, as well as observational learning (Blakemore & Decety, 2001; Jeannerod, 2001; but see Jacob & Jeannerod, 2005 for a critical discussion on their role in action understanding). They might facilitate action imitation (Hurley, 2008; Iacoboni et al., 1999; Rizzolatti, Fogassi, & Gallese, 2001) and, crucially, serve as the basis for the prediction of observed actions (Brown & Brüne, 2012; Flanagan & Johansson, 2003; Grush, 2004; Schütz-Bosbach & Prinz, 2007; Wilson & Knoblich, 2005; Wolpert & Flanagan, 2001). For example, Schütz-Bosbach and Prinz (2007) argued that the observation of an action involves not only a representation of the current action state but also a prediction of forthcoming action states allowing the evaluation and anticipation of observed actions. In line with this reasoning, Urgesi et al. (2010) showed that motor facilitation as measured by single-pulse transcranial magnetic stimulation (TMS) is highest during the beginning and middle phase compared to the end phase of an observed action. This suggests that the observers' motor system is specifically tuned to the observation of ongoing actions in order to predict future behaviors of other individuals accordingly.

The ability to predict observed actions might in turn be based on the use of multiple inverse and forward models (cf., Blakemore, Wolpert, & Frith, 2000; Miall & Wolpert, 1996; Wolpert, Doya, & Kawato, 2003; Wolpert & Flanagan, 2001; Wolpert & Kawato, 1998). According to this framework, which originated from the motor control literature, an inverse model allows the observer to infer the motor commands that would produce the observed action. The corresponding forward model, on the contrary, represents a prediction about the sensory consequences of the observed action for which an efference copy of the respective motor command is used (also termed corollary discharge; see also Chapter II on page 24 for a detailed description). This concept has been introduced originally by Von Holst and Mittelstaedt (1950) and Sperry (1950) in their seminal work on motor adaptation, which described how sensory effects of self-generated movement may be distinguished from externally generated sensory signals. During action observation, this prediction is compared to the actual sensory input and if there is a discrepancy between the two signals, an error signal is formed (i.e., prediction error) that is used to refine the internal action representation. Thus, forward modeling during action observation may reduce ambiguities, for example, when a moving person is partly occluded from view, and enables the perceiver to react quickly to changes in the social environment.

ACTION PERCEPTION AND PREDICTION IN THE HUMAN BRAIN

In this section, findings from a variety of neuroscientific studies will be reviewed that investigated how action perception may be implemented in the human brain. The majority of these studies suggest that action execution and action observation are not only closely intertwined at the behavioral level but also with respect to their neural representation. In addition, the neural underpinnings of action prediction will be introduced together with the concept of predictive coding that may constitute a fundamental functional principle of the brain (cf., Bubic et al., 2010; Friston, 2005; Friston & Kiebel, 2009). More specifically, possible neural mechanisms within relevant structures are outlined supporting the integration of predicted (top-down) and actual (bottom-up) sensory signals during action perception.

At the neurophysiological level, one of the most intriguing findings in support for a close link between action execution and action observation was the discovery of the so-called mirror neurons in premotor and parietal areas of the macaque brain (Fogassi et al., 2005; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Mirror neurons are neurons that discharge both, when an individual plans and executes an action as well when the same or a similar action performed by another individual is observed. Subsequent studies found that mirror neurons even discharged when parts of the observed action were hidden, provided that the goal of the action could be inferred, or when the monkey only heard the typical sound of an action in the absence of a visual presentation (Kohler et al., 2002; Umilta et al., 2001). Thus, activation of these neurons seems to map sensory information of an observed action onto an internal motor representation of that action (e.g., Rizzolatti & Craighero, 2004).

Evidence from a large amount of studies using neurophysiological and neuroimaging techniques suggests that a similar neural system may exist in humans as well (see Buccino, Binkofski, & Riggio, 2004; Rizzolatti 2005; Rizzolatti & Craighero, 2004 for reviews). For example, functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) experiments have frequently demonstrated that action observation engages regions in the human brain that are similarly activated during action execution, that is, the premotor cortex (PMC), the inferior frontal gyrus (IFG), and the inferior parietal lobule (IPL; e.g., Caspers, Zilles, Laird, & Eickhoff, 2010; Grafton, 2009; Grèzes & Decety, 2001; Kilner, Neal, Weiskopf, Friston, & Frith, 2009; Van Overwalle & Baetens, 2009). In action observation tasks containing biological motion, the superior temporal sulcus (STS) has additionally been shown to be involved, although this region does not appear to have motor properties itself (cf., Grossman et al., 2000; Puce & Perrett, 2003; Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004). Grafton (2009) subsequently referred to this whole set of regions as the human action observation network (AON). However, whether neural subpopulations in the frontoparietal regions of the AON indeed possess mirror-like properties still remains controversial due to confounding evidence and limited possibilities to record single-cell activity in humans (cf., Dinstein, Gardner, Jazayeri, & Heeger, 2008; Hickok, 2009; Lingnau, Gesierich, & Caramazza, 2009; Turella, Pierno, Tubaldi, & Castiello, 2009). Only one study to date provided direct evidence that neurons, which respond in a similar fashion to action observation and action execution, may actually be present in the human brain (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010). The results of this study suggested additionally that neurons of this kind exist in more brain regions than previously assumed (e.g., in the medial temporal lobe). Thus, whereas the AON seems to represent the central neural correlate of observed actions, other brain regions may similarly exhibit mirror-like properties depending on the specific task requirements and modalities involved (cf., Keysers & Gazzola, 2010; Molenberghs, Cunnington, & Mattingley, 2012).

With respect to the prediction of visual events, evidence from different neuroimaging studies indicates that these kinds of tasks engage a distributed network in the brain depending, for example, on the characteristics of the observed material (e.g., timescale, content, and context; see Bubic et al., 2010 for a review). More specifically, the prediction of observed actions has been shown to be supported by the recruitment of regions within but also beyond the classical AON (e.g., Buccino et al., 2007; Cross, Stadler, Parkinson, Schütz-Bosbach, & Prinz, 2011; Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004; Ramnani & Miall, 2004; Schiffer & Schubotz, 2011; Schubotz, 2007; Stadler et al., 2011). For example, some of these studies reported additional activity in the cerebellum during action prediction, which has been interpreted as reflecting the incorporation of temporal information about the observed movement sequences (e.g., Cross et al., 2011; see also O'Reilly, Mesulam, & Nobre, 2008). It has been further suggested that forward and/or inverse models may actually be formed in the cerebellum in order to interact with sensorimotor cortices during action observation and imitation (Miall, 2003; Miall & Wolpert, 1996). Yet other studies provided evidence for the involvement of the basal ganglia in predictive processing of observed actions and events, especially in conditions during which an initial prediction is violated (e.g., Schiffer, Ahlheim, Wurm, & Schubotz, 2012; Schiffer & Schubotz, 2011; see also den Ouden, Daunizeau, Roiser, Friston, & Stephan, 2010 for a related finding). The prediction of more complex, episodic scenarios (e.g., how

Christmas will be spent), in contrast, seems to preferentially engage medial prefrontal, medial parietal, and medial temporal structures (e.g., Addis & Schacter, 2012; Bar, 2009; Martin, Schacter, Corballis, & Addis, 2011; Schacter, Addis, & Buckner, 2007). Already these few examples illustrate that a variety of areas across the whole brain seem to be involved in some sort of predictive processing during action observation. Thus, in order to further clarify the mechanisms of action prediction in the brain, the possible role of each of these brain areas and their interactions with each other needs to be specified (Bubic et al., 2010).

Iacoboni and colleagues were among the first who described possible pathways of information processing within the AON during action imitation given that the single regions of the network are reciprocally connected (Iacoboni & Dapretto, 2006; Iacoboni et al., 2001). They proposed that a visual description of an action to be imitated is sent from the STS to the parietal lobe, which codes the motoric description of that action. This information is projected to the premotor cortex, which describes the action in terms of its goal. The sensory consequences of the action to be imitated are then sent back to the STS in order to be compared to the actual visual input. This reciprocal view on information processing was also adopted in the predictive coding account of the mirror neuron system (Friston, Mattout, & Kilner, 2011; Kilner, Friston, & Frith, 2007a, 2007b). Predictive coding is formally equivalent to empirical Bayesian inference in which the causes of sensory input (e.g., the motor commands of the observed individual) are inferred through their integration with prior expectations during visual processing (Friston, 2005; Friston & Kiebel, 2009). Accordingly, instead of only forwarding visual information from occipitotemporal to frontoparietal areas (feedforward recognition model), it is assumed that in each level of the cortical hierarchy predictive representations of the level below are formed, that is, a generative or forward model (see Figure I.1 for a schematic overview). These signals are sent back to the lower level in order to be compared to the actual representation, which produces a prediction error. The prediction error is then projected back up the hierarchy to adjust the internal representation of an observed action, which in turn changes the prediction. Thus, predictive coding provides an explanation how inferring and predicting the actions of others might be implemented at the neural level (see also Schippers & Keysers, 2011 for further evidence). In contrast to the forward and inverse model account outlined in the previous section, however, there are no separate inverse models to infer the motor commands that would produce the observed action. Instead, this interference is realized through minimizing the prediction error by adjusting the generative model based on the perceived consequences in each level of the cortical hierarchy (Friston et al., 2011).

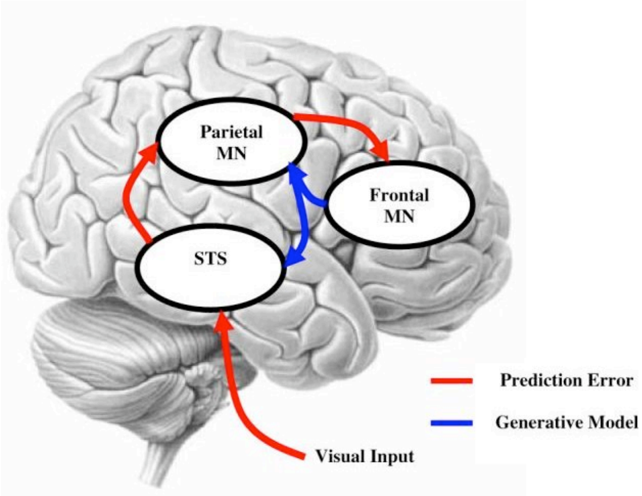


Figure I.1. Schematic overview of predictive coding in the action observation network (i.e., putative mirror neuron system). Adapted from Kilner, Friston, & Frith © 2007 Springer Verlag.

THE ROLE OF SENSORIMOTOR EXPERIENCE

If we accept the use of forward or generative models in action prediction, an efficient prediction of observed actions, that is, a small prediction error, should critically depend on the sensorimotor experience of the observer. As Friston et al. (2011) noted: "crucially, active inference does not invoke any 'desired consequences', it rests only on experience-dependent learning and inference: experience induces prior expectations, which guide perceptual inference and action" (p. 157). In line with this, studies on skilled motor performance frequently demonstrate that individual differences in sensorimotor experience correlate with the ability to infer and predict observed actions as well as modulate activity in the AON (e.g., Abernethy & Zawi, 2007; Aglioti, Cesari, Romani, & Urgesi, 2008; Buccino, Lui, et al., 2004; Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2005; Cross, Hamilton, & Grafton, 2006; Urgesi, Savonitto, Fabbro, & Aglioti, 2012). For example, Urgesi et al. (2012) asked volleyball athletes (motor experts), supporters (visual experts), and novices to predict the fate of volleyball floating services and found that the athletes outperformed the other groups in reading the body kinematics and the ball trajectory of the observed actions. Visual experts only showed an advantage compared to novices when the ball trajectory was visible. Thus, sensorimotor experience seems to play a predominant role for an efficient prediction of others' actions, whereas visual experts and non-experts rather exploit the visual dynamics of the observed actions resulting in a less accurate prediction performance. At the neural level, this assumption is supported by findings that non-experts compared to experts preferentially activate visual cortices during action imagery and prediction (e.g., Olsson, Jonsson, Larsson, & Nyberg, 2008; Wright, Bishop, Jackson, & Abernethy, 2011).

Sensorimotor experience, on the contrary, typically results in a higher engagement of the AON during the observation of actions from the observers' domain of expertise compared to unfamiliar actions (but see Cross et al., 2012 for a discussion of relevant findings on the relationship between motor familiarity and AON activity). For example, Calvo-Merino et al. (2005) reported that experts in classical ballet and capoeira showed a stronger activation in the premotor cortex, parietal cortex and the STS, when they observed actions of their own dance style compared to the other dance style. In a subsequent study, the authors further examined the role of motor versus visual familiarity in male and female expert ballet dancers during the observation of gender-specific ballet movements (Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006). Greater AON activity was found during the observation of gender specific moves compared to the observation of opposite gender moves, for which the dancers were highly familiar with but did not perform the movements themselves.

Hence, most theories on the development of shared representations emphasize the role of sensorimotor experience in order to infer the actions of others. According to the associative sequence learning (ASL) model, for example, shared representations and their neural basis are assumed to be established through the correlated experience of executing and observing the same action (e.g., during action imitation, the observation of own actions, or joint actions; Catmur, Walsh, & Heyes, 2009; Heyes, 2010; Heyes, Bird, Johnson, & Haggard, 2005). This correlated experience strengthens the connectivity between different regions of the AON through establishing links between the sensory and motor representations of a particular action (see also Keysers & Perrett, 2004 for a similar account). This hypothesis is supported by evidence that the matching properties of the AON can be reconfigured even after short amounts of incompatible training (e.g., Catmur et al., 2008; Catmur, Walsh, & Heyes, 2007; Gillmeister, Catmur, Liepelt, Brass, & Heyes, 2008). Similarly, Friston et al. (2011) argued that an efficient inference and prediction of observed actions is only possible if the observer and observed agent possess the "same kind of motor apparatus" (p. 157). In these cases, not only visual information can be predicted but also biological motion and proprioceptive information.

All these findings show that an effective prediction of observed actions requires existing representations or internal models of the respective actions in the observer. Without similar past experiences the quality of sharing with someone else is different and likely to be less sensitive which in turn affects the observers' reactions accordingly. But what happens with the ability to represent and predict observed actions with advancing age when the human brain and body substantially change? An overview about age-related changes in relevant abilities and its neural correlates will be provided in the following.

AGE-RELATED CHANGES IN ACTION PERCEPTION

Bearing in mind the findings outlined above, one important prerequisite for an effective action prediction is the correct identification and processing of relevant sensory input. With advancing age, however, the capacity to process visual information declines (see Schieber, 2006 for a general review). Therefore, this section begins with a review on age-related changes in general perceptual abilities that might affect the interpretation of an observed action, that is, motion and time perception. In addition, age-related changes in biological motion perception will be exemplified providing a first indication on how older adults might represent observed actions. Interestingly, the results of these studies suggest that this ability may remain relatively preserved with advancing age especially in conditions in which commonly encountered movement patterns are presented. A second important ability in order to predict the actions of others is the efficient utilization of one's own sensorimotor experience, which is subject to age-related change in itself. After briefly outlining typical changes in this domain over the lifespan, evidence from different studies will be presented that investigated the representations of actions in older versus younger adults more directly by using different mental imagery paradigms. The results of these studies suggest that older adults are less precise in internally representing actions, which might affect their ability to predict observed actions accordingly.

With respect to motion perception, evidence from studies using random dot motion paradigms suggests that motion detection, sensitivity, and discrimination abilities are reduced in older compared to younger adults (e.g., Bennett, Sekuler, & Sekuler, 2007; Roudaia, Bennett, Sekuler, & Pilz, 2010; Snowden & Kavanagh, 2006). Roudaia et al. (2010), for example, showed that the spatial as well as temporal range in which apparent motion direction can be discriminated is smaller in older than in younger adults. In conditions of small spatial displacement between two random-dot patterns, age-related performance declines were mainly mediated by declines in visual acuity. Thus, deficits in basic sensory processing certainly have a strong impact on general cognitive abilities of older age groups. In their seminal study on the relation between age, sensory, and cognitive functioning for which data of 156 older adults from the Berlin Aging Study (BASE) were analyzed, Lindenberger and Baltes (1994) showed that age-related variance in intellectual abilities is almost completely accounted for by differences in sensory functioning. In a later study comprising the whole BASE sample of 687 individuals between 25 and 103 years of age, it was further demonstrated that this link increases substantially from adulthood to old age (Baltes & Lindenberger, 1997). This increased coupling has been found not only between cognitive and sensory but also sensorimotor measures of performance (e.g., postural control and gait). The authors therefore proposed that this phenomenon might be the result of a common factor having domain-general consequences, that is, structural and functional changes in the aging brain (common cause hypothesis). In line with this, experimental studies frequently demonstrated that dual-task costs are higher in older than in younger adults, for example, when they are asked to perform a cognitive task (e.g., memory task) and a sensorimotor task (e.g., walking) at the same time (see Schäfer, Huxhold, & Lindenberger, 2006 for a recent review).

Although not specifically linked to one sensory modality, another perceptual ability that may be relevant in the context of action prediction is the accurate estimation of temporal intervals. If older adults perceive time differently than younger adults, their prediction of the time-course of others' actions might be systematically biased (i.e., too slow or too fast). Evidence from different timing tasks suggests that the internal clock of older adults runs faster than real-time in experimental conditions of low attentional demand (e.g., when attention focuses only on timing) but slower in conditions in which the attentional demand is higher than usual in everyday life (e.g., when attention needs to be divided between a temporal task and a non-temporal task; see Lustig, 2003 for a review). Although younger adults show effects in the same direction, they are typically more pronounced in older adults possibly due to age-related declines in attentional control. For example, age-related deficits in the allocation of attention to relevant information while inhibiting irrelevant information have been linked to performance declines in a variety of context-dependent tasks (cf., Gazzaley, Cooney, Rissman, & D'Esposito, 2005; Lustig, Hasher, & Zacks, 2007). Timing effects, however, are sensitive to feedback and older adults are able to adjust their internal clock to a given clock speed (Lustig, 2003). Based on these findings, there is little reason to assume that prediction performance of older adults will be biased due to general changes in time perception in conditions requiring low amounts of attentional control (i.e., when their full attention is directed to only one task at a time). A continuous observation of somebody else performing an action further allows them to adjust their internal timing to the respective timing of the observed action.

Crucially, the detection and discrimination of biological motion stimuli seems to be a special case within the perceptual domain because the sensitivity to differences in biological motion appears to be less affected by age. This is especially evident in conditions showing natural and highly familiar motion patterns. For example, Norman, Payton, Long, and Hawkes (2004) tested the discrimination performance of older and younger adults during the observation of point-light walkers that were walking, jogging, or skipping. The duration, direction, and temporal occlusion of the motion sequences were manipulated. They found that older adults performed almost as well as younger adults given that the exposure duration was increased from 120 ms to 400 ms, when forward instead of backward motion was depicted, and when the sequences contained motions that are frequently encountered in everyday life (e.g., simple walking). In addition, the performance of the groups was equally affected by the presence and amount of partial occlusion within the motion sequences, although the overall accuracy was lower in older compared to younger adults. Similarly, Pilz, Bennett, and Sekuler (2010) showed that older adults are less impaired in integrating form and motion information in order to discriminate the walking direction of upright compared to inverted point-light walkers. Thus, age-related differences in low-level perceptual abilities seem to account only partially for the results obtained in these kinds of tasks. Instead, it has been proposed that older adults might additionally draw on their sensory experience during the observation of biological motion, which allows them to compensate to some extent for declines in low-level visual information processing. Based on the assumption that action execution and action observation share a common representational domain, one might further speculate that older adults also use their own sensorimotor system in order to represent and predict actions that are performed by other individuals. The majority of studies investigating age-related changes in motor performance and sensorimotor control showed that movement control becomes less automatic over the lifespan involving a greater reliance on (visuospatial) attentional control (e.g., Ketcham, Seidler, Van Gemmert, & Stelmach, 2002; Panzer, Gruetzmacher, Fries, Krueger, & Shea, 2011; Sarlegna, 2006; Seidler, Bangert, Anguera, & Quinn-Walsh, 2007; Seidler et al., 2010; Verrel, Lövdén, & Lindenberger, 2012; see also Chapter II on page 26). Thus, age-related declines in this domain might additionally influence the prediction of observed actions.

One way to more directly study age-related changes in the representations of actions is to compare motor imagery abilities in older and younger adults (cf., Jeannerod, 2001). Using the vividness of movement imagery questionnaire (VMIQ), Mulder, Hochstenbach, van Heuvelen, and den Otter (2007) showed that older adults have more difficulties than younger adults when imaging movements from an internal perspective whereas no age-related differences were found in relation to motor imagery from an external perspective. Moreover, experimental research showed that older adults are less accurate than younger adults in estimating the reachability of objects in peri- and extrapersonal space (Gabbard, Caçola, & Cordova, 2011), in the mental rotation of their hands (Saimpont, Pozzo, & Papaxanthis, 2009), in the imitation of previously seen movements (Maryott & Sekuler, 2009), or in imagining the trajectory of complex action sequences involving the whole body (Saimpont, Mourey, Manckoundia, Pfitzenmeyer, & Pozzo, 2010). Studies on the temporal features of motor imagery in older versus younger adults demonstrated that older adults are less precise in covertly representing actions as evidenced by a lower temporal similarity between an imagined and executed action (e.g., Personnier, Ballay, & Papaxanthis, 2010; Personnier, Kubicki, Laroche, & Papaxanthis, 2010; Personnier, Paizis, Ballay, & Papaxanthis, 2008; Schott & Munzert, 2007; Skoura, Papaxanthis, Vinter, & Pozzo, 2005; Skoura, Personnier, Vinter, Pozzo, & Papaxanthis, 2008). Notably, these performance declines are typically more pronounced in complex conditions requiring, for example, high spatiotemporal control, whereas the actual movement execution or the imagery of very simple actions (e.g., walking short distances) often seems to be relatively preserved with age (see also Saimpont, Malouin, Tousignant, & Jackson, 2012). This indicates that age-related declines in sensorimotor control cannot fully explain age-related declines in the internal representations of actions. Instead, it was argued that they may be the result of a less efficient forward modeling in the absence of any sensory input that can be used to update the internal action representation.

Moreover, older adults have been shown to be more impaired than younger adults in incorporating episodic in contrast to non-episodic (e.g., semantic) details when they are asked to imagine possible future events (e.g., involving a vacation; Schacter, Gaesser, & Addis, 2012). This suggests that the ability to extract and recombine relevant information from memory in order to generate complex future scenarios is declining with advancing age. In how far all these changes affect the prediction of observed actions depending on the level of sensorimotor experience in the aging observer and how this might be implemented in the aging brain remains largely unknown to date, however. Based on the findings outlined above, one might speculate that previous experience (whether visual, sensorimotor, or episodic) is less organized and/or less specific in the aging mind, resulting in less precise predictions about actions and events that are performed by other individuals. General changes in the brain of older adults that might contribute to the observed deficiencies in their internal action representations will be outlined in the next section.

THE AGING BRAIN

The human brain is subject to substantial structural as well as functional changes with advancing age. These changes involve gray and white matter atrophy, lower synaptic densities and neurotransmitter levels, cerebral blood flow reductions, as well as decreases in metabolic activity (see Dennis & Cabeza, 2008; Raz & Rodrigue, 2006 for reviews). In the following, age-related changes in brain structure will be described before reviewing findings across a variety of domains on changes in task-related activation patterns. The majority of these studies showed that older adults typically recruit additional brain regions compared to younger adults in order to accomplish a given task. Possible interpretations and underlying mechanisms of these age-related differences will be discussed. The scaffolding theory of aging and cognition (STAC) will be introduced that provides an explanation on how the brain might respond to neural aging (cf., Park & Reuter-Lorenz, 2009). In addition, two studies will be presented providing first indications on how the neural representation of observed actions might change with advancing age.

Overall, gray matter volume declines roughly linearly with advancing age, while the decline in white matter volume is rather nonlinear with an accelerated decrease beginning at about the age of 55 (Raz et al., 2005; Walhovd et al., 2011). Although widespread, this age-related atrophy varies in magnitude with some brain regions that are strongly affected and other regions which remain relatively preserved (e.g., Fjell & Walhovd, 2010; Grieve, Clark, Williams, Peduto, & Gordon, 2005; Walhovd et al., 2011). Within the cerebral cortex, for example, the largest age-related declines are observed in the frontal lobes and especially in prefrontal areas, whereas more posterior regions such as the occipital lobes show only mild declines (see also Raz, 2005). The prefrontal cortex is known to play a critical role in working memory and executive control tasks, in which older adults typically show marked performance deficits compared to younger adults (cf., Braver & West, 2008). Thus, declines in specific cognitive abilities are likely to be linked to declines in specific brain regions, although the precise relation between these variables and age is still under debate in the cognitive aging literature (e.g., Salthouse, 2011).

In addition, older adults consistently show different task-related neural activation patterns compared to younger adults across a broad range of tasks (see Dennis & Cabeza, 2008; Grady, 2012 for reviews). One typically observed activity change is referred to as the hemispheric asymmetry reduction in old adults (HAROLD), which indicates that neural recruitment patterns in older adults tend to be less lateralized compared to younger adults under similar conditions (Cabeza, 2002). This age-related over-recruitment has been interpreted as a compensation for declines in brain structure and functionality in line with evidence that this pattern is predominately found in high- compared to low-performing older adults in different memory tasks (Cabeza et al., 1997; Reuter-Lorenz et al., 2000; Rosen et al., 2002). Similar results were obtained in studies comparing brain activity in older and younger adults during motor performance (see Seidler et al., 2010 for a review).

A second characteristic activity change is the so-called posterior-anterior shift in aging (PASA) that refers to an age-related decrease in occipital activity that is accompanied by an increase in prefrontal cortex activity (Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008). It has been suggested that this might serve as a compensation for processing deficits in posterior regions by recruiting high-order cognitive processes. In a series of studies on age-related changes in neural activity during motor performance, for example, Heuninckx and colleagues showed that older adults recruit additional brain areas compared to younger adults during the coordinated execution of cyclical hand and foot movements that correlated positively with their task performance (Heuninckx, Wenderoth, Debaere, Peeters, & Swinnen, 2005; Heuninckx, Wenderoth, & Swinnen, 2008). These activation differences were located in brain areas implicated in higher-level sensorimotor processing (e.g., parietal cortex) as well as in frontal areas possibly reflecting increased cognitive monitoring. In a subsequent study, the authors found evidence for a lower differentiation in relevant neural networks in older compared to younger adults during the performance of these movements in the presence or absence of visual feedback (Heuninckx, Wenderoth, & Swinnen, 2010).

Whether these additional activations in older adults are always compensatory or whether they merely reflect dysfunctional neural activity still remains controversial (e.g., Logan, Sanders, Snyder, Morris, & Buckner, 2002; Park et al., 2004). In contrast to the compensation view, the dedifferentiation hypothesis proposed by Li and Lindenberger (1999) argues that deficits in neurotransmission cause a general difficulty in recruiting specialized neural mechanisms or brain areas in older adults. According to this view, neural over-recruitment might represent a mere byproduct of aging that is not task relevant. Using multi-voxel pattern analysis (MVPA) to assess neural activation patterns in different task conditions more precisely, Carp and colleagues recently confirmed that perceptual as well as motor representations indeed seem to become less distinct in the aging brain (Carp, Park, Hebrank, Park, & Polk, 2011; Carp, Park, Polk, & Park, 2011). Older adults not only represented different visual stimuli (e.g., faces and houses) less selectively in category-specific visual areas but also showed less selectivity in the motor control network (i.e., primary motor cortex, supplementary motor area, cerebellum) during the execution of finger tapping movements (see also Bernard & Seidler, 2012; Langan et al., 2010 for related findings).

However, the compensation and dedifferentiation view on brain aging may not be mutually exclusive insofar as the difficulty in recruiting specialized brain regions with advancing age might be compensated through additional activation in other regions to perform a particular task. As proposed by the scaffolding theory of aging and cognition (STAC), not only extrinsic challenges to the neural system (e.g., unfamiliar material) but also intrinsic challenges such as biological aging may result in so-called neural scaffolding (Park & Reuter-Lorenz, 2009). This scaffolding involves a functional reorganization through the recruitment of additional neural networks or regions to compensate for noisy and/or inefficient neural processing. Notably, as neural scaffolding may be present in younger adults in response to unfamiliar material, it may already be invoked by familiar material or basic tasks in older adults. Although performance that is based on neural scaffolding (i.e., among non-experts or older adults) is likely to be less effective compared to groups who are able to exploit highly specialized and interconnected neural networks, it may be enhanced through training and practice (cf., Erickson et al., 2007). The efficiency of neural scaffolding might be further modulated by the degree of age-related declines in functional connectivity between relevant areas and white matter integrity (cf., Grady, 2012; Madden et al., 2012). For example, Davis, Kragel, Madden, and Cabeza (2012) measured cross-hemispheric communication in older versus younger adults by means of fMRI and diffusion tensor imaging (DTI) during a lateralized matching task. It was shown that cortical redistribution associated with better performance was constrained by white matter integrity in older adults.

With respect to the neural representation of observed actions, Léonard and Tremblay (2007) provided first evidence for a loss of neural selectivity with advancing age by showing that corticomotor facilitation in relevant muscles is more widespread in older compared to younger adults during action observation, imagery, and imitation. Moreover, Nedelko et al. (2010) recently showed that older adults recruit additional brain regions beyond the AON during action observation and imagery (see Chapter III on page 58 for a detailed description of these studies). Thus, neural scaffolding in regions outside of the sensorimotor system might change the weighting or precision of different sources of information (e.g., visual, sensorimotor, or episodic) during predictive processing resulting in an altered representation of observed actions in older compared to younger adults.

AIM OF THE DISSERTATION AND EXPERIMENTAL APPROACH

The main aim of this dissertation was to clarify how advancing age affects the ability to predict the actions of others. Due to a lack of specific research on this issue so far, in a first experiment, prediction performance was investigated in older adults compared to younger adults during the observation of complex but highly familiar everyday actions. A second behavioral experiment addressed the question to what extent sensorimotor experience might attenuate possible age-related declines in prediction performance given its important role in the development of shared action representations and predictive coding.

Even though expertise in a certain domain may not prevent general physical or cognitive declines typically seen in older age groups, it may attenuate age-related declines on skill-related tasks (e.g., Horton, Baker, & Schorer, 2008; Krampe, 2002; Krampe & Charness, 2006; but see Salthouse, 2006 for a critical discussion). For example, Krampe and Ericsson (1996) compared the performance of younger and older expert as well as amateur pianists on different cognitive-motor tasks and did not find any expertise-related benefits on tasks measuring general cognitive performance. On music-related tasks, however, older pianists performed only slightly worse than younger pianists. Moreover, their level of performance was modulated by the amount of deliberate practice in later adulthood. Similarly, Kattenstroth and colleagues showed that a regular engagement in amateur dancing had beneficial effects on a variety of perceptual, motor, and cognitive abilities in older adults, whereas professional experience in dancing exerted a positive influence only on performance in tasks that were closely related to dancing (e.g., balance, posture, and reaction times; Kattenstroth, Kalisch, Kolankowska, & Dinse, 2011; Kattenstroth, Kolankowska, Kalisch, & Dinse, 2010). These findings highlight the importance of selective maintenance for adaptive aging that might similarly apply to the ability to predict the actions of others (cf., Baltes, Staudinger, & Lindenberger, 1999).

Accordingly, prediction performance of older and younger figure skating experts as well as age-matched non-experts was compared during the observation of classical figure skating elements and highly familiar movement exercises. Figure skating was chosen because no objects are present during the execution of these actions that might facilitate the prediction of their trajectory. Moreover, professional figure skating movements cannot be reproduced without extensive amounts of training, which allows a clear differentiation between observers who possess sensorimotor experience in the sport and inexperienced observers. Age-related changes in neural activation patterns during action prediction were examined in a follow-up fMRI experiment in which the same action sequences were used as in the second behavioral experiment. Participants consisted of older and younger adults with varying degrees of motor familiarity with the observed actions. The majority of them had already taken part in the second behavioral experiment. Brain activity was measured by metabolic changes in blood flow, that is, the blood-oxygen-level-dependent (BOLD) signal.

In all of the experiments, participants completed beforehand different psychometric tests and a general health questionnaire, which was developed with Dr. D. V. M. Ott from the Department of Neurology of the MPI for Human Cognitive and Brain Sciences, Leipzig (see Appendix A). Only healthy older adults were included in the experiments, which allowed an examination of the effects of cognitive aging on action prediction that are unlikely to be influenced by any age-associated pathology. In addition, participants were always asked to indicate how experienced they are/were with the actions observed in the experiments (see Appendix B). Moreover, fMRI analyses focused on the interactions between the factor age group and the experimental conditions in an event-related design, which has been recommended in order to control for potential confounding effects of age-related differences at the cerebrovascular level (cf., D'Esposito, Deouell, & Gazzaley, 2003; Gazzaley & D'Esposito, 2005; Kannurpatti, Motes, Rypma, & Biswal, 2010).

MEASURING ACTION PREDICTION: THE ACTION OCCLUSION PARADIGM

To this end, an action occlusion paradigm was used to assess the predictive abilities of the different groups and their neural implementation during action observation. One version of this paradigm has been frequently used in studies on skilled motor performance in which different expert groups were asked to predict the fate of athletic movements that were partly occluded at critical time points (e.g., Abernethy & Zawi, 2007; Aglioti et al., 2008; Farrow & Abernethy, 2003; Müller & Abernethy, 2006; Müller, Abernethy, & Farrow, 2006; Wright et al., 2011). Typically, the results show a superior prediction performance and higher AON activity in experts compared to less experienced groups particularly at very early stages of an unfolding movement from the respective domain of expertise. In a slightly different version of the paradigm, which was used in the present experiments, the actions continue after a certain occlusion period in a temporally manipulated way (i.e., congruent, too early or too late). Participants are then asked to judge the temporal coherence of the continuation after occlusion. This requires them to extrapolate the trajectory of the occluded action into the future and to match this prediction with the actual continuation after occlusion in order to solve the task (see Figure I.2).

Figure I.2. Schematic overview of the action occlusion paradigm used in the present experiments: Participants observed different action sequences that were partly occluded at critical time points and whose continuation after occlusion was temporally manipulated (congruent, too early, or too late on different levels). Prediction performance should depend on the match between the prediction of the occluded action and its observed continuation afterwards.

This paradigm has been used successfully in different variations across different action observation and prediction studies (e.g., Graf et al., 2007; Parkinson, Springer, & Prinz, 2012; Prinz & Rapinett, 2008; Sparenberg, Springer, & Prinz, 2012; Stadler, Springer, Parkinson, & Prinz, 2012). Graf et al. (2007) and Sparenberg et al. (2012) tested additionally in how far the observation of inverted actions affects prediction performance and found that performance in these conditions was considerably impaired [see Chapter II on page 25 for a detailed description of the Graf et al. (2007) study]. Thus, a pure visual encoding and extrapolation of occluded actions do not seem to be sufficient in order to accomplish the task effectively. The paradigm also proved successful in measuring neural activity in the AON during action observation (e.g., Cross et al., 2011; Stadler et al., 2011). For example, Stadler et al. (2011) compared brain activity during the prediction of occluded actions to different action-related control conditions and showed that only the dynamic prediction, but not maintenance, of the occluded actions involved activation in parts of the AON.

Based on these findings, I assumed that the participants of the present experiments predict the trajectory of the ongoing actions during the occlusion period based on their internal action representations. As outlined above, sensory as well as motor representations seem to become less precise with advancing age. Therefore, I hypothesized that older adults are less efficient compared to younger adults in matching their internal predictions to the actual sensory input during action observation. More specifically, the prediction accuracy and timing (i.e., the match with the action continuation after occlusion) should be less precise in older compared to younger adults. I further assumed that sensorimotor experience with the observed actions exerts a positive influence on the prediction performance of younger and older adults. Experts compared to non-experts should be able to generate more precise prior expectations that are based on biological motion and proprioceptive information in addition to visual information. Moreover, I hypothesized that old age as well as the lack of sensorimotor experience results in different neural processing of the observed actions (i.e., neural scaffolding) in regions beyond the classical AON. The recruitment of additional brain regions might in turn imply the use of a different prediction strategy that is based, for example, predominantly on the visual dynamics of the observed actions.

In order to test these hypotheses, I analyzed the proportion of correct responses as a measure for prediction accuracy of the groups in different conditions of the two behavioral experiments. The timing in action prediction was examined by applying psychophysical methods that tested in how far the response thresholds of the groups were modulated across different stimulus levels. The two behavioral experiments are presented in Chapter II (Diersch et al., 2012). In the fMRI experiment, I investigated in how far different levels of motor familiarity modulate activity in the AON based on evidence indicating that this relationship might be non-linear (Cross et al., 2012). In addition, brain activity was analyzed as a function of age and sensorimotor experience in figure skating. The fMRI experiment is presented in Chapter III (Diersch et al., submitted).

II. REPRESENTING OTHERS' ACTIONS: THE ROLE OF EXPERTISE IN THE AGING MIND

Psychological Research (2012), 76(4), 525-541.
doi: 10.1007/s00426-011-0404-x.

Nadine Diersch[1,2], Emily S. Cross[1,3,4], Waltraud Stadler[1,5], Simone Schütz-Bosbach[1], & Martina Rieger[1,6]

[1]Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany; [2]MaxNet Aging Research School, Max Planck Institute for Demographic Research, Rostock, Germany; [3]Behavioral Science Institute, Donders Institute for Brain, Cognition and Behaviour, Radboud University Nijmegen, Nijmegen, The Netherlands; [4]Wales Institute for Cognitive Neuroscience, School of Psychology, Bangor University, Gwynedd, UK; [5]Movement Science Unit, Faculty for Sports and Health Science, Technical University Munich, Munich, Germany; [6]UMIT-The Health and Life Sciences University, Hall/Tyrol, Austria

ABSTRACT

A large body of evidence suggests that action execution and action observation share a common representational domain. To date, little is known about age-related changes in these action representations that are assumed to support various abilities such as the prediction of observed actions. The purpose of the present study was to investigate (a) how age affects the ability to predict the time course of observed actions; and (b) whether and to what extent sensorimotor expertise attenuates age-related declines in prediction performance. In a first experiment, older adults predicted the time course of familiar everyday actions less precisely than younger adults. In a second experiment, younger and older figure skating experts as well as age-matched novices were asked to predict the time course of figure skating elements and simple movement exercises. Both young age and sensorimotor expertise had a positive influence on prediction performance of figure skating elements. The expertise-related benefit did not show a transfer to movement exercises. Together, the results suggest a specific decline of action representations in the aging mind. However, extensive sensorimotor experience seems to enable experts to represent actions from their domain of expertise more precisely even in older age.

INTRODUCTION

Imagine a coach who trains amateur or professional athletes. Besides teaching new skills and knowledge about the sport, he or she is also responsible for monitoring the athletes' performance. Although coaches are often considerably older than the athletes they train, they do exceptionally well in evaluating and predicting the outcome of the athletes' efforts. Not surprisingly, many coaches are former athletes of the sport themselves. How do they translate their own motor experience obtained many years ago into evaluations and predictions based on current observations? And how do these abilities change with age in general?

There is growing support for the assumption that action execution and action observation share a common representational domain (Hommel et al., 2001; Prinz, 1997). It is assumed that observed actions are mapped onto one's own internal motor representations without any explicit reflective reasoning (De Vignemont & Haggard, 2008; Jeannerod, 2001; Wilson & Knoblich, 2005; Wolpert & Flanagan, 2001). Moreover, the observation of an action may not only involve a representation of the current action state but also a prediction of forthcoming action states, thus allowing the observer to flexibly adapt and react to changes in the social environment (cf., Perrett, Xiao, Barraclough, Keysers, & Oram, 2009; Schütz-Bosbach & Prinz, 2007; Urgesi et al., 2010). A well-documented overlap between brain regions recruited during action execution and action observation provides further support for the shared representation account (Caspers et al., 2010; Grafton, 2009; Grèzes & Decety, 2001; Rizzolatti & Craighero, 2004; Van Overwalle & Baetens, 2009).

Wolpert and Kawato (1998) suggested that in action execution, two types of internal models are active, which are closely linked in a modular network. An inverse model provides the motor commands necessary to perform an action while using all the contextual information available. Each inverse model is supplemented with a corresponding forward model. The forward model represents predictions about the sensory consequences and the next state of an action by relying on an efference copy of the motor command and the current state of the action. By creating predictions of forthcoming sensory events, the brain compensates for neural processing delays of sensory feedback. Discrepancies between the predicted and the actual action feedback, that is, the prediction error, are used to refine an internal model of an action. As in action execution, internal models may also be used in action observation

(Kilner et al., 2007b; Schippers & Keysers, 2011; Wolpert et al., 2003). Inverse models allow the observer to infer the motor commands that would produce the action based on the current state of the observed individual. Without actually performing the action, the corresponding forward models can then be used to generate predictions about the sensory outcomes of the observed action. Thus, forward modeling may reduce ambiguities in uncertain situations and may enable the observer to react flexibly in interaction with others.

For example, it happens frequently that a moving person is temporarily occluded from view. An observer is usually quite good in predicting where and when the observed person will reappear through extrapolating the trajectory of the occluded action into the future. Observers thus anticipate the trajectory of temporarily occluded actions approximately in real-time (Graf et al., 2007). Graf et al. (2007) presented different action sequences performed by point-light walkers that were temporarily occluded from view followed by a static test posture of that action. Participants had to decide whether the test posture was rotated in depth or not, compared to the action sequence before occlusion. Results showed that performance was best when the time of occlusion and the movement gap (i.e., time between the end of the visible action sequence and the test posture) matched. However, other studies also found indications for an anticipation of observed actions, that runs even faster than real-time (e.g., Perrett et al., 2009; Urgesi et al., 2010) or a slight temporal delay in action anticipation (Prinz & Rapinett, 2008; Sparenberg et al., 2012).

A question that has not been answered yet is how the representation of actions and the ability to predict the time course of observed actions change with advancing age, when cognitive, motor, and perceptual abilities are substantially changing. Whereas so-called crystallized skills that involve knowledge and depend on individual experience (e.g., verbal knowledge) show little or no decline until very late in life, basic information processing mechanisms or fluid abilities (e.g., reasoning, spatial orientation, and perceptual speed) tend to decline roughly linearly during adulthood (Baltes et al., 1999; Park et al., 2002). In addition, such changes at the behavioral level are logically linked to changes at the neural level, as the human brain is subject to substantial changes with age (see Dennis & Cabeza, 2008; Raz & Rodrigue, 2006 for reviews). Older adults also exhibit different task-related activation patterns compared to those activated in younger adults while performing the same task (e.g., Cabeza, 2002; Davis et al., 2008). These activation patterns are predominantly interpreted as compensation for declining structures and have been linked with higher performance among older adults in cognitive as well as sensorimotor processing (Heuninckx et al., 2008; Mattay et al., 2002; Park & Reuter-Lorenz, 2009).

In motor control and sensorimotor processing, aging is commonly associated with various declines such as movement slowing, coordination deficits, difficulties in balance and gait, as well as greater spatial and temporal movement variability (Seidler et al., 2007; Seidler et al., 2010). Age-related declines in motion perception and discrimination abilities have been demonstrated as well, especially in conditions with high levels of stimulus complexity (e.g., Bennett et al., 2007; Norman et al., 2004; Pilz et al., 2010; Roudaia et al., 2010; Snowden & Kavanagh, 2006).

To our knowledge, there are very few studies so far that examined age-related changes in the representations of actions, and most of these studies have investigated motor imagery but not the prediction of observed actions (e.g., Celnik et al., 2006; Gabbard et al., 2011; Léonard & Tremblay, 2007; Maryott & Sekuler, 2009; Mulder et al., 2007; Personnier, Kubicki, et al., 2010; Personnier et al., 2008; Saimpont et al., 2009; Skoura et al., 2005; Skoura et al., 2008). For example, Personnier et al. (2008) showed that imagery performance is temporally less accurate in older than in younger adults, especially for complex movements with high demands on sensorimotor control. No such age-related decline was found during movement execution, suggesting that older adults might rely more on online sensory feedback to compensate for deficiencies in their internal models. In addition, Léonard and Tremblay (2007) showed that motor facilitation as measured by transcranial magnetic stimulation (TMS) is less selective in older than in younger adults during the observation, imagery, and imitation of different hand actions. These results indicate that there might be a specific decline of action representations in the aging mind, possibly based on less precise internal models of actions. Thus, one may speculate that older adults are also less precise than younger adults in predicting the time course of observed actions.

Nevertheless, the representation of actions and their neural basis are highly plastic in response to experience. Studies on skilled performance frequently demonstrate that individual differences in sensorimotor expertise correlate with the ability to anticipate and predict observed actions (e.g., Abernethy & Zawi, 2007; Aglioti et al., 2008; Farrow & Abernethy, 2003; Mann, Williams, Ward, & Janelle, 2007;

Müller et al., 2006; Sebanz & Shiffrar, 2009) as well as modulate activity in the action observation network in the brain (e.g., Calvo-Merino et al., 2005; Cross et al., 2006). Extensive practice in a certain domain over a long time might also attenuate age-related declines on skill-related tasks or their underlying components (Horton et al., 2008; Kramer, Bherer, Colcombe, Dong, & Greenough, 2004; Krampe, 2002; Krampe & Charness, 2006; Salthouse, 2006). However, whether sensorimotor expertise might compensate for possible age-related changes in the representations of observed actions remains an open question. To the best of our knowledge, only one study has provided preliminary evidence that this might be the case, by showing that the ability to anticipate observed handball actions was largely preserved in middle-aged (M = 46.7 years) handball goal-keepers (Schorer & Baker, 2009). However, the expert group in this study comprised only three adults. Thus, the impact of expertise on action representations in older age groups that are already facing cognitive and motor declines still remains largely unexplored.

The purpose of the two experiments reported here was to investigate (a) how age affects the ability to predict the time course of observed actions; and (b) whether and to what extent sensorimotor expertise might attenuate possible age-related declines in prediction performance. In two experiments, we asked participants to predict the time course of observed actions by using an action occlusion paradigm. In Experiment 1, older and younger adults were required to judge the temporal coherence of complex but highly familiar everyday actions that were temporarily occluded. We hypothesized that prediction performance is less precise in older adults than in younger adults. In Experiment 2, by using a similar paradigm as in the first experiment, prediction performance of younger and older figure skating experts as well as age-matched novices was investigated during the observation of classical figure skating elements, as well as simple movement exercises. Figure skating was chosen to examine the impact of expertise on prediction performance because no object interactions are involved in the sport, requiring participants to focus solely on the movement patterns. In addition, the different elements in figure skating possess high levels of motor difficulty and cannot be reproduced without extensive training. We assumed that both young age and sensorimotor expertise contribute to better performance when judging the coherence of temporarily occluded figure skating actions. Young age should also result in a better performance in predicting the time course of simple movement exercises. If sensorimotor expertise has only domain-specific positive effects, figure skating expertise should have no influence on prediction performance when observing movement exercises. If, however, positive effects of sensorimotor expertise generalize at least to some extent to other movement domains, figure skating experts should also be more precise in judging the temporal coherence of movement exercises.

EXPERIMENT 1

METHODS

Participants

Twenty-five younger adults (13 women, *M* = 25.1, SD = 2.49, age range 22-31 years) and 24 older adults (12 women, *M* = 66.6, SD = 2.99, age range 61-70 years) participated in the experiment. All participants were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971) and reported normal or corrected-to-normal vision. The younger group consisted of university students who were recruited from the participant database of the MPI for Human Cognitive and Brain Sciences, Leipzig. The older group consisted of community-dwelling older adults that were recruited through a local newspaper advertisement. Participants gave written informed consent and received payment for participation. Younger adults reported on average more years of education than older adults, $t(47) = 2.49$, $p = 0.016$. Characteristics of the groups are shown in Table II.1.

Table II.1. Characteristics of the sample in Experiment 1.

	Younger adults (n = 25)	Older adults (n = 24)
Years of education	17.1 (2.72)	15.3 (2.40)
Handedness score	89.6 (13.3)	89.4 (13.3)
MMSE score	-	29.1 (0.78)
SF-36		
PCS score	51.1 (4.78)	55.1 (5.39)
MCS score	52.3 (4.18)	50.6 (6.39)
DSST		
Raw score	86.8 (14.0)	63.2 (11.3)
Standardized score	11.6 (2.80)	12.1 (1.72)
SWT		
Raw score	34.5 (2.14)	33.7 (2.70)
Standardized score	0.83 (0.53)	0.66 (0.57)

Values represent mean scores and standard deviations (parenthesized). The physical component summary (PCS) and mental component summary (MCS) scores are psychometrically aggregated summary measures with a mean of 50 (SD = 10) that are based on eight subscales of the SF-36. DSST and SWT values are shown as raw scores and as standardized scores adjusted to the following means: DSST: M = 10, SD = 3 (age-adjusted); SWT: M = 0, SD = 1.

Health and cognitive status

None of the participants reported current evidence of any major physical or neurological disease and/or use of medication that might affect perceptual or cognitive performance. In addition, none of the older adults showed indications of cognitive impairment (M = 29.1, SD = 0.78, range 28-30) as measured by the Mini-Mental State Examination (MMSE; Folstein, Folstein, & McHugh, 1975; Maximum Score: 30).

The MOS 36-Item Short Form Health Survey (SF-36; McHorney, Ware, & Raczek, 1993; Ware et al., 1995; Ware & Sherbourne, 1992) was conducted to obtain a standardized score of the physical and mental health for each age group. Older adults obtained a significantly higher physical component summary (PCS) score than younger adults, $t(47) = 2.80$, $p = 0.007$, indicating that older adults who estimated their health status as being very good participated in the study. No age group differences were found for the mental component summary (MCS) score, $t(47) = 1.10$, $p = 0.278$. In addition, fluid intelligence (processing speed) was assessed by means of the Digit Symbol Substitution Test (DSST), a subscale of the Wechsler Adult Intelligence Scale (WAIS-III; Wechsler, 1997). Older adults obtained significantly lower scores than younger adults, $t(47) = 6.48$, $p < 0.001$, in line with other cognitive aging studies (e.g., Park et al., 2002). However, the scores of both age groups equaled or exceeded age norms and the age-adjusted scores did not differ between groups, $t(47) = 0.79$, $p = 0.433$. Crystallized intelligence (verbal knowledge) was assessed by means of the Spot-the-Word Test (SWT; Baddeley, Emslie, & Nimmo-Smith, 1993). In accordance with Park et al. (2002), neither the raw scores nor the standardized scores showed indications for an age-related difference, both $t \leq 1.23$, $p \geq 0.225$, with both groups scoring above average. Performance of the age groups on these measures is summarized in Table II.1.

Stimuli and material

Six different action sequences were recorded with a Sony HDR-HC7 camera and a Sony VCL-MHG07 wide end conversion lens in HDV1080i (16:9, interlaced, 25 frames per second) showing highly familiar everyday actions (making coffee, sweeping up after breakfast, piling boxes, getting a glass of water, putting a poster on a wall, sorting groceries into a refrigerator). Each action was performed by a younger and older male and female, resulting in 24 different videos overall. Special care was taken that every actor performed the action in the same manner while the setting was exactly the same within each action sequence. A static camera position was used and camera settings were kept constant across the videos. The actions lasted 37.6 s on average (range 29.0-46.8 s).

The experiment was conducted in a dimly lit room. The videos were presented in full color with a resolution of 1,024 × 768 pixels and a screen refresh rate of 100 Hz on a 19-in. Sony Triniton Multiscan E450 monitor (NVIDIA GeForce 8500 GT graphics card). The participants were sitting approximately 65 cm in front of the monitor and responded on a custom-built response device, which was connected to the computer through a parallel port. The software "Presentation" (Neurobehavioral Systems, Albany, CA) was used to control stimulus presentation and data collection.

Design and procedure

Each video started with a fixation cross (1,500 ms), followed by the beginning of an action sequence. Each action sequence was occluded twice for 2,000 ms by a gray rectangle at critical time points, that is, shortly before a sub-goal of the action was accomplished (e.g., when the actor was returning with the water from the tap to the coffee machine). The action sequences were visible for 12.7 s (range 5.6-26.2 s) before each occlusion. The action continuations were either congruent, temporally too early or too late on two different levels (±800 ms/ ±1,600 ms; see Figure II.1.a). The congruent continuation was presented twice as often as the too early and too late continuations, which resulted in an equal number of required key presses. Participants were asked to judge the temporal coherence of the observed action continuation by pressing on one of three response keys (left key: too early, middle key: just-in-time, right key: too late) with the index finger of their right hand. Participants were instructed to respond as quickly and accurately as possible as soon as the action sequence continued after occlusion.

The experiment started with a familiarization phase, in which two action sequences (putting a poster on a wall, sorting groceries into a refrigerator) were presented first without, and second with occlusion. Participants were asked to watch carefully. The same two action sequences were used in the subsequent training phase consisting of 48 trials, in which participants were required to perform the prediction task and received feedback of their performance. Before the actual test phase started, the remaining four action sequences (making coffee, sweeping up after breakfast, piling boxes, getting a glass of water) were presented once without occlusion. The test phase, in which no feedback was given, consisted of 192 trials (4 action sequences × 4 actors × 2 occlusions per video × 6 continuations after occlusion). The action sequences were shown in a pseudo-randomized order, with the restriction that no action or actor was repeated after one another. The continuations after occlusion were randomized separately with the restriction that the same continuation should not be presented more than three times in a row. The order of the videos and continuations was counterbalanced across participants. There was a self-timed break every 15 min after 48 trials. The whole experiment lasted approximately 60 min.

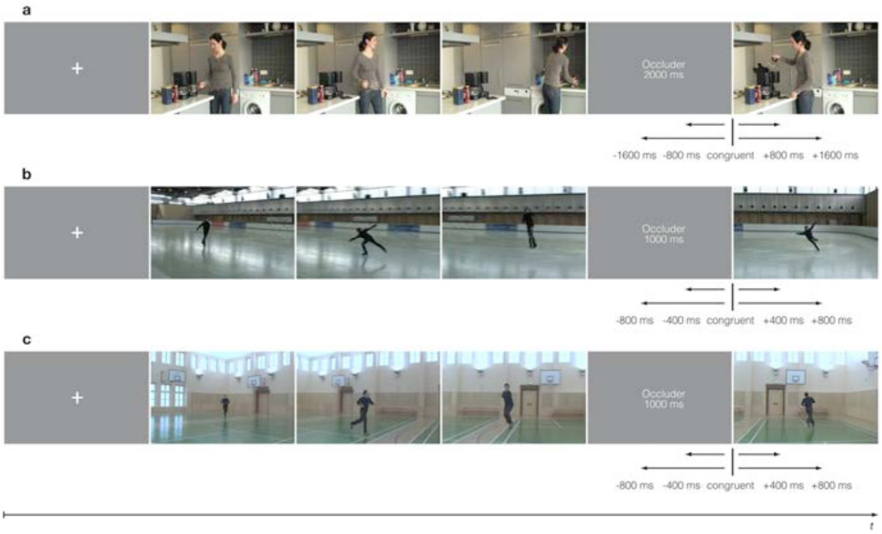


Figure II.1. Details of experimental conditions in Experiment 1 and Experiment 2: The experimental conditions in Experiment 1 are exemplified for the first occluder in a given action sequence (**a**). Each video clip started with a fixation cross (1,500 ms), followed by the beginning of an action sequence. Then the occluder was presented for 2,000 ms, followed by the continuation of the action, that was either congruent, temporally too early or too late on two different levels (±800 ms/±1,600 ms). In Experiment 2, different action sequences of classical figure skating elements (**b**) and simple movement exercises (**c**) were presented. Each video clip started with a fixation cross (1,000 ms), followed by the beginning of an action sequence. Then the occluder was presented for 1,000 ms, followed by the continuation of the action, that was either congruent, temporally too early or too late on two different levels (±400 ms/±800 ms).

Experience with the observed actions

Participants were asked to rate beforehand how often they execute activities such as those shown in the videos (e.g., lifting things, climbing stairs, bending, walking) on a 5-point rating scale ranging from 1 (*daily*) to 5 (*never*). This allowed us to check whether possible age-related differences in prediction performance might be explained by current differences in experience with the observed actions.

Data analysis

First, to analyze the accuracy in prediction, the proportion of correct responses on every continuation after occlusion was submitted into an analysis of variance (ANOVA) with continuation after occlusion (-1,600, -800, 0, +800, +1,600) as repeated measures variable and age group (younger adults, older adults) as between-subject variable. Second, to examine the timing of prediction and possible anticipation biases, the just-in-time response rate on every continuation after occlusion was analyzed by means of an ANOVA with continuation after occlusion (-1,600, -800, 0, +800, +1,600) as repeated measures variable and age group (younger adults, older adults) as between-subject variable. If appropriate, Greenhouse-Geisser corrected *F* values are reported. Post hoc pairwise comparisons (Bonferroni corrected) or *t* tests were applied to further examine significant effects.

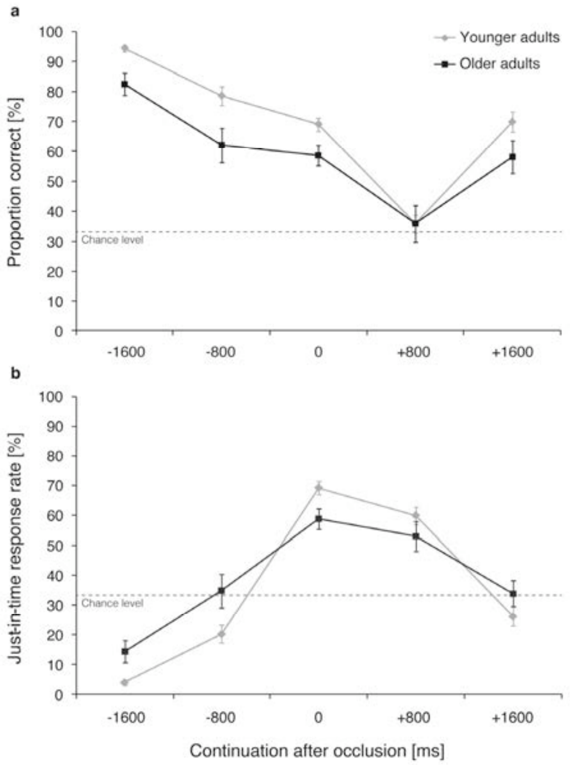
In addition, we analyzed the data psychophysically to test whether the slope of the just-in-time response rate increased (or decreased) with increasing continuations after occlusion in the two age groups. Planned polynomial contrasts tested the trend model that best described the performance of each age group (adapted from Aglioti et al., 2008). The significance of the linear, quadratic, and cubic trend model was examined. With respect to the participants' reports on the frequency of executing movements such as those shown in the videos, data were analyzed by means of a Mann-Whitney *U* test for non-parametric samples.

RESULTS AND DISCUSSION

Prediction accuracy

The ANOVA on the proportion of correct responses revealed a significant main effect of age group, $F(1,47) = 18.75$, $p < 0.001$, $\eta_p^2 = 0.285$. As expected, older adults ($M = 59.4\%$, SD = 9.86%) performed worse than younger adults ($M = 69.5\%$, SD = 6.11%). In addition, the continuations varied in difficulty as suggested by a significant main effect of continuation after occlusion, $F(4,188) = 43.54$, $p < 0.001$, $\eta_p^2 = 0.481$. Performance was best when the actions continued 1,600 ms too early ($M = 88.7\%$) compared to all the other continuations (M = 70.5, 64.1, 35.9, and 64.1% for the -800, 0, +800, and +1,600 ms continuations, respectively), all $p < 0.001$. Performance was worst when the actions continued 800 ms too late, all $p < 0.001$. The interaction between continuation after occlusion and age group did not reach significance, $F(4,188) = 1.14$, $p = 0.315$, $\eta_p^2 = 0.024$, indicating that the pattern of performance did not differ between the age groups (see Figure II.2.a).

Figure II.2. Proportion of correct responses (**a**) and just-in-time response rates (**b**) on every continuation after occlusion for younger and older adults in Experiment 1. *Error bars* represent standard errors of the means.



Prediction timing

The ANOVA on the just-in-time response rates revealed a significant main effect of continuation after occlusion, $F(4,188) = 74.26$, $p < 0.001$, $\eta_p^2 = 0.612$. The just-in-time response rates did not differ significantly between the congruent continuation ($M = 64.1\%$, SD = 14.9%) and the +800 ms continuation ($M = 56.5\%$, SD = 20.1%), $p = 0.145$, indicating that both continuations were predominantly perceived as being just-in-time. There was no significant main effect of age group, $F(1,47) = 2.01$, $p = 0.163$, $\eta_p^2 = 0.041$, but a significant interaction between continuation after occlusion and age group, $F(4,188) = 4.45$, $p = 0.018$, $\eta_p^2 = 0.087$. Compared to older adults, younger adults correctly perceived both too early continuations less often as being just-in-time, and the congruent continuation more often as being just-in-time, all $t \geq 2.26$, $p \leq 0.030$ (see Figure II.2.b).

The trend analysis on the just-in-time response rates revealed a significant linear trend model for younger adults, $F(1,24) = 77.28$, $p < 0.001$, $\eta_p^2 = 0.763$, and older adults, $F(1,23) = 6.32$, $p = 0.019$, $\eta_p^2 = 0.216$. This indicates that the proportion of just-in-time responses in both groups increased at later continuations. The quadratic trend model was also significant for younger adults, $F(1,24) = 416.71$, $p < 0.001$, $\eta_p^2 = 0.946$, and older adults, $F(1,23) = 61.56$, $p < 0.001$, $\eta_p^2 = 0.728$. Thus, the proportion of just-in-time responses correctly tended to level out at continuations that were far away from the congruent continuation. The cubic trend model was significant only for the younger adults, $F(1,24) = 65.61$, $p < 0.001$, $\eta_p^2 = 0.732$, but not for the older adults, $F(1,23) = 1.38$, $p = 0.253$, $\eta_p^2 = 0.056$. This implies that in younger adults, the increase of just-in-time responses was steeper compared to the decrease afterwards. Although the prediction performance of both age groups was biased towards the future as indicated by the results of the ANOVA and the significant linear trend models, this bias seemed to be stronger in younger than in older adults who showed a lower perceptual sensitivity.

Experience with the observed actions

Younger ($Mdn = 1.60$) as well as older adults ($Mdn = 1.64$) reported to execute actions such as those shown in the videos "several times per week" on average, $U = 246.00$, $z = 1.09$, $p = 0.276$. This shows that both groups had comparable levels of experience with the observed actions at the time of the experiment.

Summary

Experiment 1 provided evidence for an age-related decline in the representation of observed actions. Compared to younger adults, older adults were less precise in predicting the time course of observed actions in terms of accuracy and perceptual sensitivity, although they had comparable current experience with the shown actions. Both groups recognized not only the congruent continuation predominantly as being just-in-time but also the continuation that was shifted 800 ms into the future. Thus, both age groups showed an anticipation bias in the prediction of the time course of these actions and the trend analysis revealed that this bias was more pronounced in younger than in older adults.

EXPERIMENT 2

METHODS

Participants

Eighteen younger (16 women, $M = 20.6$, SD = 3.91, age range 16-29 years) and 11 older figure skating experts (7 women, $M = 62.5$, SD = 10.3, age range 51-82 years) took part in Experiment 2. In addition, 19 younger (14 women, $M = 22.2$, SD = 1.80, age range 19-25 years) and 19 older adults (12 women, $M = 64.3$, SD = 4.25, age range 56-74 years) with no visual or motor experience in figure skating participated in the experiment. The experts did not differ significantly in their age compared to the novices of the respective age group, both $t \leq 1.53$, $p \geq 0.139$. All participants were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971) and reported normal or corrected-to-normal vision. The younger novices group consisted of university students and the older novices group of community-dwelling older adults. Both novice groups were recruited from the participant database of the MPI for Human Cognitive and Brain Sciences, Leipzig. None of the participants took part in Experiment 1. Eleven younger experts and five older experts were recruited from the figure skating club "USG Chemnitz e. V.". The remaining experts were recruited via an advertisement in the German-wide published figure skating magazine "Pirouette".

Participants were asked to rate how often they engage in physical activities on a 5-point rating scale ranging from 1 (*daily*) to 5 (*less than once per month*). A Kruskal-Wallis Test for non-parametric samples with group (younger experts, older experts, younger novices, older novices) as between-subject variable revealed significant differences between the groups, $H(3) = 16.80$, $p = 0.001$. Mann-Whitney U tests for non-parametric samples were used to further examine pairwise differences between the groups. The expert groups reported to engage in physical activities "several times per week" on average (younger experts: $Mdn = 1.72$; older experts: $Mdn = 2.38$) and did not differ significantly in their reports, $U = 57.00$, $z = 2.13$, $p = 0.061$. The novice groups reported to engage in physical activities "once per week" on average (younger novices: $Mdn = 3.40$; older novices: $Mdn = 2.83$) and did not differ in their reports, $U = 163.50$, $z = 0.52$, $p = 0.624$. The reported frequency of the novices was lower than that of the experts, $U = 277.50$, $z = 3.64$, $p < 0.001$. More specifically, the younger figure skaters spent on average 11.5 h per week (SD = 5.76) on ice for 15.6 years

(SD = 4.08). All of the older experts still performed the sport on a regular basis with 4.00 h per week (SD = 4.81) on ice for 38.6 years (SD = 21.8). Seven of them pursued a professional career for a period of 10.9 years (SD = 8.19) with 10.3 h per week (SD = 7.48) on ice but ended it around the age of 23.3 years (SD = 10.8).

Participants gave written informed consent and received payment for participation. For participants under the age of 18 (6 younger experts), additional informed consent was obtained from their parents. The groups did not differ with respect to their reported years of education as revealed by an ANOVA on the reported years of education with age group (younger adults, older adults) and expertise group (novices, experts) as between-subject variables, all $F \leq 1.72$, $p \geq 0.195$, $\eta_p^2 \leq 0.027$. Characteristics of the groups are shown in Table II.2.

Table II.2. Characteristics of the sample in Experiment 2.

	Younger experts (n = 18)	Older experts (n = 11)	Younger novices (n = 19)	Older novices (n = 19)
Years of education	14.4 (3.71)	15.2 (2.52)	15.2 (2.72)	14.0 (3.21)
Handedness score	90.1 (12.1)	90.3 (12.8)	96.0 (6.44)	96.1 (7.03)
MMSE score	-	29.2 (0.75)	-	29.3 (0.75)
SF-36				
PCS score	50.7 (10.4)	58.0 (4.61)	50.9 (8.01)	55.9 (4.27)
MCS score	49.7 (7.17)	53.3 (4.49)	53.4 (4.68)	55.5 (3.58)
DSST				
Raw score	84.3 (12.7)	65.6 (14.3)	87.4 (11.7)	60.5 (14.7)
Standardized score	11.4 (2.40)	11.4 (2.80)	11.7 (2.23)	11.3 (2.65)
SWT				
Raw score	29.2 (3.38)	32.3 (2.80)	33.3 (2.61)	32.8 (2.06)
Standardized score	-0.13 (0.47)	0.39 (0.58)	0.58 (0.54)	0.46 (0.43)

Values represent mean scores and standard deviations (parenthesized). See Table II.1 for a description of the scores.

Health and cognitive status

None of the participants reported current evidence of any major physical or neurological disease and/or use of medication that might affect perceptual or cognitive performance. None of the older experts (M = 29.2, SD = 0.75, range 28-30) and none of the older novices (M = 29.3, SD = 0.75, range 28-30) showed indications of cognitive impairment as measured by the MMSE and the groups did not differ significantly from each other, $t(28) = 0.47$, $p = 0.641$.

In addition, the same tests as used in Experiment 1 were conducted to assess health and cognitive status among the groups. Group differences were examined by means of an ANOVA for each test score with age group (younger adults, older adults) and expertise group (novices, experts) as between-subject variables. The performance of the sample on these measures is summarized in Table II.2. Concerning the PCS score, a significant main effect of age group indicated that older participants obtained higher scores than younger participants, $F(1,63) = 10.74$, $p = 0.002$, $\eta_p^2 = 0.146$. In the MCS score, the reports of the groups differed as well as shown by a significant main effect of age group, $F(1,63) = 4.81$, $p = 0.032$, $\eta_p^2 = 0.071$. Thus, especially older adults who estimated their health status as being very good participated in the experiment. In addition, a significant main effect of expertise group on the MCS score implied that experts estimated their mental health as being lower than novices, $F(1,63) = 5.15$, $p = 0.027$, $\eta_p^2 = 0.076$. With respect to fluid intelligence (processing speed), a significant main effect of age group was found for the DSST raw score, $F(1,63) = 46.71$, $p < 0.001$, $\eta_p^2 = 0.426$. Older participants obtained significantly lower scores than younger participants, in line with other cognitive aging studies (e.g., Park et al., 2002). When compared with norms appropriate to the participants' age group, all groups obtained scores that equaled or exceeded age norms and the groups did not differ significantly from each other, all $F \leq 0.13$, $p \geq 0.723$, $\eta_p^2 \leq 0.002$. With respect to crystallized intelligence (verbal knowledge), a significant interaction between age group and expertise group was found for the SWT raw score, $F(1,63) = 6.81$, $p = 0.011$, $\eta_p^2 = 0.097$, as well as the SWT standardized score, $F(1,63) = 6.44$, $p = 0.014$, $\eta_p^2 = 0.093$. Planned comparisons for both test scores of the four groups revealed that the younger experts scored significantly lower than all the other groups, all $p \leq 0.045$ (Bonferroni corrected). This might be due to their age and educational level because this group also comprised some participants under the age of 18, who still went to school, whereas the younger novices were more homogenous in terms of their educational level.

Stimuli and material

The same equipment as in Experiment 1 was used to record videos of different action sequences, and the same rules concerning the equivalence of the setting and manner of performance by different actors were applied. Twelve classical figure skating elements (e.g., jumps, spins, and step sequences) were videotaped, all of which are listed in the official judging system for single skating specified by the International Skating Union (ISU, http://www.isu.org). The videos were recorded in a practice rink of the Skating Centre in Chemnitz, Germany. Each action was performed by a young male and female athlete, who both had at least 10 years of deliberate practice in singles skating. Each sequence was approved by a trainer with regard to the quality and execution of the respective element. The camera was positioned at the side of the ice rink and was kept static during the spins. During the jumps and step sequences, the camera followed the athletes in the horizontal plane to capture the whole movement (e.g., the preparation, entrance, take-off, landing, and exit of a jump). In total, 24 different figure skating videos were used in the experiment. The videos lasted 11.7 s on average (range 7.4-22.2 s).

In addition, 12 simple movement exercises (e.g., running sequences, simple jumps, and spins) were videotaped that were related to the figure skating sequences as much as possible (e.g., involving rotations or jumps) but should be feasible for nearly everyone. The videos were recorded in a sports hall of the University of Leipzig, Germany. Each action was performed by a young male and female non-athlete. The camera was positioned at the side of the sports hall and was kept static during some actions and followed them in the horizontal plane during other actions, resembling the conditions in the figure skating videos. In total, 24 different movement exercise videos were used in the experiment. The videos lasted 9.0 s on average (range 8.0-10.9 s).

A list of all action sequences from each category that were used in the experiment is provided in Table II.3. The experiment was conducted in the same environment and with the same equipment as Experiment 1.

Table II.3. Action sequences used in Experiment 2.

	Action sequences
Figure skating	*Training phase*
	Double Lutz[a]
	Double Toeloop/Double Toeloop Combination[a]
	Circular Step Sequence[a]
	Combination Spin[b]
	Test phase
	Double Toeloop[a]
	Double Salchow[a]
	Double Loop[a]
	Double Flip[a]
	Double Salchow/Double Toeloop Combination[a]
	Straight Line Step Sequence[a]
	Change Foot Sit Spin[b]
	Change Foot Combination Spin[b]
Movement exercises	*Training phase*
	Running backward[a]
	Step sequence (alternating forward and backward running)[a]
	Single spin while running forward[a]
	Jumping jack[b]
	Test phase
	Single jump while running forward[a]
	Single jumped spin while running forward[a]
	Running forward[a]
	Running forward – half spin – running backward[a]
	Step sequence (alternating single spins and running)[a]
	Double spin while running forward[a]
	Single standing spin[b]
	Knee bend[b]

Superscript letters refer to the respective viewing angle of the camera: [a] Camera followed the actors in the horizontal plane, [b] Static camera position.

Design and procedure

Each video started with a fixation cross (1,000 ms), followed by the beginning of an action sequence. Each action sequence was occluded once for 1,000 ms by a gray rectangle at critical time points, for example, when the athlete reached the highest point during the jump. For actions involving cyclic movements, the occlusions occurred only at time points in which distinct movement changes took place (e.g., a position change) to avoid ambiguities. Before each occlusion, the figure skating sequences were visible for 6.2 s (range 3.9-12.4 s) and the movement exercise sequences for 4.5 s (range 3.1-5.9 s). The action continuations were either congruent, temporally too early, or too late on two different levels (±400 ms/±800 ms, see Figure II.1.b, c for an example from each action category). Each continuation was presented equally often. In contrast to Experiment 1, participants were asked to judge the temporal coherence of the observed action continuation by pressing on one of two response keys (left key: too early, right key: too late) with their right index and middle finger. A 2-alternative instead of a 3-alternative forced choice paradigm was used in this experiment because this allowed an analysis of the prediction timing as described in Gescheider (1997) with an equal number of trials for each continuation after occlusion. Participants were instructed to respond as quickly and accurately as possible as soon as the action sequence continued after occlusion.

The experiment started with a familiarization phase, in which four action sequences from each action category were presented first without, and second with occlusion. Participants were asked to watch carefully. The same action sequences were used in the subsequent training phase, in which participants were required to perform the prediction task and received feedback of their performance. The training phase consisted of 32 trials per action category (64 in total), in which the congruent continuation was excluded because no correct response alternative was available for this continuation. Before the actual test phase started, the remaining eight action sequences from each category were presented once without occlusion. The test phase, in which no feedback was given, consisted of 320 trials (2 action categories × 8 action sequences × 2 actors × 5 continuations after occlusion × 2 repetitions). The action sequences were presented in blocks each consisting of eight videos from one action category, in which no action was repeated after one another, resulting in 20 blocks from each category (40 in total). The continuations after occlusion were randomized separately with the restriction that the same continuation should not be presented more than two times in a row with a maximum of three too early or too late continuations after one another. The order of the videos and continuations was counterbalanced across participants. There was a self-timed break every 15 min after 10 blocks. The whole experiment lasted approximately 65 min.

Experience with the observed actions

All of the participants were asked to rate how well they *are currently* able to execute the observed actions (i.e., the figure skating elements and the movement exercises). The older groups were additionally asked how well they *were* able to execute these actions in the past (i.e., when they were younger). Responses had to be given on a 5-point rating scale ranging from 1 (*very well*) to 5 (*not at all*). This allowed us to check whether possible age- and expertise-related differences in prediction performance might be explained by current and past differences in experience with the observed actions.

Data analysis

First, to analyze the accuracy in prediction, the proportion of correct responses on the too early and too late continuations after occlusion was submitted in an ANOVA with action category (figure skating elements, movement exercises) and continuation after occlusion (-400, -800, +400, +800) as repeated measures variables and age group (younger adults, older adults) and expertise group (novices, experts) as between-subject variables.

Second, we analyzed the prediction timing psychophysically and tested whether the response slope differed between the groups. Because a 2-alternative forced choice paradigm was used here, a psychometric function was fitted to the z-transformed too early response rates on every continuation after occlusion by means of a linear regression. The point of subjective equality (PSE) and the just noticeable difference (JND) were calculated for each participant and action category (Gescheider, 1997). The PSE is defined as the point at which participants judged the continuation of the action sequences on chance level, that is, at which they perceived it as being just-in-time. The JND is defined as a measure for the steepness of the psychometric function and represents the interval between 25 and 75% of too early response rates, that is, the perceptual sensitivity of the groups. ANOVAs with action category (figure skating elements, movement exercises) as repeated measures variable and age group (younger adults, older adults) and expertise group (novices, experts) as between-subject variables were applied on the PSE and JND values to analyze age- and expertise-related effects.

With respect to the participants' reports on their current and past ability to execute the observed actions, data were analyzed by means of an ANOVA with age group (younger adults, older adults) and expertise group (novices, experts) as between-subject variables. If appropriate, Greenhouse-Geisser corrected *F* values are reported. Post hoc pairwise comparisons (Bonferroni corrected) or *t* tests were applied to further examine significant effects.

RESULTS AND DISCUSSION

Prediction accuracy

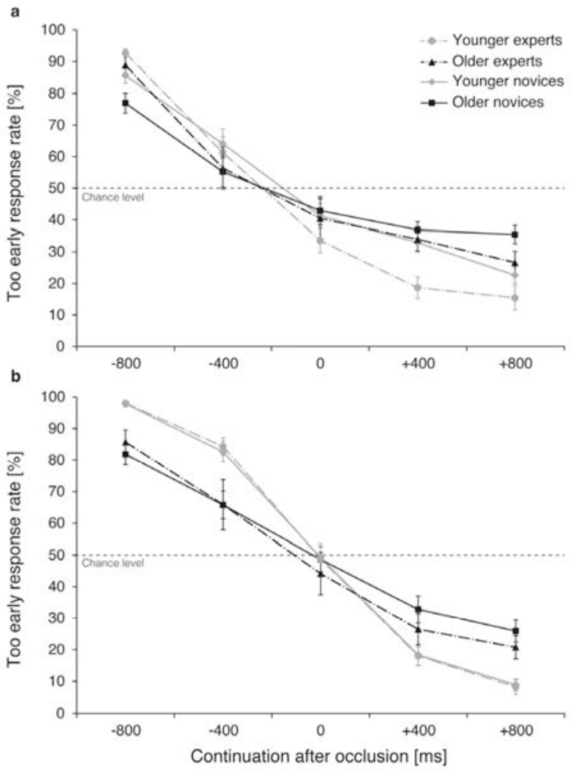
The performance of the groups (i.e., too early response rates) on every continuation after occlusion for each action category is shown in Figure II.3. The ANOVA on the proportion of correct responses on the too early and too late continuations revealed a significant main effect of action category, $F(1,63) = 86.67$, $p < 0.001$, $\eta_p^2 = 0.579$. Participants were more accurate when they observed the movement exercises ($M = 82.0\%$, SD = 10.7%) compared to the figure skating elements ($M = 72.5\%$, SD = 8.74%). There was also a main effect of continuation after occlusion, $F(3,189) = 34.53$, $p < 0.001$, $\eta_p^2 = 0.354$. Participants performed better when the actions continued 800 ms too early ($M = 88.5\%$) compared to the other too early and too late continuations ($M = 67.6$, 73.0, and 79.8% for the -400, +400, and +800 ms continuations, respectively), all $p < 0.001$. In addition, performance was better when the actions continued 800 ms too late compared to both 400 ms continuations, all $p < 0.001$. A significant interaction between action category and continuation after occlusion indicated that some continuations varied in difficulty as a function of observed action category, $F(3,189) = 6.57$, $p = 0.001$, $\eta_p^2 = 0.094$. When the figure skating elements continued 400 ms too early ($M = 59.5\%$), performance was worse than when they continued 400 ms too late ($M = 69.6\%$), $t(66) = 2.76$, $p = 0.008$. This was not found for the movement exercises, in which performance did not differ on these continuations (-400 ms: $M = 75.6\%$; +400 ms: $M = 76.3\%$), $t(66) = 0.23$, $p = 0.819$.

The ANOVA also revealed a main effect of age group, $F(1,63) = 57.41$, $p < 0.001$, $\eta_p^2 = 0.477$, showing that older adults performed less accurately ($M = 70.5\%$, SD = 7.79%) than younger adults ($M = 82.7\%$, SD = 5.07%). A significant interaction between action category and age group, $F(1,63) = 9.06$, $p = 0.004$, $\eta_p^2 = 0.126$, indicated that this age-related difference was more pronounced for the movement exercises (older adults: $M = 73.7\%$, SD = 9.85%; younger adults: $M = 88.7\%$, SD = 5.28%) than for the figure skating elements (older adults: $M = 67.3\%$, SD = 7.28%; younger adults: $M = 76.7\%$, SD = 7.53%).

In addition, a significant main effect of expertise group was found, $F(1,63) = 7.84$, $p = 0.007$, $\eta_p^2 = 0.111$, which was modulated by a significant interaction between action category and expertise group, $F(1,63) = 4.28$, $p = 0.043$, $\eta_p^2 = 0.064$. Experts ($M = 76.6\%$, SD = 8.52%) performed better than novices ($M = 69.3\%$, SD = 7.57%) when they observed the figure skating elements, $t(65) = 3.72$, $p < 0.001$. No expertise-related difference in performance was found for the movement exercises (experts: $M = 84.1\%$, SD = 10.3%; novices: $M = 80.3\%$, SD = 10.8%), $t(65) = 1.45$, $p = 0.152$.

None of the interactions containing expertise and age group became significant, possibly due to the small sample size of the older experts in particular, all $F \leq 1.91$, $p \geq 0.149$, $\eta_p^2 \leq 0.029$. However, planned comparisons on the proportion of correct responses of all groups, when the figure skating elements were observed, showed that the younger experts performed more accurately than all the other groups, all $p \leq 0.036$. The older experts' performance did not differ from the performance of younger novices, $p = 1.000$. This suggests that both young age and sensorimotor expertise had a positive effect on accuracy in the prediction of the time course of figure skating elements.

Figure II.3. Too early response rates on every continuation after occlusion for the figure skating elements (**a**) and the movement exercises (**b**) for younger and older figure skating experts and novices in Experiment 2. Higher response rates on negative continuations and lower response rates on positive continuations imply a more accurate prediction performance. *Error bars* represent standard errors of the means.



Prediction timing

The ANOVA on the PSE values did not reveal any significant main effects or an interaction, all $F \leq 3.22$, $p \geq 0.077$, $\eta_p^2 \leq 0.049$ (see Figure II.4.a). PSE values of all groups for each action category did not differ significantly from zero, all $t \leq 1.76$, $p \geq 0.097$, showing that prediction performance was not biased (M = -2.92 ms, SD = 34.1 ms).

The ANOVA on the JND values showed a significant main effect of action category, $F(1,63) = 24.15$, $p < 0.001$, $\eta_p^2 = 0.277$. This indicates that the JND was higher when the figure skating elements were observed (M = 710 ms, SD = 477 ms) than when the movement exercises were observed (M = 447 ms, SD = 322 ms) (see Figure II.4.b). In addition, a significant main effect of age group, $F(1,63) = 36.74$, $p < 0.001$, $\eta_p^2 = 0.368$, revealed that the JND of older adults (M = 966 ms, SD = 590 ms) was generally higher than that of younger adults (M = 503 ms, SD = 198 ms). This was not modulated by the type of observed actions, as implied by a non-significant interaction between action category and age group, $F(1,63) = 0.00$, $p = 0.959$, $\eta_p^2 = 0.000$. The

ANOVA also showed a significant main effect of expertise group, $F(1,63) = 8.93$, $p = 0.004$, $\eta_p^2 = 0.124$, and, more importantly, a significant interaction between action category and expertise group, $F(1,63) = 9.84$, $p = 0.003$, $\eta_p^2 = 0.135$. The JND of experts (M = 497 ms, SD = 233 ms) was significantly lower compared to the JND of novices (M = 873 ms, SD = 550 ms) when they observed the figure skating elements, $t(65) = 3.79$, $p < 0.001$. Thus, experts showed a higher perceptual sensitivity in the prediction of actions from their domain of expertise. The JNDs did not differ between experts (M = 396 ms, SD = 274 ms) and novices (M = 486 ms, SD = 354 ms) when they observed the movement exercises, $t(65) = 1.13$, $p = 0.261$. None of the interactions containing expertise and age group became significant, possibly due to the small sample size of the older experts in particular, all $F \leq 2.41$, $p \geq 0.125$, $\eta_p^2 \leq 0.037$. However, planned comparisons on the JND values of each group, when the figure skating elements were observed, showed that the older novices had a higher JND than all the other groups, all $p \leq 0.030$ (Tamhane T2 corrected due to unequal variances across groups). This suggests that both young age and expertise had a positive effect on the perceptual sensitivity in the prediction of the time course of figure skating elements.

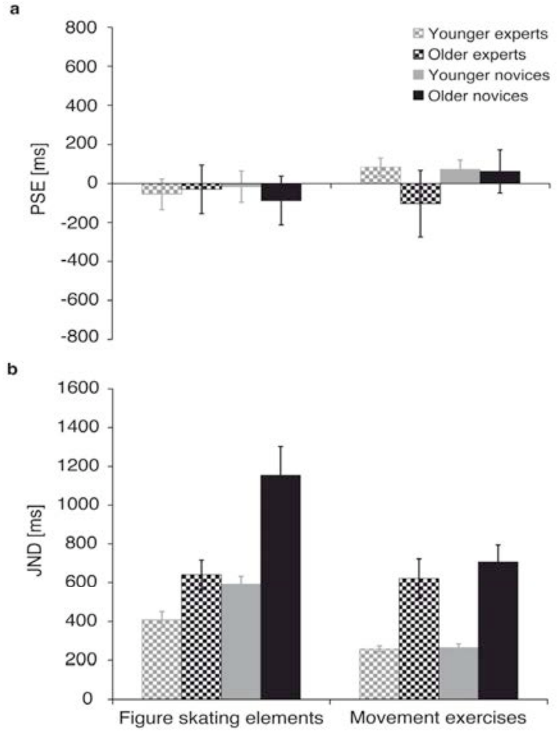


Figure II.4. The point of subjective equality (PSE, **a**) and the just noticeable difference (JND, **b**) for the figure skating elements (*left panel*) and the movement exercises (*right panel*) for younger and older figure skating experts and novices in Experiment 2. *Error bars* represent standard errors of the means.

Experience with the observed actions

For the figure skating elements, the ANOVA on the current ability to execute these actions showed a significant main effect of expertise group, $F(1,63) = 96.10$, $p < 0.001$, $\eta_p^2 = 0.604$, and a significant interaction between age group and expertise group, $F(1,63) = 21.59$, $p < 0.001$, $\eta_p^2 = 0.255$. Planned comparisons revealed that both novice groups reported to be able to execute these actions "not at all" at the time of the experiment (younger novices: $M = 4.74$, SD = 0.58; older novices: $M = 4.68$, SD = 0.65), $p = 1.000$. The older experts admitted that they would be able to execute them "not very well" at present ($M = 3.73$, SD = 1.06). The rating on their current ability was still more positive than that of the younger and older novices, all $p \leq 0.007$. In contrast, the younger experts estimated their ability to execute the observed figure skating elements as being "good" ($M = 2.06$, SD = 0.74), which was higher than the estimates of all other groups, all $p < 0.001$. With respect to the past ability to execute the figure skating elements of the older groups compared to the current ability of the younger groups, the ANOVA showed only a significant main effect of expertise group, $F(1,63) = 159.95$, $p < 0.001$, $\eta_p^2 = 0.717$. This indicates that the older novices ($M = 4.60$, SD = 0.58) were also not able to execute the actions in the past. The older experts, in contrast, estimated their past ability between "well" and "moderately" ($M = 2.55$, SD = 1.16), which did not differ from the reports of the younger experts on their current ability, $p = 0.546$.

For the movement exercises, the ANOVA on the current ability to execute these actions showed a significant main effect of age group, $F(1,63) = 17.51$, $p < 0.001$, $\eta_p^2 = 0.217$, indicating that the younger groups estimated their ability as being "very good" ($M = 1.45$, SD = 0.62), whereas the older groups estimated their current ability as being only "good" ($M = 2.30$, SD = 0.90). A significant main effect of expertise group, $F(1,63) = 11.37$, $p = 0.001$, $\eta_p^2 = 0.153$, implied that the experts ($M = 1.46$, SD = 0.69) were more positive in their ratings to perform the movement exercises than the novices ($M = 2.11$, SD = 0.89). With respect to the past ability to execute the movement exercises of the older groups compared to the current ability of the younger groups, the ANOVA revealed no significant effects, $F \leq 3.96$, $p \geq 0.051$, $\eta_p^2 \leq 0.059$, although both young age and expertise tended to result in more positive ratings (older experts: $M = 1.61$, SD = 0.76; older novices: $M = 1.93$, SD = 0.71).

Summary

In line with the findings from Experiment 1, the results from Experiment 2 suggest that there is a specific decline of action representations in the aging mind. The prediction performance in terms of accuracy and perceptual sensitivity of older adults was worse than the performance of the younger adults, irrespective of observed action category. However, extensive sensorimotor experience with the observed actions resulted in a better performance of experts compared to novices of the same age group. Indeed, the performance of older experts was comparable to the performance of younger novices when the time course of figure skating elements had to be predicted, although they reported that their ability to execute these actions had deteriorated. This expertise-related benefit did not show transfer to movement exercises, which were similar to the figure skating elements in terms of basic movement patterns (e.g., involving jumps and rotations), but were also feasible for non-athletes to perform. In contrast to the results in Experiment 1, no anticipation bias in the prediction of the time course of figure skating elements or movement exercises was found.

GENERAL DISCUSSION

The purpose of the two experiments reported here was to investigate (a) how age affects the ability to predict the time course of observed actions; and (b) whether and to what extent sensorimotor expertise might attenuate possible age-related declines in prediction performance. The results from both experiments show an age-related decline in how observed actions are internally mapped onto one's own motor representations. Older adults predicted the time course of observed actions less precisely in terms of accuracy and perceptual sensitivity than younger adults, who also possessed sensorimotor experience with the observed actions. Nevertheless, older adults were still able to accomplish the task in general and obtained scores that equaled or exceeded age norms on different physical and cognitive health measures. Sensorimotor experience with the observed actions resulted in a better prediction performance for domain-specific actions (figure skating elements) in both older and younger experts compared to novices of the respective age groups. This expertise-related benefit did not show transfer to similar actions that were also feasible for non-athletes (movement exercises). Our results further showed that the prediction performance in Experiment 1 was slightly biased towards the future, whereas this was not case in Experiment 2.

AGE-RELATED CHANGES IN THE REPRESENTATION OF OBSERVED ACTIONS

The observed age-related decline in prediction performance indicates that internal models seem to become less precise with advancing age. The results are in line with studies that used motor imagery to investigate the representation of actions in older and younger adults and argue for difficulties in the generation and control of imagined but not executed actions in the aging brain, especially for complex tasks (e.g., Gabbard et al., 2011; Personnier, Kubicki, et al., 2010; Personnier et al., 2008; Saimpont et al., 2009; Skoura et al., 2005; Skoura et al., 2008). Our results also support the notion that older adults are not as efficient as younger adults in creating and updating predictions of the sensory outcomes of an observed action when sensory feedback is not available, as in the case of temporarily occluded actions (cf., Kilner et al., 2007b; Schippers & Keysers, 2011; Wolpert et al., 2003). Even when older adults reported still being able to execute the observed actions and therefore must possess an internal model of these actions, they did not seem to represent them in a sufficiently detailed manner in order to predict their exact time course. This might indicate that these representational processes, which are thought to operate largely automatically and without any explicit reflective reasoning in younger adults, require more effort and explicit control with age. Older adults might compensate for inaccuracies in their forward models by using a higher level of abstraction, especially when no sensory feedback is available, resulting in higher uncertainties about the specific trajectory of the observed actions (see also Maryott & Sekuler, 2009).

This interpretation is supported by studies on motor performance in old age that found activation in additional brain areas in older adults compared to younger adults during movement execution and coordination. For example, in addition to activation in classical motor coordination regions, activation was found for older adults in areas known to be involved in higher-level sensory processing, as well as in frontal areas, possibly reflecting increased cognitive monitoring during complex interlimb coordination tasks (e.g., Heuninckx et al., 2005; Heuninckx et al., 2008). Thus, behavioral changes during prediction of observed actions are likely to be linked to changes at the neural level. Indeed, Nedelko et al. (2010) has provided the first evidence that besides recruiting the action observation network during action observation and imagery, older adults show stronger activation of regions involved in visual and sensorimotor processing compared to younger adults. While the recruitment of additional neural resources is likely necessary for older adults to perform the task, a more diffuse pattern of activity implies that prediction processes operate differently in the aging mind (cf., Park & Reuter-Lorenz, 2009). Léonard and Tremblay (2007) suggested that the recruitment of additional brain regions might lead to less selective motor commands in older adults, which in turn result in a more widespread corticomotor facilitation of hand muscles of older adults than in younger adults during observation, imagery, and imitation of different hand actions.

THE ROLE OF EXPERTISE

The results from Experiment 2 show that sensorimotor expertise leads to a better prediction performance for domain-specific actions. This replicates findings from previous studies that showed a better anticipation performance of experts compared to novices when they observed actions from their domain of expertise (e.g., Abernethy & Zawi, 2007; Aglioti et al., 2008; Farrow & Abernethy, 2003; Mann et al., 2007; Müller et al., 2006; Sebanz & Shiffrar, 2009). More importantly, Experiment 2 provided evidence that sensorimotor expertise indeed has the potential to compensate to some extent for age-related declines in the representation of observed actions. In line with findings from other domains of expertise, our results suggest that many years of deliberate practice enable older experts to overcome certain age-related changes in order to maintain a higher performance in skill-related tasks compared to older novices (Horton et al., 2008; Kramer et al., 2004; Krampe, 2002; Krampe & Ericsson, 1996; Salthouse, 2006). Many years of extensive participation in the sport might have resulted in more stable representations of these actions that are less prone to age-related declines. Older experts might be able to access internal models that are related to their domain of expertise more efficiently. This allows them to generate more accurate predictions about the specific time course of the observed actions without relying as much on concrete sensory feedback and/or abstract representations compared to older novices. In addition, these findings exclude the possibility that age-related declines in action prediction might be explained by general age-related declines in memory, because both older groups in Experiment 2 did not differ significantly in their age and, therefore, should possess comparable levels of memory function. However, further research is needed to clarify the possible contribution of episodic memory onto the representation of observed actions (but see Stadler et al., 2011).

An alternative explanation for the observed benefit in action prediction among older experts might be related to differing amounts of physical activity between the older groups. There is growing evidence that especially cardiovascular fitness positively affects a variety of variables that have been linked to a healthy aging mind (Colcombe & Kramer, 2003; Cotman & Berchtold, 2002; Hillman, Erickson, & Kramer, 2008). The older experts in our study indeed reported a higher frequency of engagement in physical activities than the older novices. However, the expertise-related benefit in action prediction did not show transfer to the observed movement exercises. Thus, an influence of physical activity on the representation of actions in old age seems to be rather unlikely. Because expertise-related benefits are often restricted to the domain of expertise rather than affecting cognitive tasks in general, it is assumed that experts adapt to age-related performance constraints by relying on less age-sensitive processes and mechanisms that can be maintained through increased efforts (Krampe, 2002; Krampe & Charness, 2006; Krampe & Ericsson, 1996).

One question we cannot definitely answer in the present study is whether motor and/or visual experience were responsible for the better performance of older experts during the observation of figure skating elements, as we had no control group in which participants had visual but no motor experience with the observed actions. Evidence in the literature provides support for the predominant role of motor experience in the representation of observed actions (see Aglioti et al., 2008; Calvo-Merino et al., 2006; Urgesi et al., 2012). For example, Urgesi et al. (2012) demonstrated that motor and visual expertise might result in different strategies in the prediction of observed actions. Accordingly, motor experts seem to rely mainly on body kinematics whereas visual experts rather exploit the visual dynamics of the actions and its context. The respective role of motor and visual experience may differ between younger and older experts. Although all of the older experts reported to still spend time on ice every week and had regular perceptual experience of the observed figure skating elements (e.g., as coaches or judges), they also reported that they would not be able to execute them very well anymore. The question is whether older experts still profit from the motor experience acquired many years ago or whether their visual experience also contributes to the better performance in comparison to older novices (cf., Cross et al., 2011). Older experts may use a different strategy than younger experts to solve the task (e.g., predominantly based on visual dynamics of the observed actions).

PREDICTION TIMING

Another important finding from our experiments was that the representation of the actions in Experiment 1 was slightly biased towards the future, whereas the actions in Experiment 2 were represented approximately in real-time. The results from Experiment 1 are thus in line with studies suggesting that the representation of actions is a predictive process that runs slightly ahead of the actual realization (Perrett et al., 2009; Schütz-Bosbach & Prinz, 2007; Urgesi et al., 2010), whereas the results from Experiment 2 correspond to findings of Graf et al. (2007). This discrepancy might be explained by differing setups between Experiment 1 and Experiment 2 that were related to (a) the goal-directedness of the observed actions; (b) the speed of execution of the observed movements, and (c) the respective response format.

The videos of Experiment 1 consisted of complex everyday actions in which the shown movements were always directed towards a certain goal, for example, walking from the chair to the shelf to get a glass of water. In contrast, the movement sequences in Experiment 2 were intransitive. In Experiment 1, the observation of causal events may have involved an anticipation of forthcoming action phases. The absence of such a clear anticipation bias in Experiment 2 might be due to a lack of clearly predictable goals that forced the observers to focus on the pure kinematic representation of these actions. Thus, the mere existence of a goal as such implied by the context of the action might support the prediction of observed actions (see also Iacoboni et al., 2005).

Observed differences in the timing of prediction between the experiments might also be partly related to the speed, in which the observed movements were executed. In Experiment 1, the everyday actions were executed rather deliberately. These actions are likely to be executed faster and less controlled in everyday life. The actions in Experiment 2, in contrast, were executed at a considerable faster rate, for example, the movement exercises involved running instead of walking sequences and, finally, the very fast figure skating actions. This may determine the perceptual complexity and in turn the demands on the representational processes in the observer.

In addition, whereas participants in Experiment 2 were forced to decide whether the actions continued too early or too late, participants in Experiment 1 could also judge the continuations as being just-in-time. This might have induced different response behaviors. Thus, although both experiments focused on differences in the prediction of observed actions as a function of the individual characteristics of the observer, they should be thought of as independent from each other. The degree to which particular characteristics of the setup might influence the specific timing in prediction is an important question that needs to be addressed in future research.

CONCLUSION

The results from both experiments provide evidence that the ability to predict the time course of observed actions becomes less precise with advancing age. However, the anticipation and prediction of others' actions benefits from sensorimotor expertise in the observer even in older age. Thus, the results might have useful applications in improving skill learning and skill maintenance in older adults [i.e., by targeting physical domains that older individuals were highly proficient in as younger adults or emphasizing alternative (visual) strategies that support successful performance]. As such, our findings could be taken into account when designing training and intervention programs aimed at older adults.

Acknowledgments

The authors thank Michaela Boldt, Felix Schneeweiß, Bettina Schnabel, Hans-Joachim Gehre, Luise Albrecht, Nils Ehlers, as well as Ingeburg Böhm and the athletes from the USG Chemnitz e. V., Olivia Dittrich and Martin Rappe, for their participation and invaluable help in developing the stimulus material for the experiments, Tanja Schorch for her great assistance in organizing the data collection, and two anonymous reviewers for their helpful comments on an earlier version of this manuscript.

III. ACTION PREDICTION IN YOUNGER VERSUS OLDER ADULTS: NEURAL CORRELATES OF MOTOR FAMILIARITY

PLOS ONE (submitted).

Nadine Diersch[1,2], Mueller, K. [1], Emily S. Cross[1,3,4], Waltraud Stadler[1,5], Martina Rieger[1,6], & Simone Schütz-Bosbach[1]

[1]Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany; [2]MaxNetAging Research School, Max Planck Institute for Demographic Research, Rostock, Germany; [3]Wales Institute for Cognitive Neuroscience, School of Psychology, Bangor University, Gwynedd, United Kingdom; [4]Behavioral Science Institute, Donders Institute for Brain, Cognition and Behaviour, Radboud University Nijmegen, Nijmegen, The Netherlands; [5]Movement Science Unit, Faculty for Sports and Health Science, Technical University Munich, Munich, Germany; [6]Institute for Psychology, Medical Sciences & Management Department, UMIT – The Health and Life Sciences University, Hall/Tyrol, Austria

ABSTRACT

Generating predictions during action observation is essential for efficient navigation through our social environment. With age, the sensitivity in action prediction declines. In younger adults, the action observation network (AON), consisting of premotor, parietal and occipitotemporal cortices, has been implicated in transforming executed and observed actions into a common code. Much less is known about age-related changes in the neural representation of observed actions. Using fMRI, the present study measured brain activity in younger and older adults during the prediction of temporarily occluded actions (figure skating elements and simple movement exercises). All participants were highly familiar with the movement exercises whereas only some participants were experienced figure skaters. With respect to the AON, the results confirm that this network was preferentially engaged for the more familiar movement exercises. Compared to younger adults, older adults recruited visual regions to perform the task and, additionally, the hippocampus and caudate when the observed actions were familiar to them. Thus, instead of effectively exploiting the sensorimotor matching properties of the AON, older adults seemed to create a visual image of the observed actions and evaluated its features to perform the

task. Our data further suggest that the caudate played an important role during the prediction of the less familiar figure skating elements in better-performing groups. Together, these findings show that action prediction engages a distributed network in the brain, which is modulated by the content of the observed actions and the age and experience of the observer.

INTRODUCTION

As humans, our ability to successfully navigate through our social environment and interact with others is critical for survival. It has been argued that instead of just passively relying on sensory input during the observation of others' actions, we also generate internal predictions on what we see (Brown & Brüne, 2012; Bubic et al., 2010; Schütz-Bosbach & Prinz, 2007; Wilson & Knoblich, 2005; Wolpert et al., 2003). This enables us to adapt and respond more quickly and efficiently to changes in the environment. The ability to create these action predictions is thought to be based on a shared representation between executed and observed actions (cf., Hommel et al., 2001; Prinz, 1997).

So far, research on the prediction of observed actions focused mainly on younger age groups while neglecting changes in these processes over the lifespan. Evidence suggests that there might be a specific decline in how older adults anticipate observed actions, possibly due to less precise internal action representations (e.g., Diersch et al., 2012; Gabbard et al., 2011; Personnier, Kubicki, et al., 2010; Personnier et al., 2008; Saimpont et al., 2009; Skoura et al., 2008). For example, in a recent behavioral study we showed that older adults predicted the time course of different action sequences less precisely than younger adults (Diersch et al., 2012). Although the timing in prediction was not systematically biased in older compared to younger adults (i.e., generally slower or faster), older adults did not seem to represent the observed actions in sufficient temporal detail in order to predict their exact time-course. This suggests an age-related decline in how observed actions are internally mapped onto one's own action representations. We further demonstrated that sensorimotor experience with observed actions resulted in a better prediction performance for domain-specific actions in both older and younger experts compared to non-experts. These findings, however, did not allow us to address questions concerning whether older adults might have used a different strategy to solve the task depending on their level of motor familiarity, and to what extent this might be linked to age-related changes in neural activation patterns.

In the light of a demographic change visible in many countries with lower fertility rates and rising life expectancies, a better understanding of age-related changes in these vital abilities together with its neural basis is essential in improving skill learning and skill maintenance in older adults (cf., Christensen et al., 2009). It is well known that the aging brain is subject to substantial changes at the structural as well as functional level (see Dennis & Cabeza, 2008; Fjell & Walhovd, 2010; Grady, 2012 for reviews). In addition, older adults exhibit different task-related activation patterns compared to younger adults while performing the same task that could reflect neural dedifferentiation and/or compensation (e.g., Cabeza, 2002; Davis et al., 2008; Li & Lindenberger, 1999). According to the scaffolding theory of aging and cognition (STAC), aging can be viewed as a (intrinsic) challenge to the human brain just as unfamiliar tasks pose a (extrinsic) challenge to a younger brain (Park & Reuter-Lorenz, 2009). Both types of challenges result in a functional reorganization (i.e., neural scaffolding) to maintain or improve task performance. Whereas neural recruitment patterns in younger adults become increasingly specialized with training, older adults may recruit additional regions already during the performance of familiar tasks to compensate for noisy and/or inefficient neural processing. However, even in older age groups these neural recruitment patterns are amenable to training (Erickson et al., 2007). In sensory as well as motor processing, age-related differences in neural activity together with altered functional connectivity have been demonstrated by a number of studies, possibly reflecting less specific neural representations in action *and* perception with advancing age (e.g., Carp, Park, Hebrank, et al., 2011; Carp, Park, Polk, et al., 2011; Heuninckx et al., 2005; Heuninckx et al., 2010; Langan et al., 2010; Park et al., 2004; Ward & Frackowiak, 2003; Wu et al., 2007).

In younger adults, neuroimaging studies on action observation identified regions in the premotor and inferior parietal cortex that are similarly activated during action execution (see Caspers et al., 2010; Grèzes & Decety, 2001; Molenberghs et al., 2012; Rizzolatti & Craighero, 2004 for reviews). A network comprising these sensorimotor regions as well as occipitotemporal regions implicated in biological motion processing has been referred to as the action observation network (AON; Grafton, 2009). By transforming executed and observed actions into a common code, the AON might serve as the neural substrate for the ability to predict the actions of others. According to the predictive coding account, the different regions of the AON are reciprocally connected and an actual representation of the observed action is compared to a predicted representation in each region of the network (Friston et al., 2011; Kilner et al., 2007a, 2007b). This comparison generates a prediction error, which is back propagated through the cortical hierarchy to update the internal action representation and minimize the prediction error.

Consequently, shared representations between action and perception and their neural basis are assumed to be established through sensorimotor experience that strengthens the connectivity between relevant areas (cf., Catmur et al., 2009; Heyes, 2010; Press, Heyes, & Kilner, 2011). Studies on skilled motor performance frequently demonstrate superior prediction abilities in experts when they observe actions from their domain of expertise whereas non-experts rather rely on the visual dynamics of the observed actions resulting in a less efficient anticipation performance (e.g., Abernethy & Zawi, 2007; Aglioti et al., 2008; Urgesi et al., 2012). Not surprisingly, AON activity has been shown to be modulated by the sensorimotor experience of the observer. The majority of studies investigating this issue has found increased activity in these regions during the observation of familiar actions as compared to actions that are not in the motor repertoire of the observer (e.g., Buccino, Lui, et al., 2004; Calvo-Merino et al., 2005; Calvo-Merino et al., 2006; Cross et al., 2006). Observers that are not familiar with the shown actions, in contrast, seem to recruit additional regions beyond the AON, for example, in visual cortices to perform these kinds of tasks (e.g., Olsson et al., 2008; Wright et al., 2011). In addition, recent evidence indicates that specific task requirements and stimulus characteristics might also result in the activation of regions that are not typically considered to be part of the AON during action observation (e.g., Abreu et al., 2012; Schiffer, Ahlheim, Wurm, et al., 2012; Schiffer & Schubotz, 2011). For example, Schiffer and Schubotz (2011) showed that prediction errors during action observation in ambiguous contexts are coded within a sub-region of the basal ganglia, the caudate nucleus. They suggested that the caudate might trigger the updating of the respective internal action representation if the sensory input violates the initial prediction.

To the best of our knowledge, there are only very few studies so far that examined age-related differences in the neural representation of observed actions. By using transcranial magnetic stimulation (TMS), Léonard and Tremblay (2007) showed that corticomotor facilitation in relevant muscles is less specialized in older compared to younger adults during action observation, imitation, and imagery. In addition, Nedelko et al. (2010) did not report age-related activation differences in the premotor and inferior parietal regions of the AON during observation and imagery of simple goal directed actions. The authors concluded that activity in these regions is age-independent. However, older adults recruited additional regions in the superior parietal and occipital cortices compared to younger adults, which might indicate a different processing of the observed actions (i.e., neural scaffolding). Yet, it remains unclear to what extent the prediction of an observed action is linked to similar changes at the neural level in older adults and whether they are modulated by the degree of motor familiarity in the aging observer.

By using fMRI, the present study examined the underlying neural activation patterns in younger and older adults during the prediction of action sequences that varied in their degree of motor familiarity (classical figure skating elements and simple movement exercises). All of the participants were highly familiar with the movement exercises, whereas only some of the younger and older adults possessed sensorimotor experience in figure skating. During fMRI scanning, participants were required to judge the temporal coherence of the observed action sequences that were partly occluded at critical time points and whose continuation afterwards was temporarily manipulated. Similar action occlusion paradigms have been used previously in different behavioral action observation and prediction studies and also proved successful in measuring neural activity in the AON during action observation (e.g., Cross et al., 2011; Graf et al., 2007; Parkinson et al., 2012; Saygin & Stadler, 2012; Stadler et al., 2011; Stadler et al., 2012). Brain activity was examined as a function of predicted action category and continuation after occlusion collapsed across the whole sample as well as a function of age group while controlling for the effects of sensorimotor experience in figure skating. In addition, brain activity between figure skating experts and non-experts was compared to further explore whether neural scaffolding in older adults and inexperienced observers shares a certain degree of similarity (cf., Park & Reuter-Lorenz, 2009).

We hypothesized that the type of observed action sequences modulates activity in the AON. In accordance with previous evidence, we expected to find higher AON activity during the prediction of the movement exercises for which the whole sample was highly experienced with. The less familiar figure skating elements, on the contrary, might be processed in regions beyond the AON due to less precise neural representations in an observer's AON. In addition, we assumed that older adults might recruit additional brain regions compared to younger adults, implying less specific internal action representations and/or the use of a different prediction strategy in line with the assumptions of STAC (Park & Reuter-Lorenz, 2009). Thus, older adults just as inexperienced observers might perform the task predominantly based on the visual dynamics of the observed actions, which is accompanied with a greater recruitment of visual cortices, respectively. Age-related differences in neural activation patterns might be further modulated by the degree of motor familiarity, for example, in regions known to be involved in episodic memory.

MATERIALS AND METHODS

ETHICS STATEMENT

The study was approved by the ethics committee of the University of Leipzig and was conducted in accordance with the Declaration of Helsinki. Participants gave written informed consent and received payment for participation.

PARTICIPANTS

A group of 38 participants, comprising younger and older adults, took part in the fMRI experiment. Three participants (one younger adult and two older adults) were excluded from statistical analyses after medical examination of their anatomical scans in which structural abnormalities were diagnosed that might have an influence on their functional images. In addition, one younger adult was excluded due to experience in professional modern dance for six years in adolescence. The final sample consisted of 19 younger (14 women, mean age = 22.6 ± 2.27 years, range 18-27) and 15 older adults (10 women, mean age = 61.1 ± 5.68 years, range 51-71), $t(32) = 24.7$, $p < 0.001$. The majority of the participants already took part in the behavioral action prediction experiment reported in Diersch et al. (2012). One younger adult and four older adults were additionally recruited from the participant database of the MPI for Human Cognitive and Brain Sciences, Leipzig. Before scanning, these participants were invited for a separate testing session in which they completed the relevant questionnaires and performed the behavioral action prediction task to ensure that the whole sample was scanned under the same prerequisites. Time between the two experimental sessions was 5.35 months on average (range 3-8 months). Characteristics of the sample divided by age group are shown in Table III.1.

All participants were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971) and reported normal or corrected-to-normal vision. None of the participants reported current evidence of any major physical or neurological disease and/or use of medication that might affect blood flow. None of the older adults showed indications of cognitive impairment as measured by the Mini-Mental State Examination (MMSE; Folstein et al., 1975; Maximum score: 30). The groups did not differ with respect to their reported years of education, $t(32) = 0.68$, $p = 0.500$. In addition, fluid intelligence (processing speed) was assessed by means of the Digit Symbol Substitution Test (DSST), a subscale of the Wechsler Adult Intelligence Scale (WAIS-III; Wechsler, 1997). Although older adults obtained lower DSST raw scores than younger adults, $t(32) = 5.53$, $p < 0.001$, the groups did not differ from each other, when compared with norms appropriate to the participants' age group, $t(32) = 1.09$, $p = 0.286$. With respect to crystallized intelligence (verbal knowledge) as assessed by means of the Spot-the-Word Test (SWT; Baddeley et al., 1993), no age-related differences were found, both $t \leq 0.46$, $p \geq 0.648$.

Table III.1. Characteristics of the sample.

	Younger adults ($n = 19$)	Older adults ($n = 15$)
Handedness score	92.4 (9.28)	92.5 (9.60)
MMSE score	-	29.2 (0.78)
Years of education	15.7 (3.25)	14.9 (3.11)
DSST		
Raw score	86.0 (14.2)	61.3 (11.0)
Standardized score	11.6 (2.77)	10.7 (2.29)
SWT		
Raw score	32.4 (3.24)	32.9 (2.10)
Standardized score	0.43 (0.57)	0.47 (0.44)

Values represent mean scores and standard deviations (parenthesized). DSST and SWT values are shown as raw scores and as standardized scores adjusted to the following means: DSST: $M = 10$, SD = 3 (age-adjusted); SWT: $M = 0$, SD = 1.

With respect to the action sequences used in the experiment, all participants confirmed that they were well able to perform the movement exercises (see Diersch et al., 2012 for a detailed description). In addition, 10 of the 34 participants were highly experienced in figure skating (six younger adults and four older adults). The six younger figure skaters (5 women, *M* = 21.2, SD = 2.23, range 18-24 years) spent on average 11.7 hours per week (SD = 7.06) on ice for 14.8 years (SD = 2.64). The four older figure skaters (3 women, *M* = 56.0, SD = 5.60, range 51-64 years) still performed the sport on a regular basis with 3.50 hours per week (SD = 1.29) on ice for 35.0 years (SD = 22.4). Two of them pursued a professional career for a period of 14.0 years (SD = 6.69) with 14.8 hours per week (SD = 7.41) on ice but ended it around the age of 22.7 years (SD = 11.0).

STIMULI AND DESIGN

The same video stimuli were used as in the behavioral experiment reported in Diersch et al. (2012). Half of the videos featured classical figure skating elements (e.g., jumps, spins, and step sequences), all of which are listed in the official judging system for single skating specified by the International Skating Union (ISU, http://www.isu.org). The second set of videos featured simple movement exercises (e.g., running sequences, simple jumps, and spins) that were related to the figure skating sequences as much as possible (e.g., involving rotations) but should be feasible for nearly everyone. Each action was performed by a young male and female athlete (figure skating elements) or non-athlete (movement exercises). The two sets of action sequences were carefully matched with respect to viewing perspective, camera settings, and luminance. The figure skating sequences lasted 11.7 s on average (SD = 3.70 s, range 7.40-22.2 s) and the movements exercise sequences 9.00 s on average (SD = 0.81 s, range 8.00-10.9 s). In total, 48 different videos consisting of 12 different action sequences from two action categories that were performed by two actors were used in the fMRI experiment.

Each video started with a fixation cross (1,000 ms), followed by the beginning of an action sequence. Each action sequence was occluded once for 1,000 ms by a grey rectangle at critical time points, for example, when the athlete reached the highest point during the jump. Before each occlusion, the figure skating sequences were visible for 6.24 s (SD = 2.54 s, range 3.92-12.4 s) and the movement exercise sequences for 4.50 s (SD = 0.76 s, range 3.08-5.92 s) on average, $t(46) = 3.23$, $p = 0.003$. Although the figure skating sequences were visible slightly longer than the movement exercise sequences before they were occluded, there is no reason to assume that this might have influenced the predictive processes in the observers during occlusion. Parkinson et al. (2012) recently showed that the prediction of partly occluded actions is nearly unaffected by the length of the action sequences presented before occlusion suggesting that observers engage in prediction very quickly and automatically, even when only a small fraction of human motion is visible. In addition, the critical time frame during which participants were assumed to engage in the internally guided prediction was kept constant across the two action categories (i.e., the duration of occlusion).

After an occlusion, the action sequences continued immediately. The continuations after occlusion were either congruent or incongruent (see Figure III.1 for an example from each action category). Based on the results of the previous behavioral study, in which continuations of ±400 ms and ±800 ms were used and the prediction sensitivity of the different groups (i.e., response slopes) was analyzed, a temporal shift of ±600 ms was chosen to examine age-related differences in the neural representation of the different action sequences at an intermediate level of difficulty (cf., Diersch et al., 2012).

Figure III.1. Details of experimental conditions during fMRI scanning. Different action sequences of classical figure skating elements (**A**) and simple movement exercises (**B**) were presented. Each video clip started with a fixation cross (1,000 ms), followed by the beginning of an action sequence. Then the occluder was presented for 1,000 ms, followed by the continuation of the action, that was either congruent or incongruent (±600 ms).

The action sequences were presented in full color with a resolution of 1,024 x 768 pixels and a frame rate of 25 frames per second using a back projection system in which a LCD projection on a screen in the back of the scanner was reflected by a mirror placed above the participants' eyes. The software "Presentation" (Neurobehavioral Systems, Albany, CA) was used to control stimulus presentation and behavioral data collection.

TASK AND PROCEDURE

For MRI scanning, participants were provided with ear-plugs and headphones to reduce scanner noise. Vision was corrected with MRI-compatible plastic goggles, if necessary. The participants' task was to judge for each observed action sequence whether the continuation after occlusion was correct or not by pressing on one of two response keys (left key: correct, right key: incorrect) with their index and middle finger on a response device that was placed in their right hand. Participants were instructed to respond as quickly and accurately as possible as soon as the action sequence continued after occlusion. An event-related design was used to measure neural responses during the prediction of observed action sequences.

Prior to the functional run, participants completed a short familiarization and training phase in the scanner during the acquisition of initial control sequences. This allowed them to accommodate to the task and the scanner environment. The familiarization started with two action sequences from each action category that were presented without occlusion and two action sequences from each action category that were presented with occlusion. These action sequences (four different action sequences from each action category) were also presented in a subsequent training phase, in which participants were required to perform the prediction task and received feedback of their performance. The training phase consisted of 16 trials per action category (32 in total). The remaining eight action sequences from each action category that were used in the actual test phase were presented once without occlusion before the functional run started.

The functional run, in which no feedback was given, consisted of 80 trials (8 action sequences x 2 actors x 5 repetitions) per action category (160 in total), in which the congruent and incongruent continuations were presented 40 times each. The action sequences were presented in blocks consisting of eight videos from one action category, in which no action was repeated after one another, resulting in

10 blocks from each category (20 in total). The continuations after occlusion were randomized separately with the restriction that the same continuation should not be presented more than two times in a row with a maximum of three congruent or incongruent continuations after one another. Within each action category, the congruent continuation was presented twice as often as the two incongruent continuations (i.e., too early and too late), which resulted in an equal number of congruent and incongruent continuations. The order of the videos and continuations was counterbalanced across participants. After each video block, a resting baseline showing a black screen with a grey fixation cross was presented for 8-12 s, pseudo-logarithmically distributed. The functional run lasted approximately 32 min.

Scanning was performed on a 3T TIM Trio scanner (Siemens, Erlangen, Germany) with a 12-channel head array coil. Functional images were acquired with a gradient echo echo-planar imaging (EPI) sequence with TR = 2,000 ms, TE = 30 ms, flip angle = 90°, and acquisition bandwidth = 1,815 Hz/pixel. The matrix acquired was 64 x 64 voxels with a FoV of 192 mm x 192 mm, resulting in an in-plane resolution of 3 mm x 3 mm. Twenty-six axial slices allowing for full-brain coverage were acquired in ascending order with slice thickness = 4 mm and interslice gap = 1 mm. Slices were oriented parallel to the bicommisural plane (AC-PC). A set of 1,020 functional images was collected in a single functional run. In addition to functional imaging, high-resolution anatomical images were acquired using a T1-weighted 3D magnetization-prepared rapid gradient echo (MPRAGE) sequence with selective water excitation and linear phase encoding (Mugler & Brookeman, 1990). Anatomical scanning was performed using a sagittal slice orientation with the following imaging parameters: TI = 650 ms, TR = 1,300 ms, TE = 3.5 ms, flip angle = 10°, acquisition bandwidth = 190 Hz/pixel, image matrix = 256 x 240 voxels, FoV = 240 mm x 256 mm, spatial resolution = 1 mm x 1 mm x 1 mm, 2 acquisitions.

DATA ANALYSIS

Data analysis was performed using the SPM8 software package (Wellcome Department of Imaging Neuroscience, London, UK) with Matlab 7 (Mathworks, Natick, MA). Preprocessing of the EPI volumes included correction for motion and distortion, slice timing, as well as normalization to the standard MNI space using the unified segmentation approach (Ashburner & Friston, 2005). Finally, spatial smoothing was done using an 8 mm full-width at half maximum isotropic Gaussian kernel. A two-level random effects approach as implemented in SPM8 was used for the statistical analyses. On the individual level, continuation after occlusion as a function of observed action category was modeled for each participant as separate events with 0 s duration convolved with the standard hemodynamic response function: figure skating sequences that continued congruently or incongruently and movement exercise sequences that continued congruently or incongruently. This resulted in an equal number of relevant events in each condition.

The respective beginning of occlusion was defined as the target event in order to capture the time in which participants were assumed to engage in the internally guided prediction of the occluded action sequences. The results of our previous study suggested that the sensitivity in action prediction is lower in older adults compared to younger adults and in experts compared to non-experts as evidenced by a larger temporal range during which the continuations after occlusion were predominantly perceived as being just-in-time (i.e., resulting in higher error rates; Diersch et al., 2012). In the present study, we aimed to examine the neural effects of aging and sensorimotor experience during action prediction that might accompany these differences in behavioral efficiency. Thus, both correct and incorrect trials from each critical condition were incorporated in the fMRI analyses, which also ensured that the same number of events would be included in the analyses of the between-subject effects.

The time of the button press was modeled as additional event to control for the effects of finger movements. Each baseline condition was modeled as a boxcar with the respective duration. Confounding factors from head movement, that is, six rotational and translational parameters from the rigid body transformation, obtained during image realignment, were included in the model as covariates of no interest. A high-pass filter at 1/100 Hz was used to remove low-frequency fluctuations of the MR signal. Whole brain analyses were conducted using a voxel-wise threshold of $p < 0.001$ and a minimum cluster size of 10 voxels. To control for false positive results, analyses focus on brain regions reaching a cluster-corrected significance threshold of $p < 0.05$ (FWE corrected).

On the first level, the effects of each action category, collapsed across the continuations after occlusion, were compared to baseline and directly to each other, as were the interactions with continuation after occlusion by computing contrast images combining the parameter estimates of the corresponding experimental conditions. On the second level, those contrast images were fed into one-sample *t* tests to perform inference statistics across the whole sample. Between-subject effects were tested using the general linear model as implemented in SPM. Due to the small sample size of figure skating experts in the two age-groups, two-sample *t* tests instead of a full factorial design were used to examine the effects of age while correcting for non-sphericity through assuming measurement independence und unequal variance between groups. More specifically, differences between older and younger adults on the respective first-level comparisons were examined while taking experience in figure skating as a covariate of no interest into account.

In addition, differences between figure skating experts and non-experts were tested accordingly while including age group as covariate of no interest. Although this did not allow for a direct investigation of interactions between age and experience in figure skating, the effects of motor familiarity were examined as a function of observed action category given that all of the participants were highly experienced with respect to the observed movement exercises. Significant group differences were further examined separately within the respective groups by means of one-sample *t* tests of the individual contrast images. Anatomical localization of all activations was aided by the Anatomy Toolbox in SPM8 (Eickhoff et al., 2005) in combination with the Atlas of the Human Brain (Mai, Paxinos, & Voss, 2008).

RESULTS

BEHAVIORAL RESULTS

Prediction performance during fMRI data acquisition was calculated as proportion of correct responses of every group on congruent and incongruent continuations for each action category with an equal number of trials for each condition. The proportion of correct responses was submitted into an ANOVA with action category (figure skating elements, movement exercises) and continuation after occlusion (congruent, incongruent) as repeated measures variables and age group (younger adults, older adults) and expertise group (figure skating experts, non-experts) as between-subject variables. A significant interaction between action category, continuation after occlusion, age group, and expertise group, $F(1,30) = 4.26$, $p = 0.048$, $\eta_p^2 = 0.124$, implied that the performance of the groups was modulated by the observed action category and continuation after occlusion.

To further examine this 4-way interaction, follow-up ANOVAs with continuation after occlusion (congruent, incongruent) as repeated measures variable and age group (younger adults, older adults) and expertise group (figure skating experts, non-experts) as between-subject variables were conducted for each action category separately. For the figure skating elements, a significant main effect of continuation after occlusion was revealed, $F(1,30) = 8.32$, $p = 0.007$, $\eta_p^2 = 0.217$, with better performance for congruent ($M = 65.0\%$, SD = 18.3%) than incongruent continuations ($M = 53.3\%$, SD = 16.3%). In addition, a significant main effect of age group, $F(1,30) = 18.5$, $p < 0.001$, $\eta_p^2 = 0.382$, and a main effect of expertise group, $F(1,30) = 4.54$, $p = 0.041$, $\eta_p^2 = 0.132$, was found. Thus, not only young age (younger adults: $M = 65.3\%$, SD = 12.3%; older adults: $M = 51.4\%$, SD = 7.70%) but also experience in figure skating (experts: $M = 66.0\%$, SD = 16.9%; non-experts: $M = 56.3\%$, SD = 9.21%) had a positive effect on prediction accuracy during the observation of figure skating elements.

The follow-up ANOVA for the movement exercises showed a significant main effect of continuation after occlusion, $F(1,30) = 11.2$, $p = 0.002$, $\eta_p^2 = 0.272$, and a significant main effect of age group, $F(1,30) = 11.1$, $p = 0.002$, $\eta_p^2 = 0.270$. This was modulated by a significant interaction between continuation after occlusion and age group, $F(1,30) = 6.17$, $p = 0.019$, $\eta_p^2 = 0.170$. Older ($M = 63.6\%$, SD = 18.3%) and younger adults ($M = 66.0\%$, SD = 11.0%) did not differ significantly in their performance on congruent continuations, $t(32) = 0.46$, $p = 0.648$. On incongruent continuations, however, older adults' performance dropped significantly ($M = 42.9\%$, SD = 12.8%) compared to younger adults ($M = 63.3\%$, SD = 8.80%), $t(32) = 5.51$, $p < 0.001$.

The results show that older adults predicted the observed action sequences less precisely compared to younger adults, even when they were familiar with the observed actions. In addition, the higher percentage of incongruent continuations that were incorrectly perceived as still being congruent among older adults during the observation of the movement exercises is in line with the results of our previous study suggesting that the temporal sensitivity in action prediction declines with age (cf., Diersch et al., 2012). Moreover, sensorimotor experience in figure skating exerted a positive influence on the performance of experts compared to non-experts of the same age group during the observation of the figure skating elements. Together, the behavioral data suggest that all groups attended to the action sequences and engaged in action prediction in the manner that was hypothesized during fMRI scanning.

NEUROIMAGING RESULTS

Effects of predicted action category

The prediction of both types of action sequences compared to baseline resulted in bilateral activity in frontal, parietal, occipitotemporal, and occipital regions as well as in some subcortical structures (Fig. III.2A,B and Supporting Information Table S.1 in Appendix C). The direct comparison between the action categories revealed remarkable differences. Compared to movement exercises, the visual cortex and the medial orbitofrontal cortex (OFC) were more engaged during the prediction of figure skating elements (Fig. III.2C and Table III.2A). In contrast, the premotor, parietal and occipitotemporal regions of the AON were preferentially activated during the prediction of movement exercises compared to figure skating elements (Fig. III.2D and Table III.2B). For the movement exercises only, the right posterior superior temporal sulcus (pSTS) differentiated between incongruent and congruent continuations after occlusion (Table III.2C). Thus, different regions of the AON showed selectivity for the generally familiar movement exercises whereas visual and frontal areas responded stronger to the less familiar figure skating elements.

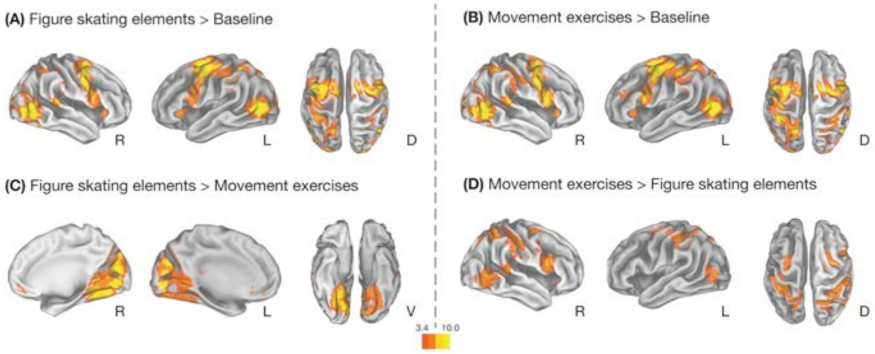


Figure III.2. Main effects of observed action category collapsed across the whole sample. Brain regions that showed greater activation during the prediction of figure skating elements (**A**) and movement exercises (**B**) compared to baseline, and direct comparisons between the action categories (**C** and **D**). Results were calculated using a voxel-wise threshold of $p < 0.001$ and a minimum cluster size of 10 voxels. Abbreviations: R – Right Hemisphere; L – Left hemisphere; D – Dorsal; V – Ventral.

Table III.2. Effects of predicted action category and continuation after occlusion.

				MNI coordinates (mm)			*t* value	*p* value
Anatomical region	Putative functional name	BA	Cluster size	*x*	*y*	*z*	*df* = [1,33]	(corr.)
(A) Figure skating elements > Movement exercises								
Midline Calcerine Gyrus	V1	17	3615	0	-88	-5	11.84	< 0.001
R Lingual Gyrus	V2/V3	18		12	-73	-5	11.38	
R Fusiform Gyrus		19		27	-64	-11	9.05	
R Superior Frontal Gyrus	vmPFC	10	117	12	50	4	4.78	0.022
R Medial Orbitofrontal Gyrus	OFC	32		12	41	-8	4.33	
L Medial Orbitofrontal Gyrus	OFC	32		-3	41	-8	3.96	
(B) Movement exercises > Figure skating elements								
R Intraparietal Sulcus	IPS	7/40	1791	36	-49	55	8.09	< 0.001
R Superior Temporal Gyrus	pSTS	22		54	-40	10	7.38	
R Supramarginal Gyrus	IPL	40		60	-22	43	7.26	

R Precentral Gyrus	PMd	6	761	30	-10	52	8.01	< 0.001
R Inferior Frontal Gyrus (pars opercularis)	PMv	44		57	11	25	7.53	
R Middle Frontal Gyrus	PMd	6		24	8	43	4.81	
L Inferior Parietal Lobule	IPL	7/40	1133	-39	-37	46	7.12	< 0.001
L Middle Frontal Gyrus	PMd	6		-27	-10	55	6.73	
L Superior Parietal Lobule	SPL	7		-18	-64	58	6.16	
L Middle Occipital Gyrus	V5/hMT+	39	194	-48	-73	4	6.78	0.003
(C) Movement exercises: incongruent > congruent								
R Middle Temporal Gyrus	pSTS	22	151	60	-49	10	4.90	0.022
R Middle Temporal Gyrus	pSTS	22		54	-43	7	4.62	

Regions activated during the prediction of figure skating elements compared to movement exercises (**A**) and vice versa (**B**). Regions activated during incongruent compared to congruent continuations after occlusion during the prediction of movement exercises are shown in section (**C**). Results are collapsed across the whole sample using a voxel-wise threshold of $p < 0.001$ and a minimum cluster size of 10 voxels. Only clusters are reported that reached cluster-corrected significance of $p < 0.05$, FWE corrected. Up to three local maxima are listed when a cluster has multiple peaks more than 8 mm apart. Abbreviations for brain regions: V1, visual area V1/striate visual cortex; V2, visual area V2/prestriate visual cortex; V3, visual area V3/extrastriate visual cortex; vmPFC, ventromedial prefrontal cortex; OFC, orbitofrontal cortex; IPS, intraparietal sulcus; pSTS, posterior superior temporal sulcus; IPL, inferior parietal lobule; PMd, dorsal premotor cortex; PMv, ventral premotor cortex; SPL, superior parietal lobule; V5/hMT+, visual area V5/extrastriate visual cortex/middle temporal.

Effects of age group

In order to evaluate regions in which activation varied as a function of age group, older and younger adults were compared to each other while the factor experience in figure skating was included as covariate of no interest. Compared to younger adults, older adults showed a greater recruitment of the prestriate and extrastriate visual cortex, bilaterally centered in the cuneus, for the figure skating elements as well as the movement exercises compared to the baseline condition (Fig. III.3A,B and Table III.3A,B). During the prediction of movement exercises, older adults engaged an additional region in the right posterior hippocampus extending to the right caudate more than younger adults (Fig. III.3B and Table III.3B). The reverse contrasts did not reveal any significant clusters that were more activated in younger adults compared to older adults. This confirms that older adults recruited areas beyond the AON, which younger adults did not, during action prediction.

Figure III.3. Brain regions more activated in older adults compared to younger adults. Patterns of brain activation during the prediction of figure skating elements (**A**) and movement exercises (**B**) compared to baseline. Results were calculated using a voxel-wise threshold of $p < 0.001$ and a minimum cluster size of 10 voxels. Only clusters are shown that reached cluster-corrected significance of $p < 0.05$, FWE corrected.

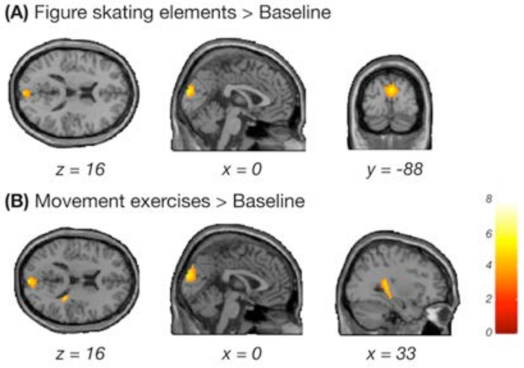


Table III.3. Main effects of age group for each predicted action category compared to baseline.

				MNI coordinates (mm)			*t* value	*p* value
Anatomical region	Putative functional name	BA	Cluster size	*x*	*y*	*z*	*df* = [1,31]	(corr.)
(A) Figure skating elements > Baseline								
R Cuneus	V2/V3	18	117	3	-91	22	5.28	0.030
R Cuneus	V3	19		3	-85	37	3.52	
(B) Movement exercises > Baseline								
R Cuneus	V2/V3	18	160	3	-91	22	5.76	0.009
R Insula		13	107	33	-34	13	4.85	0.039
R Hippocampus				36	-28	-8	4.67	
R Caudate				21	-25	22	4.17	

Regions more activated in older adults compared to younger adults while controlling for expertise group during the prediction of figure skating elements (**A**) and movement exercises (**B**) compared to baseline. Results were calculated using a voxel-wise threshold of $p < 0.001$ and a minimum cluster size of 10 voxels. Only clusters are reported that reached cluster-corrected significance of $p < 0.05$, FWE corrected. Up to three local maxima are listed when a cluster has multiple peaks more than 8 mm apart. Abbreviations for brain regions: V2, visual area V2/prestriate visual cortex; V3, visual area V3/extrastriate visual cortex.

In addition, a significant interaction between predicted action category and age group was found in the left caudate and the bilateral thalamus together with the left posterior cingulate cortex (PCC; Fig. III.4C and Table III.4A). To examine this interaction further, a comparison between both types of action sequences was conducted within each age group. The results are illustrated in the upper panels of Figure III.4 and a complete listing of suprathreshold activations in each age group can be found in Supporting Information Table S.2 in Appendix C. This analysis revealed that the interaction was due to the younger adults, who showed a greater recruitment of the visual cortex that extended to the PCC and the thalamostriatal network during the prediction of the figure skating elements compared to movement exercises. In older adults, the same comparison revealed only the visual cortex and the medial OFC. In contrast, premotor, parietal and occipitotemporal regions of the AON that were largely confined to the right hemisphere were more activated in younger adults when they predicted movement exercises compared to figure skating elements. In older adults, similar regions were found for the same contrast, although mainly bilaterally distributed. No age-related activation differences that reached cluster-corrected significance were found for the interactions between action category and continuation after occlusion.

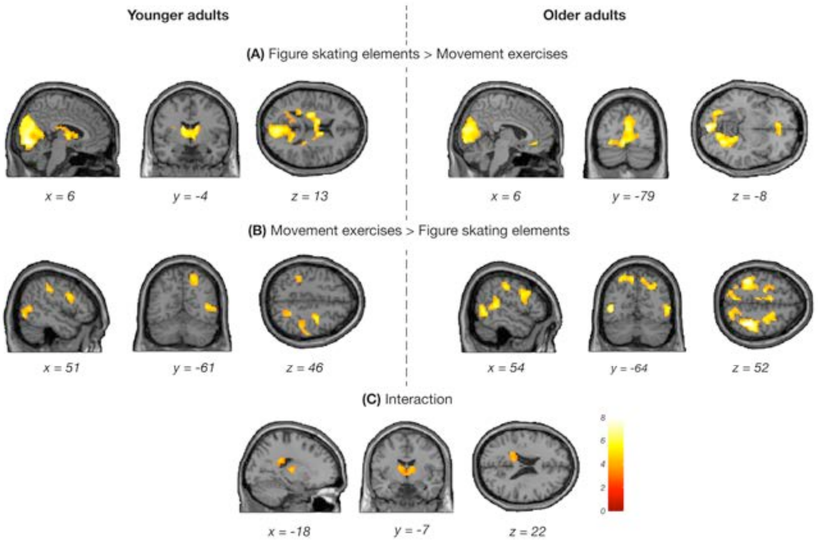


Figure III.4. Interaction between predicted action category and age group. Brain regions that showed greater activation in younger (*left panel*) and older adults (*right panel*) during the prediction of figure skating elements compared to movement exercises (**A**) and vice versa (**B**). The interaction is shown in panel (**C**). Results were calculated using a voxel-wise threshold of $p < 0.001$ and a minimum cluster size of 10 voxels. Only clusters are shown that reached cluster-corrected significance of $p < 0.05$, FWE corrected.

Table III.4. Interactions between predicted action category and group.

				MNI coordinates (mm)			*t* value	*p* value
Anatomical region	Putative functional name	BA	Cluster size	*x*	*y*	*z*	*df* = [1,31]	(corr.)
(A) Interaction with age group								
L Thalamus			271	-21	-16	10	5.36	< 0.001
Midline Thalamus				0	-22	4	5.15	
L Caudate				-9	-4	13	4.60	
L Posterior Cingulate Gyrus	PCC	23/31	105	-18	-37	28	4.70	0.027
L Posterior Cingulate Gyrus	PCC	23		-24	-43	19	4.57	
L Posterior Cingulate Gyrus	PCC	23		-9	-37	22	4.42	
(B) Interaction with expertise group								
L Caudate			195	-15	-22	13	4.58	0.002
L Caudate				-18	-7	16	4.37	
L Thalamus				-9	-10	7	4.31	

Interactions between action category and age group (**A**) and expertise group (**B**). Results were calculated using a voxel-wise threshold of $p < 0.001$ and a minimum cluster size of 10 voxels. Only clusters are reported that reached cluster-corrected significance of $p < 0.05$, FWE corrected. Up to three local maxima are listed when a cluster has multiple peaks more than 8 mm apart. Abbreviations for brain regions: PCC, posterior cingulate cortex.

Effects of expertise group

In order to explore differences in neural activation patterns as a function of experience in figure skating, figure skating experts and non-experts were compared to each other while the factor age group was included as covariate of no interest. Experts and non-experts did not differ significantly from each other for both types of action sequences compared to baseline. Interestingly, a significant interaction between predicted action category and expertise group was found again in the left caudate and the left thalamus (Fig. III.5C and Table III.4B).

The results of the comparisons between the types of action sequences within each expertise group are depicted in the upper panels of Figure III.5. A complete listing of suprathreshold activations in each expertise group is provided in Supporting Information Table S.3 in Appendix C. This analysis revealed that the interaction was due to the figure skating experts, who engaged the bilateral caudate and thalamus together with the early visual cortex more during the prediction of figure skating elements compared to movement exercises. The non-experts, in contrast, showed a greater recruitment of the whole visual cortex and the superior frontal gyrus for this comparison. The reverse contrast did not reveal any suprathreshold activations in experts whereas non-experts engaged premotor, parietal and occipitotemporal regions of the AON during the prediction of movement exercises compared to figure skating elements. No expertise-related activation differences that reached cluster-corrected significance were found for the interactions between action category and continuation after occlusion.

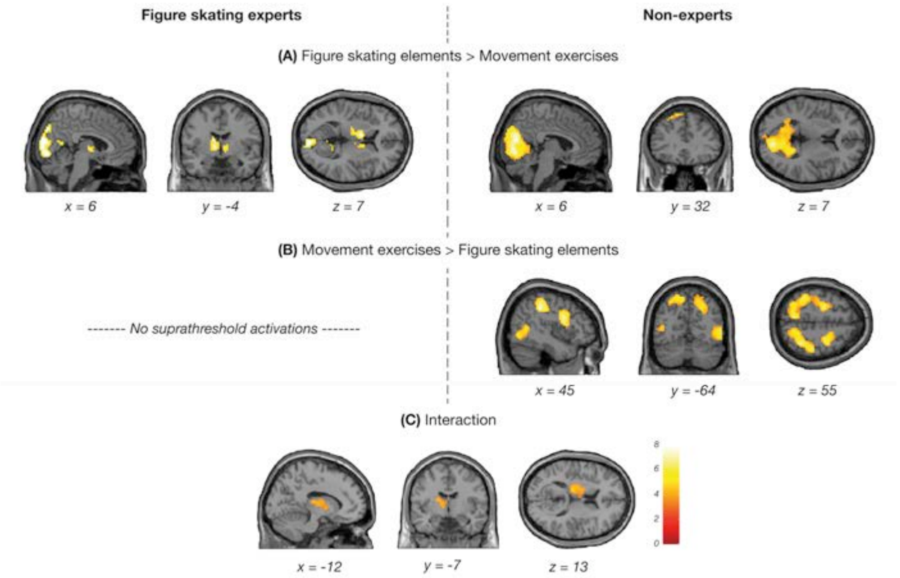


Figure III.5. Interaction between predicted action category and expertise group. Brain regions that showed greater activation in figure skating experts (*left panel*) and non-experts (*right panel*) during the prediction of figure skating elements compared to movement exercises (**A**) and vice versa (**B**). The interaction is shown in panel (**C**). Results were calculated using a voxel-wise threshold of $p < 0.001$ and a minimum cluster size of 10 voxels. Only clusters are shown that reached cluster-corrected significance of $p < 0.05$, FWE corrected.

DISCUSSION

The present study aimed to identify age-related differences in neural activation patterns during the prediction of action sequences that varied in their degree of motor familiarity (i.e., classical figure skating elements and simple movement exercises). Further, the possible role and consequences of neural scaffolding in older adults during action prediction was explored through the inclusion of observers who differed in their degree of sensorimotor experience with the observed actions. In addition, we aimed to clarify the link between AON activity and motor familiarity during action prediction in general. With respect to the AON, our results show that activity in different regions of this network was modulated by sensorimotor experience with the observed actions. Whereas the sensorimotor and occipitotemporal cortices that compose the AON showed more activation for the generally more familiar movement exercises, the prediction of figure skating elements resulted in increased engagement of the visual cortex and the medial OFC. Compared to younger adults, older adults recruited visual regions while performing the prediction task. Older adults also showed greater recruitment of the hippocampus and caudate when predicting actions that were familiar to them. During prediction of the figure skating elements, the caudate together with the thalamus seemed to play an important role in younger observers. In addition, our data indicate that this might have been similarly the case in observers who possessed sensorimotor experience in figure skating. However, due to the small sample size of the figure skating experts in particular, the interpretation of these findings has to be taken with caution. Each of these results and their implications will be considered in turn.

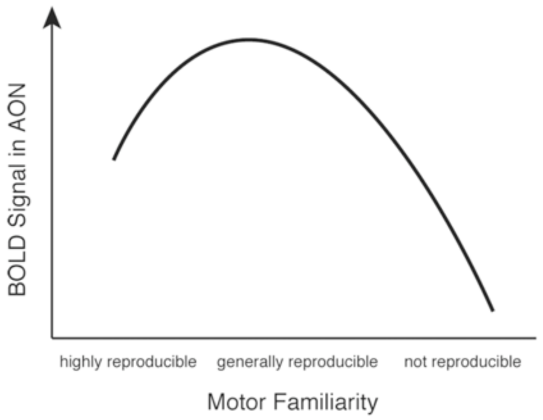
MODULATION OF AON ACTIVITY AS A FUNCTION OF PREDICTED ACTION CATEGORY

The prediction of both types of action sequences was accompanied by robust AON activation compared to baseline, in line with many others studies showing that this network is involved in the anticipation of observed actions (e.g., Caspers et al., 2010; Cross et al., 2011; Grèzes & Decety, 2001; Molenberghs et al., 2012; Oosterhof, Wiggett, Diedrichsen, Tipper, & Downing, 2010; Rizzolatti & Craighero, 2004; Stadler et al., 2011).

The direct comparison between the different action sequences revealed that AON activation was increased for the movement exercises, which is in accordance with many other studies that have shown enhanced activity in these regions for familiar actions compared to actions that are not in motor repertoire of the observer (e.g., Buccino, Lui, et al., 2004; Calvo-Merino et al., 2005; Cross et al., 2006; Olsson et al., 2008). However, the precise relation between level of familiarity and level of activation in the AON is still a matter of debate because some studies also demonstrated decreased AON activity for familiar compared to unfamiliar actions (e.g., Babiloni et al., 2010; Cross et al., 2012; Liew, Han, & Aziz-Zadeh, 2011; Vogt et al., 2007). To reconcile such seemingly discrepant findings, Cross et al. (2012) have proposed a nonlinear relationship between motor familiarity in the observer and AON activity that follows a u-shaped function. According to this model, highly unfamiliar actions produce a greater prediction error than actions of intermediate familiarity. This greater prediction error results in increased AON activity due to increased processing demands between the different regions of the AON. In contrast, highly familiar actions might also lead to enhanced AON activity compared to actions of intermediate familiarity, but for a different reason. Here, participants have generated extremely exact predictions due to a high degree of motor expertise. Any small deviations from such precise predictions might amplify the response within the AON if the sensory input does not exactly match the predicted consequences.

According to this proposal, here we might have expected increased AON activity for the less familiar figure skating elements in comparison to the generally familiar movement exercises. These discrepancies in the present as well as across previous studies might be related to the respective definition of unfamiliar actions. For example, unfamiliar actions might be defined as those that are not regularly seen, but are generally executable by the observer, such as unusual hand gestures. They might be also defined as not in the motor repertoire of the observer at all, such as figure skating elements for observers who have never ice skated before. In addition, for movement exercises, only one region of the AON, the pSTS, showed stronger activity when observing incongruent compared to congruent continuations after occlusion. Such a finding is in line with evidence that the STS is involved in the perception of biological motion and contains cells with predictive properties that are sensitive to movements that deviate from expectations (Keysers & Perrett, 2004; Perrett et al., 2009). We therefore propose an adaptation to the model put forth by Cross et al. (2012) that also considers unfamiliar actions that the observer cannot reproduce without extensive training in comparison to unfamiliar actions for which the observed kinematics might be inferable and at least to some extent reproducible (see Fig. III.6).

Figure III.6. Adapted model of the hypothesized relationship between motor familiarity and activity in the AON.



Within this adapted model, a match between observed and predicted representation of highly familiar actions should be associated with a small prediction error and, thus, intermediate AON activity. Less familiar actions might result in higher AON activity due to a less precise prediction of them that needs to be constantly updated based on the actual sensory input to minimize a larger prediction error. The use of these predictive representations might become less efficient the less familiar an observed action is, until an internal action representation will not be present at all. In these cases, the observed actions might be represented in a rather multimodal way that is supported by the recruitment of regions beyond the classical AON (cf., Olsson et al., 2008; Schiffer, Ahlheim, Wurm, et al., 2012; Schiffer & Schubotz, 2011; Wright et al., 2011).

In line with this, our data show that the less familiar figure skating elements were processed more in the visual cortex and in the medial OFC, a region that is known to be involved in adaptive decision making in unpredictable situations (Elliott, Dolan, & Frith, 2000; O'Doherty, 2007). Although special care was taken to match both types of action sequences as much as possible in terms of involved body kinematics, the figure skating elements were executed at a considerably faster speed than the movement exercises. This might have skewed the perceptual complexity and in turn biased the demands on the predictive processes in the observer to some extent. However, the activation in the medial OFC implies that differences in low-level visual features might only partially explain the observed differences in neural activity. This assumption is further supported by the observed group differences in the present study that are discussed below. Although beyond the scope of this study, the precise level of AON involvement most likely depends on the specific task demands as well. For instance, whether an action is just passively observed or whether the observer intents to infer its meaning or predicts its time course poses important differences in the neural processing demands in the observer (but see Cross et al., 2011; Kokal & Keysers, 2010; Stadler et al., 2011).

ACTION PREDICTION IN THE AGING BRAIN

With respect to the AON in particular, we did not find age-related activation differences that reached cluster-corrected significance as in Nedelko et al. (2010). However, the comparison between the action categories within each age group indicated that AON activity was mainly right lateralized in younger adults and bilaterally active in older adults during the prediction of movement exercises compared to figure skating elements. This pattern of activity change has been observed frequently in different cognitive domains and is referred to as hemispheric asymmetry reduction in old adults (HAROLD), suggesting that cortical recruitment under similar conditions tends to be less lateralized in older adults (Cabeza, 2002).

The results further show that older adults recruited regions beyond the AON, which younger adults did not, while performing the task. No matter what type of action sequence was observed, when comparing to the baseline condition, older adults showed greater recruitment of prestriate and extrastriate visual cortex compared to younger adults. In younger adults, these early visual areas, such as V2, have been shown to be recruited in mental imagery tasks that require the anticipation of objects or scenes that one is about to perceive (Kosslyn & Thompson, 2003). In older adults, however, evidence suggests that the neural representation of sensory input becomes less distinct with age, arguing for an age-related neural dedifferentiation in relevant areas (Carp, Park, Polk, et al., 2011; Park et al., 2004). In line with this assumption, behavioral evidence suggests that the correlation between sensory and cognitive abilities increases with age (Baltes & Lindenberger, 1997). The increased activation in the visual cortex might therefore partly reflect less specific sensory representations of the observed actions among older adults. These less distinct sensory representations might have been matched with motor representations that also get less selective with age (cf., Carp, Park, Hebrank, et al., 2011; Heuninckx et al., 2005; Langan et al., 2010; Ward & Frackowiak, 2003; Wu et al., 2007).

However, when examined separately, the non-experts in figure skating also demonstrated greater recruitment of a large cluster in the visual cortex during prediction of figure skating elements compared to movement exercises. In addition, Olsson et al. (2008) and Wright et al. (2011) found higher activation in very similar visual areas in non-experts compared to experts during action imagery and observation. This implies that the engagement of visual regions in older adults cannot be solely explained by neural dedifferentiation in the aging mind. The findings rather suggest that the brain's response to challenges that are due to aging or the exposure to unfamiliar material may indeed be similar during the prediction of others' actions (cf., Park & Reuter-Lorenz, 2009).

Older adults showed additional activation within the medial OFC during the prediction of the figure skating elements compared to movement exercises. The OFC has been shown to play an important role in the top-down modulation of visual processing through the generation of initial predictions about likely interpretations of the visual input in younger adults (Bar et al., 2006). In their fMRI study on expert-novice differences during the prediction of basketball throws, Abreu et al. (2012) recently found that orbito-frontal regions are specifically linked to correct action prediction in observers who are not familiar with the shown actions. Thus, one might speculate that also the older adults of the present study relied more on these higher-order regions that are involved in adaptive decision-making during the prediction of actions that were less familiar to them.

For the movement exercises, compared to younger adults, older adults recruited an additional cluster in the right hippocampus extending to the caudate compared to baseline. Neurobiological evidence suggests that these regions form a functional network that is involved in flexible decision-making with the hippocampus generating predictive (spatial) representations and the caudate learning and anticipating action-outcome contingencies (e.g., Johnson, van der Meer, & Redish, 2007; Yin & Knowlton, 2006). In addition, hippocampal activation has been found during episodic imagination of the future that is based on a recombination of past episodic events (Martin et al., 2011; Weiler, Suchan, & Daum, 2010). Recent evidence suggests that this functional differentiation, with the hippocampus mediating mainly explicit/declarative memory and the striatum mediating rather implicit/procedural memory, decreases with advancing age (Dennis & Cabeza, 2011). Thus, if older adults in the present study were familiar with the observed actions, they seemed to use learned action-outcome contingencies as well as multimodal representations of these actions stored in episodic memory to evaluate the sensory input. Age-related declines in neural selectivity in these regions together with a less efficient use of the own sensorimotor system might in turn have resulted in difficulties to recreate the observed action sequences in necessary detail in order to predict their exact time-course. This is further supported by findings that the reconstruction of episodic details comprising past and future events is reduced in older adults, which is linked to activity changes in medial temporal regions (Addis, Roberts, & Schacter, 2011; Schacter et al., 2012).

Taken together, the data provide evidence for age-related neural scaffolding in relevant areas during action prediction that is modulated by the degree of motor familiarity with the observed actions. Older adults may have created a mental image of the observed actions during the occlusion period and evaluated its visual features instead of effectively exploiting the sensorimotor matching properties of the AON. Even though it was beyond the scope of this study to examine the neural correlates of successful action prediction within the single groups, it might provide important insights on how the process of action prediction is generally implemented in the aging brain (see also Henson, 2005; Wilkinson & Halligan, 2004 for a critical discussion on the link between cognition, behavior and neural activity). Thus, future research is warranted to examine age-related changes at the neural level and their association to the ability to predict observed actions in order to determine patterns of brain activity that might be specifically linked to correct prediction performance and/or error monitoring. Based on the results of the present study, one might hypothesize that declines in prediction sensitivity in older adults are linked to neural activity that gradually shifts from the AON and areas of the motor system to areas that are involved in visual processing and frontal areas. As Park and Reuter-Lorenz (2009) noted, an efficient task performance relies on an efficient neural circuitry. To the extent that the functionality of these specialized networks declines with age and scaffolding takes place, task performance is likely to get less specific as well. One should also note that this relation presumably depends on additional factors, for example, the connectivity between different brain regions or hemispheres and how efficiently neural signals are processed (cf., Davis et al., 2012; Langan et al., 2010; Madden et al., 2012).

INVOLVEMENT OF THE CAUDATE IN ACTION PREDICTION

During the prediction of the figure skating elements compared to movement exercises, a cluster in the caudate extending to the thalamus was more engaged in younger adults compared to older adults. The activation comprised additionally the left PCC for this direction of the contrast. The caudate as the associative striatum is connected to various association cortices across the brain, including inferior frontal and inferior parietal regions of the AON (cf., Postuma & Dagher, 2006; Schmahmann & Pandya, 2006; Smith et al., 2009). Activity in the caudate is typically linked to performance monitoring in ambiguous contexts, possibly via representing and updating the value of future actions (i.e., the reward-prediction error; e.g., Balleine, Delgado, & Hikosaka, 2007; Graybiel, 2008; Schultz, 2000). Interestingly, this reward-related recruitment has been found not only in experiential but also in observational instrumental learning tasks (Cooper, Dunne, Furey, & O'Doherty, 2012). Thus, the caudate appears to be an ideal candidate for neural scaffolding in younger adults during action prediction in conditions of higher difficulty (i.e., lower motor familiarity). In line with this, Schiffer and Schubotz (2011) showed that the caudate is involved in prediction errors that are not related to some kind of reward, but violate predictions about which movements should follow after a certain cue in a movement sequence during action observation. The study also reported activation in the PCC for unexpected movement continuations, a region which has been associated with fast visuospatial orientation in unpredictable contexts (cf., Hahn, Ross, & Stein, 2007). Accordingly, PCC activity among younger adults of the present study might have reflected visuospatial monitoring of the more ambiguous figure skating elements.

Our data further show that in figure skating experts compared to non-experts a very similar cluster in the thalamostriatal network was more activated during the prediction of the figure skating elements compared to the movement exercises. Although there was no main effect of action category in the present behavioral data, the study reported by Diersch et al. (2012), which used a more fine-grained psychophysical paradigm, showed that the movement exercises were easier to predict than the figure skating elements even for figure skating experts. Due to the small sample size of the experts in the present study, however, this finding needs further confirmation from studies comprising larger sample sizes. The consistency of the results across groups that are in line with previous research still implies that higher prediction errors might not only modulate activity in the AON but also engage the caudate, possibly to adjust and optimize less precise predictions that are generated in the AON. As it was demonstrated in the putamen for stimulus-response behaviors, the caudate might similarly modulate information-transfer between visual and motor areas in action-outcome behaviors (cf., Den Ouden, Daunizeau, Roiser, Friston, & Stephan, 2010). The fact that the caudate was also active together with the hippocampus in older adults during the prediction of the movement exercises emphasizes again its importance during the prediction of actions that are rather ambiguous for the respective observer. Notably, hippocampal activity has been recently linked to the adaptation of stored action representations in younger adults in conditions in which previously encountered action sequences are repeatedly observed in a new, divergent version (Schiffer, Ahlheim, Wurm, et al., 2012). Whether the hippocampus might fulfill a similar role in older adults during the prediction of familiar actions poses an important question for future research in order to examine the role of observational learning in older adults in action-related contexts.

CONCLUSION

The present study has demonstrated that generating predictive representations of observed actions engages a distributed network in the brain, depending on the characteristics of the observer and the type of observed actions. Based on the predictive coding account, a model was outlined that considers AON activity in relation to the level of motor familiarity in the observer. Moreover, the results underline a role of the caudate during action prediction in ambiguous contexts. In older adults, evidence was found for neural dedifferentiation in relevant areas and engagement of additional regions that might be associated with an altered strategy to solve the prediction task in line with STAC (Park & Reuter-Lorenz, 2009). Older adults might be considered, metaphorically speaking, as non-experts in previously well-known domains due to internal action representations that become less precise with advancing age. Thus, emphasizing alternative (visual/mnemonic) strategies in training and intervention programs targeted at older adults may provide a promising alternative that supports successful performance in everyday life despite changes in sensorimotor processing.

Acknowledgments

The authors thank the participants, especially the older adults and figure skaters, who donated their time to take part in different sessions of the present study, Dr. Elisabeth Roggenhofer and Dr. Ilona Henseler for medical MR briefing and examination of the sample, Tanja Schorch and Franziska Ritschel for their great assistance with data collection, and Esther Kühn for fruitful discussion.

IV. DISCUSSION

Predicting the actions of others is considered to play an important role for guiding adaptive behavior in the social environment. In many countries all over the world, this social environment will consist of growing numbers of older adults in the years to come. The experiments outlined in the previous chapters used behavioral as well as neuroimaging techniques to address the question how predictive abilities during action observation may change with advancing age. In all of the experiments, an action occlusion paradigm was applied in which older and younger adults observed different action sequences that varied in their degree of motor familiarity. The actions were partly occluded at critical time points and continued after occlusion in a temporally manipulated way (congruent, too early, or too late on different levels). Participants were asked to judge the temporal coherence of the continuations after occlusion. In the following, the main results of the experiments are summarized and afterwards discussed in the context of previous research on action prediction and age-related changes in sensory and sensorimotor functioning. Putative reasons and implications of the results will be considered and placed into a broader context. Possible caveats and questions for futures research will be outlined. The discussion will focus on the behavioral results first and subsequently on its underlying neural activation patterns.

SUMMARY OF THE MAIN RESULTS

Overall, the results of this dissertation suggest that older adults are not as efficient as younger adults in predicting the sensory outcomes of observed actions when they are temporarily occluded at critical time points. In two behavioral experiments, the proportion of correct responses on the different continuations after occlusion was lower in older compared to younger adults. However, older adults were able to accomplish the task in general and obtained scores that equaled or exceeded age norms on different physical and cognitive health measures. The analyses of the prediction timing in both behavioral experiments revealed that the temporal range during which shifted continuations could not be clearly differentiated from the congruent continuation was larger in older than in younger adults. This suggests that the sensitivity in action prediction decreases with advancing age.

In the second behavioral experiment, the observer's level of sensorimotor experience was additionally taken into account. Prediction performance of older and younger figure skating experts as well as age-matched non-experts was compared during the observation of classical figure skating elements and generally familiar movement exercises. Sensorimotor experience with the observed actions resulted in better prediction performance in terms of accuracy and sensitivity for domain-specific actions in both older and younger experts compared to non-experts of the respective age groups. Prediction performance of older figure skating experts was comparable to the performance of younger non-experts during the observation of the figure skating elements. This expertise-related benefit did not show transfer to the observed movement exercises. Moreover, in the first behavioral experiment in which the observed actions were goal-directed, both age groups showed an anticipation bias directed towards the future (i.e., their prediction was slightly faster than real-time). This was not the case in the second behavioral experiment in which the observed actions were intransitive (i.e., not directed towards an object).

In the fMRI experiment, the same action sequences were used as in the second behavioral experiment. Participants consisted of older and younger adults who were all familiar with the observed movement exercises but only some of them were experienced figure skaters. Brain activity was examined as a function of action category and continuation after occlusion collapsed across the whole sample as well as a function of age group and sensorimotor experience in figure skating. The results showed that AON activity is modulated by the degree of sensorimotor experience in the observer. Higher AON activity was found during the prediction of the more familiar movement exercises. For these actions only, one region of the AON, the posterior STS, differentiated between incongruent and congruent continuations after occlusion. The prediction of the figure skating elements, in contrast, resulted in increased activity in the visual cortex and the medial OFC. Compared to younger adults, older adults recruited visual cortices to perform the task and, additionally, the hippocampus and caudate when the observed actions were familiar to them. Thus, older adults recruited brain regions beyond the AON, which younger adults did not, during action prediction. The results further suggest that the caudate together with the thalamus play an important role during the prediction of the figure skating elements compared to movement exercises in better-performing groups (i.e., younger adults compared to older adults and figure skating experts compared to non-experts).

IMPLICATIONS, CAVEATS, AND OPEN QUESTIONS

AT THE BEHAVIORAL LEVEL

The results from the behavioral experiments suggest that older in contrast to younger adults have difficulties in representing observed actions in a sufficiently detailed manner in order to predict their exact time course, even when they are still able to execute them and therefore must possess an internal representation of these actions. This supports and extends findings from previous studies using mental imagery paradigms in order to measure age-related changes in the representations of actions and events (cf., Personnier, Kubicki, et al., 2010; Personnier et al., 2008; Saimpont et al., 2012; Schacter et al., 2012; Schott & Munzert, 2007; Skoura et al., 2005; Skoura et al., 2008). Personnier et al. (2008), for example, argued that the observed temporal dissimilarities between overtly and covertly represented actions in older adults might be due to forward modeling that becomes less efficient with advancing age. During action prediction, age-related deficiencies in generating and updating prior expectations or forward models about observed actions might consequently result in larger inaccuracies about the actual trajectories of these actions. This is exactly what has been found in the present experiments.

In line with previous evidence, the results from the second behavioral experiment additionally indicate that many years of deliberate practice in a particular domain may enable older adults to maintain a better performance in skill-related tasks (cf., Horton et al., 2008; Kattenstroth et al., 2011; Krampe, 2002; Krampe & Charness, 2006). Extensive amounts of sensorimotor experience seem to result in more stable internal action representations that can be used to generate more accurate predictions about these actions even in older age groups. In younger adults, it has been suggested that experts in contrast to non-experts are able to exploit biological motion and proprioceptive information in addition to visual information in order to anticipate observed actions (e.g., Aglioti et al., 2008; Calvo-Merino et al., 2006; Friston et al., 2011; Urgesi et al., 2012). Whether the reliance on different sources of information may generally differ in older compared to younger experts during action prediction, however, cannot be determined from the behavioral data. Older experts may not only possess high degrees of sensorimotor experience but also visual experience with actions from their domain of expertise. This issue will be further discussed in relation to the results of the fMRI experiment. Importantly, the older figure skating experts did not differ significantly in their age or cognitive status from the older non-experts. This implies that age-related differences in action prediction are unlikely to be accounted for by age-related declines in general cognitive abilities such as memory and attention. Although age-related declines in attention have been linked to differences in time perception in conditions requiring high amounts of attentional control, there are no indications that this might have biased the results of the present experiments (cf., Lustig, 2003). In all of the observed action sequences, participants needed to allocate their attention towards only one moving person at a time. In addition, the ongoing action sequences were visible for several seconds before occlusion allowing participants to adjust their internal timing to the respective timing of the observed actions. Moreover, the anticipation bias found in the first but not in the second behavioral experiment was not modulated by the age of the respective observers. This difference between the two experiments might be instead related to the goal-directedness of the observed actions and/or differences in the experimental set-up (see Chapter II on page 53 for a discussion of this finding).

A completely different picture might emerge, however, if the demands on attentional control increase during action prediction. This might be the case, for example, when more than one moving person is present in the social environment – which is usually the case in everyday life. In these cases, the inhibition of information that is not relevant to one's goals may be required, an ability which has been found to be considerably reduced in older adults. According to the inhibitory deficit theory, many age-related deficits in cognition can be explained by an inability to appropriately suppress irrelevant information processing or responses (e.g., Gazzaley et al., 2005; Lustig et al., 2007). The activation of relevant information, in contrast, is considered to remain relatively preserved with age. It has been further suggested that the processing of more information by older adults may not always be disadvantageous (Healey, Campbell, & Hasher, 2008). In some situations, the relevance of (seemingly) extraneous information may either be not immediately clear or may become relevant in a later situation. Thus, one might speculate that older adults might occasionally even show a benefit compared to younger adults during action prediction, for example, when they process not only information about the actions of the person closest to them but also about the actions of persons in the background who will come closer shortly after.

Another important aspect, which cannot be determined from the present data, relates to the question of how older adults' predictions may actually guide their behavior. In the experiments outlined above, participants were only passively observing the different actions sequences. Declines in sensory, motor, and cognitive functioning, however, may require older adults to invest more effort or resources to the same task compared to younger adults. As a consequence, they may be required to flexibly allocate their resources towards more important aspects at the cost of less important ones in multiple-task situations (see Riediger, Li, & Lindenberger, 2006 for a review). In a series of experiments on age-related changes in adaptive resource allocation, Li, Lindenberger, Freund, and Baltes (2001) showed that older in contrast to younger adults tend to prioritize sensorimotor functioning (i.e., walking) at the expense of cognitive performance (i.e., memorization) during dual-task performance. They further showed that older adults preferred and benefited more than younger adults from the use of a handrail in contrast to a memory aid in order to optimize their performance. It has been suggested that this pattern of performance may reflect a loss-based selection and compensation strategy in older adults, possibly in order to reduce the risk of physical injuries due to falling (Riediger et al., 2006). Thus, if an older adult is not just passively observing but also moving, he or she may focus on his or her own movements instead of constantly monitoring and evaluating the actions of others. This might in turn result in even less precise predictions of others' actions but also in less flexible behavioral adaptations in response to changes in the social environment. Moreover, older adults are likely to be slower than younger adults in transforming their predictions into appropriate reactions. An age-related slowing in cognitive processing speed is one of the most replicated findings in aging research (cf., Salthouse, 1996). In line with this, Sarlegna (2006) showed that older adults are slower and less efficient in adjusting their hand movements in response to visual feedback when a target to be reached is displaced unexpectedly at movement onset. Studying age-related changes in prediction performance and their relation to behavioral adaptations in the aging observer in conditions of high and low attentional demand will therefore be an important avenue for future research.

Nevertheless, one might think of several factors and mechanisms that may attenuate age-related performance declines during action prediction. Besides the positive effects of sensorimotor experience that were found in the second behavioral experiment, evidence was outlined suggesting that the use of assistive devices, which reduce the attentional demands of sensorimotor functioning, may also enhance performance. Given the close link between sensorimotor and cognitive measures of performance in older age groups, physical activity, or more specifically, physical fitness, may free up resources in order to predict the actions of others more precisely (cf., Schäfer et al., 2006). Physical activity has been linked to a better performance in older adults across a variety of cognitive tasks (e.g., Colcombe & Kramer, 2003; Hillman et al., 2008; Kattenstroth et al., 2010; Kramer, 1999; Szabo, Bangert, Reuter-Lorenz, & Seidler, 2012; Voelcker-Rehage, Godde, & Staudinger, 2011). The results of these studies further suggest that executive processing in particular appears to profit from a regular engagement in physical activities. For example, Szabo et al. (2012) recently reported that a higher level of physical fitness in older adults is associated with a better reproduction of temporal intervals encompassing longer durations, which are thought to rely more on executive control mechanisms compared to shorter durations. One should note, however, that the expertise-related benefit found in the second behavioral experiment did not show transfer to the observed movement exercises, although older experts reported a slightly higher engagement in physical activities compared to older non-experts. Similarly, Kattenstroth et al. (2011) showed that the positive effects of professional dancing experience in older adults were restricted to tasks closely related to dancing. Thus, future research is warranted to disentangle the effects of sensorimotor experience and physical activity on prediction performance in older adults more clearly. For example, prediction performance could be compared between two older expert groups who are both highly fit but not experienced with the actions from the other domain of expertise. In addition to motor training, observational training might provide another useful tool to improve prediction performance in older adults. Celnik et al. (2006), for example, demonstrated that the positive effects of a combination of motor training and action observation exceeded the summation of the single effects on motor cortex excitability in a group of healthy older adults.

AT THE NEURAL LEVEL

The results of the fMRI experiment confirm that action prediction is a complex process that engages a distributed neural network, within and beyond the AON, depending on the specific stimulus characteristics and their degree of motor familiarity (cf., Bubic et al., 2010; Schubotz, 2007). In line with many other studies, activity in the AON was found to be enhanced during the prediction of generally familiar actions compared to actions that were less familiar (cf., Buccino, Lui, et al., 2004; Calvo-Merino et al., 2005; Cross et al., 2006; Olsson et al., 2008). Given that some studies also found the reverse pattern of results (i.e., higher AON activity for less familiar compared to more familiar actions; e.g., Babiloni et al., 2010; Cross et al., 2012; Liew et al., 2011; Vogt et al., 2007), Cross et al. (2012) recently suggested that the relationship between AON activity and motor familiarity in the observer may follow a U-shaped function. Based on the predictive coding account of the AON, it was argued that extremely unfamiliar but also extremely familiar actions might lead to higher AON activity compared to actions of intermediate familiarity. In these two cases, less precise *or* very exact prior expectations about the observed actions might result in higher prediction errors than intermediate expectations. Given the results of the present study, an adaptation of this model was proposed that further elaborates on the respective definition of unfamiliar actions. Within this adapted model, AON activity is assumed to be differentially modulated by actions that might be considered as unfamiliar because they are not regularly seen but are generally reproducible by the observer in contrast to actions that are not reproducible at all. Generally reproducible actions might consequently result in higher AON activity than highly reproducible actions, which are regularly executed, due to a higher degree of uncertainty about their specific trajectory. Actions that are not reproducible, in contrast, might be predominantly processed in regions outside of the AON (see Chapter III on page 78 for a detailed discussion of this relationship).

In line with this, the data of the fMRI experiment indicate that participants relied more on visual information during the prediction of the less familiar figure skating elements possibly due to a lack of direct motor and proprioceptive experience (cf., Friston et al., 2011; see also Olsson et al., 2008; Wright et al., 2011 for similar findings). The results further suggest that one region of the basal ganglia, the caudate, might play an important role during the prediction of actions that are less familiar and, as a consequence, more ambiguous for the respective observer (cf., Schiffer, Ahlheim, Wurm, et al., 2012; Schiffer & Schubotz, 2011). The caudate is directly as well as indirectly via several thalamic nuclei connected with various regions in the cerebral cortex, some of which are also part of the AON (e.g., IFG, inferior parietal regions; cf., Postuma & Dagher, 2006; Schmahmann & Pandya, 2006; Smith et al., 2009). Together with the putamen, it is known to play an essential role in motor sequence learning in which more flexible action-outcome behaviors are predominantly linked to the caudate and more rigid stimulus-response behaviors to the putamen (e.g., Balleine et al., 2007; Graybiel, 2008; Yin & Knowlton, 2006). More specifically, the caudate has been suggested to mediate performance monitoring in ambiguous contexts, possibly via representing and updating the value of future actions (i.e., the reward-prediction error). Based on their findings, Schiffer and Schubotz (2011) argued that the caudate may also encode deviations from an initial prediction during action observation, possibly in order to trigger an update of the current forward model or in order to assess the probabilities of other action alternatives. Interestingly, Den Ouden et al. (2010) showed that prediction error responses in the putamen modulated the cortical coupling between visual areas and the premotor cortex during learning of stimulus-response behaviors. The authors further suggested that this modulation might operate indirectly via the thalamus given the anatomical connections between these regions. In line with this, Sherman and Guillery (2011) provided evidence that feedforward *and* feedback connections might be mediated by transthalamic pathways instead of only being projected from one cortical area to another in sensorimotor processing (see also Smith, Surmeier, Redgrave, & Kimura, 2011; Thorn & Graybiel, 2010 for related findings). In the present study as well as in the study by Schiffer and Schubotz (2011), the activation in the caudate also extended to the thalamus. This suggests that caudate together with the thalamus might modulate information transfer between visual and motor areas during the prediction of action-outcome behaviors.

In contrast to some other studies examining predictive processing in the brain, no additional activations that reached cluster-corrected significance were found in the cerebellum for the comparisons on the effects of observed action category. This implies that differences in motor familiarity during action prediction relied less on the functional properties of the cerebellum in the present study. Previous research suggests that the cerebellum might encode temporal information about dynamic events or might even act as an internal model during action observation (e.g., Cross et al., 2011; Miall, 2003; O'Reilly et al., 2008). Thus, one might postulate that differences between the temporally manipulated continuations after occlusion might have modulated neural activity in the cerebellum. For the majority of the interactions between action category and continuation after occlusion, however, no significant activation differences were obtained. Only one region of the AON, the pSTS, was found to differentiate between incongruent and congruent continuations after occlusion during the prediction of the movement exercises (see Chapter III on page 79 for a discussion of this finding). The number of relevant events for each of the continuations after occlusion within each action category might have been too small in order to detect activation differences in additional brain regions as well. In addition, both correct and incorrect trials from each critical condition were included in the analyses of the fMRI data. This ensured that the observed differences in neural activity between groups who differed substantially in their degree of prediction sensitivity were always based on the same number of events. As a consequence, no conclusion can be drawn with respect to neural correlates that might be specifically linked to successful prediction performance, for example, when a temporally shifted continuation was correctly perceived as being incongruent.

However, in recent conceptualizations of brain function, it is argued that predictive processing during perception takes place in multiple levels in the cortical hierarchy (Friston, 2005; Friston & Kiebel, 2009; Friston et al., 2011). Thus, the connectivity between different brain regions and the way they interact with each other is emphasized (see also Bastos et al., 2012 for neurophysiological evidence). New and unexpected information generates a mismatch between predicted and actual sensory input, which is expressed through enhanced cortical activity in relevant areas. This mismatch (i.e., the prediction error) is minimized through updating the respective prior expectation, resulting in decreased neural activity over repeated iterations (i.e., learning; see also De Gardelle, Waszczuk, Egner, & Summerfield, 2012; Egner, Monti, & Summerfield, 2010; Summerfield, Trittschuh, Monti, Mesulam, & Egner, 2008 for empircal evidence in support of these assumptions during visual perception). In line with this, Saygin, Chaminade, Ishiguro, Driver, and Frith (2012) recently demonstrated that neural activity in parts of the AON was most strongly modulated by the observation of a moving android compared to a human agent or a robot, possibly due to a mismatch between appearance and motion (i.e., if an human-like agent did not move in a natural, expected manner). Thus, observed actions might be differently encoded in situations in which the actions are just familiar or unfamiliar (as in the present experiment) or in which rather familiar actions unfold in a predictable or unpredictable manner (cf., Schiffer, Ahlheim, Ulrichs, & Schubotz, 2012; Schiffer, Ahlheim, Wurm, et al., 2012). This, however, needs further empirical validation. In addition, the use of additional methods such as Granger causality mapping or dynamic causal modeling (DCM) that enables one to test different connectivity models based on fMRI or electroencephalography (EEG) data would be useful in order to describe information processing in relevant areas more precisely.

With respect to age-related changes in neural activation patterns during action prediction, the findings of the fMRI study support the implications of the behavioral data outlined in the previous section. Older adults seemed to be less efficient in exploiting the sensorimotor matching properties of the AON in order to generate predictions about the observed actions during the occlusion period. Instead, the fMRI data suggest that they predominantly relied on visual information in order to accomplish the task. A recent fMRI study measuring age-related changes in neural activation patterns during mental imagery similarly showed an increased activation in multisensory cortices in older compared to younger adults during imagined standing, walking, and running (Zwergal et al., 2012). Higher activation in visual regions was also found in non-experts of the present study during the observation of non-familiar compared to familiar actions as well as in previous studies measuring neural activity in non-experts compared to experts during action imagery and prediction (Olsson et al., 2008; Wright et al., 2011). Thus, in line with the assumptions of STAC, less distinct sensory and/or motor representations in the aging brain seem to result in a functional reorganization through the recruitment of additional regions in order to predict observed actions (cf., Park & Reuter-Lorenz, 2009). Moreover, this functional reorganization appears to resemble the response to the observation of unfamiliar actions in a younger brain. During the prediction of familiar actions, this age-related neural scaffolding further involved activity in the caudate and the hippocampus. The hippocampus has been implicated in the prediction of sequential, episodic scenarios in younger adults (Addis & Schacter, 2012; Bar, 2009; Martin et al., 2011; Schacter et al., 2007). During action prediction, activity in the caudate has been specifically linked to prediction errors in conditions of high uncertainty, whereas the hippocampus seems to be preferentially engaged during the adaption of stored action representations in conditions in which previously encountered action sequences are repeatedly observed in a new, divergent version (Schiffer, Ahlheim, Wurm, et al., 2012). In older adults, the functional specificity of the hippocampus and the striatum has been shown to decrease during explicit and implicit learning (Dennis & Cabeza, 2011). The results of the present study indicate that the functional role of each of these regions during action prediction also becomes less distinct with advancing age.

As a consequence, generally familiar actions might be evaluated based on previously learned, multimodal representations of these actions stored in different memory systems (cf., Addis et al., 2011). These age-related declines in neural selectivity may in turn be associated with the reduced sensitivity observed at the behavioral level (cf., Grady, 2012). This, however, needs further confirmation from studies examining the relation between prediction performance and neural activity directly, for example, through comparing neural activity in high- versus low-performing older adults.

Although the present fMRI study sheds light on how action prediction might be implemented in the aging brain, future research is needed in order to specify how predictive coding may actually change with advancing age. Is it predominantly the processing of sensory input or the generation of prior expectations that becomes less precise in the aging mind? Are less efficient interactions between relevant brain regions one of major sources for the observed performance declines in action prediction? Several recent studies showed, for example, that neural adaptation in sensory cortices is reduced but also less selective in older compared to younger adults over repeated stimulus presentations (e.g., Goh, Suzuki, & Park, 2010; Grady, Charlton, He, & Alain, 2011; Lee, Grady, Habak, Wilson, & Moscovitch, 2011; Park et al., 2012). This loss in selectivity has been mainly attributed to broadly tuned neurons that respond to a greater range of different stimuli possibly due to reductions in GABA-mediated cortical inhibition in the aging brain (cf., Leventhal, Wang, Pu, Zhou, & Ma, 2003; Pinto, Hornby, Jones, & Murphy, 2010; Schmolesky, Wang, Pu, & Leventhal, 2000). In addition to GABA, changes in other neurotransmitter systems such as the dopaminergic system have also been linked to neural dedifferentiation in older adults (Li & Lindenberger, 1999). Decreases in dopamine transmission have been widely studied in the context of age-related declines in motor function that are particularly pronounced in Parkinson’s disease (see Seidler et al., 2010 for a review). In the context of predictive coding, dopamine has been implicated in modulating the precision of prediction errors (or uncertainty) at different levels in the sensorimotor hierarchy (Friston et al., 2012). By using computational modeling, the authors showed that the depletion of dopamine results in a variety of physiological and behavioral consequences depending on which pathway in the cortical hierarchy is affected. A reduction of dopamine in sensory regions, for example, resulted in failures to infer changes in the context and a preservation of suboptimal movement trajectories, which constitutes one of the core symptoms in Parkinson’s disease (Bradykinesia).

Thus, one might speculate that the age-related loss in selectivity in sensory representations (but also in prior expectations) reflects declines in neurotransmitter function in the aging mind resulting in deficiencies in minimizing prediction error signals during action prediction.

In the previous section, the positive impact of physical activity on cognitive performance in older adults was briefly discussed. At the neural level, several studies showed that age-related declines in brain tissue density and white matter integrity are reduced as a function of cardiovascular fitness (e.g., Colcombe et al., 2003; Colcombe et al., 2006; Erickson et al., 2011; Marks et al., 2007). Higher levels of physical fitness have also been associated with changes in task-related activation of neural regions needed for successful task performance (e.g., Colcombe et al., 2004; Erickson et al., 2007; Godde & Voelcker-Rehage, 2010; Rosano et al., 2010; Voelcker-Rehage et al., 2011). Godde and Voelcker-Rehage (2010), for example, found increased recruitment of the motor system in high-fit older adults during motor imagery, whereas low-fit older adults showed higher activations in prefrontal regions known to be involved in cognitive monitoring. This provides further support for the assumption that physical fitness may have a positive influence on action prediction and its neural basis in the aging observer. This should be taken into account in future studies on age-related changes in predictive processing.

In general, the older participants of the present experiments were all healthy and fit as the data on the self-reported health and level of physical activity showed – even if they were not experienced in figure skating. This allowed the examination of the effects of aging and sensorimotor experience on action prediction that are unlikely to be confounded by the effects of any age-related disease. Selecting such a specific sample, however, may underestimate the "true" magnitude of age-related change, making it difficult to draw conclusions that apply to the general population. The motivation in younger and older adults to participate in experimental studies may generally differ. Only very healthy and dedicated older adults may agree to take part in such studies (cf., Hultsch, MacDonald, Hunter, Maitland, & Dixon, 2002; Lindenberger et al., 1999). The safety and data analysis requirements of MR scanning on medical conditions and medication further limit the generalizability of the obtained results. The results of this dissertation might therefore be considered as a best-case scenario on how predictive abilities may change with advancing age. In addition, all of the reported experiments were cross-sectional in design.

The interpretation of cross-sectional data may be susceptible to cohort effects compared to longitudinal data, although the way of executing the observed action sequences (e.g., the figure skating elements) did not change considerably in the last decades (see Salthouse, 2009 for a comparison between cross-sectional and longitudinal data in aging research). Thus, although the present dissertation provides new and important insights into age-related changes during the prediction of observed actions, there are numerous open questions that remain to be investigated. Studying these questions in more diverse older participant groups as well as using different methodological approaches will be an important empirical task for the future in order to gain a fuller understanding of the mechanisms underlying action prediction in the aging mind.

SUMMARY OF DISSERTATION

Action Prediction in the Aging Mind

Submitted to the Faculty of Biosciences, Pharmacy and Psychology
University of Leipzig

by Dipl. – Psych. Nadine Diersch,

Leipzig, 23 January 2013

One of the most essential abilities that enables us to navigate successfully through our social environment and interact with others is the correct prediction of actions that are performed by other individuals. Imagine, for example, you are crossing a busy street or passing an opponent's ball in a volleyball game. Without generating some kind of prediction about how the others are likely to behave, it would be difficult to react quickly and efficiently in these kinds of situations. Over the last decade, substantial evidence has been accumulated in the cognitive (neuro)sciences indicating that action execution and action observation share a common representational domain that might support a variety of human abilities such as the control of self-intended actions but also the evaluation and prediction of observed actions (Jeannerod, 2001; Prinz, 1997; Schütz-Bosbach & Prinz, 2007; Wilson & Knoblich, 2005; Wolpert & Flanagan, 2001). More specifically, it has been proposed that observed actions are mapped onto one's own internal action representations. This mapping may not only involve a representation of the current action state but also a prediction of forthcoming action states. These assumptions are supported by a vast amount of neuroimaging studies demonstrating that action observation engages regions in the human brain that are similarly activated during action execution, that is, the premotor cortex (PMC), the inferior frontal gyrus (IFG), and the inferior parietal lobule (IPL) together with the superior temporal sulcus (STS; e.g., Caspers et al., 2010; Grèzes & Decety, 2001; Rizzolatti & Craighero, 2004). Grafton (2009) subsequently referred to this whole set of regions as the human action observation network (AON). According to the predictive coding account, the different regions of the AON are reciprocally connected and an actual representation of the observed action is compared to a predicted representation in each region of the network (Kilner et al., 2007a, 2007b). This comparison generates a prediction error, which is back propagated through the cortical hierarchy to update the internal action representation and minimize the prediction error. Thus, predictive coding provides an explanation how inferring and predicting the actions of others might be implemented at the neural level. The prediction of an observed action should consequently become more effective the closer the observers' internal action representation matches the observed action. Individuals who are not able to execute the observed actions, in contrast, might rather exploit the visual dynamics of theses actions resulting in a less accurate prediction performance. In line with this, studies on skilled motor performance frequently demonstrate that individual differences in sensorimotor experience correlate with the ability to predict observed actions as well as modulate neural activity in the observers' brain (e.g., Aglioti et al., 2008; Calvo-Merino et al., 2005; Urgesi et al., 2012).

At present, however, it is still poorly understood whether and how predictive abilities and their underlying neural mechanisms change over the lifespan due to age-related changes in the brain and body. Only very few studies addressed these questions from a lifespan perspective, although the proportion of older people in many societies is constantly increasing (cf., Christensen et al., 2009). Notably, despite declines in low-level visual information processing and general motion perception, the detection and discrimination of biological motion stimuli seems to be relatively preserved with age (Norman et al., 2004; Pilz et al., 2010). This is especially evident in conditions in which highly familiar motion patterns are presented. In the light of these findings, it has been suggested that older adults might draw on their sensory experience during the observation of biological motion, which allows them to compensate to some extent for declines in low-level visual information processing. Based on the assumption that action execution and action observation share a common representational domain, one might further speculate that older adults also use their sensorimotor system in order to represent observed actions. Thus, age-related declines in sensorimotor processing might additionally influence the prediction of observed actions (cf., Seidler et al., 2010). Studies on the temporal features of motor imagery, for example, showed that the temporal similarity between an imagined and executed action is reduced in older compared to younger adults (e.g., Personnier et al., 2008; Skoura et al., 2008). Such changes at the behavioral level are logically linked to changes at the neural level given that the human brain is subject to substantial declines at the structural as well as functional level with age (Grady, 2012). Typically, older adults exhibit less distinct task-related activation patterns compared to younger adults across a variety of cognitive domains that could either reflect neural dedifferentiation or compensation for declining structures (Cabeza, 2002; Li & Lindenberger, 1999). According to the scaffolding theory of aging and cognition (STAC), aging can be viewed as a (intrinsic) challenge to the human brain just as unfamiliar tasks pose a (extrinsic) challenge to a younger brain (Park & Reuter-Lorenz, 2009). Both types of challenges result in a functional reorganization (i.e., neural scaffolding) through the recruitment of additional regions to compensate for noisy and/or inefficient neural processing. With respect to the neural representation of observed actions, Léonard and Tremblay (2007) provided first evidence for a loss of neural selectivity with advancing age. By using transcranial magnetic stimulation (TMS), the authors showed that corticomotor facilitation in relevant muscles is less specialized in older compared to younger adults during action observation, imitation, and imagery. Moreover, Nedelko et al. (2010) recently showed that older adults recruit additional brain regions beyond the AON compared to younger adults during action observation and imagery. In how far these changes affect the prediction of observed actions depending on the level of sensorimotor experience in the aging observer and how this might be implemented in the aging brain remains largely unknown to date, however.

Therefore, the aim of this dissertation was to investigate how advancing age affects the ability to predict the actions of others and its neural implementation. In a first behavioral experiment, the accuracy and timing in action prediction was investigated in older compared to younger adults during the observation of complex but highly familiar everyday actions. A second behavioral experiment addressed the question to what extent sensorimotor experience might attenuate possible age-related declines in action prediction (Diersch et al., 2012). Even though expertise in a certain domain may not prevent general physical or cognitive declines typically seen in older age groups, it may attenuate age-related declines on skill-related tasks (Krampe & Charness, 2006). Accordingly, the accuracy and timing in action prediction was compared in older and younger figure skating experts as well as age-matched non-experts during the observation of classical figure skating elements and generally familiar movement exercises. In all of the experiments, an action occlusion paradigm was used in which the observed action sequences were partly occluded at critical time points and continued after occlusion in a temporally manipulated way (i.e., congruent, too early or too late on different levels). Participants were asked to judge the temporal coherence of the continuation after occlusion. This required them to extrapolate the trajectory of the occluded action into the future and to match this prediction with the actual continuation after occlusion in order to solve the task. Similar action occlusion paradigms have been used previously in different action observation and prediction studies (e.g., Graf et al., 2007; Parkinson et al., 2012; Stadler et al., 2011).

The results of the behavioral experiments suggest that older adults are not as efficient as younger adults in creating and updating predictions of the sensory outcomes of an observed action when they are temporarily occluded at critical time points. The proportion of correct responses on the different continuations after occlusion was lower in older compared to younger adults in both experiments. However, older adults were able to accomplish the task in general and obtained scores that equaled or exceeded age norms on different physical and cognitive health measures. The analyses of the prediction timing revealed that the temporal range during which shifted continuations could not be clearly differentiated from the congruent continuation was larger in older than in younger adults. Thus, even when older adults were still able to execute the observed actions and therefore must possess an internal representation of these actions, they did not seem to represent them in a sufficiently detailed manner in order to predict their exact time course (cf., Personnier et al., 2008; Skoura et al., 2008). The results from the second behavioral experiment additionally indicate that sensorimotor experience in figure skating results in better prediction performance for domain-specific actions in both older and younger experts compared to non-experts of the respective age groups. This expertise-related benefit did not show transfer to the observed movement exercises. Thus, extensive amounts of experience seem to result in more stable internal action representations that can be used to generate more accurate predictions about these actions even in older age groups. Importantly, the older figure skating experts did not differ significantly in their age or cognitive status from the older non-experts and the timing in prediction was not systematically biased in older compared to younger adults (i.e., generally slower or faster). This implies that age-related differences in action prediction are unlikely to be accounted for by age-related declines in general cognitive abilities such as memory and time perception.

In a follow-up functional magnetic resonance imaging (fMRI) experiment, age-related changes in neural activation patterns during the prediction of temporally occluded actions were examined while using the same action sequences as in the second behavioral experiment (Diersch et al., submitted). Participants consisted of older and younger adults with varying degrees of motor familiarity with the observed actions. The majority of them had already taken part in the second behavioral experiment. Brain activity was analyzed as a function of predicted action category collapsed across the whole sample as well as a function of age group and sensorimotor experience in figure skating. The results of the fMRI experiment show that action prediction is a complex process that engages a distributed neural network, within but also beyond the AON, depending on the specific stimulus characteristics and the age and experience of the observer. In line with previous evidence, higher AON activity was found during the prediction of the more familiar movement exercises (cf., Calvo-Merino et al., 2005; Cross et al., 2006). For these actions only, one region of the AON, the posterior STS, differentiated between incongruent and congruent continuations after occlusion. The prediction of the figure skating elements, in contrast, resulted in increased activity in the visual cortex and the medial orbitofrontal cortex (OFC). This implies that generally reproducible actions are predominantly processed in the AON. Any deviations between the prediction and the actual sensory input might consequently result in higher AON activity until the prediction error is minimized. The use of these predictive representations might become less efficient the less familiar an observed action is, until an internal (sensorimotor) representation of that action will not be present at all. In these cases, the observed actions might be represented in a rather multimodal way that is supported by the recruitment of regions beyond the classical AON. In line with this, the results further suggest that the caudate together with the thalamus play an important role during the prediction of the less familiar figure skating elements compared to movement exercises in better-performing groups (i.e., younger adults compared to older adults and figure skating experts compared to non-experts). Schiffer and Schubotz (2011) recently showed that the caudate may encode deviations from an initial prediction during action observation. Thus, the prediction of actions that more ambiguous for the respective observer might engage the caudate (together with the thalamus), possibly to adjust and optimize less precise predictions that are generated in the AON.

With respect to age-related changes in neural activation patterns during action prediction, the findings of the fMRI experiment support the assumption that older adults are less efficient in exploiting the sensorimotor matching properties of the AON. Compared to younger adults, older adults recruited visual cortices to perform the task and, additionally, the hippocampus and caudate when the observed actions were familiar to them. This suggests that older adults may have created a mental image of the observed actions during the occlusion period and evaluated its visual features in order to accomplish the task. If they were familiar with the observed actions, this evaluation seemed to be based on previously learned, multimodal representations of these actions stored in different memory systems. Thus, in line with the assumptions of STAC, less distinct sensory and/or motor representations in the aging brain seem to result in a functional reorganization through the recruitment of additional regions in order to predict observed actions (cf., Park & Reuter-Lorenz, 2009). Moreover, this functional reorganization appears to resemble the response to the observation of unfamiliar actions in a younger brain. Higher activation in visual regions was also found in non-experts of the present study during the observation of the figure skating elements compared to the generally familiar movement exercises as well as in previous studies measuring neural activity in non-experts compared to experts during action imagery and prediction (Olsson et al., 2008; Wright et al., 2011).

Taken together, the results from the present dissertation provide new and important insights into how the prediction of others' actions might change with advancing age. Evidence from two behavioral experiments suggests that older adults are less precise in predicting the time course of observed actions, possibly due to age-related deficiencies in generating predictions and updating them based on actual sensory input. Nevertheless, extensive sensorimotor experience seems to enable experts to predict actions from their domain of expertise more precisely even in older age. The results of the fMRI experiment further showed that the brain's response to challenges due to aging or the exposure to unfamiliar material may share some similarities during the prediction of others' actions. Older adults might be considered, metaphorically speaking, as non-experts in previously well-known domains due to internal action representations that become less precise with advancing age.

ZUSAMMENFASSUNG DER DISSERTATION

Action Prediction in the Aging Mind

Eingereicht an der Fakultät für Biowissenschaften, Pharmazie und Psychologie
Universität Leipzig

von Dipl. – Psych. Nadine Diersch

Leipzig, 23. Januar 2013

Eine der wichtigsten Fähigkeiten, die ein erfolgreiches Navigieren in unserer sozialen Umwelt und die Interaktion mit Anderen gewährleistet, ist die korrekte Vorhersage von den Handlungen anderer Personen. Stellen Sie sich beispielweise vor, Sie überqueren eine dicht bevölkerte Straße oder versuchen, in einem Volleyballspiel den Aufschlag der generischen Mannschaft anzunehmen. Ohne dabei eine Art Prädiktion über das künftige Verhalten des Anderen zu treffen, wäre es schwierig, in derartigen Situationen schnell und effizient zu reagieren. In den letzten Jahren mehren sich Befunde in den kognitiven (Neuro-)Wissenschaften, die auf eine gemeinsame Repräsentation von Handlungsausführung und Handlungswahrnehmung hinweisen (Jeannerod, 2001; Prinz, 1997; Schütz-Bosbach & Prinz, 2007; Wilson & Knoblich, 2005; Wolpert & Flanagan, 2001). Dies könnte die Basis für eine Reihe von menschlichen Fähigkeiten bilden, wie etwa die Kontrolle von intentionalen Handlungen aber auch die Einschätzung und Prädiktion beobachteter Handlungen. Dabei wird angenommen, dass beobachtete Handlungen auf den eigenen, internen Handlungsrepräsentationen abgebildet werden, was neben einer Repräsentation des gegenwärtigen Handlungsschrittes auch eine Repräsentation zukünftiger Handlungsschritte beinhaltet. Diese Annahmen werden durch eine große Anzahl von Studien unterstützt, die mittels bildgebender Verfahren zeigten, dass die Handlungsbeobachtung ähnliche Regionen im menschlichen Gehirn beansprucht wie die tatsächliche Handlungsausführung (z.B., Caspers et al., 2010; Grèzes & Decety, 2001; Rizzolatti & Craighero, 2004). Dieses Netzwerk, von Grafton (2009) als das menschliche „Action Observation Network“ (AON) bezeichnet, umfasst den prämotorischen Kortex, den inferioren frontalen Gyrus, das inferiore Parietalläppchen zusammen mit dem superioren Teil des temporalen Sulcus. Laut dem sogenannten „Predictive Coding“-Prinzip sind die einzelnen Regionen dieses neuronalen

Netzwerkes reziprok verbunden (Kilner et al., 2007a, 2007b). In jeder Region des Netzwerkes wird die tatsächliche Repräsentation einer beobachteten Handlung mit einer intern generierten Repräsentation über den zu erwartenden Handlungseffekt verglichen. Dieser Vergleich erzeugt einen Prädiktionsfehler („prediction error"), der in der kortikalen Hierarchie zurückgesendet wird, um die interne Handlungsrepräsentation entsprechend anzupassen und den Prädiktionsfehler zu minimieren. Mittels dieses Prinzips lässt sich folglich erklären, wie die Einschätzung und Prädiktion von beobachteten Handlungen auf neuronaler Ebene implementiert sein könnte. Die Prädiktion von beobachteten Handlungen müsste daher umso effektiver werden, je mehr die interne Handlungsrepräsentation des Beobachters der beobachteten Handlung entspricht. Im Gegensatz dazu sind Personen, die die beobachtete Handlung selbst nicht ausführen können, vorwiegend auf die visuellen Eigenschaften der Handlung angewiesen, was eine weniger genaue Prädiktionsleistung zur Folge hat. Im Einklang damit wurde in zahlreichen Studien gezeigt, dass individuelle Unterschiede im Grad der sensomotorischer Erfahrung mit bestimmten Handlungen sowohl die Prädiktionsleistung während der Beobachtung dieser Handlungen beeinflussen als auch die Aktivität im Gehirn des Beobachters modulieren (z.B., Aglioti et al., 2008; Calvo-Merino et al., 2005; Urgesi et al., 2012).

Wesentlich weniger ist jedoch darüber bekannt, ob und wie sich die Prädiktionsfähigkeit und deren neuronale Grundlage über die Lebensspanne verändern, wenn das Gehirn und der Körper älter werden. Nur sehr weniger Studien haben sich bisher mit diesem Aspekt befasst, obwohl der Anteil an älteren Personen in vielen Gesellschaften stetig zunimmt (vgl., Christensen et al., 2009). Trotz altersbedingter Leistungseinbußen in der visuellen Informationsverarbeitung und in der generellen Bewegungswahrnehmung scheint das Erkennen und die Diskriminierung von biologischen Bewegungsstimuli interessanterweise über die Lebensspanne relativ gut erhalten zu bleiben (Norman et al., 2004; Pilz et al., 2010). Dies ist besonders evident in Bedingungen, in denen sehr geläufige und vertraute Bewegungsmuster präsentiert werden. Aufgrund dieser Ergebnisse wurde angenommen, dass ältere Erwachsene während der Beobachtung von biologischen Bewegungen ihre sensorischen Erfahrungen nutzen und auf diese Weise Veränderungen in der visuellen Informationsverarbeitung teilweise kompensiert werden können. Basierend auf der Idee, dass Handlung und Wahrnehmung gemeinsam repräsentiert sind, liegt außerdem der Schluss nahe, dass ältere

Erwachsene auch ihr sensomotorisches System nutzen, um beobachtete Handlungen zu repräsentieren und vorherzusagen. Altersbedingte Veränderungen in der sensomotorischen Informationsverarbeitung würden daher die Prädiktion von beobachteten Handlungen ebenfalls beeinflussen (vgl., Seidler et al., 2010). Studien zu den zeitlichen Aspekten der motorischen Vorstellungskraft („motor imagery“) haben beispielsweise gezeigt, dass die zeitliche Übereinstimmung zwischen einer vorgestellten und einer tatsächlichen Handlung bei älteren im Vergleich zu jüngeren Erwachsenen vermindert ist (z.B., Personnier et al., 2008; Skoura et al., 2008). Diese Veränderungen auf behavioraler Ebene stehen naturgemäß in einem engen Zusammenhang mit Veränderungen auf neuronaler Ebene, da das menschliche Gehirn, sowohl strukturell als auch funktionell, mit dem Alter dramatischen Abbauprozessen unterliegt (Grady, 2012). Typischerweise zeigen ältere im Vergleich zu jüngeren Erwachsenen während der Durchführung einer Aufgabe in einer Reihe von kognitiven Bereichen weniger spezifische neuronale Aktivierungsmuster. Dies könnte entweder auf eine neuronale Dedifferenzierung im alternden Gehirn oder auf eine kompensatorische Anpassung zum Ausgleich dysfunktionaler Strukturen hinweisen (Cabeza, 2002; Li & Lindenberger, 1999). Laut der sogenannten „Scaffolding Theory of Aging and Cognition“ (STAC) kann Altern als eine (intrinsische) Herausforderung für das menschliche Gehirn betrachtet werden, ähnlich wie unbekannte Aufgaben eine (extrinsische) Herausforderung für ein junges Gehirn darstellen (Park & Reuter-Lorenz, 2009). Beide Arten von Herausforderung führen zu einer funktionellen Reorganisation („neural scaffolding“), die sich in einer Aktivierung von zusätzlichen Gehirnregionen als Ausgleich von verrauschter und/oder ineffizienter neuronaler Verarbeitung manifestiert. Bezüglich der neuronalen Repräsentation von beobachteten Handlungen haben Léonard and Tremblay (2007) erste Hinweise für eine altersbedingte Verminderung der neuronalen Selektivität geliefert. Unter Anwendung von transkranieller Magnetstimulation (TMS) konnten die Autoren zeigen, dass die kortikomotorische Erregbarkeit während der Handlungsbeobachtung, -imitation, und -vorstellung in den entsprechenden Muskeln bei älteren Erwachsenen weniger spezifisch ist als bei jüngeren Erwachsenen. Des Weiteren berichteten Nedelko et al. (2010) unlängst, dass bei älteren im Vergleich zu jüngeren Erwachsenen während der Handlungsbeobachtung und –vorstellung zusätzliche Gehirnregionen aktiviert sind, die nicht als Teil des AONs gelten. Inwieweit sich diese altersbedingten

Veränderungen auf die Prädiktion von beobachteten Handlungen in Abhängigkeit des Grades an sensomotorischer Erfahrung des Beobachters auswirken und wie dies im alternden Gehirn implementiert ist, ist bisher jedoch weitgehend unbekannt.

Das Hauptziel der vorliegenden Dissertation war es daher, die Auswirkungen des Älterwerdens auf die Fähigkeit der Handlungsprädiktion und deren neuronale Grundlage zu untersuchen. In einem ersten behavioralen Experiment wurden die Genauigkeit und das Timing der Handlungsprädiktion bei älteren im Vergleich zu jüngeren Erwachsenen während der Beobachtung von komplexen, aber sehr vertrauten Alltagshandlungen untersucht. Ein zweites behaviorales Experiment befasste sich mit der Frage, inwieweit sensomotorische Erfahrung mögliche altersbedingte Leistungseinbußen bei der Handlungsprädiktion ausgleichen kann (Diersch et al., 2012). Obwohl Erfahrung in einem bestimmten Bereich physische oder kognitive Abbauprozesse, die sich typischerweise im Alter zeigen, nicht aufhalten kann, scheint sie altersbedingte Veränderungen innerhalb expertisespezifischer Fertigkeiten abzumildern (Krampe & Charness, 2006). Aus diesem Grund wurden die Genauigkeit und das Timing der Handlungsprädiktion bei älteren und jüngeren Eiskunstlauf-Experten sowie Eiskunstlauf-Laien während der Beobachtung von klassischen Eiskunstlaufelementen und einfachen, vertrauten Alltagsbewegungen untersucht. In beiden Experimenten wurde ein „Action Occlusion Paradigm“ verwendet, in dem die gezeigten Handlungen zu bestimmten Zeitpunkten teilweise verdeckt und nach der Verdeckung zeitlich manipuliert fortgesetzt wurden (d.h., zu früh, kongruent, oder zu spät). Die Aufgabe der Probanden war es, die zeitliche Kohärenz der Handlungsfortsetzung nach der Verdeckung einzuschätzen. Die Bewältigung der Aufgabe erforderte von den Beobachtern somit eine zeitliche Extrapolation des Handlungsablaufes während der Verdeckung sowie den Abgleich dieser Prädiktion mit der tatsächlichen Handlungsfortsetzung. Diese Art von Paradigma wurde bereits in einer Reihe von Studien zur Handlungsbeobachtung und –prädiktion erfolgreich eingesetzt (z.B., Graf et al., 2007; Parkinson et al., 2012; Stadler et al., 2011).

Die Ergebnisse der behavioralen Experimente legen nahe, dass ältere im Vergleich zu jüngeren Erwachsenen weniger effizient darin sind, Prädiktionen über den Verlauf von zeitweise verdeckten Handlungen zu generieren und diese entsprechend dem tatsächlichen sensorischen Input anzupassen. In beiden Experimenten war der Anteil an richtigen Antworten bei den verschiedenen

Handlungsfortsetzungen nach der Verdeckung bei älteren Erwachsenen geringer als bei jüngeren Erwachsenen. Dennoch waren die älteren Erwachsenen generell in der Lage, die Aufgabe zu bewältigen und erreichten in verschiedenen Testverfahren zum physischen und kognitiven Gesundheitszustand Testwerte, die im oder über dem Durchschnitt altersdifferenzierter Normwerte lagen. Die Auswertung des Timings der Handlungsprädiktion zeigte, dass der Bereich, in dem zeitlich manipulierte Fortsetzungen nicht eindeutig von der kongruenten Fortsetzung differenziert werden konnten, bei älteren im Vergleich zu jüngeren Erwachsenen deutlich größer war. Dies legt nahe, dass die beobachteten Handlungen von den älteren Erwachsenen nicht ausreichend im Detail repräsentiert wurden, auch wenn sie diese nach wie vor motorisch reproduzieren konnten und daher über eine entsprechende interne Handlungsrepräsentation verfügen mussten (vgl., Personnier et al., 2008; Skoura et al., 2008). Die Ergebnisse des zweiten behavioralen Experiments zeigten außerdem, dass sensomotorische Erfahrung im Eiskunstlauf während der Beobachtung von expertisespezifischen Handlungen eine bessere Prädiktionsleistung zur Folge hatte, sowohl bei älteren als auch bei jüngeren Experten im Vergleich zu Laien gleichen Alters. Dieser expertisespezifische Vorteil zeigte keinen Transfer auf die Prädiktionsleistung während der Beobachtung der allgemein vertrauten Alltagsbewegungen. Somit scheint die professionelle Ausübung einer motorischen Fertigkeit in stabileren internen Handlungsrepräsentationen zu resultieren. Diese erlauben auch im höheren Alter die Generation von genaueren Prädiktionen während der Beobachtung expertisespezifischer Handlungen. Wesentlich dabei ist, dass sich die älteren Eiskunstlauf-Experten im Alter und kognitiven Status nicht signifikant von den älteren Eiskunstlauf-Laien unterschieden. Ferner war das Timing der Handlungsprädiktion bei den älteren Erwachsenen nicht signifikant schneller oder langsamer im Vergleich zu den jüngeren Erwachsenen. Dies impliziert, dass altersbedingte Unterschiede in der Handlungsprädiktion nicht auf generelle Unterschiede in der kognitiven Leistung (z.B. in Bezug auf Gedächtnis oder Zeitwahrnehmung) zurückzuführen sind.

In einem Folgeexperiment wurden altersbedingte Veränderungen neuronaler Aktivierungsmuster während der Prädiktion von zeitweise verdeckten Handlungen mittels funktioneller Magnetresonanztomographie (fMRT) untersucht (Diersch et al., eingereicht). Dafür wurden die gleichen Handlungssequenzen wie in dem zweiten behavioralen Experiment verwendet. Die Stichprobe bestand aus älteren und jüngeren Erwachsenen, die einen unterschiedlichen Grad an Erfahrung mit den beobachteten Handlungssequenzen besaßen. Die Mehrheit der Probanden nahm bereits an dem zweiten behavioralen Experiment teil. Hirnaktivität wurde in Abhängigkeit der beobachteten Handlungsart über die gesamte Stichprobe hinweg als auch in Abhängigkeit der Altersgruppe sowie des Grades an sensomotorischer Erfahrung im Eiskunstlauf analysiert. Die Ergebnisse des fMRT-Experimentes zeigen, dass Handlungsprädiktion ein komplexer Prozess ist, der ein weit verzweigtes Netzwerk im Gehirn aktiviert, sowohl innerhalb als auch außerhalb des AONs, in Abhängigkeit von der Art der gezeigten Stimuli sowie dem Alter und der Erfahrung des Beobachters. In Übereinstimmung mit vorherigen Studien war die Aktivität im AON höher während der Prädiktion der allgemein vertrauteren Alltagsbewegungen (vgl., Calvo-Merino et al., 2005; Cross et al., 2006). Nur für diese Handlungen differenzierte eine Region des AON, der superiore Teil des temporalen Sulcus, zwischen inkongruenten und kongruenten Fortsetzungen nach der Verdeckung. Im Gegensatz dazu führte die Prädiktion von den Eiskunstlaufelementen zu erhöhter Aktivität im visuellen Kortex und im medialen Teil des orbitofrontalen Kortex. Dies impliziert, dass generell reproduzierbare Handlungen vorwiegend im AON verarbeitet werden. Etwaige Abweichungen zwischen der Prädiktion und dem tatsächlichen sensorischen Input führen demnach zu höherer Aktivität in diesem Netzwerk bis der Prädiktionsfehler minimiert ist. Die Verwendung dieser im AON generierten Prädiktionen wird dabei umso ineffektiver, je weniger motorisch vertraut die beobachtete Handlung ist, bis eine sensomotorische Repräsentation dieser Handlung überhaupt nicht mehr vorhanden ist. In diesen Fällen werden beobachtete Handlungen möglicherweise eher multimodal repräsentiert, was durch eine Aktivierung von Regionen außerhalb des klassischen AONs gekennzeichnet ist. In Übereinstimmung damit legen die Ergebnisse nahe, dass der Nucleus Caudatus zusammen mit dem Thalamus in den Gruppen, die generell eine bessere Prädiktionsleistung zeigten (d.h., bei jüngeren im Vergleich zu älteren Erwachsenen sowie bei Eiskunstlauf-Experten im Vergleich zu Eiskunstlauf-Laien), eine wichtige Rolle während der Prädiktion der weniger vertrauten Eiskunstlaufelemente spielte. Schiffer and Schubotz (2011) zeigten kürzlich, dass der Nucleus Caudatus Abweichungen von der ursprünglichen Prädiktion während der Handlungsbeobachtung kodiert. Somit könnte die Prädiktion von Handlungen, die für den jeweiligen Beobachter nicht eindeutig nachzuvollziehen sind, den Nucleus

Caudatus (zusammen mit dem Thalamus) aktivieren, um möglicherweise weniger präzisen Prädiktionen aus dem AON entsprechend anzupassen und zu optimieren.

Bezüglich altersbedingter Veränderungen neuronaler Aktivierungsmuster während der Handlungsprädiktion stützen die Ergebnisse des fMRT-Experiments die Annahme, dass ältere Erwachsene das AON weniger effizient nutzen können, um beobachtete Handlungen auf sensomotorischer Ebene abzubilden. Im Vergleich zu jüngeren Erwachsenen waren bei älteren Erwachsenen während der Handlungsprädiktion überwiegend visuelle Bereiche des Gehirns aktiviert und außerdem der Hippocampus und der Nucleus Caudatus, wenn ihnen die gezeigten Handlungen motorisch vertraut waren. Dies impliziert, dass ältere Erwachsene während der Verdeckung ein mentales Abbild der beobachteten Handlungen generierten und dessen visuelle Eigenschaften evaluierten, um die Aufgabe zu bewältigen. Wenn ihnen die gezeigten Handlungen vertraut waren, schien diese Evaluierung zudem auf gelernten, multimodalen Repräsentationen der Handlungen zu basieren, die in verschiedenen Gedächtnissystemen gespeichert sind. Übereinstimmend mit den Annahmen von STAC, scheinen somit weniger distinkte sensorische und/oder motorische neuronale Handlungsrepräsentationen im alternden Gehirn eine funktionale Reorganisation zur Folge zu haben, die sich in der Aktivierung von zusätzlichen Gehirnregionen während der Handlungsprädiktion manifestiert (vgl., Park & Reuter-Lorenz, 2009). Darüber hinaus scheint diese funktionelle Reorganisation ähnlich zu der neuronalen Antwort auf die Beobachtung von motorisch unvertrauten Handlungen in einem jüngeren Gehirn zu sein. Höhere Aktivierungen in visuellen Regionen wurden in dem vorliegenden Experiment ebenfalls bei Eiskunstlauf-Laien während der Beobachtung von den Eiskunstlaufelementen im Vergleich zu den sehr vertrauten Alltagsbewegungen gefunden. Ähnliche Befunde wurden auch in früheren Studien bei Laien im Vergleich zu Experten während der Handlungsvorstellung und –prädiktion berichtet (Olsson et al., 2008; Wright et al., 2011).

Insgesamt geben die Ergebnisse der vorliegenden Dissertation neue und wichtige Aufschlüsse darüber, wie sich die Prädiktion von beobachteten Handlungen mit zunehmendem Alter verändert. Zwei behaviorale Experimente liefern Evidenz, dass ältere Erwachsene bei der Prädiktion des zeitlichen Ablaufs von beobachteten Handlungen weniger präzise sind, möglicherweise aufgrund von altersbedingten Defiziten bei der Generierung von Prädiktionen und deren Anpassung an den tatsächlichen sensorischen Input. Dennoch scheint umfangreiche sensomotorische Erfahrung in einem Bereich Experten zu befähigen, expertisespezifische Handlungen präziser vorherzusagen, auch im höheren Alter. Die Ergebnisse des fMRT-Experimentes zeigen außerdem, dass die neuronale Antwort auf Herausforderungen, die sich durch das Altern oder die Präsentation von motorisch unvertrauten Handlungen ergeben, während der Handlungsprädiktion einige Gemeinsamkeiten aufweist. Ältere Erwachsene könnten, aufgrund von internen Handlungsrepräsentationen, die mit zunehmendem Alter an Präzision verlieren, metaphorisch gesprochen, als Laien in vorher wohlbekannten Bereichen betrachtet werden.

BIBLIOGRAPHY

Abernethy, B., & Zawi, K. (2007). Pickup of essential kinematics underpins expert perception of movement patterns. *Journal of Motor Behavior, 39*(5), 353-367.

Abreu, A. M., Macaluso, E., Azevedo, R. T., Cesari, P., Urgesi, C., & Aglioti, S. M. (2012). Action anticipation beyond the action observation network: A functional magnetic resonance imaging study in expert basketball players. *European Journal of Neuroscience, 35*(10), 1646-1654.

Addis, D. R., Roberts, R. P., & Schacter, D. L. (2011). Age-related neural changes in autobiographical remembering and imagining. *Neuropsychologia, 49*(13), 3656-3669.

Addis, D. R., & Schacter, D. L. (2012). The hippocampus and imagining the future: Where do we stand? *Frontiers in Human Neuroscience, 5*, 173. 1-15. doi: 10.3389/fnhum.2011.00173

Aglioti, S. M., Cesari, P., Romani, M., & Urgesi, C. (2008). Action anticipation and motor resonance in elite basketball players. *Nature Neuroscience, 11*(9), 1109-1116.

Ashburner, J., & Friston, K. J. (2005). Unified segmentation. *Neuroimage, 26*(3), 839-851.

Babiloni, C., Marzano, N., Infarinato, F., Iacoboni, M., Rizza, G., Aschieri, P., . . . Del Percio, C. (2010). "Neural efficiency" of experts' brain during judgment of actions: A high-resolution EEG study in elite and amateur karate athletes. *Behavioural Brain Research, 207*(2), 466-475.

Baddeley, A., Emslie, H., & Nimmo-Smith, I. (1993). The Spot-the-Word test: A robust estimate of verbal intelligence based on lexical decision. *British Journal of Clinical Psychology, 32*, 55-65.

Balleine, B. W., Delgado, M. R., & Hikosaka, O. (2007). The role of the dorsal striatum in reward and decision-making. *Journal of Neuroscience, 27*(31), 8161-8165.

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), 12-21.

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

Bar, M. (2009). The proactive brain: Memory for predictions. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*(1521), 1235-1243.

Bar, M., Kassam, K. S., Ghuman, A. S., Boshyan, J., Schmidt, A. M., Dale, A. M., . . . Halgren, E. (2006). Top-down facilitation of visual recognition. *Proceedings of the National Academy of Sciences of the United States of America, 103*(2), 449-454.

Barsalou, L. W. (2008). Grounded cognition. *Annual Review of Psychology, 59*, 617-645.

Bastos, A., Usrey, W., Adams, R., Mangun, G., Fries, P., & Friston, K. (2012). Canonical Microcircuits for Predictive Coding. *Neuron, 76*(4), 695-711.

Bennett, P. J., Sekuler, R., & Sekuler, A. B. (2007). The effects of aging on motion detection and direction identification. *Vision Research, 47*(6), 799-809.

Bernard, J. A., & Seidler, R. D. (2012). Evidence for motor cortex dedifferentiation in older adults. *Neurobiology of Aging, 33*(9), 1890-1899.

Blakemore, S.-J., & Decety, J. (2001). From the perception of action to the understanding of intention. *Nature Reviews Neuroscience, 2*(8), 561-567.

Blakemore, S.-J., Wolpert, D., & Frith, C. . (2000). Why can't you tickle yourself? *Neuroreport, 11*(11), R11-R16.

Braver, T. S., & West, R. (2008). Working memory, executive control, and aging. In F. I. M. Craik & T. A. Salthouse (Eds.), *The handbook of aging and cognition* (3rd ed., pp. 311-372). New York: Psychology Press.

Brown, E. C., & Brüne, M. (2012). The role of prediction in social neuroscience. *Frontiers in Human Neuroscience, 6*, 147. 1-19. doi: 10.3389/fnhum.2012.00147

Bubic, A., Von Cramon, D. Y., & Schubotz, R. I. (2010). Prediction, cognition and the brain. *Frontiers in Human Neuroscience, 4*, 25. 1-15. doi: 10.3389/fnhum.2010.00025

Buccino, G., Baumgaertner, A., Colle, L., Buechel, C., Rizzolatti, G., & Binkofski, F. (2007). The neural basis for understanding non-intended actions. *Neuroimage, 36, Supplement 2*(0), T119-T127.

Buccino, G., Binkofski, F., & Riggio, L. (2004). The mirror neuron system and action recognition. *Brain and Language, 89*(2), 370-376.

Buccino, G., Lui, F., Canessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., . . . Rizzolatti, G. (2004). Neural circuits involved in the recognition of actions performed by nonconspecifics: An fMRI study. *Journal of Cognitive Neuroscience, 16*(1), 114-126.

Cabeza, R. (2002). Hemispheric asymmetry reduction in older adults: The HAROLD model. *Psychology and Aging, 17*(1), 85-100.

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

Calvo-Merino, B., Glaser, D. E., Grezes, J., Passingham, R. E., & Haggard, P. (2005). Action observation and acquired motor skills: An fMRI study with expert dancers. *Cerebral Cortex, 15*(8), 1243-1249.

Calvo-Merino, B., Grèzes, J., Glaser, D. E., Passingham, R. E., & Haggard, P. (2006). Seeing or doing? Influence of visual and motor familiarity in action observation. *Current Biology, 16*(19), 1905-1910.

Carp, J., Park, J., Hebrank, A. C., Park, D. C., & Polk, T. A. (2011). Age-related neural dedifferentiation in the motor system. *PLOS ONE, 6*, 12. e29411. doi: 10.1371/journal.pone.0029411

Carp, J., Park, J., Polk, T. A., & Park, D. C. (2011). Age differences in neural distinctiveness revealed by multi-voxel pattern analysis. *Neuroimage, 56*(2), 736-743.

Caspers, S., Zilles, K., Laird, A. R., & Eickhoff, S. B. (2010). ALE meta-analysis of action observation and imitation in the human brain. *Neuroimage, 50*(3), 1148-1167.

Catmur, C. , Gillmeister, H., Bird, G. , Liepelt, R. , Brass, M., & Heyes, C. (2008). Through the looking glass: Counter-mirror activation following incompatible sensorimotor learning. *European Journal of Neuroscience, 28*(6), 1208-1215.

Catmur, C., Walsh, V., & Heyes, C. (2007). Sensorimotor learning configures the human mirror system. *Current Biology, 17*(17), 1527-1531.

Catmur, C., Walsh, V., & Heyes, C. (2009). Associative sequence learning: The role of experience in the development of imitation and the mirror system. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*(1528), 2369-2380.

Celnik, P., Stefan, K., Hummel, F., Duque, J., Classen, J., & Cohen, L. G. (2006). Encoding a motor memory in the older adult by action observation. *Neuroimage, 29*(2), 677-684.

Christensen, K., Doblhammer, G., Rau, R., & Vaupel, J. W. (2009). Ageing populations: The challenges ahead. *The Lancet, 374*, 1196-1208.

Colcombe, S. J., Erickson, K. I., Raz, N., Webb, A. G., Cohen, N. J., McAuley, E., & Kramer, A. F. (2003). Aerobic fitness reduces brain tissue loss in aging humans. *Journals of Gerontology Series A: Biological Sciences and Medical Sciences, 58*(2), 176-180.

Colcombe, S. J., Erickson, K. I., Scalf, P. E., Kim, J. S., Prakash, R., McAuley, E., . . . Kramer, A. F. (2006). Aerobic exercise training increases brain volume in aging humans. *Journals of Gerontology Series A: Biological Sciences and Medical Sciences, 61*(11), 1166-1170.

Colcombe, S. J., & Kramer, A. F. (2003). Fitness effects on the cognitive function of older adults: A meta-analytic study. *Psychological Science, 14*(2), 125-130.

Colcombe, S. J., Kramer, A. F., Erickson, K. I., Scalf, P., McAuley, E., Cohen, N. J., . . . Elavsky, S. (2004). Cardiovascular fitness, cortical plasticity, and aging. *Proceedings of the National Academy of Sciences of the United States of America, 101*(9), 3316-3321.

Cooper, J. C., Dunne, S., Furey, T., & O'Doherty, J. P. (2012). Human dorsal striatum encodes prediction errors during observational learning of instrumental actions. *Journal of Cognitive Neuroscience, 24*(1), 106-118.

Cotman, Carl W., & Berchtold, Nicole C. (2002). Exercise: A behavioral intervention to enhance brain health and plasticity. *Trends in Neurosciences, 25*(6), 295-301.

Cross, E. S., Hamilton, A. F., & Grafton, S. T. (2006). Building a motor simulation de novo: Observation of dance by dancers. *Neuroimage, 31*(3), 1257-1267.

Cross, E. S., Liepelt, R., Hamilton, A. F. de C., Parkinson, J., Ramsey, R., Stadler, W., & Prinz, W. (2012). Robotic movement preferentially engages the action observation network. *Human Brain Mapping, 33*(9), 2238–2254.

Cross, E. S., Stadler, W., Parkinson, J., Schütz-Bosbach, S., & Prinz, W. (2011). The influence of visual training on predicting complex action sequences. *Human Brain Mapping*. doi: 10.1002/hbm.21450

D'Esposito, M., Deouell, L. Y., & Gazzaley, A. H. (2003). Alterations in the BOLD fMRI signal with ageing and disease: A challenge for neuroimaging. *Nature Reviews Neuroscience, 4*(11), 863-872.

Davis, S. W., Dennis, N. A., Daselaar, S. M., Fleck, M. S., & Cabeza, R. (2008). Que PASA? The posterior-anterior shift in aging. *Cerebral Cortex, 18*(5), 1201-1209.

Davis, S. W., Kragel, J. E., Madden, D. J., & Cabeza, R. (2012). The architecture of cross-hemispheric communication in the aging brain: Linking behavior to functional and structural connectivity. *Cerebral Cortex, 22*(1), 232-242.

De Gardelle, V., Waszczuk, M., Egner, T., & Summerfield, C. (2012). Concurrent repetition enhancement and suppression responses in Extrastriate Visual Cortex. *Cerebral Cortex*. doi: 10.1093/cercor/bhs211

De Vignemont, F., & Haggard, P. (2008). Action observation and execution: What is shared? *Social Neuroscience, 3*(3), 421-433.

Decety, J. (2002). Is there such a thing as functional equivalence between imagined, observed, and executed action? In A. N. Meltzoff & W. Prinz (Eds.), *The imitative mind: development, evolution, and brain bases* (pp. 291-310). Cambridge, UK: Cambridge University Press.

Den Ouden, H. E. M., Daunizeau, J., Roiser, J., Friston, K. J., & Stephan, K. E. (2010). Striatal prediction error modulates cortical coupling. *Journal of Neuroscience, 30*(9), 3210-3219.

Dennis, N. A., & Cabeza, R. (2008). Neuroimaging of healthy cognitive aging. In F. I. M. Craik & T. A. Salthouse (Eds.), *The handbook of aging and cognition* (3rd ed., pp. 1-54). New York: Psychology Press.

Dennis, N. A., & Cabeza, R. (2011). Age-related dedifferentiation of learning systems: An fMRI study of implicit and explicit learning. *Neurobiology of Aging, 32*(12), 2318.e2317-2330.

Diersch, N., Cross, E. S., Stadler, W., Schütz-Bosbach, S., & Rieger, M. (2012). Representing others' actions: the role of expertise in the aging mind. *Psychological Research, 76*(4), 525-541.

Diersch, N., Mueller, K., Cross, E. S., Stadler, W., Rieger, M., & Schütz-Bosbach, S. (submitted). Action prediction in younger versus older adults: Neural correlates of motor familiarity. *PLOS ONE*.

Dinstein, I., Gardner, J. L., Jazayeri, M., & Heeger, D. J. (2008). Executed and observed movements have different distributed representations in human aIPS. *Journal of Neuroscience, 28*(44), 11231-11239.

Egner, T., Monti, J. M., & Summerfield, C. (2010). Expectation and surprise determine neural population responses in the ventral visual stream. *Journal of Neuroscience, 30*(49), 16601-16608.

Eickhoff, S. B., Stephan, K. E., Mohlberg, H., Grefkes, C., Fink, G. R., Amunts, K., & Zilles, K. (2005). A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *Neuroimage, 25*(4), 1325-1335.

Elliott, R., Dolan, R. J., & Frith, C. D. (2000). Dissociable functions in the medial and lateral orbitofrontal cortex: Evidence from human neuroimaging studies. *Cerebral Cortex, 10*(3), 308-317.

Erickson, K. I., Colcombe, S. J., Wadhwa, R., Bherer, L., Peterson, M. S., Scalf, P. E., . . . Kramer, A. F. (2007). Training-induced plasticity in older adults: Effects of training on hemispheric asymmetry. *Neurobiology of Aging, 28*(2), 272-283.

Erickson, K. I., Voss, M. W., Prakash, R. S., Basak, C., Szabo, A., Chaddock, L., . . . Kramer, A. F. (2011). Exercise training increases size of hippocampus and improves memory. *Proceedings of the National Academy of Sciences of the United States of America, 108*(7), 3017-3022.

Farrow, D., & Abernethy, B. (2003). Do expertise and the degree of perception - action coupling affect natural anticipatory performance? *Perception, 32*(9), 1127-1139.

Fjell, A. M., & Walhovd, K. B. (2010). Structural brain changes in aging: Courses, causes and cognitive consequences. *Reviews in the Neurosciences, 21*(3), 187-221.

Flanagan, J. R., & Johansson, R. S. (2003). Action plans used in action observation. *Nature, 424*(6950), 769-771.

Fogassi, L., Ferrari, P. F., Gesierich, B., Rozzi, S., Chersi, F., & Rizzolatti, G. (2005). Parietal lobe: From action organization to intention understanding. *Science, 308*(5722), 662-667.

Folstein, M. F., Folstein, S. E., & McHugh, P. R. (1975). "Mini-mental state": A practical method for grading the cognitive state of patients for the clinician. *Journal of Psychiatric Research, 12*(3), 189-198.

Friston, K. J. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society B: Biological Sciences, 360*(1456), 815-836.

Friston, K. J., Shiner, T., Fitzgerald, T., Galea, J. M., Adams, R., Brown, H., . . . Bestmann, S. (2012). Dopamine, affordance and active inference. *PLOS Computational Biology, 8*, 1. e1002327. doi: 10.1371/journal.pcbi.1002327

Friston, K., & Kiebel, S. (2009). Predictive coding under the free-energy principle. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*(1521), 1211-1221.

Friston, K., Mattout, J., & Kilner, J. (2011). Action understanding and active inference. *Biological Cybernetics, 104*(1), 137-160.

Gabbard, C., Caçola, P., & Cordova, A. (2011). Is there an advanced aging effect on the ability to mentally represent action? *Archives of Gerontology and Geriatrics, 53*(2), 206-209.

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain, 119*, 593-609.

Gazzaley, A., Cooney, J. W., Rissman, J., & D'Esposito, M. (2005). Top-down suppression deficit underlies working memory impairment in normal aging. *Nature Neuroscience, 8*(10), 1298-1300.

Gazzaley, A. H., & D'Esposito, M. (2005). BOLD functional MRI and cognitive aging. In R. Cabeza, L. Nyberg & D. C. Park (Eds.), *Cognitive neuroscience of aging: Linking cognitive and cerebral aging* (pp. 107-131). New York, NY: Oxford University Press.

Gescheider, G. A. (1997). The classical psychophysical methods. In G. A. Gescheider (Ed.), *Psychophysics: The fundamentals* (3rd ed., pp. 45–72). Mahwah, NJ: Lawrence Erlbaum Associates.

Gillmeister, H., Catmur, C., Liepelt, R., Brass, M., & Heyes, C. (2008). Experience-based priming of body parts: A study of action imitation. *Brain Research, 1217*, 157-170.

Godde, B., & Voelcker-Rehage, C. (2010). More automation and less cognitive control of imagined walking movements in high- versus low-fit older adults. *Frontiers in Aging Neuroscience, 2*, 139. 1-13. doi: 10.3389/fnagi.2010.00139

Goh, J. O., Suzuki, A., & Park, D. C. (2010). Reduced neural selectivity increases fMRI adaptation with age during face discrimination. *Neuroimage, 51*(1), 336-344.

Grady, C. L. (2012). The cognitive neuroscience of ageing. *Nature Reviews Neuroscience, 13*(7), 491-505.

Grady, C. L., Charlton, R., He, Y., & Alain, C. (2011). Age differences in fMRI adaptation for sound identity and location. *Frontiers in Human Neuroscience*, 5, 24. 1-12. doi: 10.3389/fnhum.2011.00024

Graf, M., Reitzner, B., Corves, C., Casile, A., Giese, M., & Prinz, W. (2007). Predicting point-light actions in real-time. *Neuroimage, 36*(Supplement 2), T22-T32.

Grafton, S. T. (2009). Embodied cognition and the simulation of action to understand others. *Annals of the New York Academy of Sciences, 1156*(1), 97-117.

Graybiel, A. M. (2008). Habits, rituals, and the evaluative brain. *Annual Review of Neuroscience, 31*(1), 359-387.

Grèzes, J., & Decety, J. (2001). Functional anatomy of execution, mental simulation, observation, and verb generation of actions: A meta-analysis. *Human Brain Mapping, 12*(1), 1-19.

Grieve, S. M., Clark, C. R., Williams, L. M., Peduto, A. J., & Gordon, E. (2005). Preservation of limbic and paralimbic structures in aging. *Human Brain Mapping, 25*(4), 391-401.

Grossman, E., Donnelly, M., Price, R., Pickens, D., Morgan, V., Neighbor, G., & Blake, R. (2000). Brain areas involved in perception of biological motion. *Journal of Cognitive Neuroscience, 12*(5), 711-720.

Grush, R. (2004). The emulation theory of representation: Motor control, imagery, and perception. *Behavioral and Brain Sciences, 27*(03), 377-396.

Hahn, B., Ross, T. J., & Stein, E. A. (2007). Cingulate activation increases dynamically with response speed under stimulus unpredictability. *Cerebral Cortex, 17*(7), 1664-1671.

Healey, M. K., Campbell, K. L., & Hasher, L. (2008). Cognitive aging and increased distractibility: Costs and potential benefits. In W. S. Sossin, J.-C. Lacaille, V. F. Castellucci & S. Belleville (Eds.), *Progress in brain research* (Vol. 169, pp. 353-363). Amsterdam: Elsevier.

Henson, R. (2005). What can functional neuroimaging tell the experimental psychologist? *Quarterly Journal of Experimental Psychology. A, Human Experimental Psychology, 58*(2), 193-233.

Heuninckx, S., Wenderoth, N., Debaere, F., Peeters, R., & Swinnen, S. P. (2005). Neural basis of aging: The penetration of cognition into action control. *Journal of Neuroscience, 25*(29), 6787-6796.

Heuninckx, S., Wenderoth, N., & Swinnen, S. P. (2008). Systems neuroplasticity in the aging brain: Recruiting additional neural resources for successful motor performance in elderly persons. *Journal of Neuroscience, 28*(1), 91-99.

Heuninckx, S., Wenderoth, N., & Swinnen, S. P. (2010). Age-related reduction in the differential pathways involved in internal and external movement generation. *Neurobiology of Aging, 31*(2), 301-314.

Heyes, C. (2010). Where do mirror neurons come from? *Neuroscience & Biobehavioral Reviews, 34*(4), 575-583.

Heyes, C., Bird, G., Johnson, H., & Haggard, P. (2005). Experience modulates automatic imitation. *Cognitive Brain Research, 22*(2), 233-240.

Hickok, G. (2009). Eight problems for the mirror neuron theory of action understanding in monkeys and humans. *Journal of Cognitive Neuroscience, 21*(7), 1229-1243.

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), 58-65.

Hommel, B., Muesseler, J., Aschersleben, G., & Prinz, W. (2001). The Theory of Event Coding (TEC): A framework for perception and action planning. *Behavioral and Brain Sciences, 24*(05), 849-878.

Horton, S., Baker, J., & Schorer, J. (2008). Expertise and aging: Maintaining skills through the lifespan. *European Review of Aging and Physical Activity, 5*(2), 89-96.

Hultsch, D. F., MacDonald, S. W. S., Hunter, M. A., Maitland, S. B., & Dixon, R. A. (2002). Sampling and generalisability in developmental research: Comparison of random and convenience samples of older adults. *International Journal of Behavioral Development, 26*(4), 345-359.

Hurley, S. (2008). The shared circuits model (SCM): How control, mirroring, and simulation can enable imitation, deliberation, and mindreading. *Behavioral and Brain Sciences, 31*(1), 1-22.

Iacoboni, M., & Dapretto, M. (2006). The mirror neuron system and the consequences of its dysfunction. *Nature Reviews Neuroscience, 7*(12), 942-951.

Iacoboni, M., Koski, L. M., Brass, M., Bekkering, H., Woods, R. P., Dubeau, M.-C., . . . Rizzolatti, G. (2001). Reafferent copies of imitated actions in the right superior temporal cortex. *Proceedings of the National Academy of Sciences of the United States of America, 98*(24), 13995-13999.

Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J. C., & Rizzolatti, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *PLOS Biology, 3*, 3. e79. doi: 10.1371/journal.pbio.0030079

Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science, 286*(5449), 2526-2528.

Jacob, P., & Jeannerod, M. (2005). The motor theory of social cognition: A critique. *Trends in Cognitive Sciences, 9*(1), 21-25.

Jacobs, A., & Shiffrar, M. (2005). Walking perception by walking observers. *Journal of Experimental Psychology - Human Perception and Performance, 31*(1), 157-169.

Jeannerod, M. (2006). *Motor cognition: What actions tell the self*: Oxford University Press, USA.

Jeannerod, M. (2001). Neural simulation of action: A unifying mechanism for motor cognition. *Neuroimage, 14*(1), 103-109.

Johnson, A., van der Meer, M. A. A., & Redish, A. D. (2007). Integrating hippocampus and striatum in decision-making. *Current Opinion in Neurobiology, 17*(6), 692-697.

Kannurpatti, S. S., Motes, M. A., Rypma, B., & Biswal, B. B. (2010). Neural and vascular variability and the fMRI-BOLD response in normal aging. *Magnetic Resonance Imaging, 28*(4), 466-476.

Kattenstroth, J. C., Kalisch, T., Kolankowska, I., & Dinse, H. R. (2011). Balance, sensorimotor, and cognitive performance in long-year expert senior ballroom dancers. *Journal of Aging Research*, 176709. 1-10. doi: 10.4061/2011/176709

Kattenstroth, J. C., Kolankowska, I., Kalisch, T., & Dinse, H. R. (2010). Superior sensory, motor, and cognitive performance in elderly individuals with multi-year dancing activities. *Frontiers in Aging Neuroscience, 2*, 31. 1-9. doi: 10.3389/fnagi.2010.00031

Ketcham, C. J., Seidler, R. D., Van Gemmert, A. W. A., & Stelmach, G. E. (2002). Age-related kinematic differences as influenced by task difficulty, target size, and movement amplitude. *Journals of Gerontology - Series B Psychological Sciences and Social Sciences, 57*(1), P54-P64.

Keysers, C., & Gazzola, V. (2010). Social neuroscience: Mirror neurons recorded in humans. *Current Biology, 20*(8), R353-R354.

Keysers, C., & Perrett, D. I. (2004). Demystifying social cognition: A hebbian perspective. *Trends in Cognitive Sciences, 8*(11), 501-507.

Kilner, J. M., Friston, K. J., & Frith, C. D. (2007a). The mirror-neuron system: A Bayesian perspective. *Neuroreport, 18*(6), 619-623.

Kilner, J. M., Friston, K. J., & Frith, C. D. (2007b). Predictive coding: An account of the mirror neuron system. *Cognitive Processing, 8*(3), 159-166.

Kilner, J. M., Neal, A., Weiskopf, N., Friston, K. J., & Frith, C. D. (2009). Evidence of mirror neurons in human inferior frontal gyrus. *Journal of Neuroscience, 29*(32), 10153-10159.

Kilner, J. M., Vargas, C., Duval, S., Blakemore, S.-J., & Sirigu, A. (2004). Motor activation prior to observation of a predicted movement. *Nature Neuroscience, 7*(12), 1299-1301.

Kohler, E., Keysers, C., Umilta, M. A., Fogassi, L., Gallese, V., & Rizzolatti, G. (2002). Hearing sounds, understanding actions: Action representation in mirror neurons. *Science, 297*(5582), 846-848.

Kokal, I., & Keysers, C. (2010). Granger causality mapping during joint actions reveals evidence for forward models that could overcome sensory-motor delays. *PLOS ONE,* 5, 10. e13507. doi: 10.1371/journal.pone.0013507

Kosslyn, S. M., & Thompson, W. L. (2003). When is early visual cortex activated during visual mental imagery? *Psychological Bulletin, 129*(5), 723-746.

Kramer, A. F. (1999). Ageing, fitness and neurocognitive function. *Nature, 400*, 418-419.

Kramer, A. F., Bherer, L., Colcombe, S. J., Dong, W., & Greenough, W. T. (2004). Environmental influences on cognitive and brain plasticity during aging. *Journals of Gerontology Series A: Biological Sciences and Medical Sciences, 59*(9), 940-957.

Krampe, R. T. (2002). Aging, expertise and fine motor movement. *Neuroscience and Biobehavioral Reviews, 26*(7), 769-776.

Krampe, R. T., & Charness, N. (2006). Aging and Expertise. In K. A. Ericsson, N. Charness, P. J. Feltovich & R. R. Hoffman (Eds.), *The cambridge handbook of expertise and expert performance* (pp. 723-742). New York, NY: Cambridge University Press.

Krampe, R. T., & Ericsson, K. A. (1996). Maintaining excellence: Deliberate practice and elite performance in young and older pianists. *Journal of Experimental Psychology: General, 125*(4), 331-359.

Langan, J., Peltier, S., Bo, J., Fling, B. W., Welsh, R. C., & Seidler, R. D. (2010). Functional implications of age differences in motor system connectivity. *Frontiers in Systems Neuroscience, 4*, 17. 1-11. doi: 10.3389/fnsys.2010.00017

Lee, Y., Grady, C. L., Habak, C., Wilson, H. R., & Moscovitch, M. (2011). Face processing changes in normal aging revealed by fMRI adaptation. *Journal of Cognitive Neuroscience, 23*(11), 3433-3447.

Léonard, G., & Tremblay, F. (2007). Corticomotor facilitation associated with observation, imagery and imitation of hand actions: A comparative study in young and old adults. *Experimental Brain Research, 177*(2), 167-175.

Leventhal, A. G., Wang, Y., Pu, M., Zhou, Y., & Ma, Y. (2003). GABA and its agonists improved visual cortical function in senescent monkeys. *Science, 300*(5620), 812-815.

Li, K. Z. H., Lindenberger, U., Freund, A. M., & Baltes, P. B. (2001). Walking while memorizing: Age-related differences in compensatory behavior. *Psychological Science, 12*(3), 230-237.

Li, S.-C., & Lindenberger, U. (1999). Cross-level unification: A computational exploration of the link between deterioration of neurotransmitter systems and dedifferentiation of cognitive abilities in old age. In L.-G. Nilsson & H. J. Markowitsch (Eds.), *Cognitive neuroscience of memory* (pp. 103-146). Seattle, WA: Hogrefe & Huber.

Liew, S.-L., Han, S., & Aziz-Zadeh, L. (2011). Familiarity modulates mirror neuron and mentalizing regions during intention understanding. *Human Brain Mapping, 32*(11), 1986-1997.

Lindenberger, U., & Baltes, P. B. (1994). Sensory functioning and intelligence in old age: A strong connection. *Psychology and Aging, 9*(3), 339-355.

Lindenberger, U., Gilberg, R., Little, T. D., Nuthmann, R., Pötter, U., & Baltes, P. B. (1999). Sample selectivity and generalizability of the results of the Berlin Aging Study. In P. B. Baltes & K. U. Mayer (Eds.), *The Berlin Aging Study: Aging from 70 to 100* (pp. 56-82). Cambridge: Cambridge University Press.

Lingnau, A., Gesierich, B., & Caramazza, A. (2009). Asymmetric fMRI adaptation reveals no evidence for mirror neurons in humans. *Proceedings of the National Academy of Sciences of the United States of America, 106*(24), 9925-9930.

Logan, J. M., Sanders, A. L., Snyder, A. Z., Morris, J. C., & Buckner, R. L. (2002). Under-recruitment and nonselective recruitment: Dissociable neural mechanisms associated with aging. *Neuron, 33*(5), 827-840.

Lustig, C. (2003). Grandfather's clock: Attention and interval timing in older adults. In W. H. Meck (Ed.), *Functional and neural mechanisms of interval timing* (pp. 261–293). Boca Raton: CRC Press.

Lustig, C. , Hasher, L. , & Zacks, R. T. (2007). Inhibitory decit theory: Recent developments in a "new view". In D. S. Gorfein & C. M. MacLeod (Eds.), *The place of inhibition in cognition* (pp. 145-162). Washington, DC: American Psychological Association.

Madden, D. J., Bennett, I. J., Burzynska, A., Potter, G. G., Chen, N.-K., & Song, A W. (2012). Diffusion tensor imaging of cerebral white matter integrity in cognitive aging. *Biochimica et Biophysica Acta, 1822*(3), 386-400.

Mai, J. K., Paxinos, G., & Voss, T. (2008). *Atlas of the human brain* (3rd. ed.). Amsterdam: Elsevier Academic Press.

Mann, D. T. Y., Williams, A. M., Ward, P., & Janelle, C. M. (2007). Perceptual-cognitive expertise in sport: A meta-analysis. *Journal of Sport and Exercise Psychology, 29*(4), 457-478.

Marks, B. L., Madden, D. J., Bucur, B., Provenzale, J. M., White, L. E., Cabeza, R., & Huettel, S. A. (2007). Role of aerobic fitness and aging on cerebral white matter integrity. *Annals of the New York Academy of Sciences, 1097*, 171-174.

Martin, V. C., Schacter, D. L., Corballis, M. C., & Addis, D. R. (2011). A role for the hippocampus in encoding simulations of future events. *Proceedings of the National Academy of Sciences of the United States of America, 108*(33), 13858-13863.

Maryott, J., & Sekuler, R. (2009). Age-related changes in imitating sequences of observed movements. *Psychology and Aging, 24*(2), 476-486.

Mattay, V. S., Fera, F., Tessitore, A., Hariri, A. R., Das, S., Callicott, J. H., & Weinberger, D. R. (2002). Neurophysiological correlates of age-related changes in human motor function. *Neurology, 58*(4), 630-635.

McHorney, C. A., Ware, J. E., & Raczek, A. E. (1993). The MOS 36-item short-form health survey (SF-36): II. Psychometric and clinical tests of validity in measuring physical and mental health constructs. *Medical Care, 31*(3), 247-263.

Miall, R. C. (2003). Connecting mirror neurons and forward models. *Neuroreport, 14*(17), 2135-2137.

Miall, R. C., & Wolpert, D. M. (1996). Forward models for physiological motor control. *Neural Networks, 9*(8), 1265-1279.

Molenberghs, P., Cunnington, R., & Mattingley, J. B. (2012). Brain regions with mirror properties: A meta-analysis of 125 human fMRI studies. *Neuroscience and Biobehavioral Reviews, 36*(1), 341-349.

Mugler, J. P., & Brookeman, J. R. (1990). Three-dimensional magnetization-prepared rapid gradient-echo imaging (3D MP RAGE). *Magnetic Resonance in Medicine, 15*(1), 152-157.

Mukamel, R., Ekstrom, A. D., Kaplan, J., Iacoboni, M., & Fried, I. (2010). Single-neuron responses in humans during execution and observation of actions. *Current Biology, 20*(8), 750-756.

Mulder, T., Hochstenbach, J. B. H., van Heuvelen, M. J. G., & den Otter, A. R. (2007). Motor imagery: The relation between age and imagery capacity. *Human Movement Science, 26*(2), 203-211.

Müller, S., & Abernethy, B. (2006). Batting with occluded vision: An in situ examination of the information pick-up and interceptive skills of high- and low-skilled cricket batsmen. *Journal of Science and Medicine in Sport, 9*(6), 446-458.

Müller, S., Abernethy, B., & Farrow, D. (2006). How do world-class cricket batsmen anticipate a bowler's intention? *Quarterly Journal of Experimental Psychology, 59*(12), 2162-2186.

Nedelko, V., Hassa, T., Hamzei, F., Weiller, C., Binkofski, F., Schoenfeld, M. A.l, . . . Dettmers, C. (2010). Age-independent activation in areas of the mirror neuron system during action observation and action imagery. A fMRI study. *Restorative Neurology and Neuroscience, 28*(6), 737-747.

Niedenthal, P. M., Barsalou, L. W., Winkielman, P., Krauth-Gruber, S., & Ric, F. (2005). Embodiment in attitudes, social perception, and emotion. *Personality and Social Psychology Review, 9*(3), 184-211.

Norman, J. F., Payton, S. M., Long, J. R., & Hawkes, L. M. (2004). Aging and the perception of biological motion. *Psychology and Aging, 19*(1), 219-225.

O'Doherty, J. P. (2007). Lights, camembert, action! The role of human orbitofrontal cortex in encoding stimuli, rewards, and choices. *Annals of the New York Academy of Sciences, 1121*(1), 254-272.

O'Reilly, J. X., Mesulam, M. M., & Nobre, A. C. (2008). The cerebellum predicts the timing of perceptual events. *Journal of Neuroscience, 28*(9), 2252-2260.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*(1), 97-113.

Olsson, C.-J., Jonsson, B., Larsson, A., & Nyberg, L. (2008). Motor representations and practice affect brain systems underlying imagery: An fMRI study of internal imagery in novices and active high jumpers. *The Open Neuroimaging Journal, 2*, 5-13.

Oosterhof, N. N., Wiggett, A. J., Diedrichsen, J., Tipper, S. P., & Downing, P. E. (2010). Surface-based information mapping reveals crossmodal vision–action representations in human parietal and occipitotemporal cortex. *Journal of Neurophysiology, 104*(2), 1077-1089.

Panzer, S., Gruetzmacher, N., Fries, U., Krueger, M., & Shea, C. H. (2011). Age-related effects in interlimb practice on coding complex movement sequences. *Human Movement Science, 30*(3), 459-474.

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), 299-320.

Park, D. C., Polk, T. A., Park, R., Minear, M., Savage, A., & Smith, M. R. (2004). Aging reduces neural specialization in ventral visual cortex. *Proceedings of the National Academy of Sciences of the United States of America, 101*(35), 13091-13095.

Park, D. C., & Reuter-Lorenz, P. A. (2009). The adaptive brain: Aging and neurocognitive scaffolding. *Annual Review of Psychology, 60*, 173-196.

Park, J., Carp, J., Kennedy, K. M., Rodrigue, K. M., Bischof, G. N., Huang, C. M., . . . Park, D. C. (2012). Neural broadening or neural attenuation? Investigating age-related dedifferentiation in the face network in a large lifespan sample. *Journal of Neuroscience, 32*(6), 2154-2158.

Parkinson, J., Springer, A., & Prinz, W. (2012). Before, during and after you disappear: Aspects of timing and dynamic updating of the real-time action simulation of human motions. *Psychological Research, 76*(4), 421-433.

Perrett, D. I., Xiao, D. K., Barraclough, N. E., Keysers, C., & Oram, M. W. (2009). Seeing the future: Natural image sequences produce "anticipatory" neuronal activity and bias perceptual report. *Quarterly Journal of Experimental Psychology, 62*(11), 2081-2104.

Personnier, P., Ballay, Y., & Papaxanthis, C. (2010). Mentally represented motor actions in normal aging: III. Electromyographic features of imagined arm movements. *Behavioural Brain Research, 206*(2), 184-191.

Personnier, P., Kubicki, A., Laroche, D., & Papaxanthis, C. (2010). Temporal features of imagined locomotion in normal aging. *Neuroscience Letters, 476*(3), 146-149.

Personnier, P., Paizis, C., Ballay, Y., & Papaxanthis, C. (2008). Mentally represented motor actions in normal aging: II. The influence of the gravito-inertial context on the duration of overt and covert arm movements. *Behavioural Brain Research, 186*(2), 273-283.

Pilz, K. S., Bennett, P. J., & Sekuler, A. B. (2010). Effects of aging on biological motion discrimination. *Vision Research, 50*(2), 211-219.

Pinto, J. G. A., Hornby, K. R., Jones, D. G., & Murphy, K. M. (2010). Developmental changes in GABAergic mechanisms in human visual cortex across the lifespan. *Frontiers in Cellular Neuroscience, 4*, 16. 1-12. doi: 10.3389/fncel.2010.00016

Postuma, R. B., & Dagher, A. (2006). Basal ganglia functional connectivity based on a meta-analysis of 126 positron emission tomography and functional magnetic resonance imaging publications. *Cerebral Cortex, 16*(10), 1508-1521.

Press, C., Heyes, C., & Kilner, J. M. (2011). Learning to understand others' actions. *Biology Letters, 7*(3), 457-460.

Prinz, W. (1997). Perception and action planning. *European Journal of Cognitive Psychology, 9*(2), 129-154.

Prinz, W. (2005). An ideomotor approach to imitation. In S. Hurley & N. Chater (Eds.), *Perspectives on imitation: From neuroscience to social science - Volume 1: Mechanisms of imitation and imitation in animals* (pp. 141-156). Cambridge, MA: MIT Press.

Prinz, W. (2012). *Open Minds: The Social Making of agency and intentionality*. Cambridge, MA: MIT Press.

Prinz, W., & Rapinett, G. (2008). Filling the gap: Dynamic representation of occluded action. In F. Morganti, A. Carassa & G. Riva (Eds.), *Enacting intersubjectivity: A cognitive and social perspective on the study of interactions* (pp. 223-236). Amsterdam: IOS Press.

Puce, A., & Perrett, D. (2003). Electrophysiology and brain imaging of biological motion. *Philosophical Transactions of the Royal Society B: Biological Sciences, 358*(1431), 435-445.

Ramnani, N., & Miall, R. C. (2004). A system in the human brain for predicting the actions of others. *Nature Neuroscience, 7*(1), 85-90.

Raz, N. (2005). The aging brain observed in vivo: Differential changes and their modifiers. In R. Cabeza, L. Nyberg & D. C. Park (Eds.), *Cognitive neuroscience of aging: Linking cognitive and cerebral aging* (pp. 19-57). New York, NY: Oxford University Press.

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.

Raz, N., & Rodrigue, K. M. (2006). Differential aging of the brain: Patterns, cognitive correlates and modifiers. *Neuroscience and Biobehavioral Reviews, 30*(6), 730-748.

Reuter-Lorenz, P. A., Jonides, J., Smith, E. E., Hartley, A., Miller, A., Marshuetz, C., & Koeppe, R. A. (2000). Age differences in the frontal lateralization of verbal and spatial working memory revealed by PET. *Journal of Cognitive Neuroscience, 12*(1), 174-187.

Riediger, M., Li, S.-C., & Lindenberger, U. (2006). Selection, optimization, and compensation as developmental mechanisms of adaptive resource allocation: Review and preview. In J. E. Birren & K. W. Schaie (Eds.), *The handbook of the psychology of aging* (6th ed., pp. 289-313). San Diego, CA: Academic Press.

Rizzolatti , G. (2005). The mirror neuron system and its function in humans. *Anatomy and Embryology, 210*(5-6), 419-421.

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience, 27*, 169-192.

Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research, 3*(2), 131-141.

Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews Neuroscience, 2*(9), 661-670.

Rosano, C., Venkatraman, V. K., Guralnik, J., Newman, A. B., Glynn, N. W., Launer, L., . . . Aizenstein, H. (2010). Psychomotor speed and functional brain MRI 2 years after completing a physical activity treatment. *Journals of Gerontology Series A: Biological Sciences and Medical Sciences, 65*(6), 639-647.

Rosen, A. C., Prull, M. W., O'Hara, R., Race, E. A., Desmond, J. E., Glover, G. H., . . . Gabrieli, J. D. E. (2002). Variable effects of aging on frontal lobe contributions to memory. *Neuroreport, 13*(18), 2425-2428.

Roudaia, E., Bennett, P. J., Sekuler, A. B., & Pilz, K. S. (2010). Spatiotemporal properties of apparent motion perception and aging. *Journal of Vision, 10*(14), 1-15.

Saimpont, A., Malouin, F., Tousignant, B., & Jackson, P. L. (2012). The influence of body configuration on motor imagery of walking in younger and older adults. *Neuroscience, 222*, 49-57.

Saimpont, A., Mourey, F., Manckoundia, P., Pfitzenmeyer, P., & Pozzo, T. (2010). Aging affects the mental simulation/planning of the “rising from the floor” sequence. *Archives of Gerontology and Geriatrics, 51*(3), e41-e45.

Saimpont, A., Pozzo, T., & Papaxanthis, C. (2009). Aging affects the mental rotation of left and right hands. *PLOS ONE, 4*, 8. e6714. doi: 10.1371/journal.pone.0006714

Salthouse, T. A. (1996). The processing-speed theory of adult age differences in cognition. *Psychological Review, 103*(3), 403-428.

Salthouse, T. A. (2006). Mental exercise and mental aging: Evaluating the validity of the "Use it or lose It" hypothesis. *Perspectives on Psychological Science, 1*(1), 68-87.

Salthouse, T. A. (2009). When does age-related cognitive decline begin? *Neurobiology of Aging, 30*(4), 507-514.

Salthouse, T. A. (2011). Neuroanatomical substrates of age-related cognitive decline. *Psychological Bulletin, 137*(5), 753-784.

Sarlegna, F. R. (2006). Impairment of online control of reaching movements with aging: A double-step study. *Neuroscience Letters, 403*(3), 309-314.

Saxe, R., Xiao, D. K., Kovacs, G., Perrett, D. I., & Kanwisher, N. (2004). A region of right posterior superior temporal sulcus responds to observed intentional actions. *Neuropsychologia, 42*(11), 1435-1446.

Saygin, A. P., Chaminade, T., Ishiguro, H., Driver, J., & Frith, C. (2012). The thing that should not be: Predictive coding and the uncanny valley in perceiving human and humanoid robot actions. *Social Cognitive and Affective Neuroscience, 7*(4), 413-422.

Saygin, A. P., & Stadler, W. (2012). The role of appearance and motion in action prediction. *Psychological Research, 76*(4), 388-394.

Schacter, D. L., Addis, D. R., & Buckner, R. L. (2007). Remembering the past to imagine the future: The prospective brain. *Nature Reviews Neuroscience, 8*(9), 657-661.

Schacter, D. L., Gaesser, B., & Addis, D. R. (2012). Remembering the past and imagining the future in the elderly. *Gerontology*. doi: 10.1159/000342198

Schäfer, S., Huxhold, O., & Lindenberger, U. (2006). Healthy mind in healthy body? A review of sensorimotor-cognitive interdependencies in old age. *European Review of Aging and Physical Activity, 3*(2), 45-54.

Schieber, F. (2006). Vision and aging. In J. E. Birren & K. W. Schaie (Eds.), *The handbook of the psychology of aging* (6th ed., pp. 129-162). San Diego, CA: Academic Press.

Schiffer, A. M., Ahlheim, C., Ulrichs, K., & Schubotz, R. I. (2012). Neural changes when actions change: Adaptation of strong and weak expectations. *Human Brain Mapping*. doi: 10.1002/hbm.22023

Schiffer, A. M., Ahlheim, C., Wurm, M. F., & Schubotz, R. I. (2012). Surprised at all the entropy: Hippocampal, caudate and midbrain contributions to learning from prediction errors. *PLOS ONE, 7*, 5. e36445. doi: 10.1371/journal.pone.0036445

Schiffer, A. M., & Schubotz, R. I. (2011). Caudate nucleus signals for breaches of expectation in a movement observation paradigm. *Frontiers in Human Neuroscience, 5*, 38. 1-12. doi: 10.3389/fnhum.2011.00038

Schippers, M. B., & Keysers, C. (2011). Mapping the flow of information within the putative mirror neuron system during gesture observation. *Neuroimage, 57*(1), 37-44.

Schmahmann, J. D., & Pandya, D. N. (2006). *Fiber pathways of the brain*. New York, NY: Oxford University Press.

Schmolesky, M. T., Wang, Y., Pu, M., & Leventhal, A. G. (2000). Degradation of stimulus selectivity of visual cortical cells in senescent rhesus monkeys. *Nature Neuroscience, 3*(4), 384-390.

Schorer, J., & Baker, J. (2009). An exploratory study of aging and perceptual-motor expertise in handball goalkeepers. *Experimental Aging Research, 35*(1), 1-19.

Schott, N., & Munzert, J. (2007). Temporal accuracy of motor imagery in older women. *International Journal of Sport Psychology, 38*(3), 304-320.

Schubotz, R. I. (2007). Prediction of external events with our motor system: Towards a new framework. *Trends in Cognitive Sciences, 11*(5), 211-218.

Schultz, W. (2000). Multiple reward signals in the brain. *Nature Reviews Neuroscience, 1*(3), 199-207.

Schütz-Bosbach, S., & Prinz, W. (2007). Prospective coding in event representation. *Cognitive Processing, 8*(2), 93-102.

Searle, J. R. (1983). *Intentionality: An essay in the philosophy of mind*. Cambridge, UK: Cambridge University Press.

Sebanz, N., & Shiffrar, M. (2009). Detecting deception in a bluffing body: The role of expertise. *Psychonomic Bulletin & Review, 16*(1), 170-175.

Seidler, R. D., Bangert, A. S., Anguera, J. A., & Quinn-Walsh, C. M. (2007). Motor Control. In J. E. Birren (Ed.), *Encyclopedia of gerontology: Age, aging and the aged* (2nd ed., Vol. 2, pp. 228-235). New York: Elsevier.

Seidler, R. D., Bernard, J. A., Burutolu, T. B., Fling, B. W., Gordon, M. T., Gwin, J. T., . . . Lipps, D. B. (2010). Motor control and aging: Links to age-related brain structural, functional, and biochemical effects. *Neuroscience & Biobehavioral Reviews, 34*(5), 721-733.

Sherman, S. M., & Guillery, R. W. (2011). Distinct functions for direct and transthalamic corticocortical connections. *Journal of Neurophysiology, 106*(3), 1068-1077.

Skoura, X., Papaxanthis, C., Vinter, A., & Pozzo, T. (2005). Mentally represented motor actions in normal aging: I. Age effects on the temporal features of overt and covert execution of actions. *Behavioural Brain Research, 165*(2), 229-239.

Skoura, X., Personnier, P., Vinter, A., Pozzo, T., & Papaxanthis, C. (2008). Decline in motor prediction in elderly subjects: Right versus left arm differences in mentally simulated motor actions. *Cortex, 44*(9), 1271-1278.

Smith, Y., Raju, D., Nanda, B., Pare, J.-F., Galvan, A., & Wichmann, T. (2009). The thalamostriatal systems: Anatomical and functional organization in normal and parkinsonian states. *Brain Research Bulletin, 78*(2–3), 60-68.

Smith, Y., Surmeier, D. J., Redgrave, P., & Kimura, M. (2011). Thalamic contributions to basal ganglia-related behavioral switching and reinforcement. *Journal of Neuroscience, 31*(45), 16102-16106.

Snowden, R. J., & Kavanagh, E. (2006). Motion perception in the ageing visual system: Minimum motion, motion coherence, and speed discrimination thresholds. *Perception,* 35(1), 9-24.

Sparenberg, P., Springer, A., & Prinz, W. (2012). Predicting others' actions: Evidence for a constant time delay in action simulation. *Psychological Research, 76*(1), 41-49.

Sperry, R. W. (1950). Neural basis of the spontaneous optokinetic response produced by visual inversion. *Journal of Comparative and Physiological Psychology, 43*(6), 482-489.

Springer, A., Brandstädter, S., Liepelt, R., Birngruber, T., Giese, M., Mechsner, F., & Prinz, W. (2011). Motor execution affects action prediction. *Brain and Cognition, 76*(1), 26-36.

Stadler, W., Schubotz, R. I., von Cramon, D. Y., Springer, A., Graf, M., & Prinz, W. (2011). Predicting and memorizing observed action: Differential premotor cortex involvement. *Human Brain Mapping, 32*(5), 677-687.

Stadler, W., Springer, A., Parkinson, J., & Prinz, W. (2012). Movement kinematics affect action prediction: Comparing human to non-human point-light actions. *Psychological Research, 76*(4), 395-406.

Summerfield, C., Trittschuh, E. H., Monti, J. M., Mesulam, M. M., & Egner, T. (2008). Neural repetition suppression reflects fulfilled perceptual expectations. *Nature Neuroscience, 11*(9), 1004-1006.

Szabo, A. N., Bangert, A. S., Reuter-Lorenz, P. A., & Seidler, R. D. (2012). Physical activity is related to timing performance in older adults. *Aging, Neuropsychology, and Cognition*. doi: 10.1080/13825585.2012.715625

Thorn, C. A., & Graybiel, A. M. (2010). Pausing to regroup: Thalamic gating of cortico-basal ganglia networks. *Neuron, 67*(2), 175-178.

Turella, L., Pierno, A. C., Tubaldi, F., & Castiello, U. (2009). Mirror neurons in humans: Consisting or confounding evidence. *Brain & Language, 108*(1), 10-21.

Umilta, M. A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C., & Rizzolatti, G. (2001). I know what you are doing: A neurophysiological study. *Neuron, 31*(1), 155-165.

United Nations. (2010). *Population Ageing and Development 2009*. New York: United Nations.

Urgesi, C., Maieron, M., Avenanti, A., Tidoni, E., Fabbro, F., & Aglioti, S. M. (2010). Simulating the future of actions in the human corticospinal system. *Cerebral Cortex, 20*(11), 2511-2521.

Urgesi, C., Savonitto, M. M., Fabbro, F., & Aglioti, S. M. (2012). Long- and short-term plastic modeling of action prediction abilities in volleyball. *Psychological Research, 76*(4), 542-560.

Van Overwalle, F., & Baetens, K. (2009). Understanding others' actions and goals by mirror and mentalizing systems: A meta-analysis. *Neuroimage, 48*(3), 564-584.

Verrel, J., Lövdén, M., & Lindenberger, U. (2012). Normal aging reduces motor synergies in manual pointing. *Neurobiology of Aging, 33*(1), 200.e201-210.

Voelcker-Rehage, C., Godde, B., & Staudinger, U. M. (2011). Cardiovascular and coordination training differentially improve cognitive performance and neural processing in older adults. *Frontiers in Human Neuroscience, 5*, 26. 1-12. doi: 10.3389/fnhum.2011.00026

Vogt, S., Buccino, G., Wohlschlager, A. M., Canessa, N., Shah, N. J., Zilles, K., . . . Fink, G. R. (2007). Prefrontal involvement in imitation learning of hand actions: Effects of practice and expertise. *Neuroimage, 37*(4), 1371-1383.

Von Holst, E., & Mittelstaedt, H. (1950). Das Reafferenzprinzip. Wechselwirkungen zwischen Zentralnervensystem und Peripherie. *Die Naturwissenschaften, 37*, 464-476.

Walhovd, K. B., Westlye, L. T., Amlien, I., Espeseth, T., Reinvang, I., Raz, N., . . . Fjell, A. M. (2011). Consistent neuroanatomical age-related volume differences across multiple samples. *Neurobiology of Aging, 32*(5), 916-932.

Ward, N. S., & Frackowiak, R. S. J. (2003). Age-related changes in the neural correlates of motor performance. *Brain, 126*(4), 873-888.

Ware, J. E., Kosinski, M., Bayliss, M. S., McHorney, C. A., Rogers, W.H., & Raczek, A. E. (1995). Comparison of methods for the scoring and statistical analysis of SF-36 health profile and summary measures: Summary of results from the medical outcomes study. *Medical Care, 33*(4), AS264-AS279.

Ware, J. E., & Sherbourne, C. D. (1992). The MOS 36-item short-form health survey (SF-36): I. Conceptual framework and item selection. *Medical Care, 30*(6), 473-483.

Wechsler, D. (1997). *Wechsler Adult Intelligence Scale - Third Edition (WAIS-III)*. San Antonio, TX: The Psychological Corporation.

Weiler, J. A., Suchan, B., & Daum, I. (2010). When the future becomes the past: Differences in brain activation patterns for episodic memory and episodic future thinking. *Behavioural Brain Research, 212*(2), 196-203.

Wilkinson, D., & Halligan, P. (2004). The relevance of behavioural measures for functional-imaging studies of cognition. *Nature Reviews Neuroscience, 5*(1), 67-73.

Wilson, M. (2002). Six views of embodied cognition. *Psychonomic Bulletin & Review, 9*, 625-636.

Wilson, M., & Knoblich, G. (2005). The case for motor involvement in perceiving conspecifics. *Psychological Bulletin, 131*(3), 460-473.

Wolpert, D. M., Doya, K., & Kawato, M. (2003). A unifying computational framework for motor control and social interaction. *Philosophical Transactions of the Royal Society B: Biological Sciences, 358*(1431), 593-602.

Wolpert, D. M., & Flanagan, J. R. (2001). Motor prediction. *Current Biology, 11*(18), 729-732.

Wolpert, D. M., & Kawato, M. (1998). Multiple paired forward and inverse models for motor control. *Neural Networks, 11*(7-8), 1317-1329.

Wright, M. J., Bishop, D. T., Jackson, R. C., & Abernethy, B. (2011). Cortical fMRI activation to opponents' body kinematics in sport-related anticipation: Expert-novice differences with normal and point-light video. *Neuroscience Letters, 500*(3), 216-221.

Wu, T., Zang, Y., Wang, L., Long, X., Hallett, M., Chen, Y., . . . Chan, P. (2007). Aging influence on functional connectivity of the motor network in the resting state. *Neuroscience Letters, 422*(3), 164-168.

Yin, H. H., & Knowlton, B. J. (2006). The role of the basal ganglia in habit formation. *Nature Reviews Neuroscience, 7*(6), 464-476.

Zwergal, A., Linn, J., Xiong, G., Brandt, T., Strupp, M., & Jahn, K. (2012). Aging of human supraspinal locomotor and postural control in fMRI. *Neurobiology of Aging, 33*(6), 1073-1084.

APPENDIX

TABLE OF CONTENTS

APPENDIX A:
DEMOGRAPHIC AND GENERAL HEALTH QUESTIONNAIRE

[Questions used in only some of the experiments are identified accordingly.]

FRAGEBOGEN ZUM GESUNDHEITSZUSTAND

Im Folgenden werden verschiedene Informationen hinsichtlich Ihres allgemeinen Gesundheitszustandes und –verhaltens erfasst.

Diese Daten werden von uns in digitaler Form gespeichert und dienen ausschließlich dazu, geeignete Teilnehmer für unsere Studie zu finden. Wir garantieren Ihnen, dass wir Ihre Angaben streng vertraulich und anonym behandeln und diese so aufbewahren, dass kein unrechtmäßiger Zugang durch Dritte möglich ist.

Wenn Sie damit einverstanden sind, beginnen Sie bitte mit dem Ausfüllen des Fragebogens. Sie können Ihr Einverständnis jederzeit widerrufen. Wir danken Ihnen für Ihre Mitarbeit und die wahrheitsgetreue Beantwortung der Fragen.

Probanden-Code:________________________

Datum:_________________________________

Statistische Angaben

A1 Geburtsdatum: ________________

A2 Geschlecht: ☐ weiblich ☐ männlich

A3 Körpergröße: _________________ cm

A4 Gewicht: _________________ kg

A5a Welches ist Ihr höchster allgemein bildender Schulabschluss?

☐ studiere derzeit an einer Fachhochschule, Hochschule oder Universität
☐ abgeschlossenes Fachhochschul- oder Hochschulstudium
☐ allgemeine oder fachgebundene Hochschulreife/Abitur
(Gymnasium bzw. EOS, auch EOS mit Lehre)
☐ Fachhochschulreife, Abschluss einer Fachoberschule
☐ Realschulabschluss/Mittlere Reife
☐ Polytechnische Oberschule (POS) mit Abschluss 10. Klasse (vor 1965: 8. Klasse)
☐ Hauptschulabschluss/Volksschulabschluss
☐ Volks-/Hauptschule ohne Abschluss
☐ Sonderschulabschluss
☐ anderer Abschluss, und zwar:____
☐ kein Abschluss
☐ weiß nicht

A5b Bitte markieren Sie durch einen Kreis um die entsprechende Zahl die Anzahl der Jahre, die Ihr Bildungsweg insgesamt in Anspruch genommen hat, bevor Sie ins Berufsleben eingestiegen sind. Bitte beziehen Sie nur erfolgreich beendete Bildungswege ein.

(Wenn Sie beispielsweise nach 12 Schuljahren Abitur gemacht haben und danach ein 4jähriges Studium abgeschlossen haben, wäre die korrekte Antwort auf der vorgegebenen Skala 16 Jahre)

1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22+

Die folgenden Fragen beziehen sich auf Ihren **allgemeinen Gesundheitszustand**.

B1 Haben Sie gesundheitliche Probleme, Einschränkungen oder chronische Krankheiten?

☐ ja ☐ nein ☐ weiß nicht

B1a Wenn ja, welche?

z.B.
☐ erhöhter Blutdruck
☐ niedriger Blutdruck
☐ Herzinfarkt
☐ Herzrhythmusstörungen
☐ Anfallsleiden (Epilepsie)
☐ Hirngefäßkrankheiten (z.B. Schlaganfall)
☐ Bewusstlosigkeit/Schwindel
☐ Sehstörungen
☐ Muskel- oder Gelenkkrankheiten (Wirbelsäulenschäden, Rheuma)
☐ Schilddrüsenerkrankungen
☐ Diabetes
☐ Allergien
☐ Lungenerkrankungen (z.B. Asthma)
☐ Parkinson-Krankheit
☐ Altersdemenz (z.B. Alzheimer)
☐ Sonstige, und zwar:

____

____

B2 Wurde bei Ihnen in den letzten 5 Jahren eine Herz-, Kopf- oder Gefäßoperation durchgeführt?

☐ ja ☐ nein ☐ weiß nicht

B2a Wenn ja, welche?

____

____

____

B3 Haben Sie psychische Beschwerden, für die Ihnen ein Arzt/Psychologe eine Diagnose gestellt hat, oder wurden Sie in den letzten 5 Jahren wegen einer psychischen Beeinträchtigung, beispielsweise wegen einer Depression oder Angstzuständen, behandelt?

☐ ja ☐ nein ☐ weiß nicht

B3a Wenn ja, welche?

____
____
____

B4 Nehmen Sie Medikamente zur Behandlung psychischer Erkrankungen, wie Depressionen oder Angstzustände, zu sich (z.B. Antidepressiva, Neuroleptika, Beruhigungsmittel)?

☐ ja ☐ nein ☐ weiß nicht

B4a Wenn ja, welche?

____
____
____

B5 Nehmen Sie Medikamente wegen eines erhöhten Blutdrucks oder einer Herzerkrankung zu sich?

☐ ja ☐ nein ☐ weiß nicht

B5a Wenn ja, welche?

____
____
____

B6 Nehmen Sie andere Medikamente regelmäßig ein
(z.B. Tabletten, Spritzen, Zäpfchen)?

☐ ja ☐ nein ☐ weiß nicht

B6a Wenn ja, welche und wofür?

____
____
____

B7 Befinden Sie sich derzeit in ärztlicher Behandlung?

☐ ja ☐ nein ☐ weiß nicht

B7a Wenn ja, weswegen?

____

____

____

B8 Tragen Sie eine Brille oder Kontaktlinsen?

☐ ja ☐ nein

B8a Wie würden Sie momentan Ihre Sehkraft auf beiden Augen (mit Brille oder Kontaktlinsen, falls Sie eine/welche tragen) einschätzen?

☐ sehr gut
☐ gut
☐ mittelmäßig
☐ schlecht
☐ sehr schlecht

B9 Rauchen Sie?

☐ ja, täglich seit insgesamt _____ Jahren
☐ ja, nur gelegentlich seit insgesamt _____ Jahren
☐ nein, ich habe aufgehört nach insgesamt _____ Jahren als Raucher
☐ nein, ich habe noch nie geraucht

B9a Wenn Sie rauchen oder geraucht haben, wie viele Zigaretten sind/waren es durchschnittlich pro Tag?

☐ 1 bis 10 Zigaretten
☐ 11 bis 20 Zigaretten
☐ 21 bis 30 Zigaretten
☐ 31 bis 40 Zigaretten
☐ 41 und mehr Zigaretten

B10 Wie oft trinken Sie im Durchschnitt Alkohol?

☐ täglich
☐ mehrmals pro Woche
☐ einmal pro Woche
☐ seltener als einmal pro Woche
☐ nie

B10a Wie viele Gläser alkoholischer Getränke haben Sie insgesamt in den vergangenen sieben Tagen konsumiert? *(Bitte alle zusammenzählen!)*

(Ein Glas entspricht ungefähr ½ Liter Bier oder ¼ Liter Wein oder 0,2 cl Spirituosen oder eine ähnliche Menge eines Getränkes mit vergleichbarem Alkoholgehalt.)

☐ keines
☐ 1 bis 5 Gläser
☐ 6 bis 10 Gläser
☐ 11 bis 20 Gläser
☐ 21 bis 30 Gläser
☐ 31 bis 40 Gläser
☐ 41 und mehr Gläser

B11 Leiden Sie unter Klaustrophobie (Angst in engen oder geschlossenen Räumen)?

☐ ja ☐ nein

B12 Tragen Sie nicht entfernbaren Metallschmuck?

☐ ja ☐ nein

B12a Wenn ja, welchen?

____
____
____

B13 Tragen Sie Metall oder Elektronik am oder im Körper (z.B. Herzschrittmacher, Shunt, Gelenkprothese, Insulinpumpe, Metallclips oder -schrauben nach Operationen, Implantate oder Zahnspange)?

☐ ja ☐ nein

B13a Wenn ja, welche?

____
____
____

[Questions B11-B13a were used only in the second behavioral and fMRI experiment as a preliminary screening for MRI compatibility.]

Jetzt möchten wir noch erfahren, inwieweit Sie **sportlich aktiv** sind.

C1 Treiben Sie momentan regelmäßig Sport?

☐ ja ☐ nein

<u>Wenn ja:</u>

C1a Wie oft durchschnittlich?

☐ täglich
☐ mehrmals pro Woche
☐ einmal pro Woche
☐ 2 – 3 mal pro Monat
☐ einmal pro Monat
☐ seltener als einmal pro Monat

C1b Um welche Sportarten handelt es sich? (mehrere Antworten möglich)

☐ Fußball
☐ Basketball
☐ Volleyball
☐ Handball
☐ Hockey
☐ Tennis
☐ Tischtennis
☐ Badminton/Squash
☐ Leichtathletik
☐ Turnen
☐ Judo, Karate oder ähnliche Selbstverteidigungstechniken
☐ Segeln, Surfen, Kanu, Rudern
☐ Schwimmen/Wassergymnastik
☐ Tauchen
☐ Fitnesstraining/Krafttraining im Fitnessstudio
☐ Joggen/Nordic Walking
☐ Klettern
☐ Wandern
☐ Aerobic/Gymnastik
☐ Yoga oder ähnliche Entspannungstechniken
☐ Tanzen (z.B. Jazztanz), Ballett
☐ Inline-Skaten/Skateboarden
☐ Fahrradfahren/Mountainbiking
☐ Reiten
☐ Skifahren/Snowboarden
☐ Eislaufen/Eiskunstlauf
☐ Sonstige, und zwar: ____

____

Im Folgenden geht es speziell um die Sportarten, die Sie in der vorherigen Frage (C1b) aufgeführt haben. Bitte geben Sie nun für jede der genannten Sportarten an, in welchem Rahmen und seit wann Sie diese ausüben. Tragen Sie dafür zunächst die entsprechende Sportart in das dafür vorgegebene Feld ein.

Haben Sie insgesamt mehr als vier Sportarten angekreuzt, wählen Sie für die folgenden Fragen die vier Sportarten aus, die Sie am häufigsten und am längsten ausüben.

ACHTUNG: Ihre Erfahrungen mit der Sportart **Eislaufen/Eiskunstlauf** werden gesondert im Anschluss an die folgenden Fragen abgefragt. Bitte beziehen Sie sich daher bei Frage C1c bis C1f auf alle anderen Sportarten (außer Eislaufen/Eiskunstlauf), die Sie gegebenenfalls ausüben. *[Used only in the second behavioral and fMRI experiment]*

C1c **Sportart 1:______________________**

In welchem Rahmen üben Sie diese Sportart aus?

☐ regelmäßig in einem Verein/einer festen Gruppe
☐ regelmäßig in der Freizeit ohne festen Rahmen
☐ unregelmäßig in der Freizeit ohne festen Rahmen
☐ auf andere Art und Weise, und zwar:

____

____

____

Wie lang üben Sie diese Sportart bereits aus?

☐ 0 bis ½ Jahr
☐ mehr als ½ Jahr bis 2 Jahre
☐ mehr als 2 bis 5 Jahre
☐ mehr als 5 bis 10 Jahre
☐ mehr als 10 Jahre

C1d **Sportart 2:______________________**

In welchem Rahmen üben Sie diese Sportart aus?

☐ regelmäßig in einem Verein/einer festen Gruppe
☐ regelmäßig in der Freizeit ohne festen Rahmen
☐ unregelmäßig in der Freizeit ohne festen Rahmen
☐ auf andere Art und Weise, und zwar:

____

____

____

Wie lang üben Sie diese Sportart bereits aus?

☐ 0 bis ½ Jahr
☐ mehr als ½ Jahr bis 2 Jahre
☐ mehr als 2 bis 5 Jahre
☐ mehr als 5 bis 10 Jahre
☐ mehr als 10 Jahre

C1e **Sportart 3:_______________________**

In welchem Rahmen üben Sie diese Sportart aus?

☐ regelmäßig in einem Verein/einer festen Gruppe
☐ regelmäßig in der Freizeit ohne festen Rahmen
☐ unregelmäßig in der Freizeit ohne festen Rahmen
☐ auf andere Art und Weise, und zwar:

____
____
____

Wie lang üben Sie diese Sportart bereits aus?

☐ 0 bis ½ Jahr
☐ mehr als ½ Jahr bis 2 Jahre
☐ mehr als 2 bis 5 Jahre
☐ mehr als 5 bis 10 Jahre
☐ mehr als 10 Jahre

C1f **Sportart 4:_______________________**

In welchem Rahmen üben Sie diese Sportart aus?

☐ regelmäßig in einem Verein/einer festen Gruppe
☐ regelmäßig in der Freizeit ohne festen Rahmen
☐ unregelmäßig in der Freizeit ohne festen Rahmen
☐ auf andere Art und Weise, und zwar:

____
____
____

Wie lang üben Sie diese Sportart bereits aus?

☐ 0 bis ½ Jahr
☐ mehr als ½ Jahr bis 2 Jahre
☐ mehr als 2 bis 5 Jahre
☐ mehr als 5 bis 10 Jahre
☐ mehr als 10 Jahre

Ihre Erfahrungen mit der Sportart **Eislaufen/Eiskunstlauf**:
[Used only in the second behavioral and fMRI experiment]

D1 Verfolgen Sie Eiskunstlauf (z.B. Wettkämpfe) während der Saison aufmerksam im Fernsehen oder als Zuschauer/Teilnehmer vor Ort?

☐ ja ☐ nein

Wenn ja:

D1a Wie oft durchschnittlich?

☐ täglich
☐ mehrmals pro Woche
☐ einmal pro Woche
☐ 2 – 3 mal pro Monat
☐ einmal pro Monat
☐ seltener als einmal pro Monat

D2 Üben Sie diese Sportart momentan aktiv aus?

☐ ja ☐ nein

Wenn ja:

D2a In welchem Rahmen üben Sie die Sportart aus?

☐ regelmäßig als Leistungssport in einem Verein
☐ regelmäßig als Freizeit-/Breitensport in einem Verein
☐ regelmäßig in der Freizeit ohne festen Rahmen
☐ unregelmäßig in der Freizeit ohne festen Rahmen
☐ auf andere Art und Weise, und zwar:

____
____
____

D2b Wie oft durchschnittlich?

☐ täglich
☐ mehrmals pro Woche
☐ einmal pro Woche
☐ 2 – 3 mal pro Monat
☐ einmal pro Monat
☐ seltener als einmal pro Monat

Wenn Sie eine der drei ersten Antwortmöglichkeiten angekreuzt haben:

D2c Wie vielen Stunden entspricht dies insgesamt pro Woche?

____ Stunden

D2d Wie lang üben Sie diese Sportart bereits aus?

Seit ____ Jahren

<u>Wenn Sie diese Sportart momentan **nicht** ausüben:</u>

D3 Haben Sie diese Sportart <u>früher</u> einmal aktiv ausgeübt?

☐ ja ☐ nein

<u>Wenn ja:</u>

D3a In welchem Rahmen übten Sie damals die Sportart aus?

☐ regelmäßig als Leistungssport in einem Verein
☐ regelmäßig als Freizeit-/Breitensport in einem Verein
☐ regelmäßig in der Freizeit ohne festen Rahmen
☐ unregelmäßig in der Freizeit ohne festen Rahmen
☐ auf andere Art und Weise, und zwar:

____
____
____

D3b Wie oft durchschnittlich?

☐ täglich
☐ mehrmals pro Woche
☐ einmal pro Woche
☐ 2 – 3 mal pro Monat
☐ einmal pro Monat
☐ seltener als einmal pro Monat

<u>Wenn Sie eine der drei ersten Antwortmöglichkeiten angekreuzt haben:</u>

D3c Wie vielen Stunden entsprach dies insgesamt pro Woche?

____ Stunden

D3d Wie lang übten Sie den Sport damals ohne große Unterbrechungen aus?

____ Jahre

D3e In welchem Alter haben Sie mit dem Sport aufgehört?

Im Alter von ____ Jahren

D3f Sind Sie auf eine andere Art und Weise in dem Bereich noch aktiv?

☐ ja ☐ nein

Wenn ja:

D3g Auf welche Art und Weise?

☐ Trainer
☐ Übungsleiter
☐ Preisrichter
☐ Funktionär
☐ Verbands-/Vereinsmitglied
☐ auf andere Art und Weise, und zwar:

____
____
____

Wenn Sie Eiskunstlauf als **Leistungssport** betreiben oder betrieben haben:

D4a In welcher(n) Disziplin(en) sind/waren Sie aktiv?

☐ Einzellauf
☐ Paarlauf
☐ Eistanz
☐ Synchroneiskunstlauf

D4b Nehmen/Nahmen Sie an nationalen/internationalen Wettbewerben (z.B. Meisterschaften, Olympia) teil?

☐ ja ☐ nein

D4c In welcher Kürklasse sind Sie momentan bzw. haben Sie in Ihrer Karriere als Leistungssportler maximal erreicht?

Kürklasse_____

D4d In welcher Leistungsklasse sind Sie momentan bzw. haben Sie in Ihrer Karriere als Leistungssportler maximal erreicht?

☐ Meister-/Seniorenklasse
☐ Juniorenklasse
☐ Nachwuchsklasse

Vielen herzlichen Dank für Ihre Mitarbeit!

APPENDIX B:
QUESTIONS ABOUT THE EXPERIENCE WITH THE OBSERVED ACTIONS

BEHAVIORAL EXPERIMENT 1

1.a Wie oft üben Sie **anstrengende Tätigkeiten**, z.B. schnell laufen, schwere Gegenstände heben, anstrengenden Sport treiben, aus?

täglich	mehrmals wöchentlich	einmal pro Woche	weniger als einmal pro Woche	nie
(1)	**(2)**	**(3)**	**(4)**	**(5)**

1.b Wie oft üben Sie **mittelschwere Tätigkeiten**, z.B. einen Tisch verschieben, staubsaugen, kegeln, Golf spielen, aus?

täglich	mehrmals wöchentlich	einmal pro Woche	weniger als einmal pro Woche	nie
(1)	**(2)**	**(3)**	**(4)**	**(5)**

1.c Wie oft tragen oder heben Sie Einkaufstaschen?

täglich	mehrmals wöchentlich	einmal pro Woche	weniger als einmal pro Woche	nie
(1)	**(2)**	**(3)**	**(4)**	**(5)**

1.d Wie oft steigen Sie **mehrere** Treppenabsätze?

täglich	mehrmals wöchentlich	einmal pro Woche	weniger als einmal pro Woche	nie
(1)	**(2)**	**(3)**	**(4)**	**(5)**

1.e Wie oft steigen Sie **einen** Treppenabsatz?

täglich	mehrmals wöchentlich	einmal pro Woche	weniger als einmal pro Woche	nie
(1)	**(2)**	**(3)**	**(4)**	**(5)**

1.f Wie oft beugen/knien/bücken Sie sich?

täglich	mehrmals wöchentlich	einmal pro Woche	weniger als einmal pro Woche	nie
(1)	**(2)**	**(3)**	**(4)**	**(5)**

1.g Wie oft gehen Sie **mehr als 1 Kilometer** zu Fuß?

täglich	mehrmals wöchentlich	einmal pro Woche	weniger als einmal pro Woche	nie
(1)	**(2)**	**(3)**	**(4)**	**(5)**

1.h Wie oft gehen Sie **mehrere** Straßenkreuzungen weit zu Fuß?

täglich	mehrmals wöchentlich	einmal pro Woche	weniger als einmal pro Woche	nie
(1)	**(2)**	**(3)**	**(4)**	**(5)**

1.i Wie oft gehen Sie **eine** Straßenkreuzung weit zu Fuß?

täglich	mehrmals wöchentlich	einmal pro Woche	weniger als einmal pro Woche	nie
(1)	**(2)**	**(3)**	**(4)**	**(5)**

1.j Wie oft baden Sie sich oder ziehen sich an?

täglich	mehrmals wöchentlich	einmal pro Woche	weniger als einmal pro Woche	nie
(1)	**(2)**	**(3)**	**(4)**	**(5)**

BEHAVIORAL EXPERIMENT 2

1. Wie gut würden Sie Ihre Fähigkeit einschätzen, die gezeigten Handlungen **momentan** selbst auszuführen?

Eiskunstlauffilme

a. Sprünge

sehr gut	gut	mittelmäßig	schlecht	gar nicht
☐	☐	☐	☐	☐

b. Schrittfolgen

sehr gut	gut	mittelmäßig	schlecht	gar nicht
☐	☐	☐	☐	☐

c. Pirouetten

sehr gut	gut	mittelmäßig	schlecht	gar nicht
☐	☐	☐	☐	☐

Alltagsfilme

d. Laufvariationen

sehr gut	gut	mittelmäßig	schlecht	gar nicht
☐	☐	☐	☐	☐

e. Drehungen

sehr gut	gut	mittelmäßig	schlecht	gar nicht
☐	☐	☐	☐	☐

f. Sprünge

sehr gut	gut	mittelmäßig	schlecht	gar nicht
☐	☐	☐	☐	☐

2. Wie gut würden Sie Ihre Fähigkeit einschätzen, die gezeigten Handlungen **früher** selbst auszuführen?

Eiskunstlauffilme

a. Sprünge

sehr gut	gut	mittelmäßig	schlecht	gar nicht
☐	☐	☐	☐	☐

b. Schrittfolgen

sehr gut	gut	mittelmäßig	schlecht	gar nicht
☐	☐	☐	☐	☐

c. Pirouetten

sehr gut	gut	mittelmäßig	schlecht	gar nicht
☐	☐	☐	☐	☐

Alltagsfilme

d. Laufvariationen

sehr gut	gut	mittelmäßig	schlecht	gar nicht
☐	☐	☐	☐	☐

e. Drehungen

sehr gut	gut	mittelmäßig	schlecht	gar nicht
☐	☐	☐	☐	☐

f. Sprünge

sehr gut	gut	mittelmäßig	schlecht	gar nicht
☐	☐	☐	☐	☐

APPENDIX C:
SUPPORTING INFORMATION TABLES – CHAPTER III.

Table S.1. Effects of each predicted action category compared to baseline collapsed across the whole sample.

				MNI coordinates (mm)			*t* value	*p* value
Anatomical region	Putative functional name	BA	Cluster size	*x*	*y*	*z*	*df* = [1,33]	(corr.)
(A) Figure skating elements > Baseline								
L Middle Occipital Gyrus	V5/hMT+	19	2101	-45	-73	4	18.71	< 0.001
R Middle Temporal Gyrus	V5/hMT+	19		48	-70	1	13.06	
R Fusiform Gyrus		37		42	-46	-20	11.30	
R Superior Frontal Gyrus	SMA	6	4931	9	5	55	14.67	< 0.001
L Superior Frontal Gyrus	SMA	6		-6	8	52	13.99	
R Middle Frontal Gyrus/R Precentral Gyrus	PMd	6		42	-1	46	13.30	
R Superior Temporal Gyrus	TPJ	22	170	66	-34	16	8.56	0.008
R Midbrain			444	6	-25	-11	7.97	< 0.001
L Midbrain				-3	-25	-11	7.84	
R Putamen/R Globus Pallidum				18	8	1	5.36	

R Superior Parietal Lobule	SPL	7	318	30	-46	46	6.77	< 0.001
R Supramarginal Gyrus	IPL	7/40		36	-34	43	6.28	
R Postcentral Gyrus	S1	2		57	-22	40	3.98	
(B) Movement exercises > Baseline								
L Middle Occipital Gyrus	V5/hMT+	19	641	-45	-73	4	15.77	< 0.001
L Middle Occipital Gyrus	V2/V3	18		-12	-100	7	8.52	
R Superior Frontal Gyrus	SMA	6	7549	9	5	55	13.45	< 0.001
R Middle Temporal Gyrus	V5/hMT+	19		48	-70	-2	13.04	
L Superior Frontal Gyrus	SMA	6		-6	5	52	12.77	
R Midbrain			320	6	-25	-11	7.69	< 0.001
L Midbrain				-6	-25	-5	6.74	

Regions activated during the prediction of figure skating elements (**A**) and movement exercises (**B**) compared to baseline. Results are collapsed across the whole sample using a voxel-wise threshold of $p < 0.001$ and a minimum cluster size of 10 voxels. Only clusters are reported that reached cluster-corrected significance of $p < 0.05$, FWE corrected. Up to three local maxima are listed when a cluster has multiple peaks more than 8 mm apart. Abbreviations for brain regions: V5/hMT+, visual area V5/extrastriate visual cortex/middle temporal; SMA, supplementary motor area; PMd, dorsal premotor cortex; TPJ, temporoparietal junction; SPL, superior parietal lobule; IPL, inferior parietal lobule; S1, primary somatosensory area; V2, visual area V2/prestriate visual cortex; V3, visual area V3/extrastriate visual cortex.

Table S.2. Effects of predicted action category within each age group.

				MNI coordinates (mm)			*t* value	*p* value
Anatomical region	Putative functional name	BA	Cluster size	*x*	*y*	*z*		(corr.)
(A) Figure skating elements > Movement exercises								
Younger adults *df* = [1,17]								
R Lingual Gyrus	V2/V3	18	3223	12	-73	-8	10.44	< 0.001
Midline Calcerine Gyrus	V1	17		0	-88	-5	8.86	
R Cuneus	V3	18/19		12	-88	34	8.23	
Older adults *df* = [1,13]								
Midline Calcerine Gyrus	V1	17	1458	0	-91	-8	8.90	< 0.001
R Fusiform Gyrus		19		24	-64	-11	8.58	
R Lingual Gyrus	V1	17		15	-64	1	7.73	
L Medial Orbitofrontal Gyrus	OFC	32	88	-6	35	-8	5.92	0.019
R Medial Orbitofrontal Gyrus	OFC	32		6	38	-8	4.96	

(B) Movement exercises > Figure skating elements

<u>Younger adults *df* = [1,17]</u>								
R Middle Frontal Gyrus/R Precentral Gyrus	PMd	6	97	33	-7	49	6.67	0.026
R Supramarginal Gyrus	IPL	40	159	54	-28	37	6.35	0.003
R Inferior Parietal Lobule	IPL	40		45	-34	46	4.61	
R Superior Parietal Lobule	SPL	7	214	33	-49	58	6.15	0.001
R Superior Parietal Lobule	SPL	7		21	-58	58	5.22	
R Inferior Temporal Gyrus	V5/hMT+	19	167	48	-73	-5	5.96	0.002
R Middle Temporal Gyrus	MTG	39		45	-61	7	5.37	
R Inferior Frontal Gyrus (pars opercularis)	PMv	44	109	57	11	25	5.77	0.017
L Inferior Parietal Lobule	IPL	40	106	-39	-31	37	4.90	0.019
<u>Older adults *df* = [1,13]</u>								
R Postcentral Gyrus	S1	2	905	36	-37	52	10.49	< 0.001
R Intraparietal Sulcus	IPS	7/40		36	-46	52	9.74	
R Intraparietal Sulcus	IPS	7		33	-67	46	5.97	

L Intraparietal Sulcus	IPS	7/40	660	-39	-43	49	9.00	< 0.001
L Intraparietal Sulcus	IPS	7/2/40		-30	-40	43	8.05	
L Superior Parietal Lobule	SPL	5/2		-30	-49	61	7.14	
L Middle Temporal Gyrus	MTG	39	98	-48	-67	7	8.62	0.012
R Superior Temporal Gyrus	pSTS	22	370	63	-46	13	8.01	< 0.001
R Superior Temporal Gyrus	STG	42		60	-37	16	7.94	
R Middle Temporal Gyrus	pSTS	22		60	-46	4	7.29	
R Inferior Frontal Gyrus (pars opercularis)	PMv	44	322	45	8	16	6.69	< 0.001
R Inferior Frontal Gyrus (pars opercularis)	PMv	44		57	17	28	6.53	
R Precentral Gyrus	PMv	6		48	5	31	5.57	
L Superior Frontal Gyrus	SMA	6	158	-9	-1	52	6.65	0.001
L Superior Frontal Gyrus	PMd	6		-24	-10	55	5.83	
L Superior Frontal Gyrus	SMA	6		-9	-19	58	5.01	

Regions activated during the prediction of figure skating elements compared to movement exercises (**A**) and vice versa (**B**) in younger and older adults while controlling for figure skating expertise. Results were calculated using a voxel-wise threshold of $p < 0.001$ and a minimum cluster size of 10 voxels. Only clusters are reported that reached cluster-corrected significance of $p < 0.05$, FWE corrected. Up to three local maxima are listed when a cluster has multiple peaks more than 8 mm apart. Abbreviations for brain regions: V2, visual area V2/prestriate visual cortex; V3, visual area V3/extrastriate visual cortex; V1, visual area V1/striate visual cortex; OFC, orbitofrontal cortex; PMd, dorsal premotor cortex; IPL, inferior parietal lobule; SPL, superior parietal lobule; V5/hMT+, visual area V5/extrastriate visual cortex/middle temporal; MTG, middle temporal gyrus; PMv, ventral premotor cortex; S1, primary somatosensory area; IPS, intraparietal sulcus; pSTS, posterior superior temporal sulcus; STG, superior temporal gyrus; SMA, supplementary motor area.

Table S.3. Effects of predicted action category within each expertise group.

				MNI coordinates (mm)			*t* value	*p* value
Anatomical region	Putative functional name	BA	Cluster size	*x*	*y*	*z*		(corr.)
(A) Figure skating elements > Movement exercises								
Figure skating experts *df* = [1,8]								
R Cuneus	V1/V2	17/18	519	6	-88	16	17.37	< 0.001
R Calcerine Gyrus	V1/V2	17/18		3	-85	-5	14.98	
R Lingual Gyrus	V2	18		9	-79	-8	12.50	
L Caudate			188	-9	-7	16	8.76	< 0.001
L Thalamus				-6	-7	1	8.33	
L Putamen				-24	-16	13	8.15	
R Thalamus			63	9	-7	-2	7.02	0.038
R Thalamus				9	-1	4	6.06	
R Caudate				9	5	10	5.60	

Non-experts *df* = [1,22]								
R Parahippocampal/Lingual Gyrus		18	2944	27	-49	-2	9.67	< 0.001
R Lingual Gyrus	V3	18/19		15	-70	-8	9.37	
Midline Calcerine Gyrus	V1	17		0	-88	-5	8.86	
L Superior Frontal Gyrus	SFG	8	92	-12	41	52	5.60	0.033
L Superior Frontal Sulcus	SFS	8/9		-24	29	55	4.99	
L Superior Frontal Gyrus	SFG	8		-12	32	58	4.83	
(B) Movement exercises > Figure skating elements								
Figure skating experts *df* = [1,8]			------- No suprathreshold activations -------					
Non-experts *df* = [1,22]								
L Precuneus		7	1050	-9	-58	58	7.95	< 0.001
L Intraparietal Sulcus	IPS	7/40		-42	-40	49	7.10	
L Superior Frontal Gyrus	PMd	6		-24	-10	55	6.74	
R Supramarginal Gyrus	IPL	2/40	1043	48	-34	43	7.61	< 0.001
R Superior Parietal Lobule	SPL	7		36	-49	58	7.09	
R Postcentral Gyrus	S1	2		54	-25	43	6.68	

R Inferior Frontal Gyrus (pars opercularis)	PMv	44	714	51	8	28	7.49	< 0.001
R Middle Frontal Gyrus	PMd	6		36	-7	52	7.27	
R Superior Frontal Sulcus	SFS	6/8		24	11	43	4.28	
R Superior Temporal Gyrus	TPJ/STG	22/42	442	60	-34	16	6.76	< 0.001
R Middle Temporal Gyrus	MTG	37/39		57	-61	1	6.41	
R Middle Temporal Gyrus	pSTS	22		57	-40	7	5.96	
L Middle Occipital Gyrus	V5/hMT+	39	139	-45	-70	4	5.44	0.007
L Middle Occipital Gyrus	V5/hMT+	19		-45	-76	-2	5.32	
L Precentral Gyrus	PMv	6/44	107	-48	5	19	4.93	0.019
L Precentral Gyrus	PMv	6		-51	5	37	4.76	
L Inferior Frontal Gyrus (pars opercularis)	PMv	44		-54	8	10	3.94	

Regions activated during the prediction of figure skating elements compared to movement exercises (**A**) and vice versa (**B**) in figure skating experts and non-experts while controlling for age group. Results were calculated using a voxel-wise threshold of $p < 0.001$ and a minimum cluster size of 10 voxels. Only clusters are reported that reached cluster-corrected significance of $p < 0.05$, FWE corrected. Up to three local maxima are listed when a cluster has multiple peaks more than 8 mm apart. Abbreviations for brain regions: V1, visual area V1/striate visual cortex; V2, visual area V2/prestriate visual cortex; V3, visual area V3/extrastriate visual cortex; SFG, superior frontal gyrus; SFS, superior frontal sulcus; IPS, intraparietal sulcus; PMd, dorsal premotor cortex; IPL, inferior parietal lobule; SPL, superior parietal lobule; S1, primary somatosensory area; PMv, ventral premotor cortex; TPJ, temporoparietal junction; STG, superior temporal gyrus; MTG, middle temporal gyrus; pSTS, posterior superior temporal sulcus; V5/hMT+, visual area V5/extrastriate visual cortex/middle temporal.

APPENDIX D:
LIST OF ABBREVIATIONS

AC-PC	Anterior Commisure - Posterior Commisure
ANOVA	Analysis of Variance
AON	Action Observation Network
ASL	Associative Sequence Learning
BASE	Berlin Aging Study
BOLD Signal	Blood-Oxygen-Level-Dependent Signal
DCM	Dynamic Causal Modeling
DSST	Digit Symbol Substitution Test
DTI	Diffusion Tensor Imaging
EEG	Electroencephalography
EPI	Echo-Planar Imaging
fMRI	Functional Magnetic Resonance Imaging
FoV	Field of View
FWE	Family-Wise Error
GABA	Gamma-Aminobutyric Acid
HAROLD	Hemispheric Asymmetry Reduction in Old Adults
IFG	Inferior Frontal Gyrus
IPL	Inferior Parietal Lobule
IPS	Intraparietal Sulcus
JND	Just Noticeable Difference
MCS Score	Mental Component Summary Score of the SF-36
MMSE	Mini-Mental State Examination
MNI	Montreal Neurological Institute
MPRAGE	Magnetization-Prepared Rapid Gradient Echo
MVPA	Multi-Voxel Pattern Analysis
OFC	Orbitofrontal Cortex

PASA	Posterior-Anterior Shift in Aging
PCC	Posterior Cingulate Cortex
PCS Score	Physical Component Summary Score of the SF-36
PET	Positron Emission Tomography
PMC	Premotor Cortex
PMd	Dorsal Premotor Cortex
PMv	Ventral Premotor Cortex
PSE	Point of Subjective Equality
pSTS	Posterior Superior Temporal Sulcus
SF-36	MOS 36-Item Short Form Health Survey
SPL	Superior Parietal Lobule
SPM	Statistical Parametric Mapping
STAC	Scaffolding Theory of Aging and Cognition
STS	Superior Temporal Sulcus
SWT	Spot-the-Word Test
TE	Echo Time
TEC	Theory of Event Coding
TI	Inversion Time
TMS	Transcranial Magnetic Stimulation
TR	Repetition Time
V1	Visual Area V1/Striate Visual Cortex
V2	Visual Area V2/Prestriate Visual Cortex
V3	Visual Area V3/Extrastriate Visual Cortex
V5/hMT+	Visual Area V5/Extrastriate Visual Cortex/Middle Temporal
VMIQ	Vividness of Movement Imagery Questionnaire
vmPFC	Ventromedial Prefrontal Cortex
WAIS-III	Wechsler Adult Intelligence Scale (3rd Edition)

APPENDIX E:
LIST OF FIGURES

APPENDIX F:
LIST OF TABLES

APPENDIX G:
AUTHOR INFORMATION

CURRICULUM VITAE

NAME	Nadine Diersch
GEBURTSDATUM, -ORT	13.03.1981 in Zwickau
STAATSANGEHÖRIGKEIT	deutsch

AKADEMISCHE AUSBILDUNG

SEIT 08/2008	Max-Planck-Institut für Kognitions- und Neurowissenschaften, Leipzig; Arbeitsbereich Psychologie/Max-Planck-Forschungsgruppe "Körperrepräsentation und Selbstkonzept" *Doktorandin* Betreuung: ao. Prof. Dr. M. Rieger & Dr. S. Schütz-Bosbach
10/2007 – 07/2008	Max-Planck-Institut für Demografische Forschung, Rostock *Doktorandin*
10/2007 – 01/2011	Forschungsstipendium der MaxNetAging Research School Max Planck International Research Network on Aging
02/2004 – 07/2004	University of Queensland, Brisbane, Australien *Auslandssemester*
10/1999 – 09/2006	TU-Chemnitz *Diplom in Psychologie* Titel der Diplomarbeit: Der Einfluss von Kontext und Fragenformat auf die Antworten von Kindern und Jugendlichen in einer Umfragesituation Betreuung: Prof. Dr. E. Walther

VERZEICHNIS ÜBER WISSENSCHAFTLICHE VERÖFFENTLICHUNGEN UND VORTRÄGE

WISSENSCHAFTLICHE VERÖFFENTLICHUNGEN

ARTIKEL IN JOURNALEN MIT BEGUTACHTUNGSSYSTEM

Diersch, N., Mueller, K., Cross, E. S., Stadler, W., Rieger, M., & Schütz-Bosbach, S. (eingereicht). Action prediction in younger versus older adults: Neural correlates of motor familiarity. *PLOS ONE*.

Diersch, N., Cross, E. S., Stadler, W., Schütz-Bosbach, S., & Rieger, M. (2012). Representing others' actions: The role of expertise in the aging mind. *Psychological Research, 76*(4), 525-541. doi: 10.1007/s00426-011-0404-x.

BUCHKAPITEL

Diersch, N., & Walther, E. (2010). Umfrageforschung mit Kindern und Jugendlichen. In E. Walther, F. Preckel, & S. Mecklenbräuker (Hrsg.), *Befragung von Kindern und Jugendlichen: Grundlagen, Methoden und Anwendungsfelder* (S. 297-318). Göttingen: Hogrefe Verlag.

WISSENSCHAFTLICHE VORTRÄGE UND POSTER

EINGELADENE VORTRÄGE

Diersch, N. (2012). *Action prediction in the aging mind.* Kolloquium zur sensomotorischen Kontrolle des Lehrstuhls für Bewegungswissenschaften, Fakultät für Sport- und Gesundheitswissenschaft, TU München, München, Deutschland. 29. November 2012.

VORTRÄGE

Diersch, N., Mueller, K., Cross, E. S., Stadler, W., Rieger, M., & Schütz-Bosbach, S. (2012). *Action prediction in the aging mind: The neural effects of motor familiarity.* MaxNetAging Annual Conference 2012 "Reflections on Living and Dying in Aging Societies". Bad Kohlgrub, Deutschland. 17.-20. Januar 2012.

Diersch, N., Stadler, W., Cross, E. S., Rieger, M., & Schütz-Bosbach, S. (2010). *The role of expertise in an aging mind for simulating the actions of others.* Doktorandenkolloquium MPI CBS, Abteilung Psychologie. Altenburg, Deutschland. 26.-28. Mai 2010.

Diersch, N., Stadler, W., Schütz-Bosbach, S., & Rieger, M. (2010). *Altersbedingte Veränderungen bei der mentalen Simulation von beobachteten Handlungen* [The role of age in simulating the actions of others]. 52. Tagung experimentell arbeitender Psychologen. Saarbrücken, Deutschland. 22.-24. März 2010.

Diersch, N. (2010). *The role of age in simulating the actions of others.* Graduate Workshop, MaxNetAging Research School, Rostock-Warnemünde, Deutschland. 17.-19. Februar 2010.

Diersch, N., Stadler, W., Schütz-Bosbach, S., & Rieger, M. (2009). *The role of age in simulating the actions of others.* Doktorandenkolloquium MPI CBS, Abteilung Psychologie. Weißenfels, Deutschland. 11.-13. November 2009.

Diersch, N. (2008). *The role of expertise in an aging mind for understanding the intentions and actions of others.* Graduate Workshop, MaxNetAging Research School, Rostock-Warnemünde, Deutschland. 21.-24. Oktober 2008.

POSTER

Diersch, N., Cross, E. S., Stadler, W., Rieger, M., & Schütz-Bosbach, S. (2011). *Representing others' actions: The role of expertise in the aging mind.* 18th Annual Meeting of the Cognitive Neuroscience Society (CNS), San Francisco, CA, USA. 02.-05. April 2011.

Diersch, N., Cross, E. S., Stadler, W., Rieger, M., & Schütz-Bosbach, S. (2010). *The role of expertise in an aging mind for simulating the actions of others.* TEMPAL Workshop "The Embodied Mind: Perspectives and Limitations", Nijmegen, Niederlande. 27.-28. Oktober 2010.

Diersch, N., Cross, E. S., Stadler, W., Rieger, M., & Schütz-Bosbach, S. (2010). *The role of expertise in an aging mind for simulating the actions of others.* MaxNetAging Annual Conference 2010 "Early Life - Late Life: An Interdisciplinary Approach towards Aging", Schlangenbad, Deutschland. 06.-08. Oktober 2010.

Diersch, N., Stadler, W., Rieger, M., & Schütz-Bosbach, S. (2010). *The role of age in simulating the actions of others.* Cognitive Aging Conference 2010 „Solving the Aging Puzzle", Atlanta, GA, USA. 15.-18. April 2010.

SELBSTÄNDIGKEITSERKLÄRUNG

Hiermit versichere ich, dass ich die vorliegende Dissertation ohne unzulässige Hilfe und ohne Benutzung anderer als der angegebenen Hilfsmittel verfasst habe und dass die aus fremden Quellen direkt oder indirekt übernommenen Gedanken in der Arbeit als solche kenntlich gemacht worden sind.

Leipzig, 23. Januar 2013	
Ort, Datum	Nadine Diersch

NACHWEIS ÜBER ANTEILE DER CO-AUTOREN

PUBLIKATION I

TITEL	**Representing others' actions: The role of expertise in the aging mind**
JOURNAL	Psychological Research (2012), 76(4), 525-541
DOI	10.1007/S00426-011-0404-X
AUTOREN	Nadine Diersch, Emily S. Cross, Waltraud Stadler, Simone Schütz-Bosbach, und Martina Rieger

ANTEIL NADINE DIERSCH (ERSTAUTOR):

Projektidee
Design der Experimente
Entwicklung des Setups und der Stimuli der Experimente
Probandenrekrutierung und Auswahl
Datenerhebung
Verarbeitung und Analyse der Daten
Schreiben der Publikation

ANTEIL EMILY S. CROSS (AUTOR 2):

Beratung beim Design des zweiten Experiments
Unterstützung beim Schreiben der Publikation

ANTEIL WALTRAUD STADLER (AUTOR 3):

Beratung beim Design der Experimente
Unterstützung beim Schreiben der Publikation

ANTEIL SIMONE SCHÜTZ-BOSBACH (AUTOR 4):

Projektidee
Beratung bei der Analyse der Daten
Unterstützung beim Schreiben der Publikation

ANTEIL MARTINA RIEGER (LETZTAUTOR):

Projektidee
Beratung bei der Analyse der Daten
Unterstützung beim Schreiben der Publikation

N. Diersch
Nadine Diersch

Emily S Cross
Emily S. Cross

Waltraud Stadler

Simone Schütz-Bosbach

Martina Rieger
Martina Rieger

PUBLIKATION II

Titel	**Action prediction in younger versus older adults: Neural correlates of motor familiarity**
Journal	PLOS ONE
Status	eingereicht
Autoren	Nadine Diersch, Karsten Müller, Emily S. Cross, Waltraud Stadler, Martina Rieger, und Simone Schütz-Bosbach

---

Anteil Nadine Diersch (Erstautor):

Projektidee
Design des Experiments
Entwicklung des Setups und der Stimuli des Experiments
Probandenrekrutierung und Auswahl
Datenerhebung
Verarbeitung und Analyse der Daten
Schreiben der Publikation

Anteil Karsten Müller (Autor 2):

Beratung bei der Verarbeitung und Analyse der Daten
Unterstützung beim Schreiben der Publikation

Anteil Emily S. Cross (Autor 3):

Beratung bei der Analyse der Daten
Unterstützung beim Schreiben der Publikation

Anteil Waltraud Stadler (Autor 4):

Unterstützung beim Schreiben der Publikation

Anteil Martina Rieger (Autor 5):

Projektidee
Unterstützung beim Schreiben der Publikation

Anteil Simone Schütz-Bosbach (Letztautor):

Projektidee
Unterstützung beim Schreiben der Publikation

Nadine Diersch

Karsten Müller

Emily S Cross

Emily S. Cross

Waltraud Stadler

Martina Rieger

Simone Schütz-Bosbach

MPI Series in Human Cognitive and Brain Sciences:

1 Anja Hahne
Charakteristika syntaktischer und semantischer Prozesse bei der auditiven Sprachverarbeitung: Evidenz aus ereigniskorrelierten Potentialstudien

2 Ricarda Schubotz
Erinnern kurzer Zeitdauern: Behaviorale und neurophysiologische Korrelate einer Arbeitsgedächtnisfunktion

3 Volker Bosch
Das Halten von Information im Arbeitsgedächtnis: Dissoziationen langsamer corticaler Potentiale

4 Jorge Jovicich
An investigation of the use of Gradient- and Spin-Echo (GRASE) imaging for functional MRI of the human brain

5 Rosemary C. Dymond
Spatial Specificity and Temporal Accuracy in Functional Magnetic Resonance Investigations

6 Stefan Zysset
Eine experimentalpsychologische Studie zu Gedächtnisabrufprozessen unter Verwendung der funktionellen Magnetresonanztomographie

7 Ulrich Hartmann
Ein mechanisches Finite-Elemente-Modell des menschlichen Kopfes

8 Bertram Opitz
Funktionelle Neuroanatomie der Verarbeitung einfacher und komplexer akustischer Reize: Integration haemodynamischer und elektrophysiologischer Maße

9 Gisela Müller-Plath
Formale Modellierung visueller Suchstrategien mit Anwendungen bei der Lokalisation von Hirnfunktionen und in der Diagnostik von Aufmerksamkeitsstörungen

10 Thomas Jacobsen
Characteristics of processing morphological structural and inherent case in language comprehension

11 Stefan Kölsch
Brain and Music
A contribution to the investigation of central auditory processing with a new electrophysiological approach

12 Stefan Frisch
Verb-Argument-Struktur, Kasus und thematische Interpretation beim Sprachverstehen

13 Markus Ullsperger
The role of retrieval inhibition in directed forgetting – an event-related brain potential analysis

14 Martin Koch
Measurement of the Self-Diffusion Tensor of Water in the Human Brain

15 Axel Hutt
Methoden zur Untersuchung der Dynamik raumzeitlicher Signale

16 Frithjof Kruggel
Detektion und Quantifizierung von Hirnaktivität mit der funktionellen Magnetresonanztomographie

17 Anja Dove
Lokalisierung an internen Kontrollprozessen beteiligter Hirngebiete mithilfe des Aufgabenwechselparadigmas und der ereigniskorrelierten funktionellen Magnetresonanztomographie

18 Karsten Steinhauer
Hirnphysiologische Korrelate prosodischer Satzverarbeitung bei gesprochener und geschriebener Sprache

19 Silke Urban
Verbinformationen im Satzverstehen

20 Katja Werheid
Implizites Sequenzlernen bei Morbus Parkinson

21 Doreen Nessler
Is it Memory or Illusion? Electrophysiological Characteristics of True and False Recognition

22 Christoph Herrmann
Die Bedeutung von 40-Hz-Oszillationen für kognitive Prozesse

23 Christian Fiebach
Working Memory and Syntax during Sentence Processing.
A neurocognitive investigation with event-related brain potentials and functional magnetic resonance imaging

24 Grit Hein
Lokalisation von Doppelaufgabendefiziten bei gesunden älteren Personen und neurologischen Patienten

25 Monica de Filippis
Die visuelle Verarbeitung unbeachteter Wörter. Ein elektrophysiologischer Ansatz

26 Ulrich Müller
Die katecholaminerge Modulation präfrontaler kognitiver Funktionen beim Menschen

27 Kristina Uhl
Kontrollfunktion des Arbeitsgedächtnisses über interferierende Information

28 Ina Bornkessel
The Argument Dependency Model: A Neurocognitive Approach to Incremental Interpretation

29 Sonja Lattner
Neurophysiologische Untersuchungen zur auditorischen Verarbeitung von Stimminformationen

30 Christin Grünewald
Die Rolle motorischer Schemata bei der Objektrepräsentation: Untersuchungen mit funktioneller Magnetresonanztomographie

31 Annett Schirmer
Emotional Speech Perception: Electrophysiological Insights into the Processing of Emotional Prosody and Word Valence in Men and Women

32 André J. Szameitat
Die Funktionalität des lateral-präfrontalen Cortex für die Verarbeitung von Doppelaufgaben

33 Susanne Wagner
Verbales Arbeitsgedächtnis und die Verarbeitung ambiger Wörter in Wort- und Satzkontexten

34 Sophie Manthey
Hirn und Handlung: Untersuchung der Handlungsrepräsentation im ventralen prämotorischen Cortex mit Hilfe der funktionellen Magnet-Resonanz-Tomographie

35 Stefan Heim
Towards a Common Neural Network Model of Language Production and Comprehension: fMRI Evidence for the Processing of Phonological and Syntactic Information in Single Words

36 Claudia Friedrich
Prosody and spoken word recognition: Behavioral and ERP correlates

37 Ulrike Lex
Sprachlateralisierung bei Rechts- und Linkshändern mit funktioneller Magnetresonanztomographie

38 Thomas Arnold
Computergestützte Befundung klinischer Elektroenzephalogramme

39 Carsten H. Wolters
Influence of Tissue Conductivity Inhomogeneity and Anisotropy on EEG/MEG based Source Localization in the Human Brain

40 Ansgar Hantsch
Fisch oder Karpfen? Lexikale Aktivierung von Benennungsalternative bei der Objektbenennung

41 Peggy Bungert
Zentralnervöse Verarbeitung akustischer Informationen
Signalidentifikation, Signallateralisation und zeitgebundene Informationsverarbeitung bei Patienten mit erworbenen Hirnschädigungen

42 Daniel Senkowski
Neuronal correlates of selective attention: An investigation of electrophysiological brain responses in the EEG and MEG

43 Gert Wollny
Analysis of Changes in Temporal Series of Medical Images

44 Angelika Wolf
Sprachverstehen mit Cochlea-Implantat: EKP-Studien mit postlingual ertaubten erwachsenen CI-Trägern

45 Kirsten G. Volz
Brain correlates of uncertain decisions: Types and degrees of uncertainty

46 Hagen Huttner
Magnetresonanztomographische Untersuchungen über die anatomische Variabilität des Frontallappens des menschlichen Großhirns

47 Dirk Köster
Morphology and Spoken Word Comprehension: Electrophysiological Investigations of Internal Compound Structure

48 Claudia A. Hruska
Einflüsse kontextueller und prosodischer Informationen in der auditorischen Satzverarbeitung: Untersuchungen mit ereigniskorrelierten Hirnpotentialen

49 Hannes Ruge
Eine Analyse des raum-zeitlichen Musters neuronaler Aktivierung im Aufgabenwechselparadigma zur Untersuchung handlungssteuernder Prozesse

50 Ricarda I. Schubotz
Human premotor cortex: Beyond motor performance

51 Clemens von Zerssen
Bewusstes Erinnern und falsches Wiedererkennen: Eine funktionelle MRT Studie neuroanatomischer Gedächtniskorrelate

52 Christiane Weber
Rhythm is gonna get you.
Electrophysiological markers of rhythmic processing in infants with and without risk for Specific Language Impairment (SLI)

53 Marc Schönwiesner
Functional Mapping of Basic Acoustic Parameters in the Human Central Auditory System

54 Katja Fiehler
Temporospatial characteristics of error correction

55 Britta Stolterfoht
Processing Word Order Variations and Ellipses: The Interplay of Syntax and Information Structure during Sentence Comprehension

56 Claudia Danielmeier
Neuronale Grundlagen der Interferenz zwischen Handlung und visueller Wahrnehmung

57 Margret Hund-Georgiadis
Die Organisation von Sprache und ihre Reorganisation bei ausgewählten, neurologischen Erkrankungen gemessen mit funktioneller Magnetresonanztomographie – Einflüsse von Händigkeit, Läsion, Performanz und Perfusion

58 Jutta L. Mueller
Mechanisms of auditory sentence comprehension in first and second language: An electrophysiological miniature grammar study

59 Franziska Biedermann
Auditorische Diskriminationsleistungen nach unilateralen Läsionen im Di- und Telenzephalon

60 Shirley-Ann Rüschemeyer
The Processing of Lexical Semantic and Syntactic Information in Spoken Sentences: Neuroimaging and Behavioral Studies of Native and Non-Native Speakers

61 Kerstin Leuckefeld
The Development of Argument Processing Mechanisms in German. An Electrophysiological Investigation with School-Aged Children and Adults

62 Axel Christian Kühn
Bestimmung der Lateralisierung von Sprachprozessen unter besondere Berücksichtigung des temporalen Cortex, gemessen mit fMRT

63 Ann Pannekamp
Prosodische Informationsverarbeitung bei normalsprachlichem und deviantem Satzmaterial: Untersuchungen mit ereigniskorrelierten Hirnpotentialen

64 Jan Derrfuß
Functional specialization in the lateral frontal cortex: The role of the inferior frontal junction in cognitive control

65 Andrea Mona Philipp
The cognitive representation of tasks – Exploring the role of response modalities using the task-switching paradigm

66 Ulrike Toepel
Contrastive Topic and Focus Information in Discourse – Prosodic Realisation and Electrophysiological Brain Correlates

67 Karsten Müller
Die Anwendung von Spektral- und Waveletanalyse zur Untersuchung der Dynamik von BOLD-Zeitreihen verschiedener Hirnareale

68 Sonja A.Kotz
The role of the basal ganglia in auditory language processing: Evidence from ERP lesion studies and functional neuroimaging

69 Sonja Rossi
The role of proficiency in syntactic second language processing: Evidence from event-related brain potentials in German and Italian

70 Birte U. Forstmann
Behavioral and neural correlates of endogenous control processes in task switching

71 Silke Paulmann
Electrophysiological Evidence on the Processing of Emotional Prosody: Insights from Healthy and Patient Populations

72 Matthias L. Schroeter
Enlightening the Brain – Optical Imaging in Cognitive Neuroscience

73 Julia Reinholz
Interhemispheric interaction in object- and word-related visual areas

74 Evelyn C. Ferstl
The Functional Neuroanatomy of Text Comprehension

75 Miriam Gade
Aufgabeninhibition als Mechanismus der Konfliktreduktion zwischen Aufgabenrepräsentationen

76 Juliane Hofmann
Phonological, Morphological, and Semantic Aspects of Grammatical Gender Processing in German

77 Petra Augurzky
Attaching Relative Clauses in German – The Role of Implicit and Explicit Prosody in Sentence Processing

78 Uta Wolfensteller
Habituelle und arbiträre sensomotorische Verknüpfungen im lateralen prämotorischen Kortex des Menschen

79 Päivi Sivonen
Event-related brain activation in speech perception: From sensory to cognitive processes

80 Yun Nan
Music phrase structure perception: the neural basis, the effects of acculturation and musical training

81 Katrin Schulze
Neural Correlates of Working Memory for Verbal and Tonal Stimuli in Nonmusicians and Musicians With and Without Absolute Pitch

82 Korinna Eckstein
Interaktion von Syntax und Prosodie beim Sprachverstehen: Untersuchungen anhand ereigniskorrelierter Hirnpotentiale

83 Florian Th. Siebörger
Funktionelle Neuroanatomie des Textverstehens: Kohärenzbildung bei Witzen und anderen ungewöhnlichen Texten

84 Diana Böttger
Aktivität im Gamma-Frequenzbereich des EEG: Einfluss demographischer Faktoren und kognitiver Korrelate

85 Jörg Bahlmann
Neural correlates of the processing of linear and hierarchical artificial grammar rules: Electrophysiological and neuroimaging studies

86 Jan Zwickel
Specific Interference Effects Between Temporally Overlapping Action and Perception

87 Markus Ullsperger
Functional Neuroanatomy of Performance Monitoring: fMRI, ERP, and Patient Studies

88 Susanne Dietrich
Vom Brüllen zum Wort – MRT-Studien zur kognitiven Verarbeitung emotionaler Vokalisationen

89 Maren Schmidt-Kassow
What's Beat got to do with ist? The Influence of Meter on Syntactic Processing: ERP Evidence from Healthy and Patient populations

90 Monika Lück
Die Verarbeitung morphologisch komplexer Wörter bei Kindern im Schulalter: Neurophysiologische Korrelate der Entwicklung

91 Diana P. Szameitat
Perzeption und akustische Eigenschaften von Emotionen in menschlichem Lachen

92 Beate Sabisch
Mechanisms of auditory sentence comprehension in children with specific language impairment and children with developmental dyslexia: A neurophysiological investigation

93 Regine Oberecker
Grammatikverarbeitung im Kindesalter: EKP-Studien zum auditorischen Satzverstehen

94 Şükrü Barış Demiral
Incremental Argument Interpretation in Turkish Sentence Comprehension

95 Henning Holle
The Comprehension of Co-Speech Iconic Gestures: Behavioral, Electrophysiological and Neuroimaging Studies

96 Marcel Braß
Das inferior frontale Kreuzungsareal und seine Rolle bei der kognitiven Kontrolle unseres Verhaltens

97 Anna S. Hasting
Syntax in a blink: Early and automatic processing of syntactic rules as revealed by event-related brain potentials

98 Sebastian Jentschke
Neural Correlates of Processing Syntax in Music and Language – Influences of Development, Musical Training and Language Impairment

99 Amelie Mahlstedt
The Acquisition of Case marking Information as a Cue to Argument Interpretation in German
An Electrophysiological Investigation with Pre-school Children

100 Nikolaus Steinbeis
Investigating the meaning of music using EEG and fMRI

101 Tilmann A. Klein
Learning from errors: Genetic evidence for a central role of dopamine in human performance monitoring

102 Franziska Maria Korb
Die funktionelle Spezialisierung des lateralen präfrontalen Cortex: Untersuchungen mittels funktioneller Magnetresonanztomographie

103 Sonja Fleischhauer
Neuronale Verarbeitung emotionaler Prosodie und Syntax: die Rolle des verbalen Arbeitsgedächtnisses

104 Friederike Sophie Haupt
The component mapping problem: An investigation of grammatical function reanalysis in differing experimental contexts using eventrelated brain potentials

105 Jens Brauer
Functional development and structural maturation in the brain's neural network underlying language comprehension

106 Philipp Kanske
Exploring executive attention in emotion: ERP and fMRI evidence

107 Julia Grieser Painter
Music, meaning, and a semantic space for musical sounds

108 Daniela Sammler
The Neuroanatomical Overlap of Syntax Processing in Music and Language - Evidence from Lesion and Intracranial ERP Studies

109 Norbert Zmyj
Selective Imitation in One-Year-Olds: How a Model's Characteristics Influence Imitation

110 Thomas Fritz
Emotion investigated with music of variable valence – neurophysiology and cultural influence

111 Stefanie Regel
The comprehension of figurative language: Electrophysiological evidence on the processing of irony

112 Miriam Beisert
Transformation Rules in Tool Use

113 Veronika Krieghoff
Neural correlates of Intentional Actions

114 Andreja Bubić
Violation of expectations in sequence processing

115 Claudia Männel
Prosodic processing during language acquisition: Electrophysiological studies on intonational phrase processing

116 Konstanze Albrecht
Brain correlates of cognitive processes underlying intertemporal choice for self and other

117 Katrin Sakreida
Nicht-motorische Funktionen des prämotorischen Kortex: Patientenstudien und funktionelle Bildgebung

118 Susann Wolff
The interplay of free word order and pro-drop in incremental sentence processing: Neurophysiological evidence from Japanese

119 Tim Raettig
The Cortical Infrastructure of Language Processing: Evidence from Functional and Anatomical Neuroimaging

120 Maria Golde
Premotor cortex contributions to abstract and action-related relational processing

121 Daniel S. Margulies
Resting-State Functional Connectivity fMRI: A new approach for assessing functional neuroanatomy in humans with applications to neuroanatomical, developmental and clinical questions

122 Franziska Süß
The interplay between attention and syntactic processes in the adult and developing brain: ERP evidences

123 Stefan Bode
From stimuli to motor responses: Decoding rules and decision mechanisms in the human brain

124 Christiane Diefenbach
Interactions between sentence comprehension and concurrent action: The role of movement effects and timing

125 Moritz M. Daum
Mechanismen der frühkindlichen Entwicklung des Handlungsverständnisses

126 Jürgen Dukart
Contribution of FDG-PET and MRI to improve Understanding, Detection and Differentiation of Dementia

127 Kamal Kumar Choudhary
Incremental Argument Interpretation in a Split Ergative Language: Neurophysiological Evidence from Hindi

128 Peggy Sparenberg
Filling the Gap: Temporal and Motor Aspects of the Mental Simulation of Occluded Actions

129 Luming Wang
The Influence of Animacy and Context on Word Order Processing: Neurophysiological Evidence from Mandarin Chinese

130 Barbara Ettrich
Beeinträchtigung frontomedianer Funktionen bei Schädel-Hirn-Trauma

131 Sandra Dietrich
Coordination of Unimanual Continuous Movements with External Events

132 R. Muralikrishnan
An Electrophysiological Investigation Of Tamil Dative-Subject Constructions

133 Christian Obermeier
Exploring the significance of task, timing and background noise on gesture-speech integration

134 Björn Herrmann
Grammar and perception: Dissociation of early auditory processes in the brain

135 Eugenia Solano-Castiella
In vivo anatomical segmentation of the human amygdala and parcellation of emotional processing

136 Marco Taubert
Plastizität im sensomotorischen System – Lerninduzierte Veränderungen in der Struktur und Funktion des menschlichen Gehirns

137 Patricia Garrido Vásquez
Emotion Processing in Parkinson's Disease:
The Role of Motor Symptom Asymmetry

138 Michael Schwartze
Adaptation to temporal structure

139 Christine S. Schipke
Processing Mechanisms of Argument Structure and Case-marking in Child Development: Neural Correlates and Behavioral Evidence

140 Sarah Jessen
Emotion Perception in the Multisensory Brain

141 Jane Neumann
Beyond activation detection: Advancing computational techniques for the analysis of functional MRI data

142 Franziska Knolle
Knowing what's next: The role of the cerebellum in generating predictions

143 Michael Skeide
Syntax and semantics networks in the developing brain

144 Sarah M. E. Gierhan
Brain networks for language
Anatomy and functional roles of neural pathways supporting language comprehension and repetition

145 Lars Meyer
The Working Memory of Argument-Verb Dependencies
Spatiotemporal Brain Dynamics during Sentence Processing

146 Benjamin Stahl
Treatment of Non-Fluent Aphasia through
Melody, Rhythm and Formulaic Language

147 Kathrin Rothermich
The rhythm's gonna get you: ERP and fMRI evidence on the interaction of metric and semantic processing

148 Julia Merrill
Song and Speech Perception – Evidence from fMRI, Lesion Studies and Musical Disorder

149 Klaus-Martin Krönke
Learning by Doing?
Gesture-Based Word-Learning and its Neural Correlates in Healthy Volunteers and Patients with Residual Aphasia

150 Lisa Joana Knoll
When the hedgehog kisses the frog
A functional and structural investigation of syntactic processing in the developing brain