Psychological Research (2012) 76:525–541
DOI 10.1007/s00426-011-0404-x

ORIGINAL ARTICLE

Representing others' actions: the role of expertise in the aging mind

Nadine Diersch · Emily S. Cross · Waltraud Stadler · Simone Schütz-Bosbach · Martina Rieger

Received: 12 July 2011 / Accepted: 5 December 2011 / Published online: 24 December 2011

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.

N. Diersch (✉) · E. S. Cross · W. Stadler · S. Schütz-Bosbach · M. Rieger
Max Planck Institute for Human Cognitive and Brain Sciences, Stephanstr. 1A, 04103 Leipzig, Germany
e-mail: diersch@cbs.mpg.de

N. Diersch
MaxNetAging Research School, Max Planck Institute for Demographic Research, Rostock, Germany

E. S. Cross
Behavioral Science Institute, Donders Institute for Brain Cognition and Behaviour, Radboud University Nijmegen, Nijmegen, The Netherlands

E. S. Cross
Wales Institute for Cognitive Neuroscience, School of Psychology, Bangor University, Gwynedd, UK

W. Stadler
Movement Science Unit, Faculty for Sports and Health Science, Technical University Munich, Munich, Germany

M. Rieger
UMIT-The Health and Life Sciences University, Hall/Tyrol, Austria

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, Muesseler, Aschersleben, & Prinz, 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, Zilles, Laird, & Eickhoff, 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, Friston, & Frith, 2007; Schippers & Keysers, 2011; Wolpert, Doya, & Kawato, 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, Springer, & Prinz, 2011).

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, Staudinger, & Lindenberger, 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, Dennis, Daselaar, Fleck, & Cabeza, 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 (e.g., Heuninckx, Wenderoth, & Swinnen, 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, Bangert, Anguera, & Quinn-Walsh, 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, Sekuler, & Sekuler, 2007; Norman, Payton, Long, & Hawkes, 2004; Pilz, Bennett, & Sekuler, 2010; Roudaia, Bennett, Sekuler, & Pilz, 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, Caçola, & Cordova, 2010; Léonard & Tremblay, 2007; Maryott & Sekuler, 2009; Mulder, Hochstenbach, van Heuvelen, & den Otter, 2007; Personnier, Paizis, Ballay, & Papaxanthis, 2008; Personnier, Kubicki, Laroche, & Papaxanthis, 2010; Saimpont, Pozzo, & Papaxanthis, 2009; Skoura, Papaxanthis, Vinter, &

Pozzo, 2005; Skoura, Personnier, Vinter, Pozzo, & Papaxanthis, 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, Cesari, Romani, & Urgesi, 2008; Farrow and Abernethy, 2003; Mann, Williams, Ward, & Janelle, 2007; Müller, Abernethy, & Farrow, 2006; Sebanz & Shiffrar, 2009) as well as modulate activity in the action observation network in the brain (e.g., Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2005; Cross, Hamilton, & Grafton, 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, Baker, & Schorer, 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 and 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 temporal 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 1.

Table 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 et al. 1975; Maximum score: 30).

The MOS 36-Item Short Form Health Survey (SF-36; McHorney et al. 1993; Ware and Sherbourne 1992; Ware et al. 1995) 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 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 Fig. 1a). 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

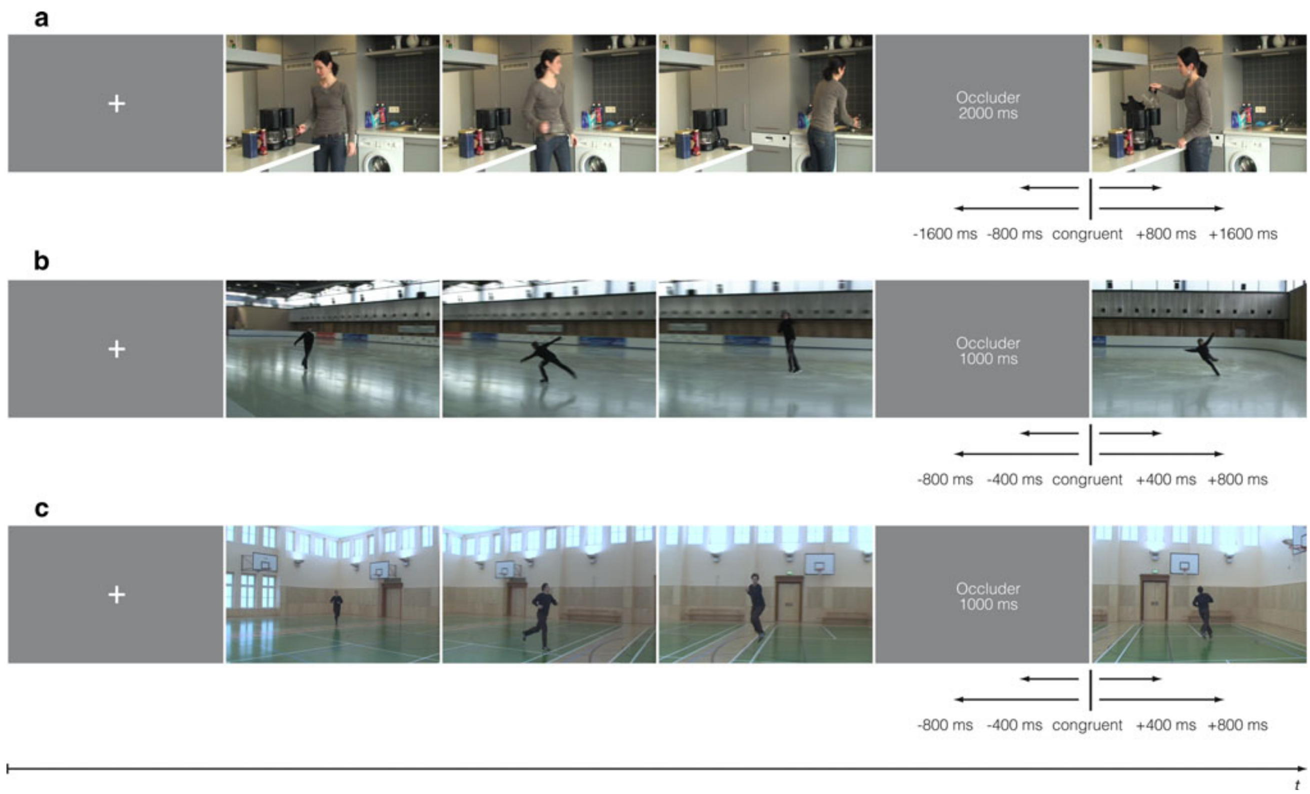

Fig. 1 Details of experimental conditions in Experiment 1 and Experiment 2: The experimental conditions in Experiment 1 are exemplified for the first occluder in a given action sequence (**a**). Each video clip started with a fixation cross (1,500 ms), followed by the beginning of an action sequence. 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)

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.

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 Fig. 2a).

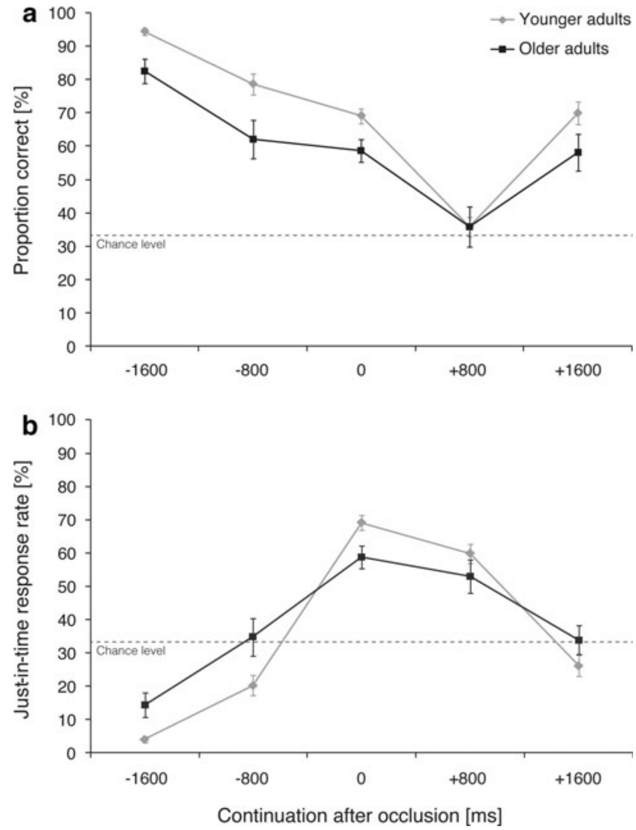

Fig. 2 Proportion of correct responses (**a**) and just-in-time response rates (**b**) on every continuation after occlusion for younger and older adults in Experiment 1. *Error bars* represent standard errors of the means

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 Fig. 2b).

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 2.

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 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 STW raw score, $F(1,63) = 6.81$, $p = 0.011$, $\eta_p^2 = 0.097$, as well as the STW 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

Table 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 1 for a description of the scores 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 3. The experiment was conducted in the same environment and with the same equipment as Experiment 1.

Table 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 Fig. 1b, 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 Fig. 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 action 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

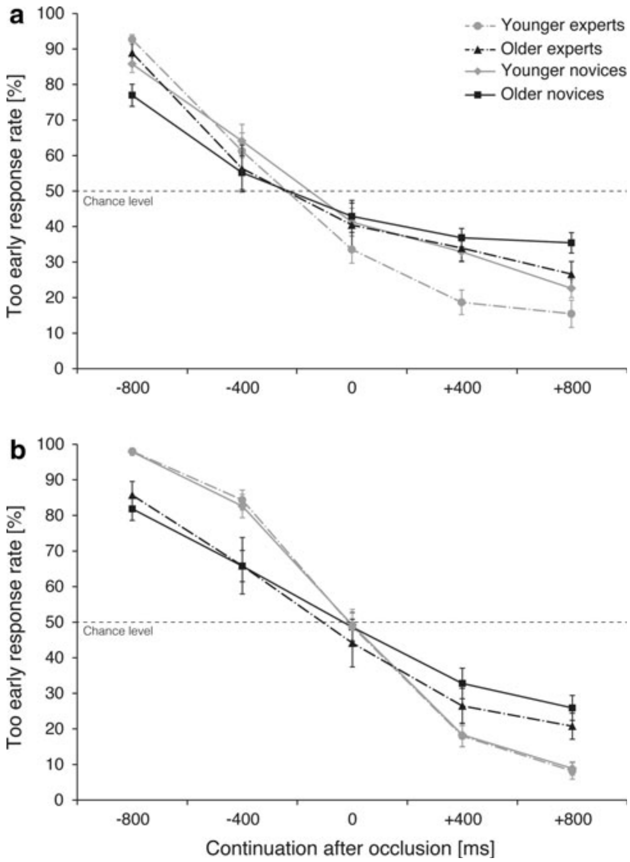

Fig. 3 Too early response rates on every continuation after occlusion for the figure skating elements (**a**) and the movement exercises (**b**) for younger and older figure skating experts and novices in Experiment 2. Higher response rates on negative continuations and lower response rates on positive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

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.

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 Fig. 4a). 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 Fig. 4b). 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

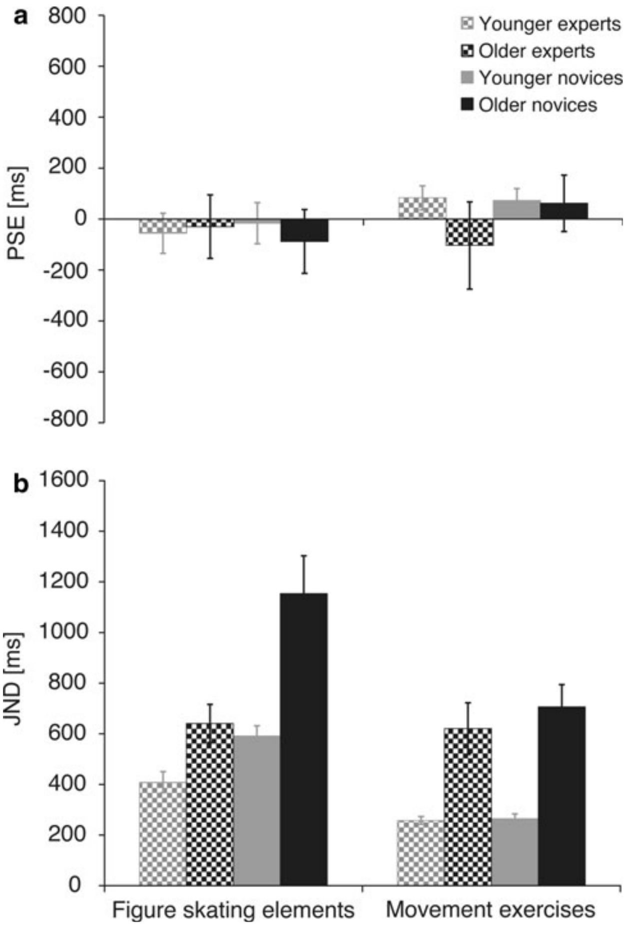

Fig. 4 The point of subjective equality (PSE, **a**) and the just noticeable difference (JND, **b**) for the figure skating elements (*left panel*) and the movement exercises (*right panel*) for younger and older figure skating experts and novices in Experiment 2. *Error bars* represent standard errors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

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.

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., 2010; Personnier et al., 2008, 2010; Saimpont et al., 2009; Skoura et al., 2005, 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., 2007; 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, Wenderoth, Debaere, Peeters, & Swinnen, 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, Schubotz, 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 Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; Aglioti et al., 2008; Urgesi, Savonitto, Fabbro, & Aglioti, 2011). For example, Urgesi et al. (2011) 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, Stadler, Parkinson, Schütz-Bosbach, & Prinz, 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.

References

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

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.

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.

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

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.

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

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.

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.

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.

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.

Cotman, C. W., & Berchtold, N. 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., 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.

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.

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

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. ed., pp. 1–54). New York: Psychology Press.

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

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.

Gabbard, C., Caçola, P., & Cordova, A. (2010). Is there an advanced aging effect on the ability to mentally represent action? *Archives*

of Gerontology and Geriatrics. doi:10.1016/j.archger.2010.10.006.
Gescheider, G. A. (1997). The classical psychophysical methods. In G. A. Gescheider (Ed.), *Psychophysics: The fundamentals* (3rd ed. ed., pp. 45–72). Mahwah, NJ: Lawrence Erlbaum Associates.
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.
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.
Heuninckx, S., Wenderoth, N., Debaere, F., Peeters, R., & Swinnen, S. P. (2005). Neural basis of aging: The penetration of cognition into action control. *The 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. *The Journal of Neuroscience, 28*(1), 91–99.
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.
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), 529–535.
Jeannerod, M. (2001). Neural simulation of action: A unifying mechanism for motor cognition. *Neuroimage, 14*(1), 103–109.
Kilner, J. M., Friston, K. J., & Frith, C. D. (2007). Predictive coding: An account of the mirror neuron system. *Cognitive Processing, 8*(3), 159–166.
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.
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.
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.
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., et al. (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.
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., & Farrow, D. (2006). How do world-class cricket batsmen anticipate a bowler's intention? *The Quarterly Journal of Experimental Psychology, 59*(12), 2162–2186.
Nedelko, V., Hassa, T., Hamzei, F., Weiller, C., Binkofski, F., Schoenfeld, M. A. l, et al. (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.
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.
Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*(1), 97–113.
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., & Reuter-Lorenz, P. A. (2009). The adaptive brain: Aging and neurocognitive scaffolding. *Annual Review of Psychology, 60*, 173–196.
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. *The Quarterly Journal of Experimental Psychology, 62*(11), 2081–2104.
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.
Prinz, W. (1997). Perception and action planning. *European Journal of Cognitive Psychology, 9*(2), 129–154.
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.
Raz, N., & Rodrigue, K. M. (2006). Differential aging of the brain: Patterns, cognitive correlates and modifiers. *Neuroscience and Biobehavioral Reviews, 30*(6), 730–748.
Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience, 27*, 169–192.
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., Pozzo, T., & Papaxanthis, C. (2009). Aging affects the mental rotation of left and right hands. *PLoS ONE, 4*(8), e6714.
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.

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.

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

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

Sebanz, N., & Shiffrar, M. (2009). Detecting deception in a bluffing body: The role of expertise. *Psychonomic Bulletin and 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., et al. (2010). Motor control and aging: Links to age-related brain structural, functional, and biochemical effects. *Neuroscience and Biobehavioral Reviews, 34*(5), 721–733.

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.

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. (2011). Predicting others' actions: Evidence for a constant time delay in action simulation. *Psychological Research*. doi:10.1007/s00426-011-0321-z.

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.

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. (2011). Long- and short-term plastic modeling of action prediction abilities in volleyball. *Psychological Research*. doi:10.1007/s00426-011-0383-y.

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

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.

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 of London Series 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.