Interference of action perception on action production increases across the adult life-span

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Accepted for publication in Experimental Brain Research (13th December 2017)

Word count: 7'727 (inclusive references)

Acknowledgements

During the work on her dissertation, Stephanie Wermelinger was a pre-doctoral fellow of the International Max Planck Research School on the Life Course (LIFE, www.imprs-life.mpg.de; participating institutions: Max Planck Institute for Human Development, Freie Universität Berlin, Humboldt-Universität zu Berlin, University of Michigan, University of Virginia, University of Zurich).

This project is funded by the Swiss National Science Foundation (grant number: S-63216-03-01).

Abstract

Action perception and action production are assumed to be based on an internal simulation process that involves the sensorimotor system. This system undergoes changes across the life span and is assumed to become less precise with age. In the current study, we investigated how increasing age affects the magnitude of interference in action production during simultaneous action perception. In a task adapted from Brass et al. (2000), we asked participants (aged 20 – 80 years) to respond to a visually presented finger movement and/or symbolic cue by executing a previously defined finger movement. Action production was assessed via participants' reaction times. Results show that participants were slower in trials in which they were asked to ignore an incongruent finger movement compared to trials in which they had to ignore an incongruent symbolic cue. Moreover, advancing age was shown to accentuate this effect. We suggest that the internal simulation of the action becomes less precise with age making the sensorimotor system more susceptible to perturbations such as the interference of a concurrent action perception.

Keywords: action simulation; sensorimotor system; motor performance; ageing; imitation inhibition

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Be it during a football game, while driving a car, or in the middle of a conversation: We constantly perceive actions of others while producing different actions ourselves. This perception of others actions is not independent of our own action production. Quite the contrary, action perception and production affect each other reciprocally, in particular, when performed simultaneously: While incongruent action perception and production interfere with each other, the opposite is true for congruent perception and production (e.g., Brass, Bekkering, & Prinz, 2001). In the current study, we investigated how age is related to the interference effects in simultaneous incongruent action perception and action production.

Action perception is modulated by a concurrent action production resulting in interference effects in case perceived and produced actions do not conform (Jacobs & Shiffrar, 2005; Kilner, Paulignan, & Blakemore, 2003). For instance, Hamilton, Wolpert, and Frith (2004) asked participants to lift boxes of different weights and at the same time make judgments about the heaviness of objects lifted by another actor. The objects lifted by another person were judged to be lighter when the participants themselves lifted a heavy box and heavier when the participants lifted a light box. In the same vein, a congruent action production (e.g., evaluation of movement durations: Hecht, Vogt, & Prinz, 2001; discrimination of hand postures: Miall et al., 2006) facilitates simultaneous action perception. Furthermore, facilitation (Edwards, Humphreys, & Castiello, 2003; Ménoret, Curie, Portes, Nazir, & Paulignan, 2013) and interference effects (Brass, Zysset, & Von Cramon, 2001; Wohlschläger & Bekkering, 2002) are found in the opposite direction, from perception on production. For instance, Hardwick and Edwards (2012) asked participants to execute finger movements while observing an experimenter executing spatially congruent or incongruent finger movements. The participants showed reduced spatial error in their own movement if the perceived action was congruent with their own action (facilitation effect) but increased spatial error if the perceived action did not match with their own action production

(interference effect; also see Press, Bird, & Heyes, 2005; Press, Bird, Walsh, & Heyes, 2008; Press, Gillmeister, & Heyes, 2007).

The simulation theory (Jeannerod, 2001; Pezzulo, Candidi, Dindo, & Barca, 2013, for a review) accounts for these interrelations between action perception and action production by stating that, in addition to the overt and observable stage of action, there is another—covert—stage of action. This simulation involves aspects of the future such as the goal of the action, the means to reach it or the consequences of the action (Jeannerod, 2001) without an overt action production. Furthermore, the production, perception, or imagination of an action are assumed to automatically elicit an internal simulation of the latter. Consequently, in cases in which the simulations associated with perception and production differ, they may interfere with each other. More precisely, since the sensorimotor system is already tuned in for a certain action when perceiving it, the concurrent production of an incongruent action interferes with this movement preparation (Blakemore & Frith, 2005).

In line with this assumption, the sensorimotor system is shown to be involved in the internal simulation process (Stadler, Springer, Parkinson, & Prinz, 2012). For instance, studies using transcranial magnetic stimulation (TMS) during action perception have shown a modulation of the motor corticospinal excitability in accordance with the perceived actions (Aglioti, Cesari, Romani, & Urgesi, 2008; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Gangitano, Mottaghy, & Pascual-Leone, 2001; Urgesi, Moro, Candidi, & Aglioti, 2006; Valchev, Tidoni, Hamilton, Gazzola, & Avenanti, 2017). In these studies, the relative sensitivity of the corticospinal tract during action perception was assessed via changes in the threshold needed to evoke responses in the effector muscles while stimulating the motor cortex. Results show a selective increase in the motor-evoked potentials (MEP) recorded from muscles normally used to produce the observed actions (D'Ausilio et al., 2014; Fadiga et al., 1995). Hence, during action perception, the activity of the sensorimotor system, as indicated by the corticospinal excitability, is highly selective for the effector that is involved in action

production (D'Ausilio et al., 2009).

However, while this is true in young adults, Léonard and Tremblay (2008) have shown that the corticomotor facilitation is less specialized in older than younger adults during action production, perception and imagination. Furthermore, studies using imaging techniques (Diersch et al., 2013; Diersch, Jones, & Cross, 2016; Mouthon, Ruffieux, Keller, & Taube, 2016; Nedelko et al., 2010) have shown that older compared to younger adults activate additional visual and sensorimotor regions during action perception. Hence, age-related de-differentiation and compensation processes with advancing age (Cabeza, 2002; Reuter, Behrens, & Zschorlich, 2015) might lead to a less precise internal representation and simulation of the actions perceived and produced.

Supporting this notion, the sensorimotor system undergoes age-related changes (Heuninckx, Wenderoth, Debaere, Peeters, & Swinnen, 2005; Sharma & Baron, 2014; Ward, 2006; Ward & Frackowiak, 2003). On the behavioural level, these changes result in greater movement variability, general slowing of movements and coordination deficits with increasing age (Seidler et al., 2010). In action production, increasing age is accompanied by less precise motor planning (Reuter et al., 2015), less interhemispheric inhibition (Talelli, Waddingham, Ewas, Rothwell, & Ward, 2008), and reduced sensorimotor control of actions (Seidler & Stelmach, 1995). With respect to action perception, the accuracy of action prediction (Diersch, Cross, Stadler, Schütz-Bosbach, & Rieger, 2012), imagination (Personnier, Kubicki, Laroche, & Papaxanthis, 2010; Personnier, Paizis, Ballay, & Papaxanthis, 2008; Saimpont, Mourey, Manckoundia, Pfitzenmeyer, & Pozzo, 2010; Skoura, Papaxanthis, Vinter, & Pozzo, 2005), and the perception of the personal action range (Gabbard, Caçola, & Cordova, 2011) decreases from younger to older adults.

Taken together, the current study is based on the following presumptions: First, action perception and production are interrelated because they are both based on an internal simulation process involving the sensorimotor system (Jeannerod, 2001). Second, along with

age-related changes in the sensorimotor system, the precision of this internal simulation process changes over age, and particularly decreases during the adult life span. This becomes evident in changes in action perception and production on the behavioural and neural level. What remains unclear is whether and how increasing age affects the interrelations of action perception and action production as indicated by interference and facilitation effects. Specifically, the less precise internal action simulation might lead to stronger interference in concurrent action perception and production in older participants. That is, if the sensorimotor system is challenged with two concurrent and contradicting simulation processes, action production should be interfered more by action perception with advancing age. Hence, in the current study we aimed to explore whether the dependence of our own action production on the perception of other's actions differs between age groups or stays constant across the life span.

To address our research question, we adapted a reaction-time task introduced by Brass, Bekkering, Wohlschläger, and Prinz (2000) and applied it to participants between the ages of 20 to 80 years. In the original task, the participants were asked to perform finger movements, which were either congruent or incongruent with finger movements or symbolic cues. The authors reported facilitation (shorter reaction times in participants' finger movements) for congruent trials and interference (longer reaction times) in incongruent trials compared to baseline trials. Importantly, interference effects were more pronounced when the participants observed an incongruent action (i.e. a finger movement) than when they observed an incongruent symbolic cue.

In accordance with Brass et al. (2000), we asked our participants to respond with an index- or middle-finger movement to a visually presented index- or middle-finger movement, or to the appearance of a symbolic cue ("spatial condition" in Brass et al., 2000). The finger movement and symbolic cue could either be congruent, implying the same response finger, or incongruent, implying a different response finger. Previous findings indicate that finger

movements, like they were presented in our study, are perceived as goal-directed actions (Bertenthal, Longo, & Kosobud, 2006). Based on the findings reported by Brass et al. (2000), we assumed longer reaction times in response to incongruent trials. In accordance with the simulation theory, this interference was assumed to be larger in trials, in which the participants' action production was interfered by an incongruent action perception. Thus, we expected reaction times to be longest in trials, in which participants were asked to respond to the symbolic cue and ignore the simultaneously presented finger movement. Furthermore, in accordance with Brass et al.'s (2000) findings, we expected reactions times to be reduced in congruent trials if participants were asked to respond to the symbolic cue (facilitation effect). Looking at the effect of age on this pattern, we expected older compared to younger participants to show longer reaction times independent of condition (Houx & Jolles, 1993). Furthermore, older participants were expected to be interfered more in the incongruent trials (Houx, Jolles, Vreeling, & Jolles, 1993; West, 1996). Finally, based on studies indicating a less precise action simulation (Diersch et al., 2016) and the activation of additional areas in older compared to younger adults (Mouthon et al., 2016), we expected older participants to be especially interfered in their action production in the presence of simultaneous action perception (motor interference). Furthermore, increasing age is associated with a decrease in health (Brazier et al., 1992) and the ability to inhibit an automatic response tendency (Korsch, Frühholz, & Herrmann, 2014, 2016). Both factors were likely to influence the results and were therefore included as control measures.

Methods

Participants

In the current study, the reaction times of $N = 171$ participants between the ages of 20 to 80 years were assessed. From this sample, $n = 157$ participants (Table 1), who passed the quality criterion of at least 10 valid trials per trial type and finger (see Data analysis), were included into further analysis. All participants reported normal or corrected-to-normal vision. All procedures were approved by the local research committee and in accordance with the ethical standards of the 1964 Helsinki declaration and its later amendments. All participants gave written informed consent. They received a reward of an approximate value of USD 30,- for their participation.

Table 1

Participant Characteristics

Age Group (years)	n	Gender (n female)	Handedness (SD)	Education (SD)
20-29	26	16	40.01(58.76)	4.23(1.37)
30-39	31	25	73.42(39.22)	5.46(1.57)
40-49	23	11	81.84(27.74)	5.90(1.66)
50-59	27	18	55.02(41.79)	4.78(2.06)
60-69	32	20	80.15(40.46)	4.61(2.00)
70-80	18	8	81.36(38.29)	4.61(1.79)

Note. Characteristics of participants that passed the quality criterion and remained in sample (participants excluded per decade: 30-39: $n = 1$, 40-49: $n = 3$, 50-59: $n = 2$, 60-69: $n = 3$, 70-80: $n = 5$). Means and standard deviations are reported for handedness and education. Handedness (% right) was assessed with the Edinburgh Handedness Inventory (Oldfield, 1971). Highest education is reported in a score ranging from 1 = High School to 7 = University. The education level did not differ between decades, $F(1,148) = 0.31$, $p = .581$.

Procedure

The current study is part of a larger longitudinal research project on the interrelations of action perception and production throughout adulthood. The tasks employed in this project were designed to assess participants' oculomotor skills (e.g. smooth pursuit, saccade velocity), their action perception (operationalized via the prediction of the action goals) and their accuracy and speed in action production. Furthermore, several control measures such as the participants' health status, handedness, motor or cognitive skills were included. Some of these control measures were used for this study. Specifically, the participants' health status was measured with the RAND 36-Item Health Survey (Hays, Sherbourne, & Mazel, 1993). This self-administered survey instrument assesses the health-related quality of life with 36 items. It fulfils criteria for reliability and validity across the life span (Brazier et al., 1992) and discriminates reliably between healthy and unhealthy participants (Hays & Morales, 2001). All participants received the survey in an online version one week prior to the lab session. Participants' inhibition of an automatic response tendency was measured via a Go/noGo task of the Tests of Attentional Performance (TAP; Zimmermann & Fimm, 2012). In this task, the participants were asked to respond to a centrally presented cross ("x") with a button press and ignore a centrally presented plus sign ("+"). Participants' reaction times in this task were assessed in the lab session prior to the reaction-time task.

For this reaction-time task, we adapted an interference task introduced by Brass et al. (2000). Like in Brass et al.'s task, participants were asked to execute finger movements in response to a visually presented finger movement or a symbolic cue. Stimulus delivery and data acquisition were achieved by means of the program Experiment Builder (SR Research, Canada). Stimuli were presented on a 17" display placed in a 60 cm distance to the participant. To record participants' reaction times (RTs), their dominant hand rested on a keyboard with the index and the middle finger on two different keys (index finger: "N"; middle finger: "M"). Task instructions were given prior to the experiment and were repeated

right before each block of trials. Participants were asked to execute their finger movements as quickly as possible.

Stimuli

Each trial of the reaction-time task consisted of a sequence of five frames (17.98 ° x 20.75 ° visual degrees; Figure 1a). The sequence started by showing a male hand resting on a black surface with the index and the middle finger elevated. The hand was positioned to appear as a mirror image of the participant's dominant hand (according to Oldfield, 1971). This initial frame was identical for all stimuli and remained visible for 560 ms. Depending on the trial type, the next three frames presented a finger movement, a symbolic cue, or both. The overall displacement of the finger movement presented was 6.95 ° for the middle finger and 8.07 ° for the index finger. The symbolic cue "x" appeared on the fingernail of the corresponding finger. Each frame of this middle section was presented for 40 ms. The presentation of the fifth frame lasted for 520 ms and showed the hand in its final resting position. The total duration of each trial was 1'200 ms. Between the trials, a fixation cross was shown for 1'840 ms.

Design

The frame sequences in the reaction-time task were presented in two experimental conditions. The order of these two blocked conditions was counterbalanced between the participants. In the symbolic condition, the participants were asked to execute an index-finger movement in response to the presentation of a symbolic cue on the index finger and to respond with a middle-finger movement to the presentation of a symbolic cue on the middle finger. Hence, the relevant stimulus dimension in the symbolic condition was the symbolic cue. In the movement condition, participants executed an index-finger movement in response to an observed index-finger movement or a middle-finger movement in response to an observed middle-finger movement. In this condition, the observed finger movements served as the relevant stimulus dimension.

Within these two conditions, trials were presented as baseline trials, congruent trials or incongruent trials (Figure 1b). In baseline trials, the presented stimuli varied only on the relevant stimulus dimension. That is, baseline trials presented in the symbolic condition showed a fixated hand with the symbolic cross appearing on either the index or the middle finger. In the movement condition, participants observed the movement of the index or the middle finger without the additional appearance of the symbolic cue. In the congruent trials of both conditions, the symbolic cue appeared on the fingernail of the moving finger. In the incongruent trials, the finger that moved differed from the finger on which the symbolic cross appeared. Each condition consisted of 72 trials (24 baseline trials, 24 congruent trials, and 24 incongruent trials). Baseline, congruent, and incongruent trials were randomly distributed within each condition. Both conditions started with the presentation of five training trials. The training trials were excluded from all further analyses.

Figure 1. a. Sequence of pictures presented to the participants. b. Sample pictures for the different trials (baseline, congruent and incongruent) per condition (symbolic or movement).

Data analysis

Participants' RTs in the reaction-time task were calculated with respect to the second frame of the stimulus sequence of each trial. The interference between action perception and action production was indicated via the difference in baseline-corrected incongruent trials between the two conditions. This baseline correction was employed to make sure that the differences in interference scores between participants were not attributable to the individuals' differences in their baseline reaction times. Therefore, reaction times in the incongruent trials were corrected for baseline reaction times by dividing the RTs in the incongruent trials of one condition by the RTs in the baseline trials of the same condition. Next, this proportion in the movement condition was subtracted from the proportion in the symbolic condition. This motor interference score represents the influence of action

perception on the simultaneous action production, controlled for the visual input and the effect of a second task. Positive values of the motor interference score represent stronger interference in the symbolic condition whereas negative values are associated with a stronger interference in the movement condition. The same score was calculated for the congruent trials.

Trials in which the participants pressed the wrong key were coded as errors and excluded from all further analysis. The mean error rate was 0.75% ($SD = 2.89$). To ensure sufficient data quality, only participants with at least 10 (out of 12) trials per trial type (baseline, congruent, incongruent) and finger were included in the analysis. This resulted in the exclusion of $n = 14$ participants (mean age: 60.00 years).

Results

The results section is divided into two parts: First, we present the differences between the reaction times in the two conditions and the three trial types across age. Furthermore, we take a closer look at the incongruent trials of both conditions and compare the interference associated with them. Second, we explore the effect of age on these result patterns.

Differences between conditions and trial types

To replicate previous findings (Brass et al., 2000), we compared the reaction times in the two conditions (symbolic and movement) and the three trial types (baseline, congruent, and incongruent) across age. A 2 conditions x 3 trial types x age repeated measures ANOVA with a Greenhouse-Geisser correction determined that the reaction times differed across conditions, $F(1,155) = 34.74, p < .001, \eta^2 = .02$, trial types, $F(2,310) = 253.91, p < .001, \eta^2 = .04$, and age, $F(1,155) = 74.18, p < .001, \eta^2 = .29$. Furthermore, significant interaction between condition and trial type, $F(2,310) = 29.12, p < .001, \eta^2 = .01$, age and condition, $F(1,155) = 7.06, p = .009, \eta^2 = .01$, age and trial type, $F(2,310) = 3.83, p = .023, \eta^2 = .00$ and a three-way interaction between age, condition and trial type, $F(2,310) = 17.22, p < .001, \eta^2 = .05$.

² = .00, emerged. To explore these results in more detail, post-hoc tests using Bonferroni correction were performed.

The participants' reaction times in baseline trials did not differ between the two experimental conditions (symbolic and movement), $p = .159$. In the symbolic condition, the reaction times in congruent ($p < .001$) and incongruent ($p < .001$) trials differed significantly from baseline trials. Furthermore, the participants' reaction times in congruent and incongruent trials were significantly different from each other, $p < .001$ (Figure 2a). Thus, in the symbolic condition participants were faster in pressing the correct key when they were presented with a symbolic cue without an additional finger movement than when two cues (finger movement and symbolic cue) were presented simultaneously. In the movement condition, only the participants' reaction times in incongruent trials differed from baseline trials ($p < .001$). The reaction times in congruent and incongruent trials were significantly different from each other, $p < .001$ (Figure 2b). Hence, the participants showed the longest reaction times when the movement of the finger and the symbolic cue contradicted each other.

Taken together, in both conditions, participants' RTs were slower when symbolic cue and finger movement contradicted each other. To explore this finding further, we performed a dependent t-test on the difference score between the RTs in incongruent and congruent trials of both conditions. Results show that this difference score differed between the two conditions, $t(156) = 2.84$, $p = .005$, $r = 0.22$. The difference between incongruent and congruent trials was larger in case the participants had to ignore the irrelevant finger movement (symbolic condition; $M_{diff} = 28.72$ ms, $SD = 29.26$ ms) than when they had to ignore the irrelevant symbolic cue (movement condition; $M_{diff} = 20.13$ ms, $SD = 23.7$ ms).

Figure 2. Means and standard errors of reaction times (RTs) in the two experimental conditions (a. movement; b. symbolic) and all three trial types (** $p < .001$; ns = non-significant).

Influence of age

Since our first analysis indicated an effect of age and an interaction of age with condition and trial type, we took a closer look at these age-related influences. Specifically, we explored age-related differences in the interference of action perception on action production. For this, a motor interference score was calculated as described above. Positive values of the motor interference score represent stronger interference in the symbolic condition whereas negative values are associated with a stronger interference in the movement condition.

A linear regression of age on this motor interference score controlling for order of conditions, health status and inhibition was performed. This model significantly predicted the motor interference score, $F(4,143) = 7.70, p < .001, R^2 = .18$. Only age ($\beta = 0.002, SE = 0.000, p < .001$), but not order ($\beta = -0.006, SE = 0.013, p = .633$), health status ($\beta = -0.000, SE = 0.000, p = .390$) or inhibition ($\beta = -0.000, SE = 0.000, p = .119$), were associated with motor interference. To explore this effect in more detail, we performed two separate linear regressions of age on the RTs in incongruent trials in both conditions. Supporting our initial analysis, the results showed that age significantly predicted the RTs in incongruent trials of the symbolic condition, $F(1,155) = 15.23, p < .001$, and in incongruent trials of the movement condition, $F(1,155) = 7.03, p = .009$. Importantly, the effect of age was greater in the symbolic condition, $R^2 = .09$, compared to the movement condition, $R^2 = .04$ (Figure 3). This result pattern was unique to incongruent trials and a similar interference score calculated for the congruent trials was not associated with age, $F(4,143) = 0.98, p = .420$.

Taken together, our results indicate that, although age was associated with increases in reaction times to incongruent stimuli in general, this effect was greater in the condition, in which the participants had to ignore the finger movement (symbolic condition) compared to the condition, in which they had to ignore the symbolic cue (movement condition).

Figure 3. Regression of age (in years) on the baseline-corrected incongruent trials, separated by condition. The baseline correction was achieved by calculating the proportion of the reaction times (RTs) in the incongruent trials over the RTs in the baseline trials (e.g., a proportion of 1.1 indicates an interference of 10% in the reaction times of incongruent compared to baseline trials). See Appendix for the respective graph on congruent trials.

Discussion

In this study, we investigated age-related differences in the interrelations between action perception and action production. We explored whether advancing age influences how participants' action production is modulated by a simultaneous but incongruent action perception. Participants were asked to respond with a finger movement to the presentation of

a congruent or incongruent finger movement and/or symbolic cue. Specifically, while finger movement and symbolic cue were present in all trials (except for baseline trials), participants were asked to respond either to the movement or the symbolic cue depending on the experimental condition. Participants' reaction times were longer in incongruent trials compared to congruent and baseline trials of both conditions. Within these incongruent trials, participants' action production was affected to a greater extent by the perception of an incongruent action (symbolic condition) than by the perception of an incongruent symbolic cue (movement condition). However, the older the participants were, the more pronounced this effect was. Thus, the influence of age was accentuated in the symbolic compared to the movement condition.

We partly replicated previous findings (Brass, Bekkering, et al., 2001; Brass et al., 2000) by showing that participants were slower in incongruent trials compared to congruent and baseline trials independent of age and experimental condition. However, only a subset of our participants showed shorter reaction times in congruent compared to baseline trials ($n = 28$, $M_{age} = 43.7$ years), and – on average – our participants did not show such facilitation effects. Compared to Brass et al. (2000) we substantially enlarged the sample size and included participants who differed strongly in their age. In addition to these changes in the sample characteristics, we reduced the number of trials per condition (reliability of reaction times: Cronbach $\alpha > .95$). Hence, our participants were less trained in completing the task than participants in prior studies. Therefore, it might very well be the case that the previously reported facilitation effects might show up only after a certain amount of experience with the stimuli and the task (Bertenthal et al., 2006) and are only found in more homogeneous samples.

In this study, we were primarily interested in the reaction times in incongruent trials since, for the reasons outlined in the introduction, we expected these to be influenced strongest by increasing age. The longer reaction times of our participants in incongruent

compared to congruent and baseline trials indicate that the processing of two conflicting cues, the finger movement and the symbolic cue, interfered with action production (i.e., the participants' finger movement). Moreover, the increase in reaction time due to this interference was larger in the symbolic condition, in which the participants had to react to the symbolic cue and ignore the finger movement as compared to the movement condition, in which the participants were asked to react to the finger movement and ignore the symbolic cue. This is in line with the assumptions of the simulation theory (Jeannerod, 2001): In the incongruent trials of the symbolic condition in this study, action perception and production were associated with concurrent but conflicting action simulations (e.g., perception of middle-finger movement during production of index-finger movement). Hence, the associated internal action simulations might have interfered with each other leading to an increase in reaction times in incongruent trials of the symbolic condition compared to incongruent trials in the movement condition.

Alternatively, the larger difference between congruent and incongruent trials in the symbolic compared to the movement condition might be explained by low-level processes. That is, ignoring a more salient finger movement in contrast to ignoring the appearance of a symbolic cue might have been more difficult and therefore led to longer reaction times. Moreover, the reported effects might be confounded with spatial compatibility since the response finger not only matched the observed finger in terms of anatomical identity, but in terms of the side on which it was presented (right or left) and the symbolic cue was displayed on the fingernail of response finger. This is also why previous studies referred to our symbolic condition as the "spatial condition" (Brass et al., 2000). However, prior findings suggest a dissociation between imitative and spatial compatibilities, implying that they are driven by different underlying processes (Boyer, Longo, & Bertenthal, 2012; Wiggett, Hudson, Tipper, & Downing, 2011). Moreover, studies using similar paradigms have shown automatic movement imitation such as the one reported in our study independent of stimulus salience or

spatial compatibility (Bertenthal et al., 2006; Catmur & Heyes, 2011; Heyes, Bird, Johnson, & Haggard, 2005). Furthermore, the suppression of an incongruent movement during action perception is shown to be accompanied by increased activity of sensorimotor areas (Koski et al., 2002). Together, these findings make it unlikely that low-level processes alone explain our findings (for a review see Heyes, 2011).

In our study, advancing age was associated with the baseline-corrected incongruent trials of both experimental conditions. While it has been shown previously that increasing age is associated with a general slowing (Salthouse, 1996) and a more wide spread and less lateralized cortical activation with age (Cabeza, 2002), older adults are shown to be especially impaired when having to process several conflicting stimuli at the same time: Studies on action production during the perception of an incongruent symbolic cue report longer reaction times (Korsch et al., 2014, 2016; Maquestiaux, 2016), over-activation of brain areas involved (Zhu, Zacks, & Slade, 2010) and the activation of additional brain areas (Nielson, Langenecker, Garavan, & Hartley, 2002) for older compared to younger participants. However, these findings do not explain why the effect of age on the baseline-corrected incongruent trials is accentuated in the case action production was interfered by a simultaneous action perception (symbolic condition) compared to the condition in which action production was interfered by the simultaneous perception of a symbolic cue (movement condition).

Action production during the perception of a human action is assumed to operate on a different basis than the interference of an action-unrelated stimulus (Valchev et al., 2017). According to the simulation theory (Jeannerod, 2001), interference effects in concurrent action perception and production are mediated by the sensorimotor system. The activity of this system is shown to change with age (Sharma & Baron, 2014; Ward, 2006; Ward & Frackowiak, 2003), which is associated with a decrease of action perception (e.g., accuracy of action prediction, Diersch et al., 2012) and action production (e.g., greater movement

variability and deficits in coordination, Seidler et al., 2010). Furthermore, older adults compared to younger adults show activation in additional brain areas during movement execution, coordination and action perception (Diersch et al., 2016; Heuninckx et al., 2005; Heuninckx, Wenderoth, & Swinnen, 2008, 2010). As age advances, action perception and production might be increasingly associated with the activation of motor programs that are irrelevant for the on-going task. This reduced specialization might make the sensorimotor system more susceptible to challenges, which shows up as increased reaction times during simultaneous action perception and production. In line with the assumption of a less specialized processing in the sensorimotor system, older compared to younger adults show less selective corticomotor facilitation during action perception, action production and imagination (Léonard & Tremblay, 2008; Mouthon et al., 2016). Furthermore, Diersch et al. (2015) have shown an age-related decline in the distinctiveness of activation in the action-observation network (AON), a set of neuronal structures including frontoparietal regions and the posterior superior temporal sulcus (Grafton, 2009), which is active during action perception. Importantly, the age-related differences in this study were measured on the behavioural level as well and older compared to younger participants were less able to capture slight variations in the temporal continuation of a partially occluded action (also see Diersch et al., 2013, 2012). Hence, the accentuated influence of action perception on the simultaneous action production in our study might be an observable lead for age-related processes associated with a less precise internal representation and simulation of the actions perceived and produced (for a review see Costello & Bloesch, 2017). In line with this, the participants' performance in the inhibition task was not related to their motor interference. That is, the ability to inhibit an automatic response tendency was already controlled for in the motor interference score by subtracting the interference in the movement condition from the interference in the cross condition. Therefore, the motor interference score represents the

influence of action perception on the simultaneous action production controlling for the effect of a second task.

Nevertheless, our results are based on the analysis of participants' behaviour. Accordingly, interpretations about the underlying physiological processes remain speculative. Future studies using TMS or imaging techniques will further explore the neural mechanisms behind the reported age-related effects in action production. Furthermore, we investigated age effects cross-sectionally. Individual differences might lead to different developmental trajectories and are better captured with longitudinal investigations.

Taken together, our findings indicate that action production is interfered by a simultaneous action perception and that this motor interference effect increases with age. Importantly, our results show that age affects action production during the perception of an incongruent action differently than action production during the perception of an incongruent symbolic cue. This indicates that the processing of perceived actions interferes with action production beyond the effect of having to process two conflicting stimuli at the same time and is especially affected by advancing age.

All procedures performed in this study were in accordance with the ethical standards of the institutional research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards. Informed consent was obtained from all individual participants included in the study. The authors declare that they have no conflict of interest.

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Appendix

Figure A1. Regression of age (in years) on the baseline-corrected congruent trials, separated by condition.