The interaction between felt touch and tactile consequences of observed actions: an action-based somatosensory congruency paradigm

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Abstract

Action observation leads to a representation of both the motor aspect of an observed action (motor simulation) and its somatosensory consequences (action-based somatosensory simulation) in the observer’s brain. In the current electroencephalography-study, we investigated the neuronal interplay of action-based somatosensory simulation and felt touch. We presented index or middle finger tapping movements of a human or a wooden hand, while simultaneously presenting ‘tap-like’ tactile sensations to either the corresponding or non-corresponding fingertip of the participant. We focused on an early stage of somatosensory processing [P50, N100 and N140 sensory evoked potentials (SEPs)] and on a later stage of higher-order processing (P3-complex). The results revealed an interaction effect of animacy and congruency in the early P50 SEP and an animacy effect in the N100/N140 SEPs. In the P3-complex, we found an interaction effect indicating that the influence of congruency was larger in the human than in the wooden hand. We argue that the P3-complex may reflect higher-order self-other distinction by signaling simulated action-based touch that does not match own tactile information. As such, the action-based somatosensory congruency paradigm might help understand higher-order social processes from a somatosensory point of view.

Key words: mirror neurons; motor simulation; somatosensory simulation; P3; sensory evoked potential (SEP); self-other distinction.

Introduction

Understanding what other people do is crucial for interacting in a social environment. Over the last two decades, evidence has accumulated that social understanding is partly based on co-representing other people’s actions and sensations in brain areas dedicated to experiencing these ourselves (we refer to this as ‘simulation’). When we observe an action for instance, we simulate the observed behavior within our own motor system (for reviews, see Rizzolatti and Craighero, 2004; Keysers, 2011; Keysers and Gazzola, 2014). However, we do not only simulate observed motor behavior, we also simulate observed somatosensory events within our own somatosensory systems (for a review, see Keysers et al., 2004, 2010). Seeing someone in pain, for instance, elicits activation in the insula, as if one undergoes the pain oneself (Bufalari et al., 2007; Lamm et al., 2011; Riečansky et al., 2014). Similarly, vicarious activations in the somatosensory cortex occur when observing someone being touched (next: ‘passive touch simulation’; Keysers et al., 2004, 2010; Blakemore et al., 2005; Schaefer et al., 2006, 2009, 2012; Ebisch et al., 2008; Pihko et al., 2010). Importantly, motor and somatosensory events usually do not occur in isolation in a social environment. When we observe somebody grasping an object, for example, this also involves the observation of somatosensory events (i.e. the person touching the object). Therefore, it is not surprising that functional magnetic imaging studies have yielded evidence for the involvement of
somatosensory brain areas in action observation (next: we refer to this as action-based somatosensory simulation; Keysers et al., 2004, 2010; Gazzola and Keysers, 2009; see also Avenanti et al., 2007).

While these findings suggest that the somatosensory consequences of observed actions are simulated simultaneously to the motor component thereof (Keysers et al., 2004, 2010; Avenanti et al., 2007; Gazzola and Keysers, 2009), direct evidence for this is still lacking. The reason is, that it is difficult to localize brain activity in the somatosensory cortex that is specific to the effector that is actually producing the action. In other words, we do not know whether the action-based touch simulation is specific to the spatial location of the touch observed on the agent’s body. One way to directly investigate this is by applying a manipulation in which the observed action-based touch of others is combined with a tactile stimulus that is either congruent or incongruent to the observed touch in terms of spatial location on the participant’s body. If action-based somatosensory simulation reflects the simulation of the actual somatosensory consequence of the observed action, and the cognitive system compares this information to own felt touch, the brain should distinguish between these spatially congruent and spatially incongruent trials. In the field of passive touch observation, studies showed that the observed passive touch activates somatotopically organized areas in S1 (Blakemore et al., 2005; Kühn et al., 2014). Likewise, in the field of action observation, studies showed that observed actions executed by different effectors (mouth, hand and foot) activate the premotor cortex in a somatotopically organized manner (Buccino et al., 2001). In addition, it was shown that the spatial congruency of observed passive touch and felt touch affects the processing of felt tactile sensations (e.g. Tsakiris, 2008; Longo et al., 2012), while the spatial congruency of observed finger movements and own motor intentions affects the execution of own finger movements (Brass et al., 2000, 2001, 2005). Accordingly, we reasoned that if action-based somatosensory simulation of fingers is specific to the location of the touch (i.e. somatotopically organized), and if the brain compares these action-based touch representations to felt touch, the cognitive system should process own somatosensory sensations differently when somatosensory consequences of the observed human action are corresponding to them in location (next: effector-specific congruency), as compared with when they are not. We therefore used a congruency manipulation where participants saw a tapping movement of the index or middle finger while receiving tactile stimulation at the finger tip of either the congruent or incongruent finger.

Interestingly, a limited amount of behavioral studies (Thomas et al., 2013; Gillmeister, 2014) has already yielded preliminary evidence for the existence of such processes, by showing for instance amplified intensity judgements of tactile stimuli presented at one’s own hand when observing a finger movement that has corresponding somatosensory consequences (Gillmeister, 2014). Neuroimaging studies combining motor observation with sensations of touch, however, provided non-realistic tactile feedback for the observed action, in which the somatosensory consequences of the observed actions never fully corresponded with the felt tactile sensations in time and space (Avikainen et al., 2002; Rossi et al., 2002; Voisin et al., 2011; see also Gillmeister, 2014). As such, they could not assess whether action-based touch simulation is specific to the spatial location of the touch observed on the agent’s body. Furthermore, existing studies did not yield insights in the temporal signature of the neuronal processes involved.

In the current electroencephalography (EEG) study, we wanted to gain insight in how somatosensory consequences of observed actions are represented in the human brain. In order to do so, we used a paradigm in which participants viewed simple finger movements and received congruent or incongruent tactile feedback (Figure 1). More specifically, we presented short series of images showing index and middle finger tapping movements, while synchronously presenting a tap-like tactile stimulation on the tip of either the middle or the index finger of the observer’s corresponding hand. As such, the tap-like stimulation at the finger was either congruent with the sensory consequence of the observed finger movement (e.g. observing a tapping movement of the index finger while getting a tactile stimulation at the tip of the index finger) or incongruent (e.g. observing a tapping movement of the index finger while getting a tactile stimulation at the middle finger). This means that in congruent trials the tactile stimulation will match the observed finger movement in terms of relative spatial location, whereas there will be a mismatch in incongruent trials. Image series of human and of wooden hands were presented. Given the observation that non-human agents engage simulation processes to a lesser extent (Tsai et al., 2004; Tsai and Brass, 2007; Holle et al., 2011; Streltsova and McCleery, 2014; Beck et al., 2013), we expected congruency differences to diminish when the observed hand is a wooden hand. While a congruency effect for human hands-only would indeed be the most straightforward result, any interaction of animacy and congruency would suggest that the interaction of action-based touch observation and felt touch is effector-specific. Indeed, an interaction effect indicates that the cognitive system distinguishes between the human and wooden hands while responding to the relative (mis)match of simulated and felt touch. Additionally, the wooden hands serve as a control for low-level visual and spatial compatibility effects (see also Hommel and Prinz, 1997; Brass et al., 2000; Catmur and Heyes, 2011). For a given congruency condition, the relative spatial compatibility will not vary between the two types of hands. Hence, a main effect of congruency could be due to effects of low-level visual or spatial compatibility, whereas a main effect of animacy is expected if action observation has a social but neither an effector-specific nor a spatial influence on the processing of own somatosensory sensations. The design thus allowed us to disentangle social effects of effector-specific congruency from non-social effects of spatial congruency.

Due to its excellent temporal resolution, EEG is a very useful method for providing insights into the neural dynamics of somatosensory consequences of observed actions. Indeed, by evaluating event-related potentials (ERPs), we can investigate at which processing stage(s) action-based somatosensory simulation interacts with felt touch in an effector-specific way. This may be of particular importance for making a functional interpretation of the observed effects. While modulations of early sensory evoked potentials (SEPs) in studies investigating passive touch simulation have been attributed to processing of body-related information in somatosensory areas (e.g. Aspell et al., 2012), later neuronal processes have been argued to underlie higher-order social cognitive processes such as self-other distinction (Synofzik et al., 2008; Spengler et al., 2009, 2010; Knyszew, 2013). Indeed, research has shown that lower-order sensorimotor and higher-order cognitive aspects of self-other distinction can be disentangled (Synofzik et al., 2008). Likewise, we will focus on two different processing stages:

First, we will investigate the influence of observed action-based touch in an early stage of tactile processing, reflected by
the SEPs P50, N100 and N140. The primary somatosensory cortex is argued to account for SEPs elicited at 50 ms or earlier (e.g. P50), whereas the secondary somatosensory cortex is said to be involved in the generation of later SEP components (Allison et al., 1992; see also Bufalari et al., 2007; Longo et al., 2011). Therefore, we expect more low-level effects in the P50, such as a main effect of congruency and/or animacy (Bufalari et al., 2007; Aspell et al., 2012; Martínez-Jauand et al., 2012). If action-based somatosensory processing would interact with felt touch in an effector-specific way already at an early stage, we would expect a larger congruency effect for human as compared with wooden hand stimuli in the N100 and N140 components (i.e. Press et al., 2008; Streltsova and McCleery, 2014; Cardini et al., 2012). If not, we would predict larger amplitudes for human as compared with wooden hand trials (main effect of animacy; see also Beck et al., 2013; see also Serino et al., 2008, 2009).

Second, we will evaluate the interplay of observed action-based touch and felt touch at a later higher-order stage: the P3-complex (see also Holeckova et al., 2006; Polich, 2007; Longo et al., 2012). We reasoned that the P3-complex is a likely neuronal index of higher-order self-other distinction (Spengler et al., 2009, 2010), because it has been implicated in congruency processing (e.g. Zhou et al., 2004; Longo et al., 2012), in self-referential processing (Knayzev, 2013) and in high-level multisensory comparison processes (Yamaguchi and Knight, 1991; Macaluso, 2006; Kühn et al., 2011; Longo et al., 2012). The effector-specificity of action-based somatosensory simulation at this stage would be expressed as a congruency effect for human hands only in the P3 components.

**Materials and Methods**

**Subject**

A total of 44 healthy Caucasian volunteers participated in the study [age range 19–49 years (M = 27.73; s.d. = 7.77), 22 male]. For 27 of them, the experiment was the first in a larger battery of studies not considered here, while the others only performed the current paradigm. The only difference in the design for the previous group was the presentation of a brief unrelated period of tactile sensations before the start of the experiment was announced. More specifically, we randomly applied 30 tactile stimulations to the index finger and an equal amount to the middle finger of the participant, identical to the ones used in the experiment. An interstimulus interval of 700 ms was applied, while continuously showing the black screen with the white fixation cross in the middle. Data patterns did not significantly differ between groups, as confirmed by a 2x2 mixed design analysis of variance (ANOVA) on pooled data for each of the ERP components of interest (with animacy and congruency as within-subjects factors and experiment as a between-subjects factor). Significant results involving the experiment factor were not detected (all P-values > 0.05), while our main experimental findings were preserved. Therefore, the data are presented as a whole. Three participants were excluded from the analyses: one did not finish the entire experiment while another one showed a large amount of slow waves due to heavy transpiration. The third person verbalized after the experiment that he had reasons to believe that he was suffering from autism spectrum disorder, although he had not received a formal diagnosis. The first author of this article has received formal training and licensing in diagnosing autism spectrum disorder and was thus able to form an educated guess. Remaining participants had normal or corrected-to-normal vision. All save one were right-handed, as indicated by the Edinburgh Handedness Inventory (Oldfield, 1971). All remaining participants reported a history free of neurological, psychiatric, sensory or motoric problems. All participants gave written informed consent and were financially compensated for their participation. The ethics committee of Ghent University approved the study.

**Materials**

The experiment was conducted in a dimly lit, electrically shielded and sound-attenuated room. The participant was...
seated at ~60 cm distance from a 17 inch monitor. All visual stimuli were 640 × 380 pixels large and were centrally presented. The participant was seated directly in front of the monitor, both hands were placed in a natural palm-down position on the table. Consequently, the participant’s left and right hand were placed, respectively, slightly left and right from the middle of the screen. A dark cloth prevented the participants from seeing their right hand. A keyboard was placed within reach of the left hand. Tactile stimulations were achieved by means of a custom made tactile stimulator (Dancer Design; www.dancerdesign.com.co.uk). We used two independently controlled piezo elements with tape, informing them that this way they would not be able to move their hand. Stimulus delivery and data acquisition were achieved by means of the program Presentation (Neurobs), ran on a HP Compaq desktop with Windows XP driver.

Design and procedure
Each trial started with showing a right hand in a neutral posture from a first person perspective, corresponding to the participant’s own right hand (1000 ms). This was followed by an index or middle finger in a tapping position (1200 ms) and ended with a black screen (700 ms). The onset of the tapping position frame was synchronized with a ‘single tap’ touch sensation to the back of the index or middle finger of the participant. In order to achieve this sensation, the piezo-element of the tactile stimulator was driven by an audio file containing a single sawtooth waveform. In congruent trials, the observed hand executed a finger movement that would, when executed by one’s self, naturally lead to the tactile sensation at the corresponding finger of the participant. In incongruent trials, the observed hand movement was incompatible with the presented tactile sensation. For human hands, a picture of the right hand of a Caucasian female was presented, whereas for wooden hands, a picture of a right mannequin hand was used. Throughout the trial presentation, a fixation mark (+ sign) was continuously presented in the center of the screen. A color change of the fixation mark accompanied the tapping position frame in 10% of the trials in each condition. Participants were instructed to attend the fixation mark and to count the number of red fixation crosses. During the breaks, the participant was asked to respond with his left hand and the number keys. Accuracy feedback was provided afterwards.

There were two within-subject variables in the design: animacy (human vs wood) and congruency (congruent vs incongruent). This leads to four experimental conditions: human congruent, human incongruent, wood congruent and wood incongruent. In the total experiment, 800 trials were presented. Human and wooden hand trials were presented in separate blocks, of which the order was counterbalanced across participants. Within each animacy block, 200 congruent and 200 incongruent trials were randomly presented, with an equiprobability of index finger and middle finger movements. Self-paced breaks occurred after every 40 trials. The experiment proper lasted 48 min.

EEG recording and analyses
EEG was recorded using a Biosemi ActiveTwo recording system at a sampling rate of 1024 Hz from 64 active electrodes, placed according to the international 10/20 setting. Bipolar electrodes were placed, respectively, above and below the left eye to measure eye blinks, and with left and right canthal montage for measuring horizontal eye movements. Electrode offsets were kept between ~25 and 25 μV at all electrodes. Additionally, two electrodes were placed on the mastoids for offline referencing.

EEG data were analyzed using BrainVision Analyzer 2 (BVA; Brain Products). The raw data were rereferenced offline to the average of the left and right mastoid. We applied a high pass filter of 0.1 Hz, a low pass filter of 30 Hz and a notch filter of 50 Hz. ERPs were time-locked to the onset of the tactile stimulation and epochs were generated running from –100 to 400 ms. Prior to averaging, the data were automatically corrected for eye movement artifacts. An automatic artifact rejection was applied including a gradient check (maximum allowed voltage step: 50 μV/ms within 200 ms before and after the locked event), a minimum/maximum amplitude check (–100 and 100 μV, respectively) and a low activity check (0.5 μV within an interval length of 100 ms). Target trials were discarded from analyses. Because we were primarily interested in congruency-related processes, the data were collapsed by congruency, over left and right finger movements observations. All statistical analyses were conducted with SPSS Statistics 20 on exported mean area amplitudes. Greenhouse–Geisser corrections were applied where needed.

Results

Behavioral results
Due to technical problems, the behavioral results of one of the remaining participants could not be analyzed. For the others, a correct counting response was given on 93.25% of break questions on average (s.d. = 6.46%). Because of the very low error rates and the focus on EEG-results, further behavioral analyses were not performed.

ERP results
Sensory evoked potentials. Visual inspection of the data revealed clear P50, N100 and N140 SEP components, at time latencies and with topographic characteristics as reported in SEP literature (e.g. Bufalari et al., 2007; Streltsova and McCleery, 2014; Cardini et al., 2012). Visual inspection showed that stable component topographies extended from 45 to 55 ms, from 85 to 100 ms and from 105 to 120 ms, respectively. With respect to both the P50 and N100, the topography was centered around electrodes AF3, AFz, F3, F1 and Fz (Figure 2A and B). Accordingly, these electrodes and fixed analyses windows were selected for analyses (Figure 3; for similar P50 and N100 topographies, see Bufalari et al., 2007; Streltsova and McCleery 2014). Given the clearly different topography of the N140 (Figure 2C) and similarly to earlier literature (e.g. Cardini et al., 2012), electrodes FC3, FC5, C3 and C5 were selected for N140 analyses (Figure 4).

P50. A 5 × 2 × 2 repeated-measures ANOVA including the factors electrode, animacy and congruency confirmed a significant interaction effect of the factors animacy and congruency (F(1,40) = 4.5, P < 0.05; Figure 5), indicating that already at a very early processing stage information about animacy and congruency is integrated. No other effects reached significance (all P > 0.05). Paired comparison tests (with pooled averages over the five electrodes) indicated that for wooden hand trials, the congruent tactile stimulations elicited a larger P50 (M = 0.78 μV),...
as compared with incongruent ones ($M = 0.50 \mu V; t(40) = 2.43, P < 0.05$) but also as compared with the human hand trials (for the human congruent condition: $M = 0.43 \mu V; t(40) = 2.70, P < 0.05$; for the human incongruent condition: $M = 0.53 \mu V, t(40) = 1.94, P = 0.06$). Paired comparisons showed no significant difference between incongruent and congruent trials for human hand trials ($t(40) = 0.75, P = 0.46$).

**N100.** At identical electrode sites, a $5 \times 2 \times 2$ repeated-measures ANOVA showed a significant main effect of animacy in the N100 amplitude ($F(1,40) = 15.52, P < 0.001$), indicating a larger amplitude for human than for wooden hand trials ($M = -1.33 \mu V$ and $M = -0.96 \mu V$, respectively). Apart from a main effect of Electrode ($F(1.7, 67) = 12.18, P < 0.000$), no other tests showed significant results (all $P > 0.05$).

**N140.** A $4 \times 2 \times 2$ repeated-measures ANOVA (including the factors electrode, animacy and congruency) identified a reliable main effect of animacy in the N140 ($F(1, 40) = 10.86, P < 0.005$). Similar to the N100, a larger N140 was found for human than for...
wooden hand stimuli (respective means: $M = 1.15 \mu V$ and $M = 0.84 \mu V$). No other effects reached significance (all $P > 0.05$).

**P3-complex.** The data showed a P3-complex, comprising an early P3 component, with a positive peak with a stable central parietal topography from 230 to 270 ms, and a later component between 310 and 360 ms, with a slightly more parietal distribution. Given the topographical maps (Figure 2D and E) and corresponding with earlier literature (e.g. Yamaguchi and Knight, 1991), electrodes Cz, CPz and Pz were selected (Figure 6) for further analyses. We performed $3 \times 2 \times 2$ repeated-measures ANOVAs with the factors electrode, animacy and congruency for both the early and the late P3 component.

**Early P3.** With regard to the early P3-component, the test showed an animacy effect ($F(2,80) = 4.70, P < 0.05$) and an electrode × animacy interaction effect ($F(1.15, 45.95) = 4.79, P < 0.05$). This interaction effect indicates larger amplitudes for wooden as compared with human trials at electrodes Pz ($t(40) = 3.61, P = 0.001; M = 4.96 \mu V$ and $M = 4.35 \mu V$) and CPz ($t(40) = 2.24, P < 0.05; M = 5.00 \mu V$ and $M = 4.45 \mu V$) but not at Cz ($t(40) = 0.75, P = 0.46; M = 5.22 \mu V$ and $M = 5.40 \mu V$). Further, an electrode × congruency interaction was detected ($F(1.51, 60.52) = 4.29, P < 0.05$). Paired comparisons showed larger amplitudes for congruent trials as compared with incongruent trials at electrode Cz ($t(40) = 2.1, P < 0.05; M = 5.44 \mu V$ and $M = 5.18 \mu V$, respectively), a marginal difference at electrode CPz ($t(40) = 1.8, P = 0.08; M = 5.32 \mu V$ and $M = 5.12 \mu V$, respectively) and no difference at Pz ($t(40) = 0.66, P = 0.51; M = 4.70 \mu V$ and $M = 4.62 \mu V$, respectively). Additionally, an animacy × congruency interaction was observed ($F(1,40) = 9.01, P = 0.005$). Interestingly, paired comparisons confirmed our hypothesis that a congruency effect should be restricted to seeing a human hand moving: for human hands, a smaller P3 was found for incongruent trials as compared with congruent trials ($t(40) = 4.24; P < 0.001; M = 4.58 \mu V$ and $M = 5.13 \mu V$, respectively), whereas no difference existed for wooden hand trials ($t(40) = -0.96; P = 0.34$; $t(40) = 0.96; P = 0.34$).

**Fig. 4.** ERP waves at electrode sites FC5, FC3, C5 and C3. The N140 peaks are labeled at electrode FC5.

**Fig. 5.** Plot of the P50 amplitudes (pooled per condition over the electrodes AF3, AFz, F3, F1 and Fz in the time frame 45–55 ms) showing an animacy × congruency interaction effect.
$M = 5.36 \, \mu V$ and $M = 5.17 \, \mu V$, respectively; Figure 7A). In effect, the P3 for human incongruent trials seceded from that of other conditions. No other effect reached significance.

Late P3. With regard to the late P3-component, the test showed a strong continuation of the congruency x animacy interaction effect ($F(1,40) = 14.45, P < 0.001$; Figure 7B), next to a main effect of Congruency ($F(1,40) = 4.79, P < 0.05$). Paired comparisons of the interaction effect confirmed the aforementioned smaller P3 for incongruent trials as compared with congruent trials for the human hand ($t(40) = 4.55; P < 0.001; M = 3.31 \, \mu V$ and $M = 4.07 \, \mu V$), with no difference for wooden hand trials ($t(40) = 0.19; P = 0.19; M = 4.12 \, \mu V$ and $M = 3.88 \, \mu V$, respectively). Apart from a main effect of electrode ($F(1.06,42.34) = 51.49, P < 0.001$), no other effects reached significance.

Discussion

Previous research has investigated the involvement of somatosensory brain areas in action observation (Keysers et al., 2004, 2010; Avenanti et al., 2007; Gazzola and Keysers, 2009). The aim of the current study was to investigate the specificity of action-based somatosensory simulation, and comparison processes of this specific type of simulation with felt touch. We investigated this by means of a congruency manipulation of observed action-based touch and felt touch: participants observed a tapping movement of an index or middle finger while simultaneously receiving a tactile stimulation at the same or a different finger. To investigate social effects and to control for non-specific effects such as spatial compatibility (Streltsova and McCleery, 2014; Gillmeister, 2014), we presented an animated wooden hand in half of the trials. Our results showed that an interaction of action-based somatosensory simulation and felt touch was present at an early stage of somatosensory processing (P50) and at a late stage of higher-order social processing (P3).

Action-based somatosensory simulation at an early stage of somatosensory processing: SEP results

As a first aim, we wanted to know whether an effector-specific interaction of action-based somatosensory simulation and felt touch already occurs at an early stage of somatosensory processing. We proposed that an interaction of animacy and congruency would most likely appear in the N100 and the N140 SEP components, next to low-level main effects in the P50.
component. Interestingly however, in contrast to our predictions, we found an interaction already in the P50, with wooden congruent trials eliciting the largest P50 amplitudes as compared with all other conditions. Importantly, although the congruency effect was found in the wooden rather than the human hand, this interaction effect nevertheless reflects a social influence. It indicates that the cognitive system distinguishes between the human and wooden hands while responding to the relative (mis)match of simulated and felt touch. As such, our data provide evidence for effector-specific action-based somatosensory simulation already at a very early neuronal processing stage. At this point however, we can only speculate about a functional interpretation of the observed pattern. Facilitation of the P50 SEP component has often been explained in terms of heightened attention in somatosensory processing (e.g. Eimer and Forster, 2003; Schubert et al., 2006, 2008; Aspell et al., 2012; Popovich and Staines, 2014). Therefore, one could assume that the human somatosensory system might engage more in sensory prediction for congruent than for incongruent animate actions (see also Cross et al., 2012). As such, the inanimate congruent trial might lead to a more severe mismatch (‘prediction error’) when the observed hand was non-human, as suggested by a significant comparison between the congruent trials of both hand types. Also, activity of the SI has been related to the attribution of observed touch to one’s own body (Schaefer et al., 2006). In line with our earlier interpretation, the congruent tactile stimulation might as well be perceived as very difficult to attribute to one’s own body when the observed hand is inanimate, leading to the larger effect in the P50 (Aspell et al., 2012; for similar effects see Streltsova and McCleery, 2014). The pattern of results in N100 and N140 SEP components is more straightforward. While no evidence for effector-specific congruency could be observed in these components, they did show larger amplitudes for human vs wooden hand movements, irrespective of congruency. As was found in earlier (though passive) visuotactile studies, our findings add to the idea that only the observed touch of a human agent is remapped onto the observer’s SII (Beck et al., 2013; see also Serino et al., 2008, 2009), similarly to research where touch applied to different types of inanimate objects did not alter the N140 (Press et al., 2008). In addition, it relates to behavioral findings that human action observation enhances the processing of felt touch (Thomas et al., 2013). Our results thus add to the evidence for a specific sensitivity of late SEPs to human stimuli (see also Blakemore et al., 2005). Interestingly, our data suggest that the early P50 SEP responds more to inanimate action, whereas the later N100 and N140 SEPs showed larger amplitudes toward observed animate action. One way to reconcile these results might be to assume different pathways from the visual system to the somatosensory system for self-related and other-related observed actions (see also Cardini et al., 2013), with the P50 seemingly tapping into the latter.

**Fig. 7.** Plot of the animacy × congruency interaction effect (pooled per condition over the electrodes Cz, CPz, Pz). (A) Effect in the early P3 in the time frame 230–270 ms. (B) Effect in the late P3 in the time frame 310–360 ms.

**Action-based somatosensory simulation at late stages of social processing: P3 results**

As a second aim, we investigated the effector-specificity of action-based somatosensory simulations in the P3-complex. We advanced the P3-complex (see also Holecakova et al., 2006; Polich, 2007) as a plausible candidate for higher-order self-other distinction (e.g. Zhou et al., 2004; Macaluso, 2006; Longo et al., 2012; Knyazev, 2013). We reasoned that if the action-based somatosensory sensations would be effector-specific, here we should find a congruency effect for human hands only. Indeed, next to a main effects of animacy and congruency, a significant animacy by congruency interaction effect was observed, which continued to be significant in the later stage of the P3. Specifically, the results showed smaller early and late P3 amplitudes for human incongruent trials than for human congruent trials, while no such congruency effect was apparent for wooden hand stimuli. As such, we provide clear evidence for the effector-specific influence of action-based somatosensory simulation at a late higher-order stage of processing.

Given this pattern of results, we suggest that the P3 in our paradigm can indeed be interpreted as a neural correlate of higher-order self-other distinction. More specifically, we argue that simulated action-based somatosensory sensations that mismatch with felt touch might help to distinguish the self from others, as reflected in smaller amplitudes for the human incongruent condition in this component. This interpretation adds to the literature where basic novel, salient or deviant sensory stimuli in a multisensory environment lead to modulations of the P3 component (Friedman et al., 2001; Escera et al., 2003; Polich, 2007). Within the social neuroscience literature, research has related late parietal components to self-referential processing (for a review, see Blank et al., 2005; Holecakova et al., 2006; Longo et al., 2012; Knyazev, 2013). In the context of joint action, it was suggested that a reduced P3 for incompatible trials indicates perceptual interference, while at the same time being sensitive to social information (Sebanz et al., 2006). In a study investigating cognitive aspects of the sense of agency, smaller P3 components reflected the judgement of stimuli as externally produced, and thus not self-generated (Kühn et al., 2011). Combining these lines of research, it is conceivable that the suppression of the late P3 reflects higher-order social processes.
of self-other distinction. Per definition, no social information can be derived without making use of our senses (Decety and Lamm, 2007). It thus makes sense to postulate a neural system that underlies cognitive aspects of self-other distinction by signaling instances where simulated sensory information does not match sensory information coming from one’s own body.

The role of the simulating somatosensory consequences of observed action in social perception

In this study, we demonstrated that the P3 signals simulated action-based touch that does not match with felt touch. Previous studies (Papeo et al., 2010; Longo et al., 2012) show, however, that the P3 acts as an indicator of (mis)matching simulated and felt somatosensory sensations also when the observed touch is passive in nature (i.e. a hand being touched; see also Gillmeister, 2014). For instance, Longo and colleagues (2012) showed smaller P3 amplitudes for incongruent vs congruent trials in a ‘mirror box’ manipulation, in which the view of passive tactile stimulations applied to the own hand was mirrored. Interestingly, when transcranial magnetic stimulation was used to disturb the activity of the right temporoparietal junction (TPJ) in the ‘mirror box’ paradigm (Papeo et al., 2010), a reduced behavioral congruency effect was observed (see also Pasalar et al., 2010). Though the P3 is quite an intangible component in terms of its generators, earlier ERP literature has implied the TPJ as one of its sources (Bledowski et al., 2004; Mulert et al., 2004; Blanke et al., 2005; Verleger, 2008; Longo et al., 2012). Other neuroimaging research is needed to confirm this, but it might suggest that the P3 signals both active and passive mismatching touch.

Therefore, one could argue that the neuronal activation signaling mismatching simulated touch is not specific to action-based sensory simulation, because it does not require a motor component. Alternatively however, one could also argue that classic passive touch paradigms very often involve motor simulation, because usually someone else is inducing the touch (e.g. Ebisch et al., 2008; Schaefer et al., 2009, 2012; Papeo et al., 2010; Longo et al., 2012). From this perspective, action-based somatosensory simulation related to the agent’s movements could underlie the reported effects in these ‘passive’ touch studies. This interpretation would also shed light on studies where no differences are found for the processing of observed touch applied to human vs inanimate objects (e.g. Keysers et al., 2004; Ebisch et al., 2008). The (implicit) presence of an agent applying the touch (see also Streltsova and McCleery, 2014) might lead to motor simulation in these inanimate conditions as well. More carefully controlled research is needed to test these two alternative interpretations.

Conclusion

In sum, our study shows that action-based somatosensory experiences of others can be used to match felt touch (see also Thomas et al., 2013; Gillmeister, 2014). Using ERPs, this study was the first to show effector-specific neuronal interactions of action-based somatosensory simulation and felt touch at two different levels of processing. First, we found an interaction of animacy and congruency in early somatosensory processing (P50). However, the pattern of this interaction is difficult to interpret. We also described animacy effects during later somatosensory processing (N100 and N140). Importantly, in the P3-complex we found the expected pattern of results, with a specific modulation of the P3 amplitude as a function of congruency for a human but not for non-human agent. The latter result adds to earlier findings where processes comparing observed passive touch and felt touch seem to underlie higher-order social cognition such as self-other distinction (Tsakiris, 2008, 2010; Kühn et al., 2011; Cardini et al., 2012; Longo et al., 2012). The action-based somatosensory congruency paradigm may thus inform us about the way healthy and clinical populations use action-based touch simulations to represent the social world.

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