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ARTICLE

It's not me, it's you - Differential neural processing of social and non-social nogo cues in joint action

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ABSTRACT

This study used a joint flanker task to investigate differences in processing of social and non-social nogo cues, i.e., between cues indicating that a co-actor should respond and cues signaling that neither actor nor co-actor should respond, using event-related potentials (ERPs) and trial-to-trial response times (RTs). It was hypothesized that a social co-actor's response should be reflected in stronger modulation (slower RTs on subsequent trials; augmented neural responses) for social compared to non-social nogo. RTs and ERPs replicated flanker compatibility effects, with faster responses and increased P3a on compatible trials. In line with the hypotheses, ERPs revealed distinct coding of social and non-social nogo in the conflict-sensitive N2 which showed a compatibility effect only for social nogo, and in the attention/memory-related P3b which was larger for social relative to non-social nogo. The P3a did not distinguish between social and non-social nogo, but was larger for compatible and smaller for go trials. Contrary to our hypotheses, RTs were faster after social relative to non-social nogo. Hence, the representation of the co-actor's response in joint action modulates conflict processing reflected in the N2 and response discrimination and evaluation reflected in the P3b and may facilitate subsequent responses in the context of social versus non-social nogo.

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Performance monitoring; task sharing; cognitive control; electroencephalography (EEG); event-related potentials (ERPs)

Introduction

A growing body of research is emphasizing the impact of social context on behavior and neural responses to imperative stimuli. Examples of social context modulations include, but are not limited to, social observation (i.e., presence or absence of an observer; Barker, Troller-Renfree, Pine, & Fox, 2015; Peterburs et al., 2017; Zajonc, 1965), sender attributions (i.e., alleged source of feedback/information; Peterburs, Sandrock, Miltner, & Straube, 2016; Schindler & Kissler, 2016), and joint action (i.e., sharing of a task between at least two actors who each respond to a specific task set; Atmaca, Sebanz, & Knoblich, 2011; Liepelt & Prinz, 2011; Sebanz, Knoblich, & Prinz, 2003).

Effects of joint action are typically investigated with interference tasks such as the Simon task (Simon, 1969) or the Eriksen flanker task (Eriksen & Eriksen, 1974). In these tasks, response times are faster if the side an imperative stimulus is presented on matches the response side ("Simon effect"; Simon, 1990), or if flankers are compatible rather than incompatible with a target stimulus (flanker task). Simon effects are evident in both standard and joint Simon tasks, but do not emerge when one person completed the joint task alone by responding only to their imperative stimulus while ignoring the other (Sebanz et al., 2003). In the joint flanker task, participants respond more slowly when flankers are potential targets for co-actors (incompatible trials) as compared to flankers compatible with the own target, or to neutral flankers (Atmaca et al., 2011).

Joint action effects have been attributed to automatic co-representation of the own and the co-actor's task rules and actions, i.e., as social phenomena (Sebanz et al., 2003; Sebanz, Knoblich, & Prinz, 2005). However, the social co-representation account has been challenged by findings of "social" Simon effects (Dolk et al., 2011; Dolk, Hommel, Prinz, & Liepelt, 2013) and Flanker effects (Dolk, Hommel, Prinz, & Liepelt, 2014b) also for non-human co-actors (e.g. a Japanese waving cat) or attention-grabbing objects (e.g. a metronome) (for a review, see Dolk et al., 2014a, 2013; Stenzel & Liepelt, 2016b). Based on these findings, an alternative account, the referential coding account (Dolk et al., 2013), proposes that both internal and external action

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events are cognitively represented in a common format – common coding (Hommel, MüSseler, Aschersleben, & Prinz, 2001; Prinz, 1997). Greater similarity between the own and the co-actor's response is associated with greater conflict at the action discrimination/selection stage and thus a stronger need to discriminate between the two responses in order to enable self-other distinction. Along these lines, in a joint action setting, discriminating features in the action representations are weighted more strongly (Memelink & Hommel, 2013). Such features may entail spatial attributes such as left and right (Dittrich, Rothe, & Klauer, 2012; Dolk et al., 2013; Guagnano, Rusconi, & Umilta, 2010), or other discriminating attributes such as color (Sellaro, Dolk, Colzato, Liepelt, & Hommel, 2015) or valence (Stenzel & Liepelt, 2016a).

The neural processes underlying joint action have been investigated with electroencephalography (EEG) and event-related potentials (ERPs), with focus particularly on two ERP components, the N2 and P3. The N2 is a fronto-central negative deflection about 200 ms after stimulus onset that has been linked to response inhibition and conflict processing (Bruin & Wijers, 2002; Falkenstein, Hoormann, & Hohnsbein, 1999). The P3, a later positive deflection approximately 300 to 500 ms after stimulus onset, has been associated with stimulus evaluation during action planning (Kok, 2001), decision making (Nieuwenhuis, Aston-Jones, & Cohen, 2005), and stimulus-response link activation (Verleger, Baur, Metzner, & Śmigasiewicz, 2014). Interestingly, the P3 has been reported to be centro-parietally distributed for go and fronto-centrally for nogo trials (Bruin & Wijers, 2002; Falkenstein, Koshlykova, Kiroj, Hoormann, & Hohnsbein, 1995; Pfefferbaum, Ford, Weller, & Kopell, 1985), reflecting different cognitive demands. The P3 is typically larger and emerges earlier on compatible as compared to incompatible trials, reflecting sensitivity to perceptual interference and response selection conflict (Valle-Inclán, 1996; Zhou, Zhang, Han, & Tan, 2004). Sebanz, Knoblich, Prinz, and Wascher (2006) showed a P3 compatibility effect on go trials in both individual and joint performance of a go/nogo task. Moreover, incompatible stimuli evoked a larger positivity in the joint than in the individual condition. For nogo trials, P3 amplitude was also larger in the joint condition, a result also reported by Tsai, Kuo, Jing, Hung, and Tzeng (2006). However, this study found the N2 on nogo trials unaffected by action context and failed to replicate the P3 compatibility effect on go trials (Tsai et al., 2006). Ruissen and De Bruijn (2015) reported increased N2 amplitudes, reflecting increased response conflict, in the social relative to the individual condition of a Simon task after nasal oxytocin administration, which is consistent with the view that oxytocin facilitates social behavior, possibly by enhancing self-other integration.

N2 and P3 joint action effects have been interpreted both in terms of task co-representation (Sebanz et al., 2006), suggesting stronger response conflict and response inhibition during co-acting, and common coding of action and perception (Hommel et al., 2001). In line with this, the P3 has also been shown to be sensitive to joint versus individual action planning (Kourtis, Sebanz, & Knoblich, 2013). Most recently, a study with an auditory oddball task which required subjects to discriminate between frequent standard tones, rare target tones, and rare non-target tones that were imperative for a co-actor reported a larger parietal P3b and a frontal nogo-P3 (P3a) to non-targets in a joint versus an individual task condition. Compared to target-related ERPs, these effects were delayed, a finding that was interpreted in terms of prioritization of own over others' task representations (Kato, Yoshizaki, & Kimura, 2016).

Previous studies have implemented joint and individual task conditions within separate task runs (e.g. Baus et al., 2014; Demiral, Gambi, Nieuwland, & Pickering, 2016; Kato et al., 2016; Sebanz et al., 2006; Tsai et al., 2006). Therefore, a central question that remains to be answered is whether neural responses differ for trials in which subjects do not respond because co-actors do (*social nogo trials)* and trials in which neither subjects nor co-actors respond (*non-social nogo)*. To this end, the present study applied an interleaved task design to investigate differential effects of social and non-social nogo in neural responses, and to determine whether such differences might also impact behavior. Note that the notion of differential neural responses for social and non-social nogo trials is in line with both the referential coding account and the task co-representation account, albeit ascribed to different mechanisms by the respective accounts. The present study was not designed to support or refute one account, but the implication of the present findings will be discussed in light of both accounts.

We applied a joint action adaptation of the Eriksen flanker task because of its suitability for the joint action setting and easy incorporation of go as well as non-social and social nogo trials in an interleaved design. Effects of joint action on neural processing of imperative stimuli were investigated in the ERP in N2 and P3a/b. Based on previous findings (Sebanz et al., 2006; Valle-Inclán, 1996; Zhou et al., 2004), we expected a larger P3a/b for compatible than for incompatible go trials. Moreover, in line with increased response inhibition due to task co-representation (Sebanz et al., 2006) and/or common coding of action and perception (Hommel et al., 2001) during co-acting, we expected a larger P3a/b for social as compared to non-social nogo trials. We hypothesized this effect to be modulated by

flanker compatibility, with stronger modulation for social relative to non-social nogo trials containing flankers compatible with the subject's position. Furthermore, we hypothesized the N2 to distinguish between social and non-social nogo trials, with increased magnitude for social nogo trials due to increased response conflict processing.

Behavioral effects of joint action were assessed in RTs in trial-to-trial sequential effects because previous work has shown that the size of the Simon effect critically depends on the characteristics of the preceding trial, with larger Simon effects on trials following compatible than trials following incompatible trials (e.g. Akçay & Hazeltine, 2007; Hommel, Proctor, & Vu, 2004), an effect that was more pronounced under joint action (Liepelt, Wenke, & Fischer, 2013; Liepelt, Wenke, Fischer, & Prinz, 2011; Yamaguchi, Wall, & Hommel, 2016). Interestingly, sequential modulation was also stronger for nogo/go transitions than for go/go transitions, independent of joint or individual action, suggesting an inhibitory tag process when responses had to be inhibited by the actor or co-actor on the preceding trial (Liepelt et al., 2011). In the present study, we were interested in whether the preceding trial type (go, social nogo, non-social nogo) would modulate RTs on subsequent go trials. Aside from a general compatibility effect, that is, faster RTs for compatible as compared to incompatible go trials, we also expected a transition effect of faster responding after go as compared to nogo trials (Liepelt et al., 2011). Furthermore, we hypothesized that RTs would be slower following social as compared to non-social nogo trials, consistent with the notion of more effective inhibitory tags in joint action (Liepelt et al., 2011).

Methods

Subjects

Twenty-four adult volunteers (6 male, 18 female) were recruited at the Institute of Medical Psychology and Systems Neuroscience at the University of Münster, Germany, by public advertisement. Exclusion criteria were current neurological or psychiatric disorders, history of head trauma or lengthy periods of unconsciousness, and current regular medication affecting the central nervous system. Mean age was 24.8 years ± 5.8 (range 19 to 43 years), and mean educational attainment was 13 ± 0 years. All subjects were right-handed as determined by self-report. Written informed consent was obtained from all subjects prior to participation. As subjects were mostly students, course credit was awarded for participation if applicable. The study conforms to the Declaration of Helsinki and has received ethical clearance by the Ethics Board of the German Society for Psychology (Deutsche Gesellschaft für Psychologie, DGPs).

Experimental task and analysis of behavioral data

The experimental task was a joint action adaptation of a modified speeded flanker task (Eriksen & Eriksen, 1974). Following the lead of a previous study, the present flanker task variant included go trials in which responses needed to be executed as well as nogo trials in which participants were required to withhold responses (Beste et al., 2013). Stimulus displays consisted of two vertically arranged arrowheads (flankers; size 1.15 degrees of visual angle) that were presented 1.15 degrees of visual angle above and below a central target stimulus (arrowhead on go trials, filled circle on nogo trials; size 1.15 degrees of visual angle). Target arrowheads pointed either to the same or opposite direction as the target. Subjects had to respond whenever the target arrowhead pointed their way (leftward, see below) by pressing a response key on a keyboard (see Figure 1) as fast and as accurately as possible and to withhold responses whenever the target arrowhead pointed to the opposite side (rightward, see below) or when a filled circle was shown (nogo trials). Flankers appeared 220 ms before target onset to increase task difficulty, target stimuli were displayed for 300 ms and switched off at the same time as the flankers. The mean duration of the inter-trial interval was 1100 ms (range 900 – 1300 ms).

The joint action aspect of the task was realized by having the task performed by two co-acting individuals, one being the subject, from whom EEG was recorded, and the other one a same-sex co-actor. Co-actors were grad students, interns or staff members from the Institute of Medical Psychology and Systems Neuroscience at the University of Münster. Throughout the study, five different individuals (3 male, 2 female) served as co-actors. Subjects were not informed that the co-actors were confederates. They were merely told that they would complete the task together with the co-actor, and that they both would be required to respond whenever the central arrowheads pointed their way. Subjects and co-actors were seated in front of the computer screen side by side at a viewing distance of 60 cm, with the subject on the left, thus responding to leftward target arrowheads (see above).

For a schematic illustration of stimulus displays and the spatial setup for subject and co-actor, see Figure 1. The setup yielded three types of trials in relation to subjects, *go trials* in which they had to respond, *social nogo trials* in which the co-actor had to respond, and *non-social nogo trials* in which co-actor and subject both had to withhold their responses. For each of these trial types, flankers could either be compatible with the subject's side

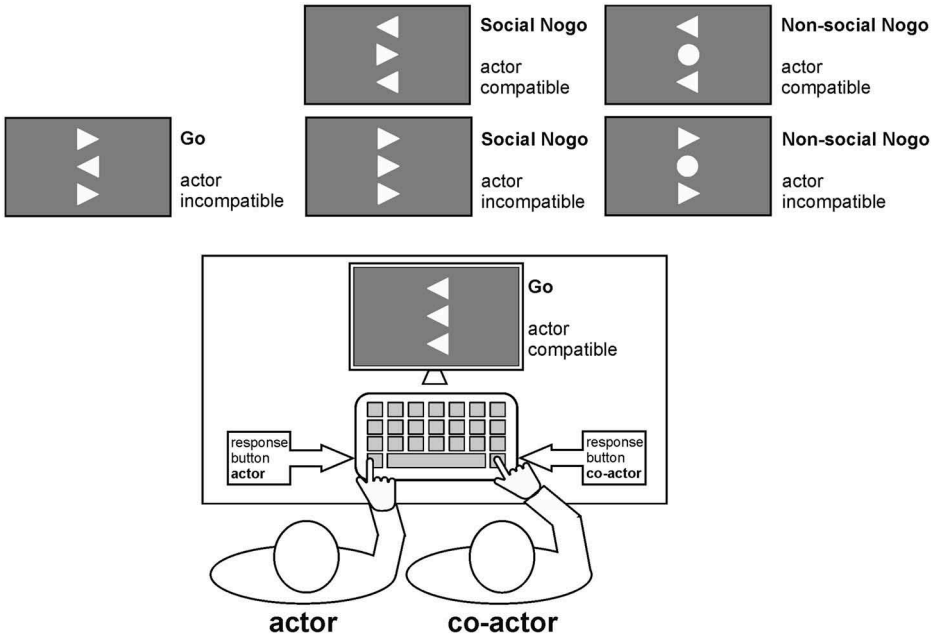

Figure 1. Schematic illustration of the experimental setup and of the possible stimulus configurations for go, social nogo, and non-social nogo trials. Co-actors were always seated on the right and subjects on the left, both responded with their right hand. Note that compatibility ("actor compatibility") is defined based on the position of the subject rather than the direction of the target.

(i.e., pointing to the left) or incompatible (i.e., pointing to the right). "Actor compatibility" will henceforth thus refer to the direction of the flankers with respect to the subject's position. Note that the task design yielded overall ratios of 66.6% for nogo trials (social and non-social) and 33.3% of go trials. Typically, go/nogo tasks contain greater ratios of go than of nogo trials. In order to tax response inhibition in the present task, time pressure was introduced. In keeping with pilot testing completed prior to the start of this study, responses on go trials had to occur within 450 ms after target onset, otherwise an auditory signal was presented to remind subjects to respond faster (1000 Hz, 60 dB SPL) before the next trial was started.

The task comprised a total of 720 trials in four runs of 180 trials each. Go, social nogo, and non-social nogo trials made up equal portions of the total trial count; actor compatibility and target direction were also balanced. Since the present study also investigated sequential effects of trial type, trial order in each run was pseudorandomized so that each combination of trial type, target direction, and actor compatibility occurred after each other combination an equal amount of times.

With regard to performance accuracy, the percentage of go trials in which the subject had correctly responded within 450 ms from target onset, and false alarm rates, that is, the percentages of social and non-social nogo trials in which subjects had wrongfully responded, were determined. Accuracy measures were acquired for descriptive purposes only and not further analyzed. Mean RTs were measured from target onset according to actor compatibility in current trial and trial type in previous trial. Due to investigation of sequential RT modulation, trials following incorrect trials and the first trials in each block were excluded from analysis. Due to repeated participation of individual confederates, RTs and accuracy scores were not analyzed for confederates.

Mean RTs for correct responses only were entered into a 2 × 3 repeated measures analysis of variance (ANOVA) with *actor compatibility* with regard to the subject's position (compatible, incompatible) and *trial type in previous trial* (go, social nogo, non-social nogo) as within-subjects factors. Greenhouse-Geisser correction was applied to account for sphericity violations when appropriate. Post-hoc paired-sample *t* tests were performed to resolve interactions, and Bonferroni correction was applied to account for multiple testing when appropriate.

Psychophysiological recordings, preprocessing and analysis of EEG data

EEG was recorded from 64 scalp electrodes and 4 ocular electrodes using a BioSemi active electrode system (BioSemi B.V., Amsterdam, Netherlands) with a sampling rate of 512 Hz using the accompanying ActiView software package. Instead of ground and reference, the BioSemi EEG system uses a CMS/DRL feedback loop with two

additional electrodes (for more information see: http://www.biosemi.com/faq/cms&drl.htm). Electrodes were mounted to an elastic cap according to the international 10–20 system (FP1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, FC1, C1, C3, C5, T7, TP7, CP5, CP3, CP1, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, FPz, FP2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FC6, FC4, FC2, FCz, Cz, C2, C4, C6, T8, TP8, CP6, CP4, CP2, P2, P4, P6, P8, P10, PO8, PO4, O2). Vertical and horizontal eye movements were recorded with two electrodes attached above and beneath the left eye (VEOG) and two electrodes attached to the right and left outer canthi (HEOG).

EEG data were processed offline using BrainVision Analyzer 2 (Brain Product GmbH, Munich, Germany) and Matlab (Mathworks, Natick, Massachusetts, USA). Raw EEG data were filtered with a 30 Hz low-pass and 0.1 Hz high-pass filter. Ocular correction was performed using the Gratton, Coles, and Donchin (1983) algorithm as implemented in BrainVision Analyzer 2 using VEOG and HEOG channels. For one subject, ocular-corrected EEG data still contained noticeable blink-related artefacts so that an automated ocular correction independent component analysis (ICA; also implemented in BrainVision Analyzer 2) was performed additionally to remove ocular artifacts. Subsequently, automatic artifact rejection was performed based on the following criteria: maximum allowed voltage step 50 µV, maximal difference of values in intervals 150 µV, and minimal/maximal amplitudes of ±200 µV. EEG data were then segmented into 1000 ms epochs ranging from −400 to 700 ms relative to target onset. Baseline correction was applied based on the 400 ms pre-target. Note that flanker onset preceded target onset by 220 ms, hence flanker-related visually-evoked potentials are clearly visible in the ERPs. Segments were averaged according to *trial type* (go, social nogo, non-social nogo) and *actor compatibility* with regard to the subject's position (compatible, incompatible).

ERP components were characterized based on visual inspection of the target-locked ERP waveforms and topographical scalp distributions. The N2 was defined as the amplitude difference between the maximum negative peak within 350 ms after target onset and the preceding positive peak (P2) at electrode Fz. The P3a was defined as amplitude difference between the negative N2 peak and the following positive peak within 450 ms after target onset at electrode FCz. The P3b was defined as average amplitude in the time window from 400 to 600 ms after target onset at CPz.

N2, P3a, and P3b were analyzed by means of separate 2 × 3 ANOVAs with *actor compatibility* with regard to the subject's position (compatible, incompatible) and *trial type* (go, social nogo, non-social nogo) as within-subjects factors. Greenhouse-Geisser correction was applied to account for sphericity violations when appropriate. Main effects of trial type were further investigated by linear trend analysis. Post-hoc paired-sample *t* tests were performed to resolve interactions when appropriate, with Bonferroni correction applied to account for multiple testing if necessary.

Results

Behavior

In general, performance accuracy was high. The average percentage of correct responses on go trials was 88.94% ± 6.18. Mean false alarm rates for social and non-social nogo trials were 2.74% ± 1.36 and 1.77% ± 1.82, respectively. Mean RTs on correct trials according to actor compatibility as well as trial type in previous trial are provided in Figure 2.

The ANOVA yielded significant main effects of *actor compatibility* ($F_{[1, 23]} = 89.112$, MSE = 96,620.63, $p < .0001$, $\eta_p^2 = .795$), reflecting shorter RTs on compatible (target leftward, flanker leftward) as compared to incompatible (target leftward, flanker rightward) trials, and of *trial type in previous trial* ($F_{[1, 23]} = 22.731$, MSE = 19,973.60, $p < .0001$, $\eta_p^2 = .497$). Here, post-hoc tests showed that RTs were longer following go relative to social nogo trials ($t_{23} = 6.577$, $p < .0001$), while there was no difference between RTs following go relative to non-social nogo trials ($p = .205$). Moreover, RTs were shorter following social nogo as compared to non-social nogo trials ($t_{23} = -5.694$, $p < .0001$). Main effects were further qualified by a significant two-way *actor compatibility* by *trial type in previous trial* interaction ($F_{[2, 46]} = 7.943$, MSE = 1870.31, $p = .002$, $\eta_p^2 = .257$). In order to resolve this interaction and clarify if compatibility effects were differentially affected by previous trial type, post-hoc t tests were performed, comparing RTs for compatible

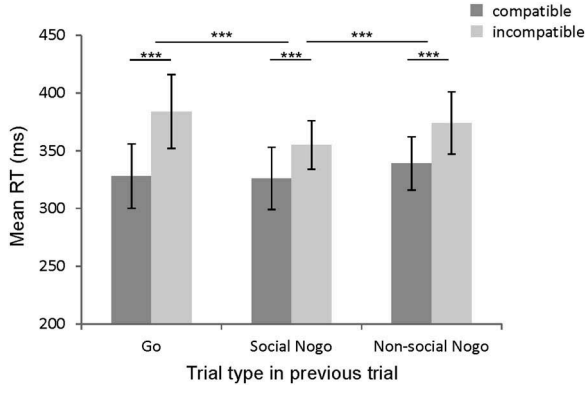

Figure 2. Mean reaction times (RTs) in milliseconds according to trial type in previous trial (go, social nogo, non-social nogo) and actor compatibility in current trial.

and incompatible trials for each trial type. While significant compatibility effects (compatible < incompatible) were found following all trial types (go: $t_{23} = -9.960$, $p < .0001$; social nogo: $t_{23} = -11.342$, $p < .0001$; non-social nogo: $t_{23} = -6.991$, $p < .0001$), the effect was strongest following go trials and smallest following social nogo trials. Moreover, descriptively, RTs were lowest following social nogo trials for both compatible and incompatible trials (327 ms and 355 ms, respectively).

EEG

Target-locked grand-average ERP waveforms at Fz, FCz, and CPz and scalp topographies of N2, P3a, and P3b according to trial type and actor compatibility are provided in Figure 3. Visual inspection revealed differences between neural responses to social versus non-social nogo cues in the N2 and P3 time windows. Generally, differences were most pronounced at fronto-central sites. Differences between go and both types of nogo trials were most pronounced fronto-centrally in the P3a time window, likely due to response execution on go trials after 300 to 400 ms.

N2

Mean N2 amplitudes according to trial type and actor compatibility are provided in Figure 4. The ANOVA yielded a significant main effect of *trial type* ($F_{[1, 23]} = 21.913$, MSE = 664.71, $p < .0001$, $\eta_p^2 = .488$).

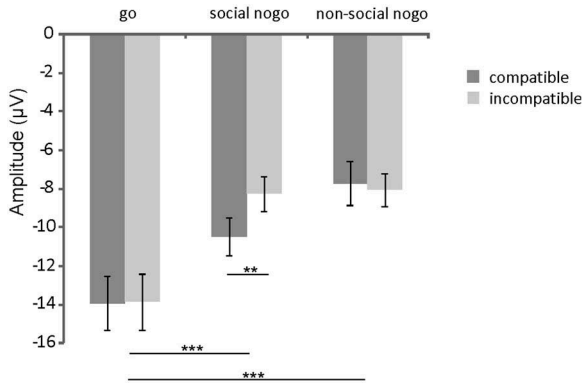

Figure 4. Mean N2 amplitudes according to trial type and actor compatibility with respect to position of subject ("compatible" thus refers to leftward flankers).

Post-hoc tests revealed more negative amplitudes for go as compared to social ($t_{23} = -4.930$, $p < .0001$) as well as non-social nogo trials ($t_{23} = -5.051$, $p < .0001$). The difference between social and non-social nogo was not significant after Bonferroni correction ($p = .032$, Bonferroni corrected significance level $p < .017$). The main effect of *actor compatibility* was not significant (MSE = 15.39, $p = .277$). Crucially, the two-way interaction was significant ($F_{[2, 46]} = 8.886$, MSE = 24.97, $p = .001$, $\eta_p^2 = .279$). Post-hoc tests comparing N2 amplitudes for actor compatibility separately for the three trial types only showed significantly more negative amplitudes for compatible relative to incompatible flankers for social nogo trials ($t_{23} = -3.556$, $p = .002$).

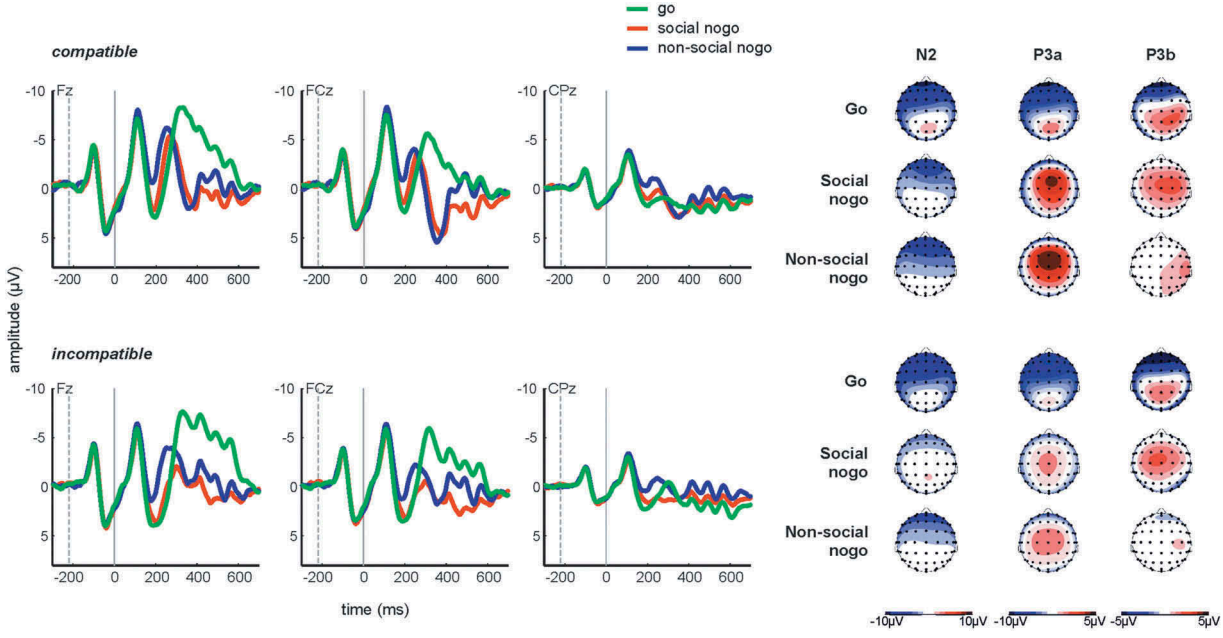

Figure 3. Target-locked grand-average ERPs at electrodes Fz, FCz, and CPz and scalp topographies of N2, P3a, and P3b according to trial type (go, social nogo, non-social nogo) and actor compatibility with respect to position of subject ("compatible" refers to leftward flankers). Dotted grey line demarks flanker onset at −220 ms.

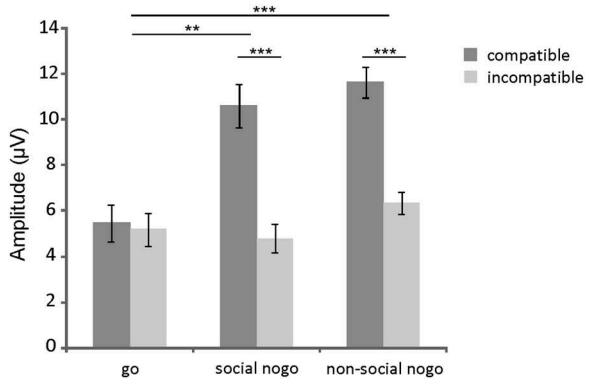

Figure 5. Mean P3a amplitudes according to trial type and actor compatibility with respect to position of subject ("compatible" thus refers to leftward flankers).

Actor compatibility did not modulate amplitudes for non-social nogo trials or go trials (both $p > .626$).

P3a

Mean P3a amplitudes according to trial type and actor compatibility are provided in Figure 5. A significant main effect of *actor compatibility* ($F_{[1,\ 23]} = 68.440$, MSE = 520.14, $p < .0001$, $\eta_p^2 = .748$) reflected more positive P3a amplitudes for compatible than incompatible flankers. Moreover, a significant main effect of *trial type* emerged ($F_{[2,\ 46]} = 13.659$, MSE = 191.66, $p < .0001$, $\eta_p^2 = .373$). Post-hoc tests showed a significantly larger P3a on social ($t_{23} = -3.018$, $p = .006$) as well as non-social nogo trials ($t_{23} = -4.802$, $p < .0001$) relative to go trials, while the difference between the two types of nogo was not significant after Bonferroni correction ($p = .032$, Bonferroni corrected significance level $p < .017$). Furthermore, the two-way interaction was significant ($F_{[2,\ 46]} = 22.139$, MSE = 145.95, $p < .0001$, $\eta_p^2 = .490$). Post-hoc tests comparing P3a amplitudes for actor compatibility separately for the three trial types showed that compatibility effects were evident on both types of nogo trials (social nogo: $t_{23} = 6.949$, $p < .0001$; non-social nogo: $t_{23} = 8.298$, $p < .0001$), but not on go trials ($p = .652$).

P3b

Mean P3b amplitudes according to trial type and actor compatibility are provided in Figure 6. The ANOVA yielded a significant main effect of *trial type* ($F_{[1,\ 23]} = 8.963$, MSE = 30.92, $p = .002$, $\eta_p^2 = .280$). Post-hoc tests revealed a significantly larger P3b on go relative to non-social nogo trials ($t_{23} = 3.415$, $p = .002$) and on social relative to non-social nogo trials ($t_{23} = 2.792$, $p = .010$), while the difference between go and social nogo trials was not significant after Bonferroni correction ($p = .035$, Bonferroni corrected significance level $p < .017$). The other effects failed to reach significance (actor compatibility: MSE = 0.93, p = .309; interaction: MSE = 0.91, $p = .411$).

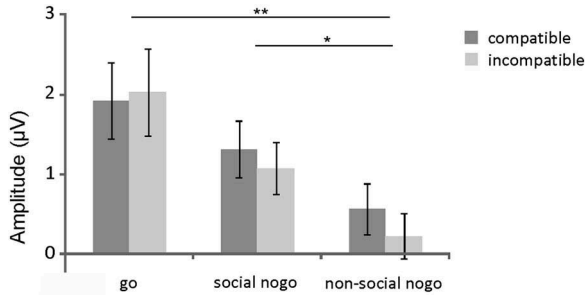

Figure 6. Mean P3b amplitudes according to trial type and actor compatibility with respect to position of subject ("compatible" thus refers to leftward flankers).

Discussion

The present study investigated potential differences between social and non-social nogo trials in a joint go/nogo Eriksen flanker task. ERPs revealed distinct processing of social and non-social nogo cues, which is in accordance with task co-representation and referential coding accounts of joint action. These results were complemented by shorter RTs and a reduced compatibility effect on trials following social nogo compared to go and non-social nogo trials. The present findings thus add to a growing body of evidence for modulation of performance monitoring processes and behavior by social context.

With regard to neural responses in joint action, most previous studies have investigated the P3 and N2 (e.g. Kato et al., 2016; Sebanz et al., 2006; Tsai et al., 2006). In line with these studies, modulation of neural responses by actor compatibility and trial type was evident in the time windows typical for these components in the present study. The N2 was more pronounced for go as compared to both types of nogo trials, which is consistent with the N2's role in response conflict processing (Bruin & Wijers, 2002; Falkenstein et al., 1999) in the sense that conflict may be greatest when a response is actually executed. Interestingly, N2 amplitudes only showed compatibility effects (more negative amplitudes for compatible as compared to incompatible flankers) for social nogo trials. This may indicate that compatible flankers, due to matching the subject's imperative stimulus, induced a propensity to respond in the subject and thereby increased response conflict for compatible relative to incompatible social nogo trials.

The P3 has been interpreted as an index of stimulus evaluation during action planning (Kok, 2001), decision making (Nieuwenhuis et al., 2005), and stimulus-

response link activation (Verleger et al., 2014), and is sensitive to response conflict and perceptual interference (Valle-Inclán, 1996; Zhou et al., 2004). Previous findings regarding P3 compatibility effects are somewhat inconsistent. Zhou et al. (2004) and Valle-Inclán (1996) reported increased amplitudes on compatible relative to incompatible trials. In contrast, Tsai et al. (2006) failed to find a P3 compatibility effect on go trials, which is in line with the present findings. It is conceivable that response execution effects in the ERP coincided with the P3 and masked potential compatibility effects on go trials in the present study.

Previous studies also did not distinguish between P3a and P3b although a functional distinction between these components has been emphasized (Polich, 2007) and may help to explain inconsistencies. According to Polich (2007), the P3a reflects stimulus-driven frontal attention mechanisms, while the P3b is linked to temporo-parietal attention and memory processes. This distinction between P3a and P3b appears to be further supported by engagement of different neurotransmitter systems in the generation of the components (Huang, Chen, & Zhang, 2015). In the present study, a compatibility effect was only observed for P3a but not P3b, and specifically on social and non-social nogo trials, likely due to the higher inhibitory demands of the two nogo as compared to go trials. This explanation is further supported by generally increased P3a amplitudes for both types of nogo as compared to go trials.

Contrary to our hypotheses, there was no difference between P3a amplitudes on social and non-social nogo trials. This result is in contrast to a previous study which applied a speeded joint go/nogo task with interleaved social and non-social go and nogo trials (De Bruijn, Miedl, & Bekkering, 2008). In this task, two subjects competed to respond most quickly to stimuli that signaled either the need for both subject to respond, for one but not the other subject to respond, or for both subjects to inhibit their response. Subjects were grouped into slow and fast responders, depending on whether they were more often slower or faster than their competitor. P3 amplitudes were increased for trials in which neither one of the two competitors responded (i.e., non-social nogo trials) compared to trials in which one competitor responded and the other had to withhold the response (i.e., social nogo) in slow responders only. While this study thus provided the first evidence for differential neural processing of social and non-social nogo, it is unclear to what extent the emphasis on competition between the co-acting subjects may have affected the results. Moreover, this study also did not distinguish between P3a and P3b. In the present study, P3b amplitudes did differentiate between social and non-social nogo trials (with increased positivity for social nogo), thus supporting a functional distinction between P3a and P3b (Polich, 2007) and aligning with previous reports of increased P3 under joint as compared to individual task conditions (Kourtis et al., 2013; Sebanz et al., 2006; Tsai et al., 2006). P3b enhancement in social relative to non-social nogo trials may reflect an enhanced response discrimination/selection process which would be expected from a referential coding perspective. The co-representation account would also assume P3b enhancement for social relative to non-social nogo due to stronger evaluative processing of the no/go decision, that is, more elaborate processing of the own decision to not have responded in relation to the co-represented response of the co-actor. The lack of a difference between social and non-social nogo trials in the P3a may suggest that "late" stimulus-driven attentional processes reflected in the P3a (as opposed to earlier stimulus-driven processes reflected e.g. in the N2) were not altered by social nogo cues because "conflicts" might have already been solved at the preceding processing stages.

Interestingly, the present findings of differential neural responses to social and non-social nogo were complemented by the behavioral data. Generally, RTs replicated the typical RT compatibility effect, with faster responses on compatible relative to incompatible trials (Atmaca et al., 2011). Somewhat unexpectedly, the transition effect of faster responding after go as compared to nogo trials found in the joint Simon effect (Liepelt et al., 2011) was not observed, possibly due to the increased ratio of nogo trials in the present task (66.67%). RTs following go and non-social nogo trials did not differ, while RTs were reduced following social nogo trials compared to both other trial types. Moreover, compatibility effects, while present following all trial types, were weakest after social nogo trials. This result pattern may indicate that differential neural coding of social and non-social nogo cues due to increased conflict processing may impact behavior on subsequent trials. It is also conceivable that own responses on subsequent trials are facilitated by an additional self-other discrimination process needed when another person is responding on (social) nogo trials (Liepelt et al., 2011; Philipp & Prinz, 2010) due to the representation of an alternative action (Sebanz et al., 2003) or an alternative event (Dolk et al., 2013), all of which could lead to heightened attention or readiness to respond. Altered RT patterns following social nogo trials could also indicate a Gratton-like effect. The Gratton effect (Gratton, Coles, & Donchin, 1992) describes a reduced congruency effect following incongruent as compared to congruent trials on a Stroop or flanker interference task.

According to the conflict adaptation hypothesis (Botvinick, Cohen, & Carter, 2004; Carter et al., 1998), this is attributed to response conflict from the previous trial signaling a need for control that manifests as a modulation of response times (and error rates) on the subsequent trial. With regard to the present data, this might indicate that response conflict from the preceding social nogo trial (that might arise from co-representation or common coding) results in stronger conflict adaptation in the following trials in this manner. The notion that RTs were nominally lowest following social nogo trials is well in line with that.

To summarize, the present study provides direct evidence for differential neural coding of social versus non-social nogo. Neural responses for social and non-social nogo trials differed particularly in the conflict-sensitive N2, but also in the later P3b time window. Increased conflict processing and response inhibition (N2) and decision making (P3b) seem to be involved in resolving the additional self-other discrimination process (Liepelt et al., 2016) needed when representing own and other actions (Sebanz et al., 2003) or events (Dolk et al., 2013) in a common representational format (Prinz, 1997). Differential sequential modulation of RTs furthermore indicated that distinct processing of social and non-social nogo might facilitate own responses on subsequent trials. Of note, recently, Baess and Prinz (2015) reported smaller amplitudes of the N1, an early component associated with perceptual processing, in joint versus individual performance of a go/nogo task. This was interpreted in terms of early task co-representation and top-down modulation of perceptual processes in a social setting, with lower N1 amplitudes reflecting decreased recruitment of attentional capacities when acting together with a co-actor due to sharing of the work load. Contrary to these findings, additional explorative analyses of the N1 in the present study showed reduced amplitudes for non-social nogo trials as compared to the other trial types.

One possible limitation of the present study pertains to differences between trial types with regard to low-level perceptual features. Social and non-social nogo trials differed with regard to the nature of the target (arrowhead vs. circle), and on social but not non-social nogo trials the response of the co-actor may have affected neural responses in the subject by eliciting a clicking sound when the response key was pressed, which has been shown to affect action coding of the actor in previous studies (e.g. Dolk et al., 2013). We do not think that these low-level perceptual differences can account for the present N1 findings, given that the effect of trial type appeared to be gradual (i.e., there did not seem to be a larger difference between trials with more visually different targets), and it was further modulated by flanker compatibility. Low level perceptual differences could indeed have confounded the P3b, but they cannot fully account for the observed differences in neural responses to social and non-social nogo cues for two reasons. First, differences in the N2 were also modulated by actor compatibility and thus cannot be attributed solely to such low level perceptual differences. Second, such clicking sounds do increase the similarity of responses between actor and co-actor (Dolk et al., 2013; Hommel et al., 2001). While previous studies showed how similarity between actions (Stenzel & Liepelt, 2016b) and actors (Philipp & Prinz, 2010) affect the size of the compatibility effect, our study shows how enhanced similarity produces a distinct neural coding of social and non-social nogo in the N2 and the P3b. Future studies should either try to eliminate low level perceptual differences between trial types, e.g., by implementing eye tracking and using saccadic eye movements as responses, or parametrically manipulate the similarity of actions in order to systematically test effects of action similarity on N2 and P3b components .

Recently, studies have investigated joint action in clinical populations. Patients suffering from schizophrenia as compared to healthy individuals showed a reduced joint Simon effect and a lack of nogo-P3 enhancement in joint action, pointing to impaired self-other integration as potential deficit underlying social interactive dysfunctions in schizophrenia (De La Asuncion, Bervoets, Morrens, Sabbe, & De Bruijn, 2015; Liepelt et al., 2012). Along these lines, future studies could investigate neural deficits with respect to differences between social and non-social nogo processing in schizophrenia and other clinical groups.

Conclusion

The present study for the first time investigated differential processing of interleaved social and non-social nogo cues in a joint Flanker task. In line with the hypotheses, ERPs revealed distinct coding of social and non-social nogo in N2 and P3b. These results were complemented by differential RT modulation, with shorter RTs and a reduced compatibility effect on trials following social nogo compared to go and non-social nogo trials. The present findings suggest that the presence of the additional response of a co-actor during a nogo trial alters response conflict processing and response discrimination/evaluative processing. The present study adds to a growing body of evidence for modulation of performance monitoring processes and behavior by social context.

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