NEURAL MARKERS OF SELF-OTHER DIFFERENTIATION DURING DYNAMIC JOINT ACTION

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ABSTRACT

Joint actions, in which two or more people coordinate their actions with each other to achieve a common goal, are ubiquitous in daily life. Examples range from moving furniture with a friend to musical ensemble performance. Despite the ubiquity of joint actions, researchers know relatively little about the underlying neural processes that operate during real-world, dynamic joint action. Furthermore, recent research emphasizes the importance of using one's own sensorimotor system to represent and simulate others' contributions to the joint action to facilitate coordination. However, the notion that people represent their own and others' contributions to a joint action using the same neural resources raises the question of how people nevertheless maintain a distinction between each person's individual contributions. This dissertation will focus on delineating neural markers of self-other differentiation during dynamic joint action. In four experiments, I employ a joint sequence production paradigm in which pairs of participants take turns producing tones to match a metronome pace. I use electroencephalography (EEG) to examine the time course of neural activity associated with each person's actions (i.e., taps) and sensory consequences (i.e., tones) as the sequence unfolds. In Chapters 2 and 3 (Experiments 1 and 2), I investigate whether there is a *perceptual* differentiation in the processing of sensory consequences that result from one's own vs. others' actions by measuring auditory event-related potentials (ERPs) elicited by self- and partner-produced tones. Together, the findings from Experiments 1 and 2 indicate that self-specific attenuation of the auditory P2 provides a neural marker of self-other differentiation at a perceptual level. The findings from Experiment 2 also show that orienting processes associated with the coordination requirements of a joint action *enhance* P2 amplitude for *partner*-produced tones, suggesting that people direct their attention to their partner's tone onsets to better coordinate with them. In Chapter 3 (Experiment 3 and 4), I investigate whether there is a differentiation in the *motor* activity that is associated with each person's actions by conducting novel analyses of the data previously reported in Experiments 1 and 2 to examine motor-related cortical oscillations during self- and partner-produced taps. Together, the findings from Experiments 3 and 4 indicate that motor-related suppression provides a neural marker of self-other differentiation at a motor level. The findings from Experiment 3 and 4 also show that the coordination requirements of a joint action affect the degree of motor-related suppression for a *partner's* actions, suggesting that people simulate their partners action timing to better coordinate with them. Overall, this research suggests that distinct neural activity for one's own contributions to a joint action is dynamically coupled with periods of neural activity that reflect the integration of a partner's actions based on the coordination demands of the joint action. Together, the experiments presented in this dissertation provide important and direct implications for theoretical accounts of joint action, as they further our understanding of how people maintain a distinction between their own and their partners' contributions to a joint action, while also dynamically integrating information about the timing of their partners' actions and sensory consequences to better coordinate with them. More broadly, these experiments contribute to our understanding of disorders associated with self-other processing deficits, such as schizophrenia, and provide valuable insight into the development of effective paradigms for motor training and rehabilitation.

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LIST OF ABBREVIATIONS

-2LL	-2 log-likelihood
AO	Action observation
EEG	Electroencephalography
ERP	Event-related potential
ERSP	Event-related spectral perturbation
fMRI	Functional magnetic resonance imaging
FSR	Force-sensitive resister
ICA	Independent component analysis
ITI	Inter-tap interval
MEG	Magnetencephalography
MI	Motor imagery
MMN	Mismatch negativity
PJAM	Predictive Joint Action Model
rTPJ	Right temporal parietal junction
TMS	Transcranial magnetic stimulation

CHAPTER 1

An Introduction to Self-Other Differentiation in Joint Action

Portions of this chapter have been previously published or submitted for publication and redundant information has been removed. I was involved in every aspect of the research process for each project and made a substantial individual contribution to each of these works that merits their inclusion in this dissertation.

Bolt, N. K., & Loehr, J. D. (2023). The auditory P2 differentiates self- from partner-produced sounds during joint action: Contributions of self-specific attenuation and temporal orienting of attention. *Neuropsychologia, 182,* 108526.

I contributed to this work in the following ways: Conceived the presented idea, developed the theory and hypotheses, programmed the experiment, carried out the experiments (including testing the EEG participants), analyzed the data, interpreted the results, drafted the manuscript and submitted and revised it for publication.

Bolt, N. K., & Loehr, J. D. (2021a). Sensory attenuation of the auditory P2 differentiates self- from partner-produced sounds during joint action. *Journal of Cognitive Neuroscience, 33*(11), 2297-2310.

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Bolt, N. K., & Loehr, J. D. (2021b). The motor-related brain activity that supports joint action: A review. *Acta Psychologica, 212*, 103218.

I contributed to this work in the following ways: Conceptualized the idea, carried out the literature review, drafted the manuscript and revised it for publication.

The ability to coordinate actions with other people is one of the earliest achievements that occurs in human development. Dyadic interactions between infants and their caregivers already show evidence of coregulation, that is, the continuous and mutual adjustment of actions and intentions between partners (Fogel & Garvey, 2007). Further along in development, humans become remarkably skilled at adapting their actions in light of others' behaviours. For example, teammates playing a game of hockey continuously monitor and adapt to their partners' actions to coordinate passing a puck. Musicians in small ensembles make subtle and precise adjustments to produce cohesive sounds. Partners paddling together in a single kayak coordinate their rowing with each other to stay on path with their planned trajectory. All of these interactions are considered ***joint actions***, in which two or more people coordinate their actions with each other to achieve a common goal (Sebanz, Bekkering, & Knoblich, 2006). We engage in joint action all the time, whether it be moving a piece of furniture together with a friend or retrieving a cup of coffee from a server's grasp.

Despite the ubiquity of joint actions in our daily lives, researchers know relatively little about the underlying neural processes that operate during online, dynamic joint action. Much of cognitive neuroscience research has historically focused on solo action, investigating processes that occur in individuals performing tasks in isolation. Even supposed "social interaction" research typically creates a social context through lens of observation, for example, by using a paradigm where an observer watches another person performing actions on a screen (Schilbach, 2014). The conceptualization of the field of "joint action" in recent decades explicitly addressed this gap (Sebanz et al., 2006), initiating investigations into the neural processes that allow people to coordinate their actions with each other. Since then, research is beginning to recognize that joint action relies on some of the same neural processes as isolated action (Wilson & Knoblich, 2005), but also involves fundamentally different processes that depend on the dynamic and mutual adjustment that is central to joint action (Schilbach et al., 2019). Recent developments in joint action therefore highlight the need for investigations into real-time joint actions that are truly interactive, calling on researchers to rethink their approaches to make theoretical advances in the field of joint action (Dumas, Kelso, & Nadel, 2014; Schilbach et al., 2019). The overarching goal of this dissertation is to reveal more about the processes that allow us to coordinate with others during real-world, dynamic joint action.

More specifically, the goal of this dissertation is to directly investigate potential neural mechanisms of self-other differentiation in joint action. As I will argue in the sections that follow, there is extensive evidence in solo action that people use their own motor system to represent and simulate the actions of others (Blakemore & Frith, 2005). The notion of similar sensorimotor representations (i.e., representing another person's action in a functionally equivalent way to one's own) raises the question of how we attribute actions to ourselves vs. another person. Recent research in joint action emphasizes the importance of similar sensorimotor representations to make accurate predictions about one's own and others' actions to facilitate joint action planning (for reviews see, Bekkering et al., 2009; Bolt & Loehr, 2021b). Moreover, a certain degree of agent specificity becomes of utmost importance during joint action so that partners can successfully monitor and generate their actions without ambiguity. Despite the importance of a differentiation between self and other to joint action coordination, little research has investigated how the brain achieves this. This dissertation presents evidence that there is a differentiation in the perception of each partners' sensory consequences, and there is a differentiation in the motor activity associated with each partners' actions.

1.1 Similar Neural Resources for Action Execution and Observation

Research in solo action contexts provides foundational evidence for the idea that one's own sensorimotor system is highly involved in *observing* others' actions. This research in solo action has implications for theorizing about the neural processes that allow people to represent and coordinate with others' actions during *joint action*. In this section, I review the evidence of similar neural resources for action execution and observation during solo action. I argue that this evidence raises a question about how people distinguish between their own action vs. others' actions. Moreover, I propose that research in solo action reveals potential neural mechanisms of self-other differentiation that could also occur in the context of joint action, as I discuss further in Section 1.3.

Numerous studies in solo action have shown that observing an action leads to activation of the same neural resources that are required for action execution. Early support for this idea comes from the discovery of mirror neurons in the macaque monkey (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996), which discharge both when a monkey observes an experimenter produce a grasping action and when the monkey executes that same action. A body of behavioural and neuroimaging evidence has since shown that the processes involved in perception and action also overlap in the human brain (Muthukumaraswamy & Johnson, 2004; Prinz, 1997; Rizzolatti & Craighero, 2004; Rizzolatti & Sinigaglia, 2010). Representations of others' actions in one's own motor system have been argued to facilitate a multiplicity of social behaviours, from social mimicry (Rizzolatti & Craighero, 2004) to understanding the intention of actions (Iacoboni, Molnar-Szakacs, Gallese, Buccino, & Mazziotta, 2005; Ortigue, Sinigaglia, Rizzolatti, & Grafton, 2010), and coordination in joint action (Sebanz, Bekkering, & Knoblich, 2006). However, since then researchers have argued that the role of mirror neurons in complex social interactions is much more limited (Hickok, 2014). Current perspectives instead argue that sensorimotor representations do play a direct role in the low-level processing of observed actions, and may contribute to higher-level social cognition with the additional involvement of higher-level non-motor systems (Heyes & Catmur, 2022).

There is extensive behavioural and neuroimaging evidence that simulating an observed action in one's own sensorimotor system can be used to generate predictions about how the observed action will unfold (Ikegami & Ganesh, 2017; Sebanz & Knoblich, 2009; Wilson & Knoblich, 2005). This process allows people to anticipate the consequences of others' actions using the same internal forward models that predict the consequences of one's own actions (Keller, Novembre, & Loehr, 2016). Evidence that people use their own sensorimotor system to predict the outcomes of others' actions comes from research showing that an observer's own motor repertoire influences their ability to predict others' actions. For example, expert basketball players are more accurate at predicting the outcome of passes and free-throws than novices, and show an increase in motor activity during their observation of free-throws (Aglioti, Cesari, Romani, & Urgesi, 2008). Thus, the more similar an action is to one's own action repertoire, the more accurate people are at predicting the outcome of that action. The same study also found that experts further displayed increased corticospinal excitation, measured via motor-evoked potentials in hand muscles, when observing the precise moment that the ball left the player's hand, a critical time point for predicting the trajectory of the ball. Such specificity in motor activation preceding the prediction of outcomes suggests motor expertise can be used to predict skill-related actions.

The notion of representing others' actions in a functionally equivalent way to one's own raises the question of how people distinguish between their own and others' actions. People typically do not confuse their own actions with others' observed actions, and they typically feel a sense of agency, or sense of self-control, over the consequences of their own actions. For example, when witnessing a colleague flick a switch to turn on a light, we are not confused about whose actions turned on the light. How, then, are people able to make these attributions and avoid ambiguity if their own actions and others' actions activate equivalent representations in one's own motor system? In contrast to such sensorimotor equivalence, the *sensorimotor differentiation hypothesis* posits that, despite the activation of similar neural resources, there is some degree of agent specificity in the way actions and their sensory consequences are represented in one's sensorimotor system (Schütz-Bosbach, Avenanti, Aglioti, & Haggard, 2009).

One possibility is that there is a perceptual differentiation that occurs during the processing of sensory consequences that result from one's own vs. others' actions. *Sensory attenuation*, the selective neural and perceptual dampening of sensory activity that results from one's own actions, could distinguish between sensory consequences produced by one's own vs. others' actions (Weiss, Herwig, & Schütz-Bosbach, 2011a). For example, self-produced tactile stimuli are perceived as less intense than externally-generated tactile stimuli, explaining why it's difficult to tickle yourself (Blakemore, Wolpert, & Frith, 1998). In the auditory domain, many studies find evidence that self-produced sounds (e.g., a tone produced via a button press) have an attenuated neural response compared to sounds produced by a computer (Baess, Horváth, Jacobsen, & Schröger, 2011; Baess, Jacobsen, & Schröger, 2008; Lange, 2011; Martikainen, Kaneko, & Hari, 2005; Schafer & Marcus, 1973). This attenuated response for self-produced sounds has been localized to the primary auditory cortex (e.g., Heins et al., 2020; Martikainen et al., 2005; Stenner, Bauer, Heinze, Haggard, & Dolan, 2015). However, studies that examine sensory attenuation for self-produced sounds compared to sounds produced by an observed other person have found mixed results, with some studies finding similar attenuation for both self and other compared to a computer (Poonian, McFadyen, Ogden, & Cunnington, 2015; Sato, 2008), and other studies finding only attenuation for self (Weiss et al., 2011a; Weiss, Herwig, & Schütz-Bosbach, 2011b).

Another possibility is that, before sensory consequences are processed in their respective sensory systems, there is a qualitative differentiation in the motor activity associated with one's own actions vs. others' actions. Here, the motor system would partially activate the same neural resources required to execute an observed action, but not to the same degree as if one were performing the action themselves (Schütz-Bosbach et al., 2009; Schütz-Bosbach, Mancini, Aglioti, & Haggard, 2006). In line with this, there is corticospinal suppression, reflective of inhibition of the primary motor cortex, when observing an action that is attributed to oneself compared to observing an action that is attributed to another person (using a rubber hand illusion; Schütz-Bosbach et al., 2009, 2006). In a similar manner, there is considerable evidence that imagining oneself act (i.e., motor imagery) produces distinct motor activity compared to observing another person act (e.g., Gonzalez-Rosa et al., 2015; Ménoret, Bourguignon, & Hari, 2015). Importantly, the possibilities of perceptual and motor differentiation are not mutually exclusive since they could operate in parallel to provide a differentiation between one's own and others' actions and their corresponding sensory consequences.

Together, the evidence presented in this section raises the question of whether there is some degree of agent specificity in the neural activity associated with actions and their sensory consequences. I proposed that two potential neural mechanisms could underlie a self-other differentiation during action execution and observation. Specifically, sensory attenuation could allow for the differentiation of one's own vs. others' sensory consequences at a perceptual level and the degree of motor activation could serve to differentiate one's own from others' actions. In the following section, I summarize evidence that *joint action* relies on the ability to represent others' actions in one's own motor system, and to predict the outcome of others' actions based on such representations. Furthermore, I argue that self-other differentiation is critical for joint action success, and that the same potential mechanisms of self-other differentiation identified from research in solo action could serve to provide such an important distinction between neural activity that is associated with one's own and others' contributions to the joint action.

1.2 Similar Neural Resources for Representing Self and Other in Joint Action

Substantial evidence now exists that people use their own motor systems to represent and simulate the actions of others during joint action (Bekkering et al., 2009; Knoblich & Sebanz, 2006; Novembre & Keller, 2014). Many studies show increased motor-related activity during joint action compared to solo action, despite the participant's action kinematics being identical in both contexts (Dumas, Martinerie, Soussignan, & Nadel, 2012; Konvalinka et al., 2014; Kourtis, Woźniak, Sebanz, & Knoblich, 2019; Naeem, Prasad, Watson, & Kelso, 2012a; Perry, Stein, &

Bentin, 2011; Zimmermann, Lomoriello, & Konvalinka, 2022). Increased motor activity in joint action may, in part, reflect the representation and simulation of a partner's actions (Bolt & Loehr, 2021b). Consistent with this idea, studies that investigate joint hand movements show that motor activity is enhanced when participants produce a unimanual movement that is part of a joint action compared to when they produce a unimanual movement alone (Kourtis, Knoblich, Woźniak, & Sebanz, 2014; Ménoret et al., 2015). More specifically, these studies show that motor activity when producing a unimanual movement in joint action is more similar to motor activity when producing a bimanual movement alone. These findings indicate that people represent their own and their partner's actions during joint action planning much like they would for left- and right-hand movements in bimanual action planning, with anticipatory motor activity for both parts of the action occurring in parallel. In the same regard, producing a complementary (rather than identical) joint action activates areas involved in integrating non-identical movements, indicating that people simultaneously represent their own and others' action in their motor system. For example, Era et al. (2018) showed that inhibiting a region of the brain involved in motor functions (i.e., the anterior intraparietal sulcus) impaired coordination of complementary joint actions relative to imitative ones, and this effect was further dependant on the partner's ability to mutual adapt to each other, suggesting that the motor system is directly involved in the integration of non-identical observed and executed actions. Thus, involvement of one's own motor system in simulating the actions of a joint action partner is well-established.

Simulations of others' action are guided by knowledge about the shared goal to make accurate predictions about others' actions (Sebanz & Knoblich, 2009; Sebanz, Knoblich, & Prinz, 2003; Wilson & Knoblich, 2005; Wolpert, Doya, & Kawato, 2003). Sacheli et al. (2019) found that the presence of a shared goal increased activity in the left ventral premotor cortex, which specifically reflected the predictive decoding of a partner's actions (i.e., the researchers could predict whether the partner was pointing or grasping from the fMRI activation pattern during joint performance). Their findings therefore suggest that motor involvement is selectively recruited to make predictions about the outcome of a partner's actions during joint action. Another study by Kourtis, Sebanz, and Knoblich (2013) also showed that knowledge about the shared goal allows partners to engage in predictive motor planning of each other's actions, much like they would their own actions, which in turn facilitates interpersonal coordination. When participants prepared to receive an object from their partner, they displayed increased anticipatory motor activity (as indexed by increased amplitude of the Contingent Negative Variation, an ERP that peaks at the onset of a motor response) compared to when simply observing another person lift an object in isolation. This anticipatory motor activity peaked at the onset of their partner's action, suggesting that people represent their partner's action in their own motor system to predict the timing of their partner's actions and thereby better coordinate with them.

Such predictions allow for complementary adjustments to be made to one's own actions in advance, which are essential for efficient interpersonal coordination (Wolpert, Diedrichsen, & Flanagan, 2011). For example, a pianist may anticipate their partner's onset timing and adjust the timing of their own playing accordingly. Partners will often adopt strategies to make their actions more predictable to their partner, such as reducing the variability in their movements, resulting in improved interpersonal coordination (Sacheli, Tidoni, Pavone, Aglioti, & Candidi, 2013; Vesper, van der Wel, Knoblich, & Sebanz, 2013; Vesper, Van Der Wel, Knoblich, & Sebanz, 2011). For example, a study by Vesper and colleagues showed that people can use their knowledge of the shared goal to predict their partner's actions and adjust their own action accordingly (Vesper et al., 2013). The researchers asked participants to jump variable distances with the goal of landing at the same time as their partner. Participants received visual information indicating their own and their partner's jump distance prior to a go signal, and then received auditory feedback to indicate when each partner had landed. They found that participants who had a shorter jump distance (i.e., the easier action) adjusted the timing and spatial trajectory of their jump to land at the same time as their partner who had a longer distance to jump (i.e., the more difficult action). Furthermore, they did this even without seeing their partner jump, indicating that action observation is not required for simulating the outcome of their partner's action. Moreover, predicting how another person's actions will unfold occurs even when it is not strictly necessary for the joint action, but may prove to be advantageous to facilitate interpersonal coordination (Bolt & Loehr, 2021b).

Predictive models of joint action coordination delineate how predictions about others' actions might be integrated with predictions about one's own actions to guide motor control (Keller et al., 2016; Pesquita, Whitwell, & Enns, 2018; Sacheli, Arcangeli, & Paulesu, 2018; Wolpert et al., 2003). According to such predictive models, separate internal models operate for both one's own and a partner's actions when engaging in joint action. These internal models recruit the motor system to simulate actions and compute predictions about an individual's contributions to the shared goal (Wilson & Knoblich, 2005; Wolpert et al., 2003). Partners monitor deviations between their predictions and the resulting sensory consequences of each person's actions (Loehr, Kourtis, Vesper, Sebanz, & Knoblich, 2013). Deviations (i.e., prediction errors) are then used to recalibrate the individual internal models and to guide the adjustment to subsequent actions so that the shared goal can be achieved. Importantly, separate internal models for self and other are inherently linked by information about the joint goal (Pesquita et al., 2018). Information about the shared goal can be used to make predictions about the joint outcome, which cascades down to inform predictions in self and other internal models. In turn, partners monitor deviations from their expectations about the joint outcome, in addition to monitoring deviations from each person's individual contributions. In support of this claim, there is evidence that people monitor their own and their partner's action outcomes, as well as the joint outcome when they play musical duets together (Loehr et al., 2013; Loehr & Vesper, 2016). For example, Loehr et al. (2013) showed that people display similar neural responses to one's own and others' errors initially (as indexed by the feedback-related negativity, an ERP that peaks about 250 ms after feedback about an error) but display a distinction between one's own and others' errors later in processing (as indexed by the P300, an ERP that peaks about 300 ms after a task-relevant stimuli). Moreover, later in processing there was also a stronger neural response to errors that affected the joint outcome compared to errors that only affected individual outcomes. Together, the findings from this study suggest that people monitor each person's separate contributions to the joint goal, as well as the joint outcome overall, consistent with the hypothesis that people use separate self and other internal models to predict each person's parts of the joint action, as well as to predict the joint outcome. Thus, predictive models of joint action control provide a framework for explaining how similar sensorimotor representations of one's own and others' actions are recruited to make separate predictions about each person's actions with respect to the joint goal.

1.3 Self-Other Differentiation in Joint Action

How, then, do people maintain separate predictions about their own and their partner's actions if models of joint action propose that these predictions are computed in a functionally equivalent way? Pesquita et al. (2018) propose that incoming sensory information is compared to the separate predictions about each person's actions, and then is parsed into self or other internal models based on whether the incoming sensory information closely matches the predictions about each person's actions. For example, when two people are carrying a table, both receive haptic feedback from the table, which provides information about the position of the table relative to the direction they wish to move (i.e., the joint goal). Each person carrying the table is applying force to move the table, and predictions can be generated about the expected haptic feedback generated by each person's force. The comparison between the resulting haptic feedback and the separate predictions about each person's actions is argued to be what differentiates this feedback into separate self and other internal models. Thus, Pesquita et al.'s predictive joint action model (PJAM) argues that partners maintain a differentiation in their *motor* representation of each persons' actions to compute separate *sensory* predictions for one's own and others' actions.

Maintaining some degree of agent specificity between each person's actions and their sensory consequences is critical to joint action success. As discussed previously, self-other differentiation is a crucial component to predictive models of joint action, as it allows individuals to maintain separate predictions for each person's actions with respect to the shared goal (Keller, Novembre, & Loehr, 2016; Pesquita et al., 2018; Wolpert et al., 2003). Self-other differentiation also allows for the autonomous control of one's own actions (Keller et al., 2016). Individuals can only adjust their own actions if the shared goal is not being met. Thus, knowing which motor commands and sensory consequences belong to oneself is crucial to make such adjustments (Fairhurst, Janata, & Keller, 2019). For example, in ensemble music performance, it is each performer's responsibility to make sure their own part is played accurately. Although the shared goal guides the overall performance, each individual performer must be aware of their own contributions to remain in control of correcting their own errors. This is in line with the previously discussed finding that people display distinct neural activity for errors that result from their own actions, their partner's actions, and the joint action (Loehr et al., 2013). Thus, people indeed monitor the consequences of their actions in an agent-specific way, suggesting that there is a differentiation between self and other to maintain control over one's own actions.

Recent research in joint music performance emphasizes the importance of integrating information related to one's own part, partners' parts, and the joint outcome, while also maintaining a distinction between individual parts of the joint action (Keller et al., 2016;

Liebermann-Jordanidis, Novembre, Koch, & Keller, 2021; Novembre, Sammler, & Keller, 2016). For example, in ensemble performance, musicians use “prioritized integrative attending” to maintain attention to their own part, their partners’ parts, and the relationship between them (Keller, 2001). Balancing self-other integration and distinction as the joint action unfolds allows people to monitor and adapt to a partner’s actions to reach a shared goal, while maintaining control over their own actions and sensory consequences. Sensorimotor activity during the joint action may reflect periods of integration and distinction between parts of the joint action (Novembre et al., 2016). For example, in live orchestra performance, performers display increased sensorimotor activity during periods that promote an integration between parts by requiring performers to act in congruent ways compared to periods that promote a distinction between parts by requiring performers to act in highly incongruent ways (Christensen, Slavik, Nicol, & Loehr, 2022). More importantly, these shifts in sensorimotor activity change dynamically within the course of a single joint action, as the coordination demands of the joint action unfold. Overall, the findings in this paragraph provide evidence that manipulating the relations between self and other in joint music performance affects the degree of sensorimotor activity that performers display during synchronous joint action.

Thus, there is indirect evidence that sensorimotor activity could allow people to maintain a distinction between individual parts of the joint action, despite the notion that others’ actions are represented in a functionally equivalent way to one’s own. This idea is explicitly proposed by the sensorimotor differentiation hypothesis, which posits that there is some degree of agent specificity in the way actions and their sensory consequences are represented in one’s sensorimotor system (Schütz-Bosbach et al., 2009). Based on research discussed in the previous section, one possibility is that *perceptual* differentiation occurs during the processing of sensory consequences that result from each person’s actions. Sensory attenuation is one candidate for perceptual differentiation in joint action. However, to date only two studies have examined sensory attenuation in joint action (Loehr, 2013; Weiss et al., 2011b). Both studies measured attenuation for *jointly* produced sensory consequences, in which both partners worked together to produce a single shared tone, and found that people displayed more attenuation when their actions were closer in time to the onset of the tone. Based on these studies, however, it is unclear whether people display distinct attenuation for each person’s separate contributions to the joint action. That is, when agents make separate contributions to a joint action, do they display more sensory attenuation for their own compared to their partner's sensory consequences?

Another possibility is that differentiation occurs in the *motor* activity that is related to one's own vs. others' actions. Only one study to date has examined whether motor activity shows some degree of agent specificity in joint action (Novembre, Ticini, Schutz-Bosbach, & Keller, 2012). This study had participants perform the right-hand part of a musical duet that they had previously learned bimanually, while the left-hand part was either not played or was believed to be played by a partner. This paradigm served to create a motor representation of the left-hand part that was either associated with the one's own or a partner's imagined actions, respectively. Motor activity (i.e., corticospinal excitability) was modulated by whether the left-hand part was thought to be associated with oneself (less motor activity) or was thought to be played by a partner (more motor activity). However, this study examined motor activity related to one's own and a partner's imagined actions, and did not directly compare motor activity elicited by self- versus partner-produced actions in joint action. Thus, it is unclear whether people display agent specificity in the motor activity associated with each person's part of the joint action. That is, when agents make separate contributions to a joint action, do they display distinct motor activity for their own actions compared to their partner's actions?

1.4 Measuring Self-Other Differentiation in Joint Action

To address the questions in the previous section, research needs to investigate self-other differentiation while individuals are involved in real-time, dynamic joint action, as these questions cannot be answered by examining individuals acting in isolation. Moreover, research needs to measure neural activity as the joint action *unfolds over time* to disentangle neural activity that is associated with each agent's respective contributions to the joint action, as these questions cannot be answered by examining neural activity that captures both parts of the joint action simultaneously. Electroencephalography (EEG) provides a neuroimaging technique that is best suited to measure the *time course* of sensorimotor electrical activity in the brain because of its excellent temporal resolution. EEG measures changes in voltage at the scalp that reflect the activity of groups of cortical pyramidal neurons. Furthermore, because of its ease-of-use and relative portability, EEG can be used during real-world joint actions from simple dyadic finger-tapping paradigms (Bolt & Loehr, 2021a) to live musical orchestra performance (Christensen et al., 2022). Different methodological and analytical techniques can be used with EEG to examine the perceptual and motor aspects of self-other differentiation during joint action, as I explain next.

Neural responses to sensory stimuli can be measured with the ERP technique, which measures neural activity elicited by a specific environmental event, such as the onset of an auditory stimulus. Sensory attenuation is displayed in auditory ERPs, in that the ERP response to self-produced auditory stimuli, such as a tone produced by a button press, is reduced compared to the ERP response to externally-produced auditory stimuli, such as the same tone that is produced by a computer (e.g., Baess, Jacobsen, & Schröger, 2008). For example, both the auditory N1, a frontocentral, negative-going ERP that peaks approximately 100 ms after a tone onset, and the auditory P2, a subsequent frontocentral positive-going potential that peaks approximately 160 ms after tone onset, are attenuated for self-produced tones compared to computer-produced tones (for reviews, see Horváth, 2015; Hughes, Desantis, & Waszak, 2012). Examining sensory attenuation via its cortical response provides the most direct measure of sensory processing changes (Roussel, Hughes, & Waszak, 2014), whereas behavioural indices of sensory attenuation, such as rating the loudness of auditory stimuli, may be further modified by later processing and/or influenced by post-hoc interpretative reconstruction (Stenner, Bauer, Haggard, Heinze, & Dolan, 2014). Furthermore, by subtracting ERPs elicited when producing movements that do not elicit an auditory outcome (e.g., silent taps), it is possible to isolate the activity associated with *listening* to auditory stimuli and remove activity associated with *producing actions*. This subtraction can allow for the direct comparison of *sensory* activity that is elicited by self- and partner-generated sensory consequences.

The degree of motor involvement in a given task can be measured with suppression or enhancement of motor-related brain rhythms during an action. For example, suppression of beta oscillations (defined as power in the 15–35 Hz frequency band, measured over central scalp electrodes) is an established marker of *enhanced* activity in primary motor areas (Pfurtscheller & Lopes da Silva, 1999). Also for example, suppression of mu oscillations (defined as power in the 8–13 Hz frequency band, measured over central scalp electrodes) reflect *enhanced* activity in the sensorimotor system during action and perception (Hari, 2006) and may reflect mirror neuron activation (Arnstein, Cui, Keysers, Maurits, & Gazzola, 2011; Fox et al., 2016), although this idea remains controversial (Hobson & Bishop, 2017). Both mu and beta oscillations are suppressed during the execution and observation of actions alike, indicating the increased involvement of one's sensorimotor system (for review see Fox et al., 2016). Furthermore, by subtracting activity that occurs in response to auditory-only stimuli in the absence of movement, it is possible to isolate activity associated with self- and other-produced *actions* and remove activity associated with *listening* to externally produced sensory information. This subtraction can allow for the direct comparison of *motor-related* activity that is associated with one's own and others' actions.

1.5 Research Goals

The primary goal of the current research was to establish whether people show some degree of agent specificity in neural activity associated with actions and their sensory consequences during online joint action, in line with the sensorimotor differentiation hypothesis. I employed a joint sequence production paradigm in which pairs of participants took turns producing sequence tones to match a pace set by an initial metronome (see Figure 1.1). Based on previous work using this paradigm, it is expected that participants will continually monitor and adapt to each other's actions to produce a sequence whose overall timing matches the metronome pace (Bolt & Loehr, 2017). Importantly, each person's action immediately elicits a tone, but critically, tones are separated in time by approximately 500 msec (the required pace). Thus, the joint task requires ongoing coordination, yet each partner produces independent actions and sensory consequences. It remains unknown whether social differentiation occurs for each person's contributions to the joint action because previous research has only examined the potential neural measures when agents act simultaneously, therefore capturing periods in which *both partners are contributing* to the joint action. Therefore, by having participants produce their actions and sensory consequences at separate time intervals, I was able to examine agentive differences in the neural activity corresponding to *each person's contributions* as the joint action unfolded over time. This detail was key to disentangling the dynamic neural activity related to one's own contributions and a partner's contributions while people coordinated together over time.

In four experiments, I used EEG to examine potential neural markers of social differentiation while participants performed the joint action task described in the previous paragraph. Experiment 1 and 2 investigated whether perceptual differentiation occurs when processing the sensory consequences that result from each agent's actions. Specifically, Experiment 1 examined whether sensory attenuation distinguishes self- from partner-produced sensory consequences during joint action by measuring auditory ERPs that are typically attenuated for self- compared to computer-generated sounds (i.e., N1 and P2 auditory ERPs). Experiment 2 aimed to replicate the effect of self-specific sensory attenuation found in Experiment 1 and to further elucidate the role of attention-related enhancement of auditory ERPs during joint action, which occurred during the same time window as sensory attenuation. Experiments 3 and 4 investigated whether differentiation occurred in the motor activity related to each agent's actions. Specifically, Experiment 3 investigated whether motor-related cortical oscillations showed increased suppression (indicative of more motor activity) during one's own actions compared to during a partner's actions as a joint action unfolds. Experiment 4 aimed to replicate the agentive differences in motor-related suppression that were found in Experiment 3 while also accounting for potential overlapping motor activity between adjacent actions. Overall, these four experiments directly investigate potential neural markers of self-other differentiation during joint action to delineate whether people display a differentiation between one's own and others' actions and their corresponding sensory consequences.

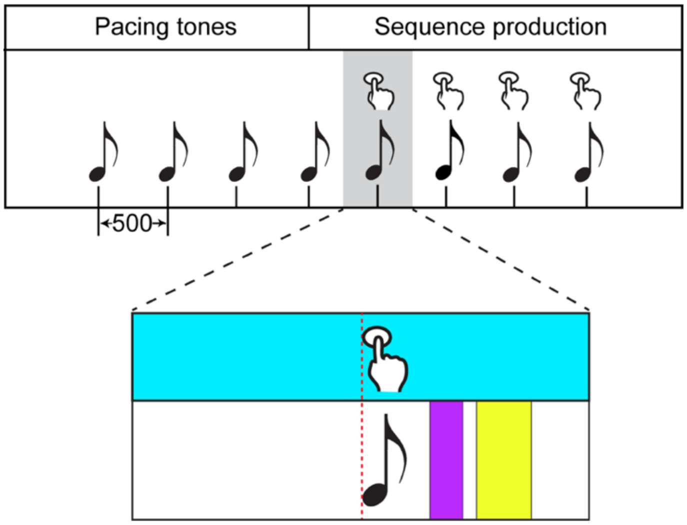

Figure 1.1. Top Panel: Schematic illustration of the basic experimental paradigm used for all experiments in this dissertation. Participants heard four pacing tones and then produced four sequences tones. The 500ms interval surrounding the first sequence tone (shaded grey) is enlarged below to show details about the analysis for each experiment. *Bottom Panel:* The dotted red horizontal line denotes the button press and onset of the tone. Experiment 1 and 2 investigated auditory ERP activity time-locked to the first sequence tone (time period for the auditory N1 shown in purple and the auditory P2 shown in yellow) after subtracting motor-related activity. Experiment 3 and 4 investigated motor-related cortical oscillations surrounding the button presses (time period shown in blue) after subtracting auditory-related activity.

CHAPTER 2

Portions of this chapter have been previously published or submitted for publication and redundant information has been removed.

Bolt, N. K., & Loehr, J. D. (2021a). Sensory attenuation of the auditory P2 differentiates self- from partner-produced sounds during joint action. *Journal of Cognitive Neuroscience, 33*(11), 2297-2310.

Sensory Attenuation of the Auditory P2 Differentiates Self- from Partner-Produced Sounds During Joint Action

When coordinating with others to produce joint actions, people plan, monitor, and adjust their own actions based on predictions about their partners' actions and the resulting consequences of those actions (Sebanz & Knoblich, 2009; Vesper et al., 2017). Such predictions are facilitated by the use of one's own motor system, allowing people to respond quickly to their partners' ongoing actions using their pre-existing knowledge about the parameters of human movement (Bolt & Loehr, 2021b; Vesper et al., 2017; Wilson & Knoblich, 2005; Wolpert et al., 2003). However, using one's own motor system to make predictions about one's own and others' actions raises the question of how people maintain a distinction between the sensory consequences of their own and others' actions. One potential mechanism for this self-other distinction is sensory attenuation, or the selective neural and perceptual dampening of self-produced sensory consequences. Most studies that have investigated sensory attenuation have compared self-produced to computer-produced sensory consequences in solo action contexts (for a review see Horváth, 2015). To date, the little research that has examined sensory attenuation during joint action has focused on joint actions in which partners' combined actions produce a single shared sensory consequence (Loehr, 2013; Weiss et al., 2011b). The purpose of Experiment 1 was to investigate whether sensory attenuation differentiates self- from other-produced sensory consequences during joint actions in which partners produce complementary actions that elicit separate rather than shared sensory consequences.

Anticipating and adapting to the sensory feedback produced by a partner's actions is critical for joint action success (Sacheli et al., 2018). People represent partners' actions in their own motor systems because doing so allows them to better predict the outcomes of their partners' actions and thereby facilitates coordination (Bekkering et al., 2009; Bolt & Loehr, 2021b; Wilson & Knoblich, 2005). In turn, sensory feedback from a partner's actions is integrated into one's own action plans. For example, when people learn a new joint action, they form representations that include both partners' action effects (Loehr & Vesper, 2016). Furthermore, receiving sensory feedback about a partner's actions facilitates people's ability to learn to coordinate (Knoblich & Jordan, 2003) and joint action performance is enhanced when the sensory consequences of a partner's actions match the predicted consequences (Sacheli et al., 2018). Computational models of motor control during joint action account for these findings by incorporating internal models for both one's own and a partner's actions (Keller, Novembre, & Loehr, 2016; Pesquita et al., 2018; Wolpert et al., 2003). Specifically, internal forward models are thought to generate predictions about the sensory consequences of both one's own and a partner's actions, which are compared with desired states and actual sensory feedback to guide subsequent actions. According to these accounts, sensory feedback from the environment must therefore be routed into separate (but interdependent) models for one's own and others' actions. This idea raises the question of how the sensory consequences of one's own and others' actions are differentiated during joint action.

One potential mechanism for differentiating between sensory feedback produced by one's own and others' actions is sensory attenuation for the consequences of one's own, but not others', actions (Pesquita et al., 2018; Weiss et al., 2011a). Although this question has received little attention in the joint action literature, research in solo action contexts has shown that perceptual and cortical responses to self-produced sensory consequences are attenuated relative to responses to externally-produced sensory effects. For example, both the auditory N1, a frontocentral, negative-going event-related potential (ERP) that peaks approximately 100 ms after a tone onset, and the auditory P2, a subsequent frontocentral positive-going potential that peaks approximately 160 ms after tone onset, are attenuated for self-produced tones compared to computer-produced tones (for reviews see Horváth, 2015; Hughes, Desantis, & Waszak, 2013). Attenuation is also evident in perceptual ratings, whereby self-produced tones are perceived as less loud than computer-produced tones (Sato, 2008), and for sensory consequences in other modalities, including the visual (Roussel, Hughes, & Waszak, 2013; Roussel et al., 2014) and somatosensory domains (Blakemore et al., 1998). We focus here on sensory attenuation in the auditory domain as measured by auditory ERPs.

Most ERP studies of sensory attenuation in the auditory domain have focused on the auditory N1 (for a review see Schröger, Marzecová, & SanMiguel, 2015). Numerous studies show that self-generated tones, produced at self-paced intervals of ~2-5 seconds, elicit an attenuated N1 compared to the same tones replayed by a computer (Baess et al., 2008; Klaffehn, Baess, Kunde, & Pfister, 2019; Lange, 2011; Martikainen et al., 2005; Schafer & Marcus, 1973). Notably, N1 attenuation for self-produced tones is stronger in mixed settings, in which self-produced tones are interspersed with computer-produced tones rather than presented in separate blocks (Baess et al., 2011; Ghio, Scharmach, & Bellebaum, 2018). This finding suggests that N1 attenuation may be particularly critical for discriminating one's own from external sensory consequences when multiple sources are present, as would be the case in joint action. N1 attenuation has typically been attributed to self-specific predictive processes arising from voluntary action (Hughes, Desantis, & Waszak, 2013a; Klaffehn et al., 2019; Timm, SanMiguel, Keil, Schröger, & Schönwiesner, 2014). However, recent findings cast doubt on whether self-specific predictive processes underlie N1 attenuation, suggesting instead that general predictive processes may account for the effect. For example, Kaiser and Schütz-Bosbach (2018) showed that N1 attenuation for self-produced tones is eliminated when tone onset timing is equally predictable for self- and computer-produced tones. Such findings suggest that N1 attenuation may be driven by accurate predictions about the timing of sensory events irrespective of the source of those predictions.

The possibility that N1 attenuation may not be self-specific has led some researchers to propose that the P2 may instead be the neural marker that distinguishes self- from externally-produced sensory consequences (e.g., Ghio et al., 2018; Sanmiguel, Todd, & Schröger, 2013; Timm, Schönwiesner, Schröger, & SanMiguel, 2016). Of the handful of studies that have examined both the N1 and the P2, most have shown attenuation of both components for self- compared to computer-produced tones (e.g., Saupe, Widmann, Trujillo-Barreto, & Schröger, 2013). However, recent work has demonstrated functional dissociations between the two components. For example, Knolle et al. (2013) showed that the P2 is attenuated for self-produced tones in patients with cerebellar lesions whereas the N1 is not. Moreover, recent studies linking sensory attenuation to people's experiences of agency (that is, their feelings of control over actions and their consequences; Gallagher, 2000) suggest that P2 attenuation may be more strongly linked to agency than N1 attenuation. For example, Timm et al. (2016) showed that P2 attenuation for self-generated tones correlates with perceived agency whereas N1 attenuation is independent of perceived agency. However, the auditory P2 has received relatively little attention in the sensory attenuation literature, so evidence for its role in distinguishing self- from externally-produced sensory consequences remains scant.

Only a handful of studies have compared sensory attenuation for self-produced tones to attenuation for tones produced by another person. Studies of action observation have had somewhat mixed results. Whereas Weiss and colleagues found that self-produced tones were perceptually attenuated relative to computer-produced tones but other-produced tones were not (Weiss et al., 2011a; Weiss & Schütz-Bosbach, 2012), Sato (2008) found that both self- and other-produced tones were perceptually attenuated relative to computer-produced tones. Two EEG studies showed that both self-produced and observed tones elicited an attenuated N1 compared to computer-produced tones (Ghio et al., 2018; Poonian et al., 2015), but Ghio and colleagues additionally found that self-produced tones elicited stronger P2 attenuation than observed tones, suggesting that the P2 may be a key marker of the self-other distinction in action observation contexts (Ghio et al., 2018). To date, two studies have examined sensory attenuation in joint action contexts, and both showed stronger attenuation of self- than partner-produced tones. Weiss et al. (2011b) showed that self-produced tones were perceived as less loud than other-produced tones in a joint task that required one person to prompt the other to produce the tone (by touching the other’s arm). Loehr (2013) examined attenuation in a joint task that required two participants to press their respective buttons nearly simultaneously to elicit a tone that was presented immediately after the second press. The N1 was only attenuated when the participant’s button press elicited the tone, and not when the partner’s button press elicited the tone. However, in both of these joint action studies, people worked together to produce a single shared action effect. Researchers have not yet examined sensory attenuation in joint actions that require people to produce complementary actions that elicit separate rather than shared sensory consequences. Moreover, researchers have not yet examined sensory attenuation in joint actions that require ongoing coordination that unfolds over time. Distinguishing between sensory feedback generated by one’s own and a partner’s actions may be particularly critical in such joint actions, if sensory feedback is to be used to continually update and adjust separate internal models for one's own and a partner's actions (Pesquita et al., 2018).

2.1 Experiment 1

The goal of Experiment 1 was to examine auditory ERPs elicited by the sensory consequences of one's own and a partner's actions, in a joint action that requires people to produce independent actions and sensory consequences that are coordinated over time. We employed a joint action task in which pairs of participants alternated their actions to produce a sequence of tones that matched the pace set by an initial metronome, as illustrated in the top two rows of Figure 2.1. Based on previous work using this paradigm, it is expected that participants will continually monitor and adapt to each other's actions to produce a sequence whose overall timing matches the metronome pace (Bolt & Loehr, 2017). Importantly, each person's action immediately elicits a tone, but, critically, tones are separated in time by approximately 500 ms (the required pace). Thus, the joint task requires ongoing coordination, yet each partner's actions produce distinct sensory consequences. To assess attenuation relative to computer-produced sounds as in previous studies, we also employed a computer task in which participants listened to previously-recorded tone sequences produced by a computer. We also included a solo task in which participants produced tone sequences alone, which allowed us to examine attenuation in solo action, similar to previous studies, but within the sequence production task employed in the current study.

The primary question of interest was whether ERP attenuation would occur for both self- and partner-produced tones in the joint task relative to computer-produced tones. Two predictions can be made based on the literature discussed above. One possibility is that auditory ERPs during joint action may show a *social differentiation* effect (Weiss et al., 2011a), whereby self-produced tones are attenuated but partner-produced tones are not. A social differentiation effect would be consistent with studies showing that ERP attenuation differentiates self- from externally-produced sounds in solo action contexts (e.g., Baess et al., 2011, 2008; Lange, 2011; Martikainen et al., 2004; Schafer & Marcus, 1973) and from other-produced sounds when people interact to produce a single shared action effect (Loehr, 2013; Weiss et al., 2011b). The second possibility is that auditory ERPs during joint action may instead show a *social equivalence* effect (Weiss et al., 2011a), whereby self- and other-produced tones show similar attenuation compared to computer-produced tones. A social equivalence effect would be consistent with studies of action observation showing similar sensory attenuation for self- and other-produced sounds (Poonian et al., 2015; Sato, 2008). Such an effect would indicate that sensory attenuation in joint action depends on the degree to which people need to distinguish their own actions from their partner's: differential processing may only occur when the need to distinguish between self and partner is high (when people work together to produce a single shared action effect) but not when it is low (when partners produce complementary actions with independent sensory consequences).

2.2 Methods

2.2.1 Participants

Eighty undergraduate students (29 males, mean age = 22, *SD* = 4.1) participated in the study in pairs. An additional two pairs completed the testing session but were excluded (and replaced with new participants) because of excessive artifacts in their EEG recording. Of the 40 pairs included in the analysis, 19 were mixed-gender, 16 were pairs of women, and 5 were pairs of men. Four pairs knew each other before the experiment. EEG was measured from one randomly chosen member of each pair (referred to as *participants*; 19 males, mean age = 21, *SD* = 3.3). The other person in each pair served as the partner, from whom only behavioural data were collected (referred to as *partners*). An a priori power analysis using MorePower 6.0 (Campbell & Thompson, 2012) indicated that a sample size of 40 EEG participants would be sufficient to detect, with 80% power, a difference of 1.75 μV between auditory N1 amplitudes elicited by self- compared to computer-produced tones (i.e., the most well-established effect reported in previous literature). Mean differences between self- and computer-produced tones ranged from 2μV – 5μV in previous studies, but additional parameters needed for effect size calculations (e.g., standard deviations) were seldom reported. We therefore performed our sample size calculation using the mean difference and standard deviation for solo- vs. computer-produced tones from Loehr (2013). Furthermore, we calculated the sample size needed to detect a difference of half the size reported by Loehr to ensure that we could detect even small differences between conditions in the current study. Ethical approval was obtained from the institutional review board prior to participant recruitment, and all participants gave informed consent before beginning the study. Participants were compensated with either partial credit for their undergraduate psychology course or $25.

2.2.2 Task and Target of Analysis

We employed a sequence production paradigm in which participants and partners first heard four pacing tones at 500-ms intervals and then produced (or listened to) a four-tone sequence that matched the initial pace (see Figure 2.1). We focused our analysis on ERPs elicited by the first tone or tap of the sequence, highlighted by a grey box around the event of interest in Figure 2.1, for three reasons. First, the event immediately preceding the first tone or tap in the sequence was identical across conditions (i.e., in all conditions, the immediately preceding event was the final pacing tone). Second, because sequence tones were presented at a different frequency than the preceding pacing tones, the first sequence tone was unlikely to be attenuated due to refractoriness (reduced amplitude when tones of the same frequency are repeated at relatively short intervals; Pereira et al., 2014). Third, examining the first tone ensured that the temporal predictability of the tone onset was equated across conditions (Lange, 2009). That is, in all conditions, participants should have expected the first tone to occur 500 ms after the last pacing tone, whereas the expected onset of subsequent sequence tones could differ depending on the timing of the preceding sequence tones (e.g., if error correction mechanisms were induced by timing errors). To ensure that the temporal predictability of the first sequence tone was as similar as possible across conditions, participants were instructed to produce the first sequence tone "where the fifth pacing tone would be if there was one," and they were required to practice the task until a strict timing criterion was achieved before beginning the test trials (see Procedure).

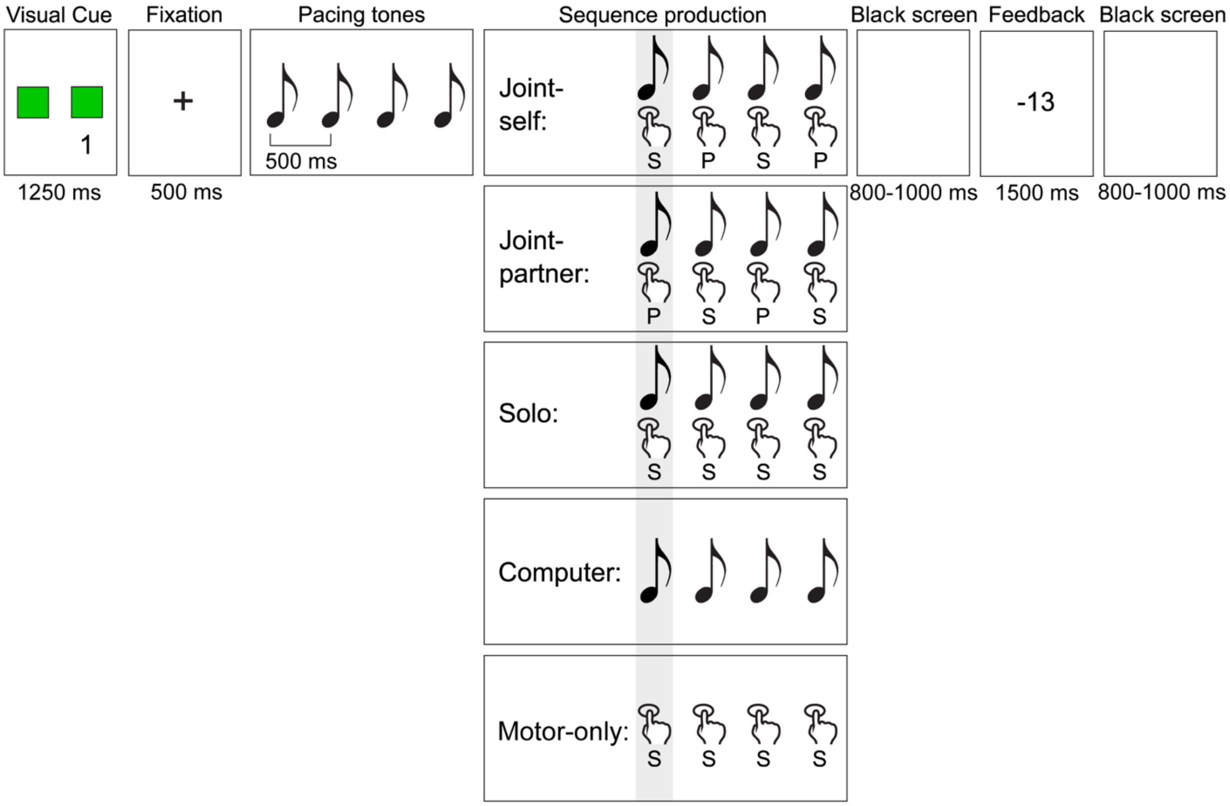

Figure 2.1. Schematic illustration of the experimental task and conditions for Experiment 1. The top row shows that, after instructions and fixation, participants heard a series of isochronous pacing tones (illustrated by eighth note symbols) and then produced a sequence of tones (illustrated by combined finger-tap and eighth note symbols, labeled S for the participant and P for the partner). After the last sequence tone, the pair received feedback about the pace of the sequence tones. The column labeled "Sequence production" shows the five experimental conditions, in which participants produced or listened to sequences of tones or taps, as described in the Design section.

2.2.3 Design

The experimental design included five conditions, as shown in Figure 2.1. Participants completed two joint conditions, in which they alternated actions with their partner to produce four-tone sequences. In one joint condition, the participant produced the first tone (i.e., ABAB, where A refers to the participant and B refers to the partner). In the other joint condition, the partner produced the first sequence tone (BABA). We henceforth refer to tones in the joint condition by the agent who produced them, i.e., *joint-self* for tones the participant produced and *joint-partner* for tones the partner produced. Participants also completed a solo condition, in which they produced sequences alone (AAAA). We refer to tones produced in the solo condition as *solo* tones. In the computer condition, participants listened to sequences of tones produced by the computer. In this condition, participants heard the same four pacing tones as in the other conditions, followed by four sequence tones whose timing was randomly selected without replacement from 715 trials of the joint task produced by five pairs of pilot participants.[1] We used timing from pilot pairs to ensure that tone timing in the computer condition matched tone timing in the joint conditions as closely as possible, while also ensuring that participants did not recognize the timing from their own previous performances. We refer to sequence tones in the computer condition as *computer* tones. Finally, participants also completed a motor-only condition, in which they produced sequences alone (AAAA), but their taps did not elicit any tones. We used ERPs elicited by taps in the motor-only condition to correct for movement-related activity in the ERPs elicited by joint-self and solo tones, as detailed in the Data Processing section.

Trials in all five conditions followed the same procedure described in the Procedure section. In all but the joint conditions, the partner sat quietly beside the participant.

2.2.4 Apparatus and Materials

Participants and partners sat next to each other on the same side of a table. Participants always sat on the right and partners on the left. An LCD computer screen was centered between them and positioned approximately 40 cm from the edge of the table. Participants and partners each had an Interlink force-sensitive resister (FSR; 3.81 cm^2) placed directly in front of them, approximately 20 cm from the edge of the table. Participants used the index finger of their dominant hand to tap the FSR during the experiment. Each FSR was connected to an Arduino micro-controller, which signaled PsychoPy software (Peirce, 2006) when a tap was registered. PsychoPy recorded each tap and, in the joint and solo conditions, presented an 880 Hz tone (100 ms duration, 10 ms rise/fall) with a tap-to-tone latency of approximately 8 ms. PsychoPy also presented the remaining auditory and visual stimuli, including the computer tones (also 880 Hz) and the pacing tones (1000 Hz, 100 ms duration, 10 ms rise/fall). Tones were presented through speakers placed on both sides of the screen, which were adjusted to a comfortable volume for each pair.

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[1] Sequences from pilot pairs were excluded if the timing of one or more inter-tone intervals (ITIs) in the sequence was less than 250 ms or greater than 750 ms. These same criteria were used to exclude behavioural outliers in the other conditions (see Data Analysis).

2.2.5 Procedure

After fitting the participant with an EEG cap, participants and their partners completed a series of training blocks to ensure that the pair could produce the four-tone sequences with accurate and stable timing, both separately and together. Training always began with blocks of solo sequence production, with separate blocks for the participant and the partner, followed by blocks of joint sequence production, with separate blocks for the joint conditon in which the participant produced the first tone and the joint condition in which the partner produced the first tone. Whether the participant or partner went first was counterbalanced across pairs and followed the same order for both the solo and joint tasks. For each task, two pre-training trials were completed first, during which the experimenter controlled the presentation of the events that comprised a trial and explained the task. The remainder of the first training block comprised five trials whose events followed the timing described below. For each trial, the mean inter-tap interval (ITI) of the four sequence tones was calculated, beginning with the ITI from the last pacing tone to the first sequence tone. If the mean ITI fell between 480 – 520 ms (inclusive) for at least four of the five training trials, the pair advanced to the next task. If performance did not meet this criterion, the training continued with another block of five trials. On average, each member of the pair performed 2.40 blocks (*SD*=1.70) of the solo condition and each pair completed 3.35 blocks (*SD*=2.76) of each joint condition.

Participants then performed the test phase of the experiment. Participants completed 8 blocks of 10 trials for each of the five conditions in the experiment (i.e., a total of 80 trials per condition). As in the training phase, conditions were always administered in separate blocks. The order of conditions was counterbalanced across pairs using a balanced Latin square design. Each block began with on-screen instructions indicating the task to be performed and, in the joint conditions, whether the participant or the partner would produce the first sequence tone. After reading the instructions, the pair pressed a button to begin the trials. A black screen was presented for 5000 ms before the first trial to allow the EEG participant to settle into a still position (reduced to 1000 ms in the training blocks).

As shown in Figure 2.1, each trial began with a visual cue that reminded the pair which task they were to complete during the trial. The visual cue consisted of two squares that were presented 4 cm to the right and left of the center of a black screen, respectively. Each square was coloured green if the person on the corresponding side of the screen was required to produce taps in the upcoming sequence and white if they were not. In the joint conditions, the number "1" appeared below one of the squares indicating which person would produce the first sequence tone. The squares remained on the screen for 1250 ms and were then replaced by a fixation cross in the center of the screen. The fixation cross was presented for 500 ms before the first pacing tone and remained on the screen until the last sequence tone was produced. The four pacing tones were presented at 500-ms intervals and were followed by sequence production (in the joint, solo, and motor-only conditions) or by the computer tones (in the computer condition). A black screen appeared for 800-1000 ms, randomly selected from a uniform distribution, after the last sequence tone/tap. Performance feedback (the difference between the mean sequence ITI and the required 500 ms pace) was then presented in the center of the screen for 1500 ms. Pairs were informed that positive numbers indicated that performance was slower than the required pace, whereas negative numbers indicated that performance was faster than the required pace. Feedback was presented to promote timing accuracy throughout the experiment and was also presented in the computer condition. Feedback was followed by another black screen for 800-1000 ms, randomly selected from a uniform distribution.

2.2.6 Data Acquisition

EEG data were recorded continuously from each participant using 32 active electrodes (actiCAP, Brain Products GmbH, Gilching, Germany), arranged according to an extended version of the 10–20 system at F7, F3, Fz, F4, F8, FC5, FC1, FCz, FC2, FC6, T7, C3, Cz, C4, T8, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, O1, CPz and O2, using carefully positioned nylon caps. All electrodes were referenced to the right mastoid during recording. Vertical eye movements were monitored using a pair of electrodes positioned above and beneath the right eye, and horizontal eye movements were monitored using a pair of electrodes positioned at the outer canthi of the eyes. Impedance was kept below 25 kOhm. EEG signals were amplified within a band width of 0.01–125 Hz and digitized with a sampling frequency of 1000Hz. Auditory events (i.e., pacing and sequence tones) were marked in the data using a StimTrak device (StimTrak, Brain Products GmbH, Gilching, Germany). This device sent a signal to the EEG recording software when auditory stimuli passed through the output cable of the audio interface. Thus, in the joint, solo, and computer conditions, triggers were time-locked to the onset of each tone. In the motor-only condition, Psychopy sent a trigger to the EEG recording software when a tap was registered.

2.2.7 Data Processing

EEG data processing was performed off-line using the EEGlab (version 14.1.1; Delorme & Makeig, 2004) and ERPlab (version 7.0.0; Lopez-Calderon, Luck, & Heekeren, 2014) toolboxes in Matlab®. EEG data were first re-referenced to the average of the two mastoid electrodes and then high-pass filtered with a half-amplitude cutoff of 0.1 Hz (12 dB/octave). The data were then segmented into epochs from 100 ms before to 300 ms after the onset of the first sequence tone in the joint, solo, and computer conditions. Epoch length was chosen to capture the N1 and the P2 while excluding motor activity related to preparing a subsequent tap.[2] Because the motor-only condition was used to correct for movement-related activity accompanying the production of joint-self and solo tones, and because PsychoPy presented tones an average of 8 ms after registering tap onsets, epochs in the motor-only condition were time-locked to 8 ms after the tap's event marker. This ensured that movement-related activity aligned with tone onset was subtracted from the joint-self and solo ERPs.

EEG artifact rejection was carried out semi-automatically. Thresholds for each of the following tests were adjusted for each participant based on visual inspection of the data. Blinks were identified using ERPLAB's step-like artifacts function (window width: 200 ms, step: 10 ms, median threshold: 50 µV) applied to a bipolar VEOG channel created by taking the difference in activity between the electrodes above and below the eyes. Horizontal eye movements were identified using the same function (window width: 400 ms, step: 10 ms, median threshold: 20 µV) applied to a bipolar HEOG channel calculated in the same way using electrodes on the outer canthi of the eyes. Extreme absolute voltage differences within an epoch were identified using a peak-to-peak test (window width: 400, step: 10 ms, median threshold: 125 µV) on all electrodes. Trials were also excluded from analysis if they contained a sequence production error in which participants and partners produced their tones in the wrong order. Trials were also excluded if the ITI from the last pacing tone to the first sequence tone/tap fell outside the range of 250-750 ms, or if the ITI from the first sequence tone/tap to the second

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[2] To check whether motor activity differed in the first 300 ms after a tap depending on whether or not that tap was followed by a subsequent tap, we compared ERPs elicited by the first and last taps in the motor-only condition (after which there was, or was not, a subsequent tap, respectively). We submitted the ERPs at electrodes FCz and Cz to repeated measures, two-tailed permutation tests based on the tmax statistic (Blair & Karniski, 1993), including all time points from 1 to 300 ms after tap onset and using a family-wise alpha level of 0.05. Although electrode FCz showed significant differences over an 11-ms period from 30-41 ms (corrected *p*s ranging from .026 – .046), no significant differences were found at either electrode in the time window of the N1 or the P2.

sequence tone/tap was less than 250 ms. The former criterion was implemented to ensure that the timing of the first tone/tap was temporally predictable, and the latter to ensure that the ERP response to the second sequence tone was not captured in the epoch for the first sequence tone. Finally, 6 trials were lost due to technical error. In total, 6.59% of all recorded trials were excluded from analysis following these criteria.

Average ERP waveforms were calculated separately for each participant for each tone type (joint-self, joint-partner, solo, and computer). Baseline correction was performed on averaged ERP waveforms using the 100 ms period before tone onset. ERPs elicited by joint-self and solo tones were corrected for movement-related activity by subtracting the mean ERP in the motor-only condition. This procedure for correcting for movement-related activity is standard in the sensory attenuation literature (Martikainen et al., 2005; Mifsud & Whitford, 2017). It ensures that movement-related activity that is present in ERPs elicited by self-produced tones (here, joint-self and solo tones, which participants elicited through tapping movements) but is not present in ERPs elicited by externally-produced tones (here, joint-partner and computer tones, which were not elicited by participant taps) is removed from comparisons between these respective ERPs.[3] Hereafter, references to ERPs elicited by joint-self and solo tones refer to motor-corrected ERPs.

2.2.8 Data Analysis

We first examined whether auditory N1 and P2 ERPs elicited by the first sequence tone differed across the four tone types: joint-self, joint-partner, solo, and computer. Electrodes and time windows for analysis were chosen based on the grand average waveforms collapsed across tone types and participants (collapsed localizer approach; Luck & Gaspelin, 2017) as well as on previous literature and individual difference plots of N1 and P2 waveforms collapsed across tone types. The grand average N1 amplitude was maximal over electrode FCz and the grand average P2 amplitude over electrode Cz, consistent with previous research showing attenuation effects at midline electrodes (e.g., Baess et al., 2011; Ghio et al., 2018; Lange, 2011). The N1 was therefore defined as the mean amplitude at electrode FCz from 75–115 ms after tone onset. The

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[3] We also confirmed through visual inspection that there was a slow-going positivity that began after tone onset and continued throughout the 300-ms epoch in the ERPs elicited by participant taps (joint-self, solo, and motor-only) but not in the ERPs not elicited by participants taps (joint-partner and computer), in line with previous reports (e.g., Baess et al., 2011; Horváth, Maess, Baess, & Tóth, 2012; Klaffehn et al., 2019) and further supporting the need to correct for movement-related activity in the joint-self and solo ERPs.

P2 was defined as the mean amplitude at electrode Cz from 125–185 ms after tone onset. Mean amplitudes were compared across tone types using separate one-way within-subject ANOVAs for each ERP component. Post-hoc tests were conducted using paired-sample *t*-tests.

Because the planned P2 analysis described in the preceding paragraph unexpectedly revealed an enhanced P2 for joint-partner tones compared to computer tones, we conducted two additional analyses to determine whether P2 enhancement could be attributed to the passage of time leading up to each tone's onset (Jones, Hsu, Granjon, & Waszak, 2017) or to heightened familiarity with the tones built up over the course of the experiment (Ross, Barat, & Fujioka, 2017; Tremblay, Shahin, Picton, & Ross, 2009). To examine the effect of the passage of time leading up to tone onset, we examined P2 amplitude as a function of the inter-tone interval (ITI) from the last pacing tone to the first sequence tone (measured in ms). To examine the effect of increasing familiarity over the course of the experiment, we examined P2 amplitude as a function of experimental block (1-8). For both analyses, we first extracted the P2 amplitude on each trial (calculated using the same definition as in the previous analysis, that is, mean amplitude from 125-185 ms at electrode Cz). We then analyzed the trial-level data using linear mixed-effect model analyses, which allowed us to examine the effects of both a continuous variable (ITI or block, respectively) and the categorical variable tone type (joint-partner vs. computer).

For each mixed-effects model analysis, we began with a maximal model (Barr, Levy, Scheepers, & Tily, 2013; Bates, Kliegl, Vasishth, & Baayen, 2015) that included the fixed effects of ITI (or block), tone type, and their interaction, as well as a random effects structure that included an intercept and slopes for ITI (or block), tone type, and their interaction at the participant level. For the analysis of ITI, we first centered ITI values at 500 ms (the required ITI) so that they were normally distributed around zero. Model fits were estimated using restricted maximum likelihood via the MIXED command in SPSS Version 25. Our strategy for refining the random effects was as follows. First, if the model fitting procedure failed to converge, we removed random effects whose covariance was estimated as zero. Then, we iteratively refined the random effects structure by checking whether the goodness of fit was significantly reduced after the random effect that accounted for the least variance was removed. Specifically, we compared the estimated deviances (-2 log-likelihood; -2LL) using a likelihood ratio test. This procedure allowed us to remove random effects not supported by the data (Bates et al., 2015). Last, we tested whether goodness of fit improved by fitting correlation parameters for the remaining variance components (Bates et al., 2015). For the ITI analysis, the final model included a random intercept and random slopes for tone type and ITI. For the block analysis, the final model included a random intercept and a random slope for tone type.

2.3 Results

2.3.1 Auditory N1

Figure 2.2 shows the grand average ERP waveforms elicited by joint-self, joint-partner, solo, and computer tones at electrode FCz, along with scalp voltage topographies and mean amplitudes across the N1 time window. As Figure 2.2 shows, mean N1 amplitudes did not differ significantly across conditions, $F(3, 117) = 0.99$, $p = .40$, $\eta^2_p = 0.25$, $\eta^2_G = 0.01$. However, the N1 itself was robust, as confirmed by a one-sample t-test against zero on mean N1 amplitudes collapsed across tone type ($M_{diff} = -3.36$, 95% CI [-4.12, -2.61], $t(39) = -9.02$, $p < .001$, $d = 1.43$). Thus, N1 amplitudes were not significantly attenuated for either self- or partner-produced tones in the joint task, nor for self-produced tones in the solo task, relative to computer-produced tones.

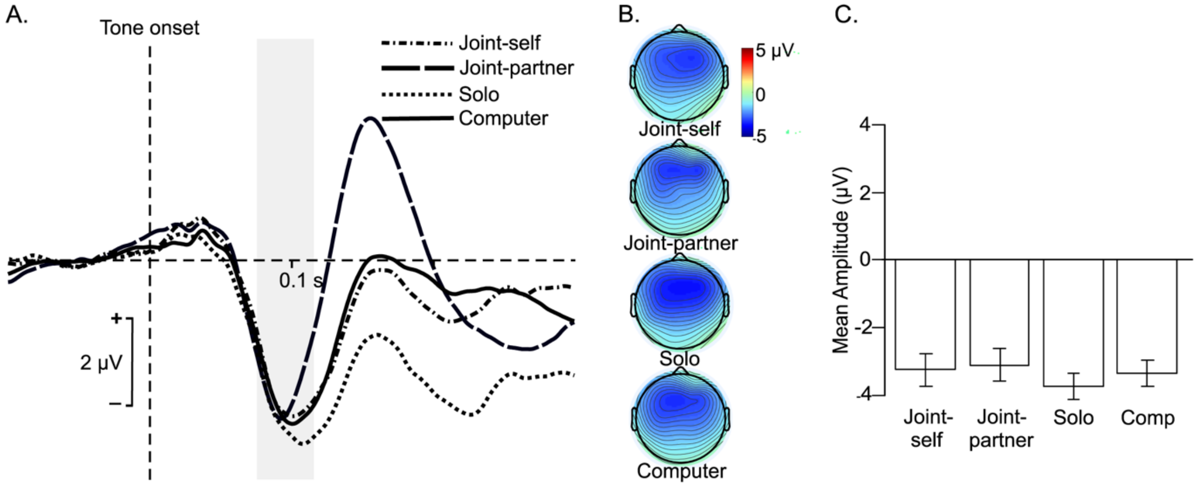


Figure 2.2. Auditory N1 Results: *(A)* Grand-averaged ERP waveforms for each tone type at electrode FCz, time-locked to tone onset. Gray bar indicates the time window of analysis for the N1. *(B)* Scalp voltage topographies averaged across the N1 time window. *(C)* Mean N1 amplitude (±*SEM*) for each tone type.

2.3.2 Auditory P2

Figure 2.3 shows the grand average ERP waveforms elicited by joint-self, joint-partner, solo, and computer tones at electrode Cz, along with scalp voltage topographies and mean amplitudes across the P2 time window. As Figure 2.3 shows, mean P2 amplitudes differed significantly across tone types, $F(3, 117) = 33.96$, $p < .001$, $\eta^2_p = 0.47$, $\eta^2_G = 0.27$. Post-hoc tests indicated that the P2 amplitude for solo tones was significantly reduced compared to the P2 amplitude for computer-produced tones ($M_{diff} = -1.97$, 95% CI [-2.84, -1.10], $t(39) = -4.58$, $p < .001$, Hedges' $g_{av} = 0.80$) and compared to the P2 amplitudes for both joint-self tones ($M_{diff} = -1.48$, 95% CI [-2.00, -.90], $t(39) = -5.33$, $p < .001$, Hedges' $g_{av} = 0.49$) and joint-partner tones ($M_{diff} = -4.86$, 95% CI [-6.05, -3.68], $t(39) = -8.29$, $p < .001$, Hedges' $g_{av} = 1.52$). The P2 amplitude for joint-self tones was significantly reduced compared to the P2 amplitude for joint-partner tones ($M_{diff} = -3.41$, 95% CI [-4.66, -2.17], $t(39) = -5.54$, $p < .001$, Hedges' $g_{av} = 1.00$), but did not differ from the P2 amplitude for computer tones ($M_{diff} = -0.52$, 95% CI [-1.59, 0.54], $t(39) = -0.99$, $p = .33$, Hedges' $g_{av} = 0.20$). The P2 amplitude for joint-partner tones was significantly larger than the P2 amplitude for computer tones ($M_{diff} = 2.89$, 95% CI [1.97, 3.82], $t(39) = 6.33$, $p < .001$, Hedges' $g_{av} = 1.00$). Thus, as expected, the P2 amplitude was attenuated for self-produced tones in the solo task compared to computer-produced tones. Also as expected based on the social differentiation hypothesis, the P2 amplitude was attenuated for self-produced tones in the joint task compared to partner-produced tones in the joint task. However, unexpectedly, the P2 amplitude for self-produced tones in the joint task was not attenuated relative to computer-produced tones, and the P2 amplitude for partner-produced tones in the joint task was enhanced relative to computer-produced tones.

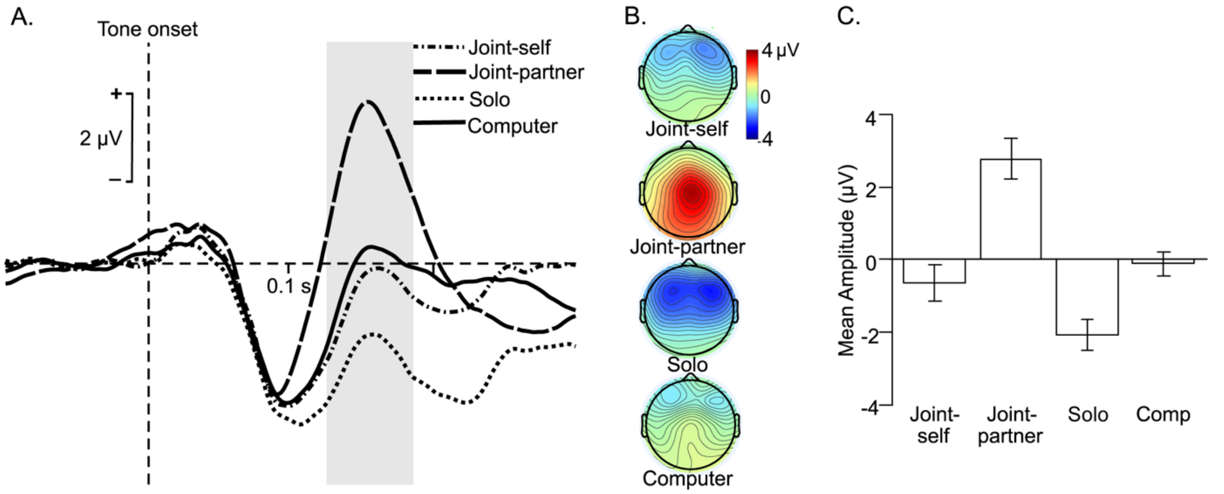


Figure 2.3. Auditory P2 Results: *(A)* Grand-averaged ERP waveforms for each tone type at electrode Cz, time-locked to tone onset. Gray bar indicates the time window of analysis for the P2. *(B)* Scalp voltage topographies averaged across the P2 time window. *(C)* Mean P2 amplitude (±*SEM*) for each tone type.

2.3.3 P2 Amplitude as a Function of ITI and Block

We next examined whether the passage of time leading up to tone onset (i.e., ITI) contributed to the enhanced P2 for joint-partner tones compared to computer tones. The mixed-effects model analysis revealed a significant effect of ITI, *b* = 0.02, 95% CI [.01, .03], $\beta = .08$, *F*(1, 41.21) = 24.67, $p < .001$, indicating that P2 amplitudes increased as the interval preceding the tone onset increased. Critically, however, the effect of tone type was also significant, *F*(1, 41.28) = 38.38, *p* = < .001, indicating that the enhanced P2 amplitude for joint-partner compared to computer tones remained significant even after controlling for ITI effects, and the tone type by ITI interaction was not significant, *F*(1, 5037.23) = 1.07, *p* = .30, indicating that the effect of ITI on P2 amplitude did not differ significantly between joint-partner and computer tones. Thus, although P2 amplitudes were influenced by the passage of time leading up to tone onset, this difference did not account for the enhanced P2 for joint-partner tones relative to computer tones.

Finally, we examined whether increasing familiarity over the course of the experiment contributed to the enhanced P2 for joint-partner tones compared to computer tones. The mixed-effects model analysis revealed a significant effect of tone type, *F*(1, 188.35) = 13.33, *p* = < .001, indicating that the enhanced P2 amplitude for joint-partner compared to computer tones remained significant even after controlling for potential amplitude changes across blocks. Moreover, the effect of block itself was not significant, *F*(1, 5825.90) = 1.25, *p* = .26, nor was the tone type by block interaction, *F*(1, 5826.47) = .71, *p* = .40.

2.4 Discussion

Experiment 1 investigated whether sensory attenuation differentiates self- from partner-produced sounds when two people engage in a joint action that requires ongoing coordination of complementary actions that elicit independent, rather than shared, sensory consequences. Specifically, we tested whether auditory ERPs elicited by self- and partner-produced tones would show social differentiation, that is, stronger attenuation for self-produced tones than partner-produced tones, or social equivalence, that is, similar attenuation for both self- and partner-produced tones (Weiss et al., 2011a). We examined both the auditory N1 and P2 ERPs, because both are considered potential neural markers of the distinction between self- and externally-produced sensory consequences (e.g., Baess et al., 2008; Ghio et al., 2018; Klaffehn et al., 2019; Timm et al., 2016). We did not find evidence of attenuation of the auditory N1 for either self- or partner-produced tones. Instead, we found evidence of social differentiation in the auditory P2:

Self-produced tones elicited an attenuated P2 amplitude relative to partner-produced tones. These findings demonstrate that self-specific attenuation of the auditory P2 differentiates between sensory feedback produced by one's own and others' actions during turn-taking joint actions.

Experiment 1 did not find evidence of self-specific attenuation of the auditory N1. However, we also did not find evidence of sensory attenuation of the N1 at all, for either self- or partner-produced tones, in solo or joint action, relative to computer-produced tones. This finding differs from those of numerous studies that have shown attenuation of self-produced tones compared to computer-produced tones (Baess et al., 2011, 2008; Mifsud et al., 2016; Schafer & Marcus, 1973; Timm et al., 2014). Our findings align with recent evidence that N1 attenuation for self-produced tones may be driven by general predictive processes, such as predictability of the timing and identity of tones, instead of self-specific predictions arising from voluntary action (Hughes et al., 2013a; Klaffehn et al., 2019; Timm et al., 2014). We carefully designed our sequence production task to hold tone identity constant across all conditions (880 Hz) and to ensure that tone timing was similarly predictable for human- and computer-produced tones, due to the isochronous tone timing required by the task, extensive practice of both solo and joint conditions, and the use of human-produced sequence timing in the computer condition. Other studies have likewise shown that when the predictability of self- and computer-produced tones are equated, for example, by providing a countdown before the onset of the computer's tone (Kaiser & Schütz-Bosbach, 2018; Lange, 2009), self-produced tones are not attenuated relative to computer-produced tones. Thus, our findings provide further evidence that general predictive processes account for the self-specific attenuation of the auditory N1 demonstrated in previous studies (Dogge, Hofman, Custers, & Aarts, 2018; Horváth, 2015; Hughes et al., 2013b; Kaiser & Schütz-Bosbach, 2018).

Experiment 1 did find evidence for self-specific attenuation of the auditory P2. First, we showed that self-produced tones within a *solo* action elicited an attenuated P2 relative to computer-produced tones. This finding demonstrates that the auditory P2 is attenuated for self-produced tones relative to externally-produced tones, even in the context of a sequence production task that equates the predictability of tone identity and timing for self- and computer-produced tones. Together with the N1 findings discussed in the preceding paragraph, this finding corroborates recent studies indicating that the P2 may be a better marker of the distinction between self- and externally-produced sensory consequences than the N1 (Ghio et al., 2018;

Knolle et al., 2013; SanMiguel, Todd, et al., 2013; Timm et al., 2016). Second, and more importantly, self-produced tones within a *joint* action elicited an attenuated P2 relative to partner-produced tones in the joint action. This finding is in line with the social differentiation hypothesis and demonstrates that self-specific attenuation does occur in a joint action in which people's actions elicit independent sensory consequences. Before discussing the implications of this finding, however, we first address two unexpected findings that indicate that P2 amplitudes in the joint task do not only reflect self-specific attenuation. Instead, they appear to reflect the combined effects of self-specific attenuation plus non-self-specific enhancement of sensory processing due to the coordination requirements imposed by the joint task, as we explain next.

Two unexpected findings together demonstrate that P2 amplitudes for *both* self- and partner-produced tones were enhanced in joint task. First, the P2 for partner-produced tones in the joint task was enhanced relative to computer-produced tones. Second, the P2 for self-produced tones in the joint task was not attenuated relative to computer-produced tones as we had expected; instead, it was enhanced relative to self-produced tones in the solo task. We speculate that the enhanced P2 for both self- and partner-produced tones could be due to enhanced attention to tone onsets in the joint task. In contrast to the solo and computer tasks, the joint task uniquely required each person to perceive and adjust to millisecond-level fluctuations in the timing of both their own and their partner's tones relative to a joint goal that is the product of both people's action timing (see, e.g., Dell'Anna, Buhmann, Six, Maes, & Leman, 2020). When people coordinate their actions to achieve such a joint goal, they monitor not only their own individual contributions but also the relation between them with respect to the joint goal (Sebanz & Knoblich, 2021; Vesper, Butterfill, Knoblich, & Sebanz, 2010). Computational models of joint action account for this by including predictive models for self and other relative to individual goals as well as their integration with respect to the joint goal (Keller et al., 2016; Pesquita et al., 2018). The need to integrate self- and partner-produced tones with respect to the joint timing goal could enhance overall attention, that is, attention to both self- and partner-produced tones. An attention-based interpretation of P2 enhancement for self- and partner-produced tones would align with recent work showing that the auditory P2 is enhanced when expected tone onsets occur under the focus of controlled attention (Sanabria & Correa, 2013). This interpretation would also be in line with behavioural studies that show that controlled attention enhances sensory processing (e.g., Rohenkohl, Coull, & Nobre, 2011). Moreover, enhanced overall attention could explain both the enhanced P2 for partner-produced tones and the enhanced P2 for self-produced tones in the joint task compared to self-produced tones in the solo task; in the joint task, the participant's tone timing was relevant for both matching the pace and for integrating their timing with their partner's, whereas in the solo task, integrating with the partner's timing was not required. However, further research is needed to confirm these speculations regarding how coordinating toward a joint goal influences attention to tone onsets and, in turn, P2 amplitude.

Importantly, our findings also rule out several potential alternative explanations for P2 enhancement of partner-produced tones. First, P2 enhancement can result from heightened expectations due to the passage of time, that is, because the probability that an expected event will occur increases linearly with the passage of time (e.g., Jones, Hsu, Granjon, & Waszak, 2017). Although we did find that P2 amplitudes increased as the delay from the preceding pacing tone increased, this effect did not account for the enhanced P2 for partner-produced tones relative to computer-produced tones. Second, P2 enhancement can result from heightened perception due to increased exposure to and interaction with specific sounds, e.g., over the course of learning (Ross et al., 2017; Tremblay et al., 2009). However, tone exposure is unlikely to account for P2 enhancement in Experiment 1 because we used the same tone identity across conditions and because P2 amplitudes did not change across blocks. A third possibility is that the enhanced P2 for partner-produces tones could have resulted from motor activity related to preparing to produce a subsequent tone, because partner tones were always followed by self-produced tones. However, preparatory motor activity is unlikely to account for the enhanced P2 because a) the P2 was not enhanced after self-produced tones in the solo task, which were likewise followed by self-produced tones, and b) an analysis of the motor-only condition showed that motor activity in the timeframe of the N1 and P2 was the same regardless of whether the participant had to produce a subsequent tone or not (as described in Footnote 2).

Having addressed the relative enhancement of the P2 for both self- and partner-produced tones within the joint task, we now return to our key finding that the P2 for self-produced tones was nevertheless still attenuated relative to the P2 for partner-produced tones. Our finding of self-specific attenuation of the auditory P2 in a joint action context complements those of several other studies that also showed stronger attenuation for self-produced tones compared to other-produced tones, in both action observation and joint action contexts (Ghio et al., 2018; Loehr, 2013; Weiss et al., 2011b). Although some studies found evidence of social differentiation as early as the N1, our findings suggest that self-other differences in N1 amplitude could result from small differences in action timing that arise in certain action contexts. For example, the joint action task employed by Loehr (2013) included small differences in the temporal intervals between each partner's action and the shared sensory consequence, because people coordinated actions that were nearly but not completely simultaneous, and therefore only one partner's action immediately elicited a tone. Our finding that self-specific P2 attenuation occurs when partners' actions are clearly separated in time (rather than simultaneous) indicates that P2 attenuation does not simply function to resolve temporal ambiguity about which person produced a given sensory consequence.

What mechanisms might account for self-specific attenuation of the auditory P2 in Experiment 1? Our findings are in line with recent evidence that P2 attenuation results from self-specific predictions (SanMiguel, Todd, et al., 2013; Timm et al., 2014). These self-specific predictions could arise from motor-related processes, as posited by forward model and pre-activation accounts of sensory attenuation, which attribute attenuation to motor-based prediction or activation of expected sensory consequences, respectively (e.g., Hughes et al., 2013; Waszak, Cardoso-Leite, & Hughes, 2012). Alternatively, self-specific predictions could arise from cognitive rather than motor-related processes. For example, Dogge et al. (2019) argue that when sensory consequences arise not from the body itself but via the external environment (as was the case in our study, in which finger taps triggered the computer to produce tones), predictions about sensory consequences may be based on cognitive sources such as intentions, goals, or beliefs. Computational models of motor control during joint action posit that predictions about the sensory consequences of actions can arise from both bottom-up and top-down sources (Keller et al., 2016; Pesquita et al., 2018). Thus, regardless of the source of sensory predictions, self-specific attenuation of the P2 could provide a way to route feedback from one's own and others' actions into their respective processing streams within internal models of action control. However, further research is needed to confirm that attenuation results from predictions that occur at cognitive and/or motor levels during joint action, as well as to directly link self-specific P2 attenuation to improvements in the specificity of prediction errors and ultimately to improvements in joint action coordination (Keller et al., 2016; Pesquita et al., 2018).

An alternative perspective to consider is that the self-specific P2 attenuation evident in Experiment 1 could instead reflect deviance detection. Specifically, because the first sequence tone was a different frequency than the four preceding pacing tones, ERP amplitudes elicited by the first sequence tone could potentially reflect a mismatch negativity (MMN), which overlaps in time with both the N1 and the P2 (Näätänen, Paavilainen, Rinne, & Alho, 2007). In line with this, recent research suggests that predictions based on self-produced actions contribute to the MMN (Korka, Schröger, & Widmann, 2019). However, we suggest two reasons why a MMN is unlikely to account for self-specific P2 attenuation in Experiment 1. First, Korka et al.'s (2019) findings show that predictions based on self-produced actions and predictions based solely on the probability of a specific tone frequency both elicit similar MMN responses and, more importantly, that these two sources of prediction integrate rather than show additive effects when they are both present. Thus, in Experiment 1, self-produced tones, which are subject to both sources of prediction, would not be expected to differ from tones in other conditions, which are subject to only one of these two sources. Second, other studies have shown self-specific P2 attenuation for tones that do not differ in frequency from preceding tones (e.g., Timm et al., 2016). That said, further research will be needed to directly investigate which mechanism(s) account for self-specific P2 attenuation in joint action contexts.

Finally, an interesting avenue for future research would be to examine auditory ERPs across all sequence tones. We limited our analysis to the first sequence tone so that we could control for factors that could differentially impact ERP amplitudes on subsequent sequence tones, such as differences in temporal predictability that arise when people adapt their timing based on the timing of preceding actions, differences in refractoriness when sequence tones of the same frequency are repeated, and differences in the agent responsible for producing preceding or upcoming tone(s). Future research examining auditory ERPs across all sequence tones would need to carefully disentangle the influence of each of these factors. For example, future research could examine whether N1 attenuation changes as a function of temporal predictability over the course of the sequence, by directly manipulating temporal predictability by having participants produce sequences with a confederate or a virtual partner (see, e.g., Bolt & Loehr, 2017; Fairhurst, Janata, & Keller, 2013) while simultaneously controlling for refractoriness by varying tone frequency across sequence positions. Manipulating tone frequency across sequence positions would also allow future research to investigate how higher-level sequence planning processes influence sensory ERPs. For example, some accounts of sequence planning in solo action argue that people plan all items in a sequence before action begins (competitive queuing accounts; Kornysheva et al., 2019; Mantziara, Ivanov, Houghton, & Kornysheva, 2020). To date, these accounts have focused primarily on "what" sequence items are planned; further work is needed to account for "who" is responsible for each item and how agency interacts with planning when multiple people produce sequences together in joint action contexts.

In sum, Experiment 1 demonstrates that self-specific attenuation of the auditory P2 ERP differentiates the sensory consequences of one's own and others' actions in joint actions that require coordination of complementary, non-simultaneous actions with independent sensory consequences. Experiment 1 also shows that self-specific attenuation of the P2 occurs concurrently with non-self-specific P2 enhancement due to the coordination requirements of a joint action task. This finding highlights a need for future research to consider the influence of attention on sensory processing during joint action, including its potential consequences for coordination performance. Finally, Experiment 1 corroborates recent evidence that N1 amplitudes are driven by general rather than action-specific predictive processes, which contributes to recent efforts to account for mixed findings in the N1 attenuation literature (Hughes et al., 2013b) and supports a recently proposed functional dissociation between N1 and P2 attenuation (Knolle et al., 2013; Timm et al., 2016).

CHAPTER 3

Portions of this chapter have been previously published or submitted for publication and redundant information has been removed.

Bolt, N. K., & Loehr, J. D. (2023). The auditory P2 differentiates self- from partner-produced sounds during joint action: Contributions of self-specific attenuation and temporal orienting of attention. *Neuropsychologia, 182,* 108526.

Experiment 1 provided evidence that auditory P2 ERP amplitudes were attenuated for self-produced tones compared to partner-produced tones within the joint action. This finding indicates that self-specific attenuation of the auditory P2 differentiates the sensory consequences of one's own from others' actions during joint action, providing a neural marker of perceptual differentiation and supporting the social differentiation hypothesis. Furthermore, Experiment 1 provided preliminary evidence that increased orienting to tone onsets in a joint task might simultaneously contribute to *enhancing* auditory P2 amplitudes. Experiment 2 manipulated the coordination requirements of a joint action to directly assess the hypothesis that orienting processes associated with such requirements would *enhance* auditory P2 amplitudes elicited by a partner's tones, while self-specific processes would *attenuate* auditory ERPs elicited by one's own tones. By doing so, Experiment 2 aimed to test the replicability that self-specific attenuation of the auditory P2 provides a neural marker of self-other differentiation and to determine whether attenuation is modulated by coordination requirements.

The auditory P2 differentiates self- from partner-produced sounds during joint action: Contributions of self-specific attenuation and temporal orienting of attention

When two people perform a task together, they typically monitor the sensory consequences produced by their own actions as well as the sensory consequences produced by their partner's actions with respect to a joint goal (Keller et al., 2016; Vesper et al., 2017). While doing so, each partner must also maintain some degree of distinction between the sensory consequences of each person's actions, so that they can actively adjust their own actions when the joint goal is not being met (Keller et al., 2016; Pesquita et al., 2018). In a previous study, we provided evidence that sensory attenuation, the selective neural or perceptual dampening of self-generated sensory consequences, provides a mechanism for differentiating self- from partner-produced sounds during joint action (Bolt & Loehr, 2021a). However, in that same study, *attenuation* of the auditory P2 ERP elicited by self- compared to partner-produced sounds occurred simultaneously with an overall *enhancement* of the auditory P2 during joint action compared to solo action. We speculated that this enhancement might have occurred because of increased attention to tone onsets in joint action. The goal of Experiment 2 was to directly investigate whether joint actions elicit attention-related enhancement of the auditory P2 during the time window of self-other differentiation. As such, Experiment 2 provides a starting point for disentangling the roles of self-specific attenuation and attention-related enhancement of auditory ERPs in differentiating one's own from a partner's sensory consequences in joint action.

Although sensory attenuation has received relatively little attention in the joint action literature, research in solo action contexts provides considerable evidence for the selective suppression of self-generated sounds. The auditory N1, a frontocentral, negative-going ERP that peaks approximately 100 ms after a tone onset, and the auditory P2, a subsequent frontocentral positive-going ERP that peaks approximately 160 ms after a tone onset, are both attenuated for self- compared to computer-produced sounds (for reviews see Horváth, 2015; Hughes, Desantis, & Waszak, 2012; Kiepe, Kraus, & Hesselmann, 2021). Researchers have recently argued that sensory attenuation of the auditory P2 might be a better marker of self-other differentiation than attenuation of the N1, because the P2 is more strongly linked to self-specific, action-related processes than the N1 (Ghio, Egan, & Bellebaum, 2020; Ghio et al., 2018; SanMiguel, Todd, et al., 2013; Timm et al., 2016). N1 attenuation might instead occur as a result of non-action-specific differences in the predictability of self- versus externally-produced sounds (e.g., differences in the predictability of tone onset timing; Dogge, Hofman, Custers, & Aarts, 2018; Harrison et al., 2021; Horváth, 2015; Hughes et al., 2012; Kaiser & Schütz-Bosbach, 2018).

In a previous study, we examined whether sensory attenuation differentiated self- from partner-produced sounds in *joint* action, and when the predictability of tone onset timing was equated between them (Bolt & Loehr, 2021a). We did so by comparing auditory ERPs for self- versus partner-produced tones in a joint action that required pairs of participants to produce tones in alternation with each other to create four-tone sequences that matched a metronome pace. In line with the sensory attenuation studies discussed above, we found that the auditory P2, but not the N1, was attenuated for self- compared to partner-produced tones. However, we also found initial evidence for an overall *enhancement* of the P2 for both partner- and self-produced tones in joint action. Specifically, we unexpectedly found that both partner- and self-produced tones in the joint action elicited enhanced P2 amplitudes compared to their respective control conditions (i.e., the P2 was enhanced for partner-produced tones in the joint action compared to computer-produced tones, which required the participant to listen to tones produced by an external agent but not to coordinate their own actions with them; and the P2 was enhanced for self-produced tones in the joint action compared to self-produced tones in solo action, which required the participant to produce an action but not to coordinate with their partner). We tentatively hypothesized that this P2 amplitude enhancement might have resulted from increased attention to tone onsets in the joint task, caused by the coordination requirements of the joint task. In other words, an attention-related enhancement of the P2 might occur simultaneously with self-specific attenuation in joint action. We aimed to test this hypothesis directly in Experiment 2.

The possibility of attention-related P2 enhancement in joint action aligns with evidence that controlled attention can influence auditory ERPs during solo action production. When the sensory consequences of one's actions are temporally predictable, as is often the case, attention can be directed towards task-relevant time points to enhance the neural processing of, and boost responding to, the expected sensory consequence (Lange, 2013). Such *temporal orienting of attention* can occur not only for self-produced sounds but also for externally produced sounds that are relevant for a given task (Nobre & Heideman, 2015; Nobre & Van Ede, 2018). For example, the auditory P2 is enhanced when an auditory sequence's rhythm can be used to as a cue to orient attention towards the forthcoming onset of a relevant sequence tone (Sanabria & Correa, 2013). A small number of studies also provide evidence that temporal orienting and sensory attenuation produce independent, but overlapping, effects on auditory processing during solo action (Lange, 2013; Saupe et al., 2013; Timm, SanMiguel, Saupe, & Schröger, 2013). However, further research is needed to determine whether temporal orienting and sensory attenuation produce independent but overlapping effects on auditory processing during joint action.

There are at least three ways that coordinating with a partner could enhance temporal orienting in joint action. First, coordinating with a partner to achieve a joint goal could produce a general enhancement of attention that increases orienting towards both self- and partner-produced tone onsets. According to computational models of joint action, attention can be directed towards self- and partner-produced sensory consequences to make predictions about upcoming actions that facilitate coordination (Harry & Keller, 2019). Second, the need to immediately adjust one's own tone timing in light of a partner's preceding tone timing could enhance attention specifically to the partner's tone onsets. Previous work shows that when partners produce sequences of alternating tones, as they did in our previous study, they correct for small timing errors on any given tone by adjusting the timing of the next tone in the sequence (Bolt & Loehr, 2017; Dell'Anna et al., 2020, 2018). For example, if one person produces their tone later than would be expected based on isochronous intervals, the other partner would produce their next tone relatively earlier to compensate. Third, the need to immediately adjust one's own timing *and* the overall coordination goal might enhance attention to partner-produced tones in an *additive* fashion. This possibility would account for another unexpected finding in our previous study, which was that within the joint action, the P2 elicited by partner-produced tones appeared to be relatively more enhanced than the P2 elicited by self-produced tones compared to their respective control conditions. We designed Experiment 2 to test these three possibilities.

3.1 Experiment 2

The goals of Experiment 2 were twofold. First, we sought to determine whether the coordination requirements of joint action enhance the auditory P2 elicited by a *partner's* tones. Second, we sought to replicate our previous findings of sensory attenuation for *self*-produced tones at the auditory P2 but not the auditory N1, and to determine whether attenuation of self-produced tones is modulated by the coordination requirements of the joint action. We employed the same sequence production task as in our previous study: pairs of participants coordinated their actions to produce four-tone sequences that matched a metronome pace (Bolt & Loehr, 2021; see Figure 3.1A). Also as in our previous study, we recorded EEG from one member of the pair (the *participant*), and we examined auditory ERPs elicited by the first sequence tone, which was produced by either the participant or the partner.

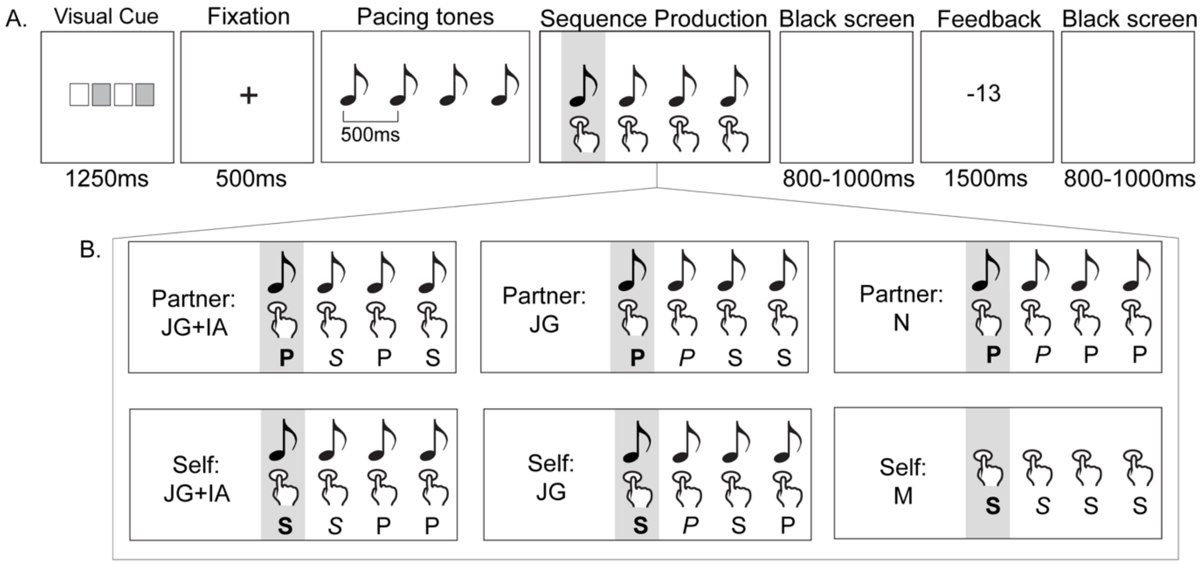


Figure 3.1. (A) Schematic illustration of the experimental task for Experiment 2. After instructions and fixation, participants heard a series of isochronous pacing tones (illustrated by eighth note symbols) and then produced a sequence of tones (illustrated by combined finger-tap and eighth note symbols). After the last sequence tone, the pair received feedback about the sequence pace (catch trial events not shown). Analysis focused on the first sequence tone, highlighted by a grey box. (B) The six experimental conditions, labeled according to which agent produced the first tone (Partner, top row, or Self, bottom row) and the coordination requirements from the participant's perspective (JG+IA = Joint Goal + Immediate Adjustment; JG = Joint Goal; N = No Coordination; M = Motor-only). The agents that produced each tone are labelled below the finger taps as "S" for self (i.e., the participant) and "P" for partner. Labels in **bold** denote the agent who produced the first sequence tone, and labels in *italics* denote the agent who produced the second sequence tone.

To test our hypothesis that the coordination requirements of joint action enhance auditory P2 amplitudes elicited by the *partner's* tones, we compared ERP responses to the partner's first tone across three conditions that differed in coordination requirements from the participant's perspective (Figure 3.1B, top row). 1) In a *joint goal + immediate adjustment* condition, the *participant* produced the second sequence tone (i.e., the pair produced the sequence PSPS, where P refers to partner and S refers to self). This condition required the participant to coordinate with their partner to achieve the joint goal, *and* to adjust the timing of their own action which immediately followed the partner's tone. 2) In a *joint goal only* condition, the *partner* produced the second sequence tone (i.e., PPSS). This condition required the participant to coordinate with their partner to achieve the joint goal, but did *not* require the participant to adjust the timing of their own immediately following action. 3) In a *no coordination* condition, the participant listened to the partner produce all four sequence tones (i.e., PPPP). This condition required neither coordination toward a joint goal nor immediate adjustment. We hypothesized that if coordinating with a partner to achieve a joint goal enhances P2 amplitudes elicited by a partner's tones, then the P2 should be enhanced in the joint goal only condition compared to the no coordination condition. Alternatively, if the need to immediately adjust one's own action enhances P2 amplitudes, then the P2 should be enhanced in the joint goal + immediate adjustment condition compared to the joint goal only condition. Finally, if coordinating toward a joint goal and the need to immediately adjust have additive effects, then P2 amplitudes should be largest in the joint goal + immediate adjustment condition, intermediate in the joint goal only condition, and smallest in the no coordination condition.

To replicate our previous findings of attenuation of the auditory P2 for *self*-produced tones, and to determine whether attenuation is modulated by coordination requirements, we included two conditions in which the *participant* produced the first sequence tone (Figure 3.1B, bottom row). Mirroring the manipulation of coordination requirements described above, in a *joint goal + immediate adjustment* condition, the participant produced the first *and* second sequence tones (i.e., SSPP). In a *joint goal only* condition, the participant produced the first but not the second sequence tone (i.e., SPSP). We expected smaller P2 amplitudes to be elicited by the first sequence tone when it was self-produced compared to partner-produced under both coordination conditions, replicating our previous findings of attenuation of self- relative to partner-produced tones when coordinating with a partner toward a joint goal. In addition, we tested whether the need to adjust one's immediately following action concurrently enhances the P2 amplitude for self-produced tones, which would be evident if self-produced tones were enhanced (or, less attenuated) in the joint goal + immediate adjustment condition compared to the joint goal only condition.

3.2 Methods

3.2.1 Participants

Forty-eight undergraduate students (31 women, 17 men, mean age = 21.2 years, *SD* = 4.6) participated in the study in pairs. An additional two pairs completed the testing session but were excluded (and replaced with new participants) because of excessive artifacts in their EEG recording. Of the 24 pairs included in the analysis, 7 were mixed-gender, 12 were pairs of women, and 5 were pairs of men. Four pairs knew each other before the experiment. EEG was measured from one randomly chosen member of each pair (referred to as *participants*; 15 women, 9 men, mean age = 20.6 years, *SD* = 2.1). The other person in each pair served as the partner, from whom only behavioural data were collected (referred to as *partners*). A power analysis was conducted to determine the required sample size and the required number of trials for each participant in each condition. Briefly, we began by analyzing a previous dataset to obtain the required parameter values, and then we used SIMR (Green & Macleod, 2016) to estimate power at a range of sample sizes and trial numbers using Monte Carlo simulation. The simulation results indicated that a sample size of 24 participants and 70 trials per condition would be required to achieve adequate power (>80%) to detect minimum differences of interest for key comparisons (e.g., self-produced vs. partner-produced tones). Ethical approval was obtained from the institutional review board prior to participant recruitment, and all participants gave informed consent before beginning the study. Participants were compensated with credit for their undergraduate psychology course.

3.2.2 Task and Target of Analysis

We employed a sequence production paradigm in which participants and partners first heard four pacing tones at 500-ms intervals and then produced a four-tone sequence that matched the initial pace (Figure 3.1A). As in our previous study (Bolt & Loehr, 2021a), we focused our analysis on ERPs elicited by the first tone or tap of the sequence to a) control for differences in temporal predictability that may arise later in the sequence when people adjust their timing based on their preceding actions, b) avoid overlapping effects of refractoriness (i.e., reduced auditory ERP amplitudes when tones of the same frequency are presented in succession; Pereira et al., 2014), and c) ensure that the event that immediately preceded the first sequence tone was always the same (i.e., the last pacing tone). To ensure that the temporal predictability of the first sequence tone was as similar as possible across conditions, participants were instructed to produce the first sequence tone “where the fifth pacing tone would be if there was one,” and they were required to practice the task until a strict timing criterion was achieved before beginning the test trials (see Procedure).

3.2.3 Design

The experimental design included six conditions, shown in Figure 3.1B. Condition names reflect which agent’s tone was analyzed (i.e., which agent produced the first sequence tone; *Partner* or *Self*) and what the sequence’s coordination requirements were (from the participant’s perspective). Thus, in the *joint goal plus immediate adjustment* conditions (abbreviated as *JG+IA*), the participant had to coordinate with their partner to achieve a joint goal *and* produce the second sequence tone, which required them to adjust the timing of their own action that immediately followed the first tone. In the *joint goal only* condition (abbreviated as *JG*), the participant had to coordinate with their partner to achieve a joint goal, but they did not produce the second sequence tone. In the *no coordination* condition (abbreviated as *N*), the participant listened to the partner produce the sequence and therefore did not have to coordinate with their partner or adjust their own immediately following action. Thus, the three conditions in which the partner produced the first tone are denoted Partner:JG+IA (sequence produced: PSPS), Partner:JG (sequence produced: PPSS), and Partner:N (sequence produced: PPPP). Two conditions in which the participant produced the first sequence tone are denoted Self:JG+IA (sequence produced: SSPP) and Self:JG (sequence produced: SPSP). Finally, we also included a control condition in which the participant produced the sequence alone (SSSS), but their taps did not elicit any tones (labeled Self:M, where *M* denotes *motor only*). We subtracted ERPs elicited by the first tap in the Self:M condition from ERPs elicited by tones in the Self:JG+IA and Self:JG conditions, to remove movement-related activity that was present in self- but not partner-produced tones (see, e.g., Martikainen, Kaneko, & Hari, 2005; Mifsud & Whitford, 2017).

3.2.4 Apparatus and Materials

Participants and partners sat next to each other on the same side of a table. Participants always sat on the right and partners on the left. An LCD computer screen was centered between them and positioned approximately 40 cm from the edge of the table. Participants and partners each had an Interlink force-sensitive resister (FSR; 3.81 cm^2) placed directly in front of them, approximately 20 cm from the edge of the table. Participants used the index finger of their dominant hand to tap the FSR during the experiment. Each FSR was connected to an Arduino micro-controller, which signaled PsychoPy software (Peirce, 2006) when a tap was registered. PsychoPy recorded each tap and, in all conditions but the motor condition, presented an 880 Hz tone (100 ms duration, 10 ms rise/fall) with a tap-to-tone latency of approximately 8 ms. PsychoPy also presented the remaining auditory and visual stimuli, including the pacing tones (1000 Hz, 100 ms duration, 10 ms rise/fall). Tones were presented through speakers placed on both sides of the screen, which were adjusted to a comfortable volume for each pair.

3.2.5 Procedure

After fitting the participant with an EEG cap, participants and their partners completed a series of training blocks to ensure that the pair could produce the four-tone sequences with accurate and stable timing, both separately and together. Training always began with blocks of solo sequence production, separately for the participant and the partner, followed by blocks of joint sequence production, separately for each coordination condition (i.e., Partner:JG+IA, Partner:JG, Self:JG+IA, and Self:JG). Whether the participant (self) or partner went first was counterbalanced across pairs and followed the same order for both the solo and joint blocks. Whether the first joint block required the participant to produce the second sequence tone (JG+IA) or not (JG) was also counterbalanced across pairs.

The first training block started with two pre-training trials, during which the experimenter controlled the presentation of events and explained the task. Subsequent training blocks had one pre-training trial each. Each training block then proceeded with five trials whose events followed normal trial timing. For each trial, the mean inter-tap interval (ITI) of the four sequence tones was calculated, beginning with the ITI from the last pacing tone to the first sequence tone. If the mean ITI fell between 470 – 530 ms (inclusive) for at least four of the five trials, the pair advanced to the next task. If performance did not meet this criterion, the training continued for another block. On average, each member of the pair performed 1.77 blocks (*SD* = 1.24) of solo sequence production and each pair completed 2.10 JG+IA training blocks (*SD* = 1.67) and 2.23 JG training blocks (*SD* = 1.99).

Participants then performed the test phase of the experiment. Participants completed 7 blocks of 10 trials for each of the 6 conditions in the experiment (i.e., a total of 70 trials per condition). The order of conditions was counterbalanced across pairs using a balanced Latin square design. Each block began with on-screen instructions indicating the task to be performed. After reading the instructions, the pair pressed a button to begin the trials. A black screen was presented for 5000 ms before the first trial to allow the EEG participant to settle into a still position (reduced to 1000 ms in the training blocks).

As shown in Figure 3.1A, each trial began with a visual cue that reminded the pair which task they were to complete. The visual cue remained on the screen for 1250 ms and was then replaced by a central fixation cross, which was presented for 500 ms before the first pacing tone and remained on the screen until the last sequence tone was produced. The four pacing tones were presented at 500-ms intervals and were followed by sequence production. After the last sequence tone/tap, a black screen appeared for 800-1000 ms, randomly selected from a uniform distribution. Performance feedback (the difference between the mean sequence ITI and the required 500 ms pace) was then presented in the center of the screen for 1500 ms. Pairs were informed that positive numbers indicated that performance was slower than the required pace, whereas negative numbers indicated that performance was faster than the required pace. Feedback was presented to promote timing accuracy throughout the experiment. Feedback was followed by another black screen for 800-1000 ms. On two or three trials per block, one member of the pair was randomly selected to enter an estimate of the pair's sequence pace (in ms) before the feedback appeared. These catch trials were included to make sure that participants were paying attention to tones in all conditions. The number of catch trials and the trial numbers on which they occurred was randomly selected, separately for each block, with the constraints that one or two catch trials appeared within the first 7 trials and one catch trial appeared within the last 3 trials of each block. Catch trials were presented on the screen until the participant entered a number and pressed 'enter'. Following this, a black screen appeared for 500 ms, followed by feedback and a black screen as previously described.

3.2.6 Data Acquisition

EEG data were recorded continuously from each participant using 32 active electrodes (actiCAP, Brain Products GmbH, Gilching, Germany), arranged according to an extended version of the 10–20 system at F7, F3, Fz, F4, F8, FC5, FC1, FCz, FC2, FC6, T7, C3, Cz, C4, T8, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, O1, CPz and O2, using carefully positioned nylon caps. All electrodes were referenced to the right mastoid during recording. Vertical eye movements were monitored using a pair of electrodes positioned above and beneath the right eye, and horizontal eye movements were monitored using a pair of electrodes positioned at the outer canthi of the eyes. Impedance was kept below 25 kOhm. EEG signals were amplified within a band width of 0.01–125 Hz and digitized with a sampling frequency of 1000Hz. Auditory events (i.e., pacing and sequence tones) were marked in the data using a StimTrak device (Brain Products GmbH, Gilching, Germany). This device sent a signal to the EEG recording software when auditory stimuli passed through the output cable of the audio interface. Thus, in all conditions other than the Self:M condition, triggers were time-locked to the onset of each tone. In the Self:M condition, Psychopy sent a trigger to the EEG recording software when a tap was registered.

3.2.7 Data Processing

EEG data processing was performed off-line using the EEGlab (version 2020.0.0; Delorme & Makeig, 2004) and ERPlab (version 8.0.0 and v14.1.2; Lopez-Calderon, Luck, & Heekeren, 2014) toolboxes in Matlab® (version R2018A). EEG data were first re-referenced to the average of the two mastoid electrodes and then high-pass filtered with a half-amplitude cutoff of 0.1 Hz (12 dB/octave). The data were then segmented into epochs from 100 ms before to 300 ms after the onset of the first sequence tone in all conditions except the Self:M condition. Epoch length was chosen to capture the N1 and the P2 while excluding motor activity related to preparing a subsequent tap. Because the Self:M condition was used to correct for motor activity accompanying self-produced *tones*, and because PsychoPy presented tones an average of 8 ms after registering a *tap*, epochs in the Self:M condition were time-locked to 8 ms *after* the tap's event marker.

EEG artifact rejection was carried out semi-automatically. Thresholds for each of the following tests were adjusted for each participant based on visual inspection of the data. Blinks were identified using ERPLAB's step-like artifacts function (window width: 200 ms, step: 10 ms, median threshold: 30 µV) applied to a bipolar VEOG channel created by taking the difference in activity between the electrodes above and below the eyes. Horizontal eye movements were identified using the same function (window width: 400 ms, step: 10 ms, median threshold: 20 µV) applied to a bipolar HEOG channel calculated in the same way using electrodes on the outer canthi of the eyes. Extreme absolute voltage differences within an epoch were identified using a peak-to-peak test (window width: 400, step: 10 ms, median threshold: 200 µV) on all electrodes. Trials were also excluded from analysis if they contained a sequence production error in which participants and partners produced their tones in the wrong order. Trials were also excluded if the ITI from the last pacing tone to the first sequence tone/tap fell outside the range of 250-750 ms, or if the ITI from the first sequence tone/tap to the second sequence tone/tap was less than 250 ms. The former criterion was implemented to ensure that the timing of the first tone/tap was temporally predictable, and the latter to ensure that the ERP response to the second sequence tone was not captured in the epoch for the first sequence tone. Finally, one trial was lost due to technical error. In total, 8.85% of all recorded trials were excluded from analysis following these criteria.

Average ERP waveforms were calculated separately for each participant for each condition. Baseline correction was performed on averaged ERP waveforms using the 100 ms period before tone onset. ERPs elicited by self-produced tones (i.e., in the Self:JG+IA and Self:JG conditions) were corrected for movement-related activity by subtracting the mean ERP in the Self:M condition. Hereafter, references to ERPs elicited by self-produced tones refer to motor-corrected ERPs.

3.2.8 Data Analysis

Electrodes and time windows for analysis were chosen based our previous study (a priori measurement parameters; Luck & Gaspelin, 2017). The P2 was therefore defined as the mean amplitude at electrode Cz from 125–185 ms after tone onset. The N1 was defined as the mean amplitude at electrode FCz from 75–115 ms after tone onset. We confirmed that the P2 was maximal over electrode Cz and the N1 was maximal over electrode FCz, consistent with our previous study and with research showing a central maximum for P2 and a more frontocentral maximum for N1 (e.g., Han, Jack, Hughes, Elijah, & Whitford, 2021; Harrison et al., 2021).

We compared mean amplitudes elicited by the first sequence tone across conditions as follows. First, we assessed the effects of coordination requirements on mean P2 amplitudes elicited by the *partner's* tones by comparing P2 amplitudes across coordination conditions (Partner:JG+IA, Partner:JG, and Partner:N) using a one-way within-participants ANOVA. We then conducted planned comparisons using paired samples *t*-tests to check for an effect of coordinating towards a joint goal (Partner:JG vs. Partner:N), an effect of immediate adjustment (Partner:JG+IA vs. Partner:JG), and an additive effect (Partner:JG+IA vs. Partner:N). To further assess the potential additive effect, we conducted a linear trend analysis across the three coordination conditions.

Next, we assessed whether P2 amplitudes were attenuated for *self*- compared to *partner*-produced tones, and whether attenuation was modulated by the need to immediately adapt one's own following action, using a 2 (Agent: Self, Partner) x 2 (Coordination condition: JG+IA, JG) within-participants ANOVA. We planned to conduct follow-up paired-samples *t*-tests as needed.

Last, we conducted two additional sets of analyses to confirm that Experiment 2's findings aligned with findings from prior research. First, we used the Partner:N condition to confirm that self-produced tones in our joint action task were attenuated relative to tones produced by an external agent (here the partner, with whom the participant did not coordinate in the Partner:N condition). This analysis was conducted for comparison to previous research that showed attenuation of self-produced tones relative to an external agent (i.e., tones produced by an observed other person or a computer). It was carried out using planned paired-samples *t*-tests comparing the Self:JG+IA and Self:JG conditions to the Partner:N condition. Second, we confirmed that attenuation of self-produced tones was evident in the auditory P2, but not the auditory N1, by repeating the 2 (Agent: Self, Partner) x 2 (Coordination condition: JG+IA, JG) within-participants ANOVA, and the paired-samples *t*-tests comparing the Self:JG+IA and Self:JG conditions to the Partner:N condition, on mean auditory N1 amplitudes.

3.3 Results

3.3.1 Effects of coordination requirements on P2 amplitudes elicited by partner-produced tones

Figure 3.2 shows the mean P2 amplitudes across all conditions in the study. Our first set of analyses examined P2 amplitudes elicited by *partner*-produced tones, shown in the rightmost three bars in Figure 3.2C. The one-way ANOVA comparing P2 amplitudes across the three coordination conditions (Partner:JG+IA, Partner:JG, Partner:N) did not reveal a significant effect, $F(2, 46) = 2.32$, $p = .110$, $\eta^2_p = .09$, $\eta^2_G = .03$). However, planned comparisons indicated that the mean P2 amplitude was enhanced when participants were required to coordinate toward a joint goal *and* immediately adjust their following action, compared to when they did not need to coordinate (Partner:JG+IA vs. Partner:N; top row of Table 3.1). Mean P2 amplitudes were not enhanced by either the need to coordinate toward a joint goal alone (Partner:JG vs. Partner:N) or the need to immediately adjust a following action alone (Partner:JG+IA vs. Partner:JG; bottom rows of Table 3.1). These findings suggest that coordination requirements had an additive effect, which was further supported by a significant linear trend across the three coordination conditions, $F(1, 23) = 4.507$, $p = .045$, whereby P2 amplitudes increased linearly from the Partner:N to the Partner:JG to the Partner:JG+IA condition.

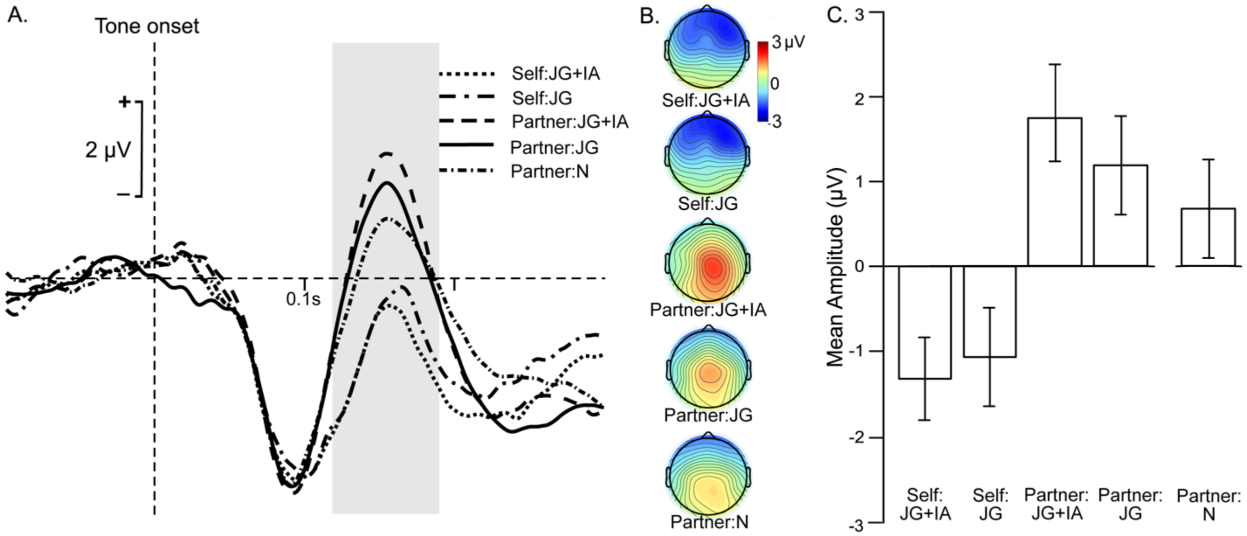


Figure 3.2. Auditory P2 Results: (A) Grand-averaged ERP waveforms for each tone type at electrode Cz, time-locked to tone onset. Gray bar indicates the time window of analysis for the P2. (B) Scalp voltage topographies averaged across the P2 time window. (C) Mean P2 amplitude (±*SEM*) for each condition.

Table 3.1. Differences in P2 amplitudes between partner-produced tones.

Comparison[a]	M_{diff}	[95% CI]	*t*(23)	*p*	g_{av}
Partner:JG+IA vs. Partner:N	1.09	[0.03, 2.15]	2.12	.045*	0.40
Partner:JG vs. Partner:N	0.51	[– 0.59, 1.62]	0.96	.346	0.18
Partner:JG+IA vs. Partner:JG	0.57	[– 0.39, 1.54]	1.23	.232	0.21

[a] Comparisons were ordered such that the condition listed second was subtracted from the condition listed first.
*$p < .05$

Table 3.2. Differences in P2 amplitudes between self- and partner-produced tones.

Comparison[a]	M_{diff}	[95% CI]	*t*(23)	*p*	g_{av}
Self:JG+IA vs. Self:JG	– 0.25	[– 1.07, 0.56]	– 0.64	.526	0.10
Self:JG+IA vs. Partner:N	– 1.98	[– 3.46, – 0.51]	– 2.78	.011*	0.74
Self:JG vs. Partner:N	– 1.73	[– 3.15, – 0.30]	– 2.51	.020*	0.60

[a] Comparisons were ordered such that the condition listed second was subtracted from the condition listed first.
*$p < .05$

3.3.2 Attenuation of P2 amplitudes elicited by self- compared to partner-produced tones

Our next set of analyses examined attenuation for self- compared to partner-produced tones. The leftmost four bars in Figure 3.2C show that P2 amplitudes elicited by self-produced tones were smaller than P2 amplitudes elicited by partner-produced tones, which was confirmed by a main effect of Agent, $F(1, 23) = 17.07$, $p < .001$, $\eta^2_p = 0.43$, $\eta^2_G = 0.21$. Attenuation of self- relative to partner-produced tones did not differ depending on the need to immediately adjust one's own following action; neither the main effect of coordination condition, $F(1, 23) = 0.31$, $p = .586$, $\eta^2_p = 0.01$, $\eta^2_G < 0.01$, nor the interaction, $F(1, 23) = 1.65$, $p = .212$, $\eta^2_p = 0.07$, $\eta^2_G = 0.01$, were significant. In fact, the difference in P2 amplitudes between the Self:JG+IA and Self:JG conditions was in the opposite direction numerically than would be expected if the need to immediately adjust one's following action enhanced the P2 elicited by self-produced tones, although this difference was not significant (first row of Table 3.2).

Furthermore, self-produced tones in the joint action task were attenuated relative to partner-produced tones in the Partner:N condition, as confirmed by significantly smaller P2 amplitudes in the Self:JG+IA and Self:JG conditions compared to the Partner:N condition (second and third rows of Table 3.2).

3.3.3 Auditory N1 amplitudes elicited by self- compared to partner-produced tones

There was no evidence that the auditory N1 was attenuated for self- compared to partner-produced tones. The 2x2 ANOVA revealed no effect of Agent, $F(1, 23) = 0.92$, $p = .347$, $\eta^2_p = 0.04$, $\eta^2_G = 0.01$, no effect of coordination condition, $F(1, 23) = 0.57$, $p = .457$, $\eta^2_p = 0.02$, $\eta^2_G < 0.01$, and no interaction, $F(1, 23) = 0.19$, $p = .670$, $\eta^2_p = 0.01$, $\eta^2_G < 0.01$. Furthermore, N1 amplitudes in the Self:JG+IA and the Self:JG conditions were not significantly different from N1 amplitudes in the Partner:N condition, both *t*s < 0.62, both *p*s > .547.

3.4 Discussion

Experiment 2 investigated the impacts of temporal orienting and self-specific sensory attenuation on auditory ERPs during joint action. Our primary goal was to investigate whether temporal orienting processes associated with the coordination requirements of joint action *enhance* auditory P2 ERPs elicited by a partner's tones, while self-specific processes *attenuate* auditory ERPs elicited by one's own tones. We found that auditory P2 amplitudes elicited by a partner's tones were enhanced under the combined requirements to coordinate with a partner toward a joint goal *and* adjust the timing of one's own immediately subsequent action. We also found that auditory P2 amplitudes elicited by self-produced tones were attenuated relative to partner-produced tones when coordinating with a partner toward a joint goal, regardless of the need to adjust the timing of a following action. These findings demonstrate that the coordination requirements of joint action differentially impact auditory P2s elicited by self- and partner-produced tones, and indicate that self-specific attenuation influences the former while temporal orienting impacts the latter. Our findings additionally confirmed that a) self-produced tones elicited attenuated P2 amplitudes relative to tones produced by an external agent, and b) there was no indication of self-specific attenuation of the auditory N1 during joint action or relative to an external agent. Taken together, the current findings corroborate and extend previous work showing that self-specific attenuation of the auditory P2, and not the N1, differentiates between sensory feedback produced by one's own and partners' actions during joint action (Bolt & Loehr, 2021a).

Experiment 2 revealed a modest, additive effect of coordinating with a partner toward a joint goal *and* adjusting the timing of one's upcoming action on P2 amplitudes elicited by a joint action partner's tones. This finding provides initial evidence that the combination of sharing a goal with an interaction partner, and adjusting one's own actions in light of theirs, shapes how people direct attention towards a partner's tone onsets and thereby contributes to auditory processing of the partner's tones. This finding complements previous research showing that the presence of a joint goal modulates processing of other people's actions, and that attention can be specifically directed towards the timing of sounds that are immediately relevant to planning one's own upcoming action. With respect to the former, previous research has shown that the presence of a joint goal increases activity in sensorimotor areas related to the anticipation of a partner's actions (Sacheli et al., 2019) and that a history of engaging in joint actions with a partner enhances the degree to which people anticipate the partner's actions in their own motor system (Kourtis, Knoblich, & Sebanz, 2013; Kourtis, Sebanz, & Knoblich, 2010). Co-representation accounts of joint action posit that enhanced anticipatory motor and sensorimotor activity related to a partner's actions facilitates prediction of the partner's prospective contribution as well as integration of both parts of the joint action into a unitary representation (Era et al., 2018; Keller et al., 2016; Pesquita et al., 2018; Sacheli et al., 2018). Directed orienting toward the sensory consequences of a partner's actions (here, tone onsets) might likewise facilitate prediction and integration of both people's action timing to enhance joint performance.

With respect to directed attention toward action-relevant sounds, reaction time studies show that enhanced temporal orienting can elicit a behavioural advantage, such that temporally attended stimuli can be responded to faster than unattended stimuli (e.g., Lange & Röder, 2006). In a joint action that requires precise temporal coordination as performed in Experiment 2, temporal orienting might facilitate people's ability to detect small discrepancies in their partners' tone timing relative to the joint timing goal and subsequently make compensatory adjustments to their own action timing (e.g., Dell'Anna et al., 2020). Notably, however, in Experiment 2 the need to adjust one's subsequent action timing influenced auditory P2 amplitudes elicited by *partner*-produced tones, but did not influence auditory P2 amplitudes elicited by *self*-produced tones. Thus, the need to adjust an upcoming action did not appear to increase temporal orienting toward one's *own* tones. The finding that immediate adjustment enhances orienting only toward partner-produced tones could be interpreted as evidence that adjusting to a partner is based more on reactive error correction processes (Harry & Keller, 2019), wherein adjustment is made based on the onset of sensory consequences, rather than on anticipatory processes, wherein adjustment is made based on internal predictions. However, further research would be needed to directly test this interpretation, and further work is also needed to establish a causal link between temporal orienting and enhanced online error correction processes during joint action.

Turning next to our findings regarding sensory attenuation, Experiment 2 corroborates previous work showing that attenuation of the auditory P2 distinguishes self- from other-produced sensory consequences in joint action as well as in action observation (Bolt & Loehr, 2021a; Ghio et al., 2018; Timm et al., 2016). We replicated our previous work by confirming that the P2 was attenuated for self- compared to partner-produced tones in joint action and that there was no evidence of self-specific sensory attenuation at the auditory N1 (Bolt & Loehr, 2021a). These findings add to a growing body of evidence that self-specific attenuation of the auditory P2 underlies self-other differentiation, whereas the auditory N1 does not differentiate self from other when temporal predictability is equated between them (Bolt & Loehr, 2021; Kaiser & Schütz-Bosbach, 2018; Lange, 2009). Importantly, Experiment 2 also rules out the possibility that sensory attenuation for self-produced tones is an artefact of activity related to producing an immediately following action, as attenuation of the first self-produced sequence tone was evident regardless of whether or not the participant also had to produce the second sequence tone. Finally, Experiment 2 also confirmed that self-produced tones were attenuated relative to tones produced by an external agent, i.e., relative to tones produced by a partner under no requirement to coordinate with them. This finding aligns with our own and others' work showing that self-produced tones are attenuated relative to those produced by an external agent, whether that is a computer, another person's observed action, or a human partner with whom one has to interact in other conditions in the experiment (Ghio et al., 2020, 2018; Weiss et al., 2011a, 2011b; Weiss & Schütz-Bosbach, 2012).

The idea that sensory attenuation allows people to differentiate self- from partner-produced sensory consequences within joint action, while temporal orienting might concurrently facilitate the integration of both people's contributions to the joint action, might initially seem contradictory. However, the current findings align with previous work showing separate, but overlapping, effects of sensory attenuation and temporal orienting on auditory ERPs during solo action (Lange, 2013; Saupe et al., 2013; Timm et al., 2013). Moreover, recent research highlights the importance of balancing self-other differentiation with self-other integration during joint action, and provides evidence that both processes occur concurrently as a joint action unfolds (Keller et al., 2016; Liebermann-Jordanidis et al., 2021; Novembre et al., 2016). Specifically, successful joint action performance is thought to rely on a balance between integrating information related to one's own part, partners' parts, and the joint outcome, while also differentiating between individual parts of the joint action. Balancing self-other integration and differentiation allows people to monitor and adjust to a partner's actions to reach a shared goal, while maintaining control over their own actions and sensory consequences. Previous work has shown that dynamic shifts between integration and differentiation are evident in centroparietal alpha oscillations measured on a seconds-long time scale (e.g., Christensen, Slavik, Nicol, & Loehr, 2022; Novembre et al., 2016). Our findings suggest that the balance of self-other integration and differentiation might also be evident on a shorter time scale (i.e., the few hundred milliseconds following the onset of a single sequence tone). How these neural processes work together and shift dynamically as a joint action unfolds remains an intriguing avenue for further research.

In sum, Experiment 2 demonstrates that the coordination requirements of joint action enhance auditory P2 ERPs elicited by a partner's tones, while self-specific processes attenuate auditory P2 ERPs elicited by one's own tones. These findings further our understanding of how the sensory consequences of one's own and others' actions are processed during joint action, and contribute to ongoing work investigating how people balance the need to integrate versus differentiate their own from others' actions while engaged in joint action. The current findings also contribute to ongoing work investigating the concurrent impacts of self-specific sensory attenuation and temporal orienting of attention on sensory processing in solo action and other contexts (Lange, 2013; Saupe et al., 2013; Timm et al., 2013). In addition, by providing further evidence of self-specific sensory attenuation of the auditory P2, but not the auditory N1, Experiment 2 supports a recently proposed functional dissociation between auditory N1 and P2 attenuation (Knolle et al., 2013; Timm et al., 2016). Together, then, findings from Experiment 2 elucidate how the sensory consequences of actions are processed both within and beyond joint action.

CHAPTER 4

Experiment 1 and 2 provide evidence that self-specific attenuation of the auditory P2 differentiates the sensory consequences of one's own from others' actions during joint action. Together, these experiments demonstrate that sensory attenuation of the auditory P2 provides a neural marker of perceptual differentiation. Previous research in solo action contexts further suggests that, before sensory consequences are processed in their respective sensory systems, there is a qualitative differentiation in the *motor* activity associated with one's own actions vs. others' actions (Schütz-Bosbach et al., 2009, 2006). However, research has not yet directly investigated whether each person's individual contributions to a joint action are associated with distinct activity in one's own motor system. To address this gap in the literature, Experiments 3 and 4 conducted a novel analysis of the data from Experiments 1 and 2 to examine motor-related cortical oscillations associated with self- versus partner-produced actions while removing auditory-related activity associated with listening to tones (i.e., sensory consequences). Based on the idea of social differentiation, I hypothesized that motor-related cortical oscillations would provide a neural marker of self-other differentiation, in that people would display increased suppression (indicative of more motor activity) during one's own actions compared to during a partner's actions.

Motor-related Cortical Oscillations Distinguish One's Own from a Partner's Contributions to a Joint Action

Joint action, in which two or more people coordinate their actions towards a common goal, may be facilitated by the activation of similar motor processes for one's own and others' actions (Sebanz et al., 2003; Wilson & Knoblich, 2005; Wolpert et al., 2003). Recent research indeed indicates that when people engage in joint action, they represent both their own and their partner's part of the joint action in their motor system to successfully coordinate with others (e.g., Kourtis, Knoblich, Woźniak, & Sebanz, 2014; Kourtis, Woźniak, Sebanz, & Knoblich, 2019; for a review see Bolt & Loehr, 2021b). The question then becomes, how do people differentiate between each person's actions in their own motor systems? The ability to differentiate between each person's actions is not only essential for the autonomous control of one's own actions, but it is also a requirement for joint action success (Keller et al., 2016;

Pesquita et al., 2018). It is therefore likely that, despite similar neural mechanisms, there is some degree of specificity in the motor activity that corresponds to each partner's actions (Novembre et al., 2012). However, it is still unclear to what extent such a differentiation exists during joint action. Experiment 3 and 4 sought to address this question by investigating whether motor-related brain activity associated with self- versus partner-produced actions differs over the course of a turn-taking joint action.

Numerous studies provide evidence for the idea that similar neural resources support action execution and action observation in solo action contexts (e.g., Muthukumaraswamy & Johnson, 2004; Prinz, 1997; Rizzolatti & Craighero, 2004; Rizzolatti & Sinigaglia, 2010). Early work identified mirror neurons in the macaque monkey that discharge both when the monkey executes a grasping action and when the monkey observes the experimenter performing the same action (Rizzolatti et al., 1996). Despite the lack of evidence for analogous neurons in the human cortex, several functional magnetic resonance imaging (fMRI) studies demonstrate that there are regions of the human cortex that show mirroring properties. These regions show a pattern of activation elicited by observed actions that is similar to the pattern of activation elicited by executing these actions (for review see Molenberghs, Cunnington, & Mattingley, 2012). Increased activity in these regions corresponds to a decrease – or suppression – in spectral power of cortical oscillations measured via EEG (Arnstein, Cui, Keysers, Maurits, & Gazzola, 2011). Specifically, both mu (~8 – 13Hz) and beta (~13 – 35Hz) oscillations measured at central electrode sites are suppressed (reflecting an enhanced state of the motor system) during the execution and observation of actions alike (for review see Fox et al., 2016). Furthermore, for oscillations in both frequency bands, there is typically a substantial rebound of activity about 0.5 – 2 seconds after the cessation of executed and observed actions, with beta rebounding about 200 ms faster and showing a larger increase in power (Avanzini et al., 2012; Salmelin & Hari, 1994).

Although central mu and beta oscillations typically show similar patterns of suppression for both executed and observed actions, recent studies suggest that beta suppression is more directly related to motor system involvement than mu suppression (e.g., Angelini et al., 2018; Avanzini et al., 2012; Press, Cook, Blakemore, & Kilner, 2011). Magnetencephalography (MEG) studies examining beta oscillations during action observation and execution indicate that they are generated in the motor cortex (Hari, 2006; Ménoret et al., 2015; Salmelin & Hari, 1994). Furthermore, beta oscillations are specifically sensitive to the kinematic parameters of executed and observed actions (Brinkman, Stolk, Dijkerman, De Lange, & Toni, 2014). For example, the degree of beta suppression, but not mu suppression, corresponds to the velocity of an observed (Avanzini et al., 2012; Press et al., 2011) or executed action (Kilner, Baker, Salenius, Hari, & Lemon, 2000). The dynamic modulation of beta suppression by the kinematic parameters of observed and executed actions alike suggests a role for beta oscillations in the motoric simulation of other people's actions. Mu suppression is also related to motor system involvement during action execution and observation, although studies provide evidence that it is predominantly generated in the somatosensory cortex (Hari, 2006; Ménoret et al., 2015; Salmelin & Hari, 1994) and it appears to have a functional role in representing others' actions as well as the sensory consequences of these actions (Hari, 2006). Mu suppression is selectively modulated by top-down knowledge about the action context. For example, mu suppression is increased when observed actions are part of a social context instead of a solo context (Perry et al., 2011), when observers have a social history with the actor (Kourtis, Knoblich, et al., 2013), and when actions are observed from a first-person perspective (Angelini et al., 2018). These findings all support the idea that mu suppression during action observation depends on the degree to which people represent the observed others' actions in their own motor system. Both beta and mu suppression could thus play a role in supporting joint action, since the simulation and representation of others' actions are both key processes that allow people to coordinate their actions with each other (Bolt & Loehr, 2021b; Knoblich, Butterfill, & Sebanz, 2011; Wilson & Knoblich, 2005; Wolpert & Flanagan, 2001). Accordingly, in Experiment 3 and 4 we examined self-partner differences in both beta and mu suppression, and we used sensory-only control conditions to isolate motor-related activity in both frequency bands.

Evidence that mu and beta suppression occur during both one's own and observed others' solo actions raises the possibility that in joint action, self- and partner-produced actions might be associated with similar degrees of motor-related suppression, referred to as *social equivalence* (Schütz-Bosbach et al., 2009). Although there is very little research examining whether the motor activity associated with each person's actions shows social equivalence during joint action, several studies provide evidence for an overall increase in mu and beta suppression during joint action compared to solo action (Dumas et al., 2012; Konvalinka et al., 2014; Kourtis et al., 2019; Naeem et al., 2012a; Perry et al., 2011; Zimmermann et al., 2022). There is also evidence that mu suppression is increased when people can represent how their partner's actions relate to their own (Kourtis et al., 2019) and that mu suppression occurs during periods of joint action that promote integration of own and partners' actions by requiring to performers act in congruent ways (Christensen et al., 2022; Novembre et al., 2016). The degree of mu and beta suppression during synchronous joint action in turn corresponds with the amount of behavioural synchrony between partners' actions (Dumas et al., 2012; Naeem et al., 2012a; Naeem, Prasad, Watson, & Kelso, 2012b; Novembre, Knoblich, Dunne, & Keller, 2017), suggesting a link between motor-related suppression in joint action and coordination success.

At the same time, however, the possibility of social equivalence during joint action raises the question of how people would nevertheless distinguish between each person's actions in their own motor systems. The ability to differentiate one's own actions from that of a partner's is essential for maintaining autonomous control of one's own actions (Keller et al., 2016; Pesquita et al., 2018). Computational models of motor control during joint action posit that separate internal models for both one's own and a partner's actions are important for making predictions about the outcomes of a joint action (Keller, Novembre, & Loehr, 2016; Pesquita et al., 2018; Wolpert et al., 2003). From this perspective, successful joint action therefore depends on maintaining a certain degree of agent specificity between partners' actions. This constraint could potentially imply that people's motor activity during joint action may therefore display *social differentiation*, whereby self- and partner-produced actions would be associated with different degrees of motor-related suppression (Schütz-Bosbach et al., 2009). Indirect evidence for social differentiation during joint action comes from studies showing that mu suppression is reduced under conditions that promote distinction between one's own and others' actions, such as when ensemble musicians have to play at different tempi or produce different pitches, rhythms, or dynamics (Christensen et al., 2022; Novembre et al., 2016) or when people are instructed to ignore their partners' actions and focus only on their own (Naeem et al., 2012a).

Thus, there is indirect evidence to support both social equivalence and social differentiation in joint action. One reason why the evidence might appear to be somewhat mixed is that studies that have examined mu or beta suppression in joint action have done so by comparing joint action to solo action and/or by manipulating the relations between self and partner during joint performance. Few studies have directly compared motor activity associated with partners' individual contributions to a joint action. To our knowledge, only one study to date has examined motor activity as a function of the agent producing actions (i.e., self vs.

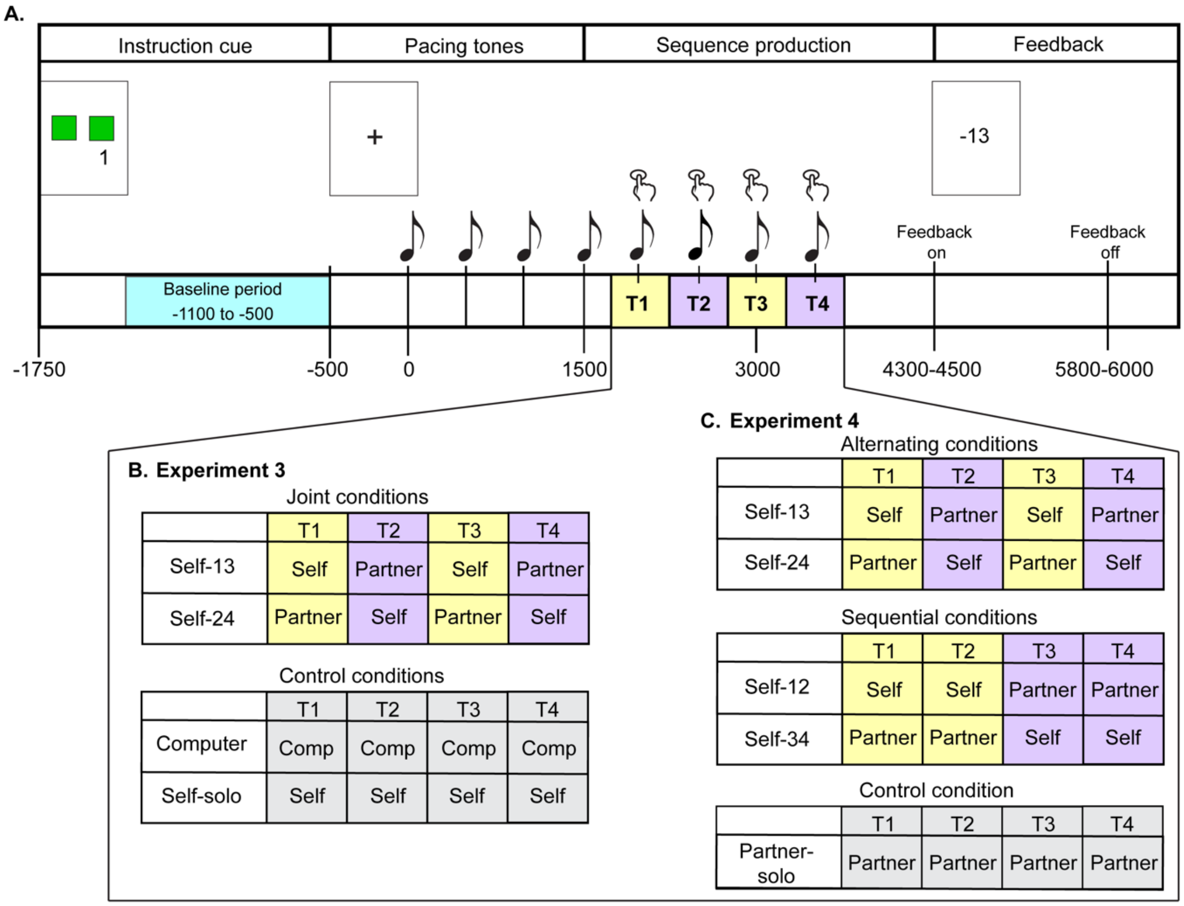
partner, henceforth referred to as *agent-related* or *agentive* influences on motor activity). Novembre et al. (2012) had participants perform the right-hand part of a musical duet, previously learned bimanually, when the left-hand part was either not played (and associated with one's own actions) or was thought to be played by a co-performer (and associated with their co-performer's actions). They found that the degree of motor activity (measured via corticospinal excitability) differed depending on whether the left-hand part was associated with oneself (less motor activity) or another person (more motor activity). However, as in the studies cited in the preceding paragraph, this evidence for agentive differences is also indirect, because the study examined activity during self-produced actions that were performed in relation to one's own versus a partner's imagined actions, and did not directly compare motor activity elicited by self- versus partner-produced actions in joint action. In two recent studies, we (Bolt & Loehr, 2021a, 2023) provided direct evidence of agentive differences in people's responses to actions' sensory consequences during joint action: People displayed stronger attenuation of ERP responses to self- versus to partner-produced tones when they performed a turn-taking joint tapping task, which allowed their responses to self- and partner-produced tones to be examined separately and compared directly. However, these studies only examined participants' sensory responses and did not determine whether agentive differences are also evident in motor activity associated with each partner's actions.

4.1 Current Study

In Experiment 3 and 4, we investigated whether motor-related cortical oscillations show a degree of agent specificity for each partner's distinct contributions to a joint action. Specifically, we investigated whether the motor activity associated with each person's actions shows evidence of social *differentiation* (whereby the degree of mu and beta suppression is significantly increased during one's own actions compared to their partner's actions) or social *equivalence* (whereby the degree of mu and beta suppression is similar during both one's own and a partner's actions). We tested these possibilities using data collected in our studies of agentive differences in responses to the sensory consequences of own and partners' actions (Bolt & Loehr, 2021a, 2023). These studies used a joint tapping paradigm in which pairs of participants coordinated their actions to produce sequence of tones that matched a metronome pace. Importantly, participants took turns producing their taps, so each tap was separated in time by approximately 500 ms (i.e., the metronome pace). Because partners produced their actions at separate times while still coordinating their actions to meet a joint timing goal, we were able to directly compare motor activity associated with each partner's individual contributions to the joint action, by examining mu and beta during separate tap intervals that each encompassed a single tap produced by one partner or the other. Experiment 3 examined whether motor activity shows agent specificity over the time course of a joint action. Experiment 4 aimed to replicate the findings of Experiment 3 and to determine whether agentive differences were more pronounced under conditions that reduced the potential for overlapping motor activity between partners' adjacent turns.

4.2 Experiment 3

In Experiment 3, we conducted novel analyses of data previously reported in Bolt & Loehr (2021a). That dataset included a joint tapping task in which participants produced tones in alternation with a partner. For half of the joint sequences, the participant (referred to as *self*) produced the first and third taps (i.e., the sequence SPSP, where S and P represent self and partner, respectively; see Figure 4.1). For the other half of the joint sequences, the participant produced the second and fourth taps (i.e., PSPS). We tested for agentive differences in motor-related suppression by comparing suppression during taps *within* each joint sequence (e.g., comparing self-produced Tap 1 to partner-produced Tap 2, within the SPSP sequence) and by comparing suppression at equivalent taps *between* the two joint sequences (e.g., comparing self-produced Tap 1 in the SPSP sequence to partner-produced Tap 1 in the PSPS sequence). Social *differentiation* between motor activity associated with each person's actions would be evident in greater mu and beta suppression during self- compared to partner-produced taps. Social *equivalence* would be evident in similar mu and beta suppression during self- and partner-produced taps.



B. Experiment 3

Joint conditions

	T1	T2	T3	T4
Self-13	Self	Partner	Self	Partner
Self-24	Partner	Self	Partner	Self

Control conditions

	T1	T2	T3	T4
Computer	Comp	Comp	Comp	Comp
Self-solo	Self	Self	Self	Self

C. Experiment 4

Alternating conditions

	T1	T2	T3	T4
Self-13	Self	Partner	Self	Partner
Self-24	Partner	Self	Partner	Self

Sequential conditions

	T1	T2	T3	T4
Self-12	Self	Self	Partner	Partner
Self-34	Partner	Partner	Self	Self

Control condition

	T1	T2	T3	T4
Partner-solo	Partner	Partner	Partner	Partner

Figure 4.1. (A) Schematic illustration of a single trial. After an instruction cue, a fixation cross appeared, and participants heard a series of isochronous pacing tones (illustrated by eighth note symbols) and then produced a sequence of tones (illustrated by combined finger-tap and eighth note symbols). Analyzed tap intervals are depicted in purple and yellow squares (e.g., T1 denotes the time window for analysis of motor activity that occurred during the first tap). After the last sequence tone, the pair received feedback about the pace of the sequence tones. (B and C) The experimental conditions for Experiment 3 and 4. Labels within coloured cells denote the agent for each tap (self, partner, or comp = computer). Joint condition names denote which taps the participant produced (see Experiment 3 Design section). Purple and yellow are used to highlight when participants alternated turns with their partner (i.e., after every tap in self-13 and self-24 joint sequences, and between taps 2 and 3 in self-12 and self-34 joint sequences).

4.2.1 Methods

Here we summarize the key methods for Experiment 3 with respect to the current paper. Complete details for the full experiment are reported in Bolt and Loehr (2021a).

4.2.1.1 Participants

The original sample included 80 undergraduate students who participated in the study in pairs. EEG was measured from one randomly chosen member of each pair (referred to as *participants*). The other person in each pair served as the partner, from whom only behavioural data were collected (referred to as *partners*). Because the oscillations of interest were lateralized to the left hemisphere (see Data Analysis section), only data from pairs with right-handed participants were included in the final data set. Four pairs were excluded because the participant was left-handed. An additional pair completed the testing session but was excluded because the participant had excessive artifacts in their EEG recording. Of the 35 pairs included in the analysis, 18 were mixed gender, 14 were pairs of women, and 3 were pairs of men. Four pairs knew each other before the experiment. Of the 35 participants included in the EEG analysis, 24 were male (mean age = 22, *SD* = 4.3). Ethical approval was obtained from the institutional review board prior to participant recruitment, and all participants gave informed consent before beginning the study. Participants were compensated with either credit for their undergraduate psychology course or $25.

4.2.1.2 Task

We employed a sequence production paradigm in which participants and partners first heard four pacing tones at 500-ms intervals and then produced (or listened to) a four-tone sequence that matched the initial pace. A schematic depiction of a single trial is shown in Figure 4.1A and the conditions that were analyzed in Experiment 3 are shown in Figure 4.1B.

4.2.1.3 Design

Experiment 3 examined data from four conditions (see Figure 4.1B). In two joint conditions, participants alternated actions with their partner to produce a four-tone sequence. We refer to the joint conditions according to which taps the participant produced. Thus, we refer to the joint condition in which the participant produced the first and third tones (i.e., SPSP, where S refers to the participant, i.e., *self*, and P refers to the *partner*) as the *self-13* condition. Likewise, we refer to the condition in which the participant produced the second and fourth sequence tones (PSPS) as the *self-24* condition. These two joint conditions allowed us to assess motor activity associated with self- and partner-produced taps during the joint action. In the *self-solo* condition, the participant produced the sequence alone (SSSS). We used the self-solo condition to confirm that motor-related suppression occurred for all self-produced taps across the course of the sequence, replicating previous research on motor-related suppression during action execution (e.g., Neuper, Wörtz, & Pfurtscheller, 2006). We also used the self-solo condition to choose parameters for the time-frequency analysis (see the Time-Frequency Analysis Parameters section and Figure 4.2). Finally, in the *computer* condition, participants listened to sequences of tones produced by the computer. We calculated suppression in all other conditions relative to the computer condition, in order to remove activity associated with hearing tones and thereby isolate motor-related activity. In the computer condition, participants heard the same four pacing tones as in the other conditions, followed by four sequence tones whose timing was randomly selected without replacement from 715 trials of the joint task produced by five pairs of pilot participants.[4] We used the timing produced by pilot pairs during the same joint action as the participants performed to ensure that tone timing in the computer condition matched tone timing in the joint conditions as closely as possible, while also ensuring that participants did not recognize the timing from their own previous performances.

Trials in all four conditions followed the same procedure, described in the Procedure section. In the self-solo and computer conditions, the partner sat quietly beside the participant.

4.2.1.4 Apparatus and Materials

Participants and partners sat next to each other on the same side of a table. Participants always sat on the right and partners on the left. An LCD computer screen was centered between them and positioned approximately 40 cm from the edge of the table. Participants and partners each had an Interlink force-sensitive resister (FSR; 3.81 cm^2) placed directly in front of them, approximately 20 cm from the edge of the table. Participants used the index finger on their dominant hand to tap the FSR during the experiment. Each FSR was connected to an Arduino micro-controller, which signaled PsychoPy software (Peirce, 2007) when a tap was registered. PsychoPy recorded each tap and presented an 880 Hz tone (100 ms duration, 10 ms rise/fall) with a tap-to-tone latency of approximately 8 ms. PsychoPy also presented the remaining auditory and visual stimuli, including the computer tones (also 880 Hz) and the pacing tones (1000 Hz, 100 ms duration, 10 ms rise/fall). Tones were presented through speakers placed on both sides of the screen, which were adjusted to a comfortable volume for each pair.

4.2.1.5 Procedure

After fitting the participant with an EEG cap, participants and their partners completed a series of training blocks to ensure that the pair could produce the four-tone sequences with

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[4] Sequences from pilot pairs were excluded if the timing of one or more inter-tone intervals (ITIs) in the sequence was less than 250 ms or greater than 750 ms. These same criteria were used to exclude behavioural outliers in the other sequences (see Data Analysis).

accurate and stable timing, both separately and together. Details of the training condition are reported in Bolt & Loehr (2021a).

Participants then performed the test phase of the experiment. Participants completed 8 blocks of 10 trials for each of the conditions in the original experiment (i.e., a total of 80 trials per condition). The order of conditions was counterbalanced across pairs using a balanced Latin square design. Each block began with on-screen instructions indicating the task to be performed and, in the joint conditions, whether the participant or the partner would produce the first sequence tone. After reading the instructions, the pair pressed a button to begin the trials. A black screen was presented for 5000 ms before the first trial to allow the EEG participant to settle into a still position.

As shown in Figure 4.1A, each trial began with a visual cue that reminded the pair which task they were to complete during the trial. The cue remained on the screen for 1250 ms and was then replaced by a fixation cross in the center of the screen. The fixation cross was presented for 500 ms before the first pacing tone and remained on the screen until the last sequence tone was produced. The four pacing tones were presented at 500-ms intervals and were followed by sequence production (in the self-13, self-24, and self-solo conditions) or by the computer-produced sequence tones (in the computer condition). A black screen appeared for 800-1000 ms, randomly selected from a random uniform distribution, after the last sequence tone/tap. Performance feedback (the difference between the mean sequence ITI and the required 500 ms pace) was then presented in the center of the screen for 1500 ms to promote timing accuracy throughout the experiment. Feedback was also presented in the computer condition, and was followed by another black screen for 800-1000 ms, randomly selected from a uniform distribution.

4.2.1.6 Data Acquisition

EEG data were recorded continuously from each participant using 32 active electrodes (actiCAP, Brain Products GmbH, Gilching, Germany), arranged according to an extended version of the 10–20 system at F7, F3, Fz, F4, F8, FC5, FC1, FCz, FC2, FC6, T7, C3, Cz, C4, T8, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, O1, CPz and O2, using carefully positioned nylon caps. All electrodes were referenced to the right mastoid during recording. Vertical eye movements were monitored using a pair of electrodes positioned above and beneath the right eye, and horizontal eye movements were monitored using a pair of electrodes positioned at the outer canthi of the eyes. Impedance was kept below 25 kOhm. EEG signals were amplified within a band width of 0.01–125 Hz and digitized with a sampling frequency of 1000Hz. Auditory events (i.e., pacing and sequence tones) were marked in the data using a StimTrak device (StimTrak, Brain Products GmbH, Gilching, Germany). This device sent a signal to the EEG recording software when auditory stimuli passed through the output cable of the audio interface. Thus, in all conditions analyzed here, triggers were time-locked to the onset of each tone.

4.2.1.7 Data Pre-Processing

EEG data pre-processing was performed off-line using the EEGLab (version 2021.1; Delorme & Makeig, 2004) and ERPLab toolboxes (version 8.30; Lopez-Calderon & Luck, 2014) run in Matlab (version R2018.a). Raw EEG data were high-pass filtered with a half-amplitude cutoff of 0.1 Hz (12 dB/octave). We removed ocular artifacts using an Independent Component Analysis (ICA). To prepare for ICA, we first removed noisy periods of data that occurred between testing blocks and in the first two seconds of each testing block, before the onset of the first visual instruction cue. We then removed brief periods of noise (typically less than one trial in duration) that were identified using ERPLab's pop_continuousartdet function and visual inspection of the data. We then ran the ICA using the AMICA EEGLab plugin (version 1.6.1). Next, we used the SASICA EEGLab plugin (version 1.3.8) alongside the guidelines for its use (Chaumon et al., 2015) to identify components representing blinks and saccades, which we removed from the data. On average, two components were removed from each participant. Next, we epoched the data from 1750 ms before to 5000 ms after the first pacing tone. The data were then re-referenced to an average of the two mastoid electrodes.

Epochs that still contained large voltage excursions were removed from the data. EEG artifact rejection was carried out semiautomatically using ERPLAB's step function, starting with a threshold of 80 *u*V, a window size of 2000 ms, and a window step of 500 ms. Voltage thresholds were adjusted for each participant based on visual inspection of the data. We also excluded any trials that contained a sequence production error in which participants and partners produced their tones in the wrong order, as well as any trials whose timing included one or more inter-tap intervals (ITIs) that were less than 250 ms or greater than 750 ms. We chose these criteria to match the criteria used to create the sequences in the computer condition. Finally, 6 trials were lost due to technical error. In total, 7.19% of all recorded trials were excluded from analysis following these criteria.

4.2.1.8 Time-Frequency Analysis Parameters

Time-frequency analyses were conducted using the EEGlab toolbox (version 2021.1) run in Matlab (version R2018a). Time-frequency transforms were computed on the single-trial data by means of a continuous Morlet wavelet transform for the frequency range 3 to 40 Hz (incrementing linearly by 0.25 Hz), with the number of cycles increasing from 3 cycles at the lowest frequency to 30 cycles at the highest frequency (calculated with a scale expansion factor of 0.25). The prestimulus period during which participants observed the visual instruction cue (from –1100 to –600 ms from the last pacing tone; see Figure 4.1A) served as a baseline. We then calculated the mean event-related spectral perturbation (ERSP) for each condition, separately for each participant. The ERSP is the mean change in spectral power (averaged across trials) relative to the baseline period (dividing each time-frequency point value by the average spectral power across the baseline period at the same frequency), at each of 200 equally-spaced timepoints within the epoch. For all conditions, we then computed suppression relative to the computer control condition, i.e., we subtracted the ERSP in the computer condition from the ERSP in each other condition (self-13, self-24, and self-solo). Hereafter, references to "mean power" in the self-13, and self-24, and self-solo conditions refer to the difference between each of these conditions and the computer condition.

To identify the electrodes of interest, we assessed the topography plots for the self-solo condition (see Figure 4.2A). Specifically, we plotted the topographies for the mu (8 – 13Hz) and beta (15 – 35Hz) frequency bands; frequency ranges were selected based on previous research showing modulation of mu and beta oscillations during joint action and action observation (e.g., Avanzini et al., 2012). For each frequency band, we plotted the topography of power values averaged across the entire sequence production period (i.e., from the onset of the last pacing tone to 500 ms after the last sequence tone) in the self-solo condition. As Figure 4.2A shows, suppression was lateralized over the left hemisphere at electrode C3 for both mu and beta frequency bands. We therefore restricted the following analysis to electrode C3. To further refine the frequency ranges for mu and beta using a data-driven approach (e.g., Angelini et al., 2018), we plotted the ERSP for the self-solo condition at electrode C3, as shown in Figure 4.2B. Based on the maximal suppression over the time course of sequence production in these plots, we defined mu as 11 – 13 Hz and beta as 20 – 26 Hz.

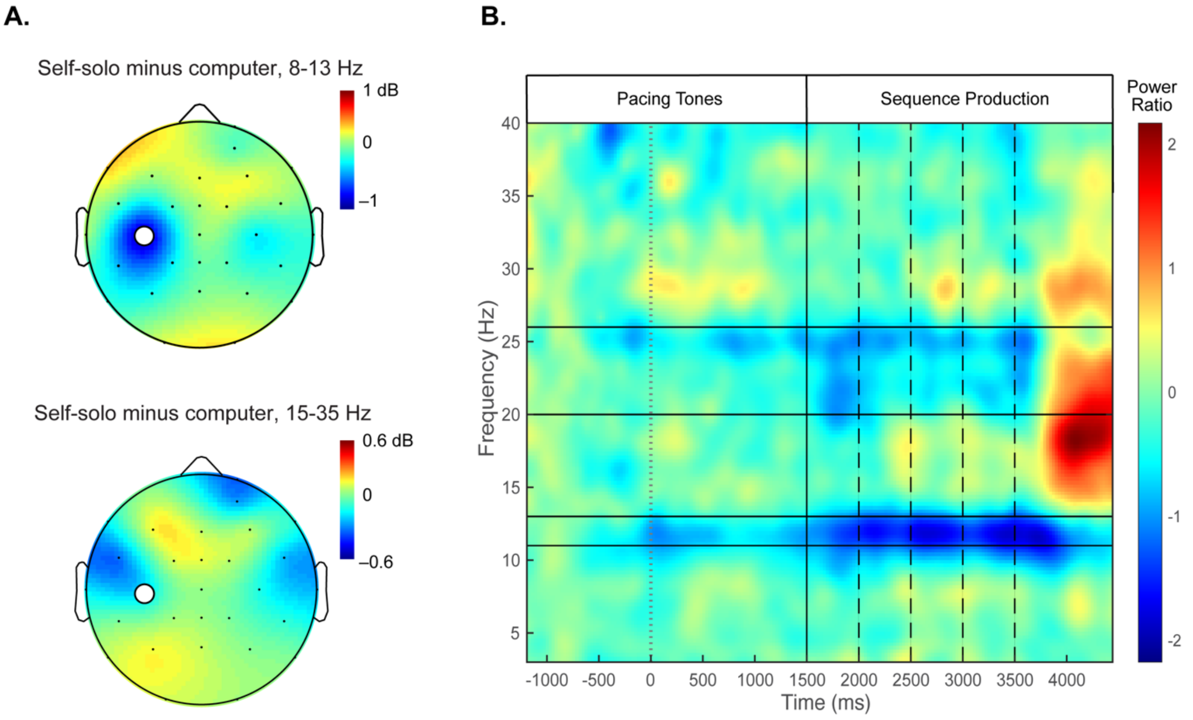

Figure 4.2. (A) Topography plots showing mean power (dB) averaged across the time window of sequence production in the self-solo condition for the predicted mu (8 – 13 Hz) and beta (15 – 35 Hz) frequency bands. Based on these plots, analyses were restricted to electrode C3 (highlighted). (B) The time-frequency plot for electrode C3. The dotted black vertical line indicates the first pacing tone. The solid black vertical line indicates the last pacing tone (i.e., the start of sequence production). The dashed black lines indicate the sequence tones. The horizontal lines indicate the frequency range for mu (11-13 Hz) and beta (20-26 Hz) which were selected based on the maximal suppression over sequence production in this plot.

We next checked whether mean power fluctuated before and after taps based on the cyclic nature of participants' finger movements. In our sequence production task, people moved their index finger cyclically from flexion (i.e., tapping finger down on the FSR) to extension (i.e., raising finger up in the air). Hand movements that are cyclic show fluctuations in beta that correspond with movement velocity (e.g., Avanzini et al., 2012; Kilner et al., 2003). Because flexion occurs immediately before each tap, and extension occurs after each tap, we calculated the mean power in the self-solo condition over intervals lasting 250 ms, starting 250 ms after the last pacing tone. These intervals corresponded approximately to intervals of flexion and extension before and after taps, respectively. We examined the mean power across these 8 intervals using a one-way ANOVA with the within-subjects factor of Interval, separately for mu and beta frequency bands. Mean power did not significantly differ across intervals in the mu band, $F(3.44, 117) = 1.18$, $p = .322$, $\eta^2_p = .03$, $\eta^2_G < .01$, or the beta band, $F(4.72, 160.44) = 1.89$, $p = .103$, $\eta^2_p = .05$, $\eta^2_G = .01$. Because we did not find evidence of flexion/extension-based effects in the self-solo condition, we divided the time course of sequence production in the joint condition into four 500-ms intervals that encompassed the entire movement (i.e., both flexion and extension) surrounding each agent-produced sequence tone, henceforth referred to as taps 1-4.

4.2.1.9 Statistical Analysis

We conducted the following analyses separately for mu and beta frequency bands. We first examined mean power in the self-solo condition to check if there was consistent suppression across the sequence during solo action execution. To confirm that suppression occurred at each tap, we conducted four one-sample *t*-tests comparing the mean power for each tap against zero. We then checked whether suppression differed across taps using a one-way ANOVA with the within-subjects factor of Tap (1-4).

We then examined mean power in the joint conditions to test whether there were differences between self- and partner-produced taps, using a 2 (Condition: self-13, self-24) x 4 (Tap: 1-4) within-subjects ANOVA. In this analysis, social differentiation would be supported by a Condition by Tap interaction, because the participant and partner produced opposite taps in the two conditions. Because the Condition by Tap interaction was significant in both the mu and beta frequency bands, we next conducted planned paired-samples *t*-tests in two steps. First, we compared mean power between adjacent taps *within* each joint condition; in this analysis, social differentiation would be supported by significant differences between adjacent self- versus partner-produced taps. Second, we compared mean power at each tap *between* the two joint conditions; in this analysis, social differentiation would be supported by significantly greater suppression for self- compared to partner-produced taps at each of taps 1-4. For all ANOVAs, Greenhouse-Geisser corrections were applied to degrees of freedom and *p* values whenever Mauchly's test of sphericity indicated the assumption of sphericity was violated ($p < .05$). For all t-tests, *p* values were adjusted for multiple comparisons using the Holm-Bonferroni method with a family size of 3 for within sequence comparisons and 4 for between sequence comparisons.

4.2.2 Results

4.2.2.1 Mu Band

4.2.2.1.1 Solo Sequence Production.

The top left panel of Figure 4.3 shows that mu suppression occurred at all taps in the self-solo condition. Mean power was significantly lower than zero for taps 1-4, all $t(34)$s < -3.56, all ps $< .002$. Mean power did not significantly differ across taps, $F(2.38, 81.04) = 0.98$, $p = .393$, $\eta^2_p = .03$, $\eta^2_G < .01$, indicating that suppression was consistent across the sequence.

4.2.2.1.2 Joint Sequence Production.

The bottom left panel of Figure 4.3 shows the mean power in the mu frequency band for each tap in the two joint conditions. The ANOVA confirmed that there was a significant Condition by Tap interaction, $F(1.78, 60.57) = 11.52$, $p < .001$, $\eta^2_p = .25$, $\eta^2_G = .01$, but no main effect of Condition, $F(1, 34) = 0.04$, $p = .836$, $\eta^2_p < .01$, $\eta^2_G < .01$, nor Tap, $F(2.15, 73.11) = 1.50$, $p = .228$, $\eta^2_p = .04$, $\eta^2_G < .01$.

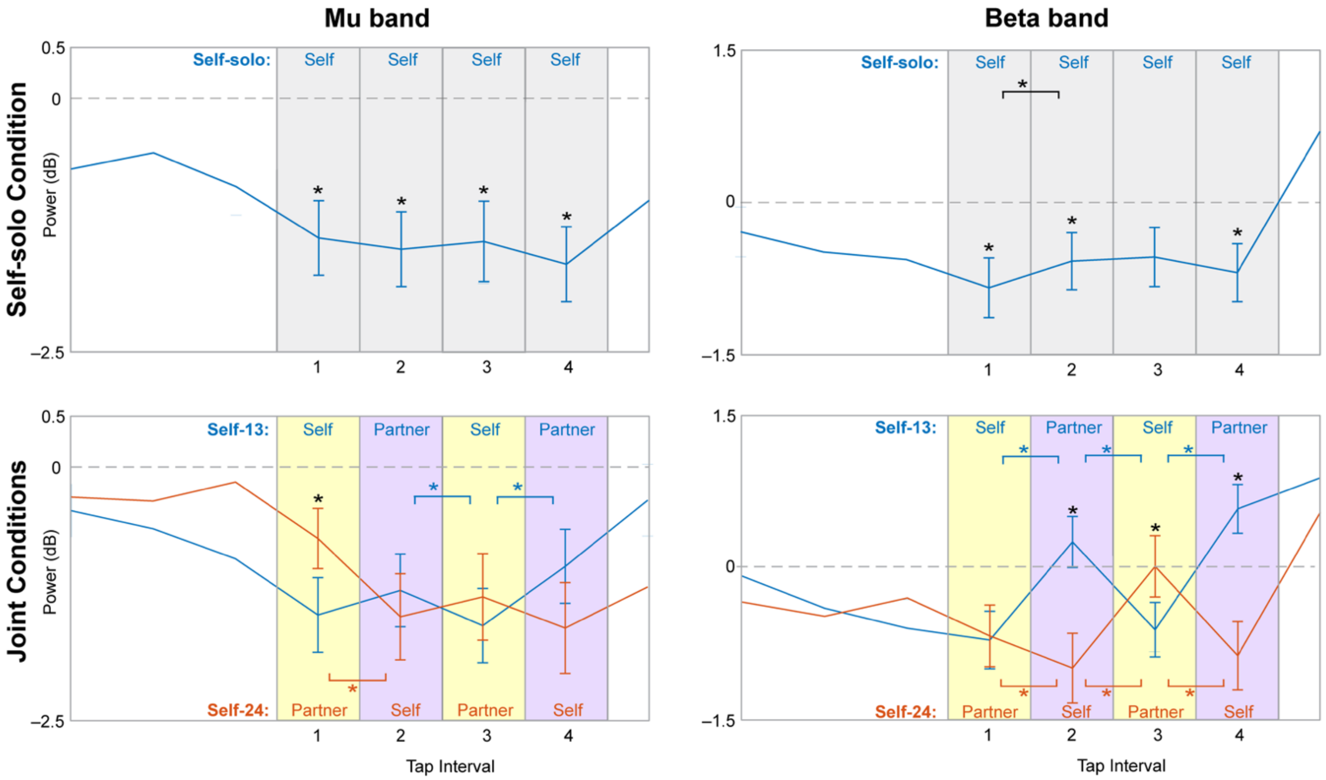

Figure 4.3. Mean power (± *SEM*) in the mu (left panels) and beta (right panels) bands at electrode C3 across taps, relative to the computer condition (represented by the dotted horizontal line at 0 dB). Top panels: Mean power in the self-solo condition. Significant differences from zero are denoted with an asterisk above the error bars. Bottom panels: Mean power in each joint condition (self-13: blue line and agent labels at the top of the plot; self-24: red line and agent labels at the bottom of the plot). Significant differences between adjacent taps *within* each joint condition are denoted with square brackets and an asterisk, at the top of the plot for the self-13 condition and at the bottom of the plot for the self-24 condition. Significant differences *between* joint conditions at each tap are denoted with an asterisk above the error bars.

Table 4.1. Power differences between adjacent taps *within* each joint condition in the mu (left) and beta (right) bands.

Joint Cond.	Taps Compared[a]	*mu*					*beta*				
		M_{diff}	95% CI	$t(34)$	p_{adj}	g_{av}	M_{diff}	95% CI	$t(34)$	p_{adj}	g_{av}
Self-13	1 vs. 2	−0.24	[−0.67, 0.18]	−1.2	.255	0.11	**−0.97**	[−1.24, −0.70]	−7.3	**<.001**	0.60
	3 vs. 2	**–0.35**	[–0.63, –0.06]	–2.5	**.038**	0.16	**–0.87**	[–1.27, –0.61]	–6.8	**<.001**	0.56
	3 vs. 4	**−0.58**	[−0.95, −0.22]	−3.3	**.008**	0.27	**−1.19**	[−1.53, −0.86]	−7.3	**<.001**	0.78
Self-24	2 vs. 1	**–0.77**	[–1.25, –0.29]	–3.3	**.008**	0.36	**–0.32**	[–0.55, –0.09]	–2.8	**.008**	0.16
	2 vs. 3	−0.20	[−0.52, 0.13]	−1.2	.232	0.08	**−1.00**	[−1.30, −0.71]	−7.0	**<.001**	0.52
	4 vs. 3	–0.31	[–0.65, 0.04]	–1.8	.165	0.12	**–0.86**	[–1.14, –0.62]	–6.8	**<.001**	0.46

[a]In all Tables, comparisons are ordered such that self-produced taps are always compared to partner-produced taps (i.e., self minus partner, so that negative values indicate greater suppression for self- compared to partner-produced taps). Comparisons that reached significance ($p_{adj} < .05$) are indicated by bolded means and p_{adj} values.

Table 4.2. Power differences *between* joint conditions at each tap in the mu (left) and beta (right) bands.

Tap	*mu*					*beta*				
	M_{diff}[a]	95% CI	$t(34)$	p_{adj}	g_{av}	M_{diff}	95% CI	$t(34)$	p_{adj}	g_{av}
Tap 1	**−0.75**	[−1.18, −0.33]	−3.60	**.004**	0.38	−0.04	[−0.40, −0.32]	−0.23	1	0.02
Tap 2	−0.26	[−0.82, 0.30]	−0.95	.365	0.11	**−1.25**	[−0.79, −1.70]	−5.54	**<.001**	0.70
Tap 3	−0.28	[−0.70, 0.14]	−1.36	.365	0.12	**−0.63**	[−1.01, −0.24]	−3.30	**.005**	0.37
Tap 4	−0.61	[−1.23, 0.01]	−1.99	.163	0.25	**−1.45**	[−1.01, −1.89]	−6.65	**<.001**	0.84

[a]Comparisons were ordered so that negative values indicate greater suppression for self- compared to partner-produced taps.

The left half of Table 4.1 shows the mean power differences between taps *within* each joint condition in the mu frequency band, along with confidence intervals, t statistics, p values, and measures of effect size for each comparison. In the self-13 condition, mean power was not significantly different between tap 1 (self tap) and tap 2 (partner tap), but was more suppressed for tap 3 (self tap) than taps 2 and 4 (partner taps). In the self-24 condition, mean power was more suppressed for tap 2 (self tap) than tap 1 (partner tap), but was not significantly different for other tap comparisons. The left half of Table 4.2 shows the mean power differences and supporting statistics for comparisons *between* joint conditions for each tap in the mu frequency band. Mean power was more suppressed at Tap 1 in the self-13 condition (self tap) compared to the self-24 condition (partner tap). Mean power did not significantly differ between sequences for taps 2-4.

4.2.2.2 Beta Band

4.2.2.2.1 Solo Sequence Production.

The top right panel of Figure 4.3 shows that suppression (i.e., mean power significantly lower than zero) occurred at tap 1, $t(34) = -2.85$, $p = .029$. Mean power was marginally lower than zero at tap 2 ($t(34) = -2.06$, $p = .095$), tap 3 ($t(34) = -1.85$, $p = .095$), and tap 4 ($t(34) = -2.42$, $p = .062$).. The difference in mean power across taps was likewise marginal, $F(2.34, 79.59) = 2.72$, $p = .064$, $\eta^2_p = .07$, $\eta^2_G < .01$).

4.2.2.2.2 Joint Sequence Production.

The bottom right panel of Figure 4.3 shows the mean power for each tap in the two joint conditions. The ANOVA confirmed that there was a significant Condition x Tap interaction, $F(2.17, 74.07) = 65.48$, $p < .001$, $\eta^2_p = .66$, $\eta^2_G = .06$. There was also a significant main effect of Condition, $F(1, 34) = 8.64$, $p = .006$, $\eta^2_p = .20$, $\eta^2_G = .02$, indicating that mean power was less suppressed overall for the self-13 condition (when the participant led the sequence) compared to the self-24 condition (when the partner led the sequence), $M_{diff} = 0.51$, 95% CI [0.16, 0.86]. There was also a significant main effect of Tap, $F(2.31, 78.47) = 8.57$, $p < .001$, $\eta^2_p = .20$, $\eta^2_G = .01$, whereby tap 1 was more suppressed compared to all other taps, all ts > -3.38, all ps $< .007$. None of the other taps differed from each other, all ts < -1.93, all ps > 0.19. More importantly, planned comparisons confirmed that *within* both the self-13 and self-24 conditions, mean power differed between self-produced and partner-produced taps at all adjacent taps, with self-produced taps showing more suppression than partner-produced taps (right half of Table 4.1). Mean power also differed *between* the two joint conditions at taps 2, 3, and 4, with self-produced taps showing more suppression than partner-produced taps (right half of Table 4.2).

4.2.3 Discussion

Experiment 3 investigated whether motor activity shows agent specificity over the time course of a joint action. We found evidence that mu and beta suppression fluctuate over the time course of joint sequence production, with more suppression occurring during self-produced actions compared to partner-produced actions. Given that solo sequence production showed suppression across the sequence, our findings are consistent with a social differentiation effect.

There were notably more agentive differences in the beta frequency band compared to the mu frequency band during joint sequence production. This finding may suggest that social differentiation is more pronounced in the beta frequency band, and, in turn, that activity associated with the motoric simulation of a partner's actions differs from the activity associated with producing one's own actions. However, it is also possible that agentive differences in the mu frequency band were reduced when agents produced actions in alternation because for most taps, the participant's own tap immediately preceded the partner's tap. Mu suppression rebounds about 200 ms later than beta after action cessation (Avanzini et al., 2012; Salmelin & Hari, 1994), making it possible for mu suppression associated with a preceding self-produced tap to overlap with the following partner-produced tap. Consistent with this possibility, we *did* find agentive differences in the mu band when the partner's tap occurred at the beginning of the sequence, which would not be obscured by overlapping activity from preceding self-produced taps. We therefore analyzed data from a second experiment to explore the possibility that agentive differences would be more pronounced when not obscured by overlapping motor activity, and to replicate our findings that agentive differences in mu and beta suppression occur across the time course of a joint action.

4.3 Experiment 4

In Experiment 4, we conducted novel analyses of data first reported in Bolt and Loehr (2022), in which partners performed the same joint tapping task as Experiment 3. In addition to having participants produce tones in *alternation* with their partner (i.e., SPSP or PSPS), this dataset also included a *sequential* task in which partners' contributions to the joint action were successive (i.e., SSPP or PPSS). When agents produced tones in succession, partner-produced taps that occurred at taps 1, 2 and 4 were not preceded by self-produced taps, thus eliminating the possibility that suppression related to self-produced taps would overlap with partner-produced taps. Only partner-produced taps that occurred at tap 3 would potentially contain overlapping suppression from a preceding self-produced tap. As in Experiment 3, social differentiation would be evident in greater suppression during self-produced compared to partner-produced taps. Social differentiation would be further supported by agentive differences in the mu frequency band when partners produce successive actions, particularly when examining partner-produced taps that are not preceded by self-produced taps.

4.3.1 Methods

Here we summarize the key methods for Experiment 4. Complete details are reported in Bolt & Loehr (in prep).

4.3.1.1 Participants

The original sample included 48 undergraduate students who participated in the study in pairs (17 men, mean age = 21.2 years, *SD* = 4.6). As in Experiment 3, pairs consisted of a *participant* (from whom EEG was measured) and a *partner* (from whom only behavioural data were collected). Three pairs were excluded because the participant was left-handed. Of the 21 pairs included in the analysis, 7 were mixed gender, 10 were pairs of women, and 4 were pairs of men. Four pairs knew each other before the experiment. Of the 21 participants included in the EEG analysis, 8 were male (mean age = 20.4, *SD* = 1.4). Ethical approval was obtained from the institutional review board prior to participant recruitment, and all participants gave informed consent before beginning the study. Participants were compensated with either credit for their undergraduate psychology course or $25.

4.3.1.2 Task

Experiment 4 employed the same sequence production paradigm as Experiment 3; participants and partners first heard four pacing tones at 500-ms intervals and then produced (or listened to) a four-tone sequence that matched the initial pace. A schematic depiction of a single trial is shown in Figure 4.1A and the conditions that were analyzed in Experiment 4 are shown in Figure 4.1C.

4.3.1.3 Design

Experiment 4 examined data from five conditions (see Figure 4.1C). As in Experiment 3, Experiment 4 included two joint conditions in which pairs performed an alternating sequence production task: in the *self-13* condition, the participant produced taps 1 and 3 (SPSP), and in the *self-24* condition, the participant produced taps 2 and 4 (PSPS). The alternating conditions allowed us to test the replicability of agentive differences found in Experiment 3. Experiment 4 also included two joint conditions in which pairs performed a sequential task, whereby one member of the pair produced successive actions before the other member produced their successive actions (e.g., SSPP). In the *self-12* condition, the participant produced the first two taps (SSPP), and in the *self-34* condition, the participant produced the last two taps (PPSS). The sequential conditions allowed us to examine agentive differences without overlap from preceding self-produced taps. Finally, in the *partner-solo* condition, participants passively listened to sequences of tones produced by their partner. The partner-solo condition served as the control condition for Experiment 4 because our previous study (Bolt & Loehr, 2023) did not include a computer condition as in Experiment 3. Thus, we calculated suppression in all other conditions relative to the partner-solo condition.

Trials in all five conditions followed the same procedure described in the Procedure section. In the partner-solo condition, the partner sat quietly beside the participant.

4.3.1.4 Apparatus and Materials

Experiment 4 used the same apparatus and materials as Experiment 3.

4.3.1.5 Procedure

As in Experiment 3, participants were fitted with an EEG cap and then participants and their partners completed a series of training blocks to ensure that the pair could produce the four-tone sequences with accurate and stable timing, both separately and together. Details of the training condition are reported in (Bolt & Loehr, 2023).

Participants then performed the test phase of the experiment. Participants completed 7 blocks of 10 trials for each of the conditions in the original experiment (i.e., a total of 70 trials per condition). The order of conditions was counterbalanced across pairs using a balanced Latin square design. Block instructions were presented following the same procedure as Experiment 3.

Trials in Experiment 4 followed the same procedure as Experiment 3 (see Figure 4.1A), with the addition of catch trials in Experiment 4. These catch trials were included to make sure that participants were paying attention to tones in all conditions. On two or three trials per block, one member of the pair was randomly selected to enter an estimate of the pair's sequence pace (in ms) before the feedback appeared. The number of catch trials and the trial numbers on which they occurred was randomly selected, separately for each block, with the constraints that one or two catch trials appeared within the first 7 trials and one catch trial appeared within the last 3 trials of each block. Catch trials were presented on the screen until the participant entered a number and pressed ‘enter’. Following this, a black screen appeared for 500 ms, followed by feedback and a black screen as described in Experiment 3.

4.3.1.5 Data Acquisition

Experiment 4 used the same data acquisition as Experiment 3.

4.3.1.6 Data Pre-Processing

Experiment 4 used the same data pre-processing as Experiment 3. In Experiment 4, 7.19% of all recorded trials were excluded from analysis following these criteria.

4.3.1.7 Time-frequency Analysis Parameters

Experiment 4 used the same time-frequency analysis parameters as Experiment 3 except that in Experiment 4, we subtracted the ERSP in the partner-solo condition from the ERSP in all other conditions. Hereafter, references to “mean power” in the self-13, self-24, self-12, and self-34 conditions refer to the difference between each of these conditions and the partner-solo condition.

4.3.1.8 Statistical Analysis

As in Experiment 3, we conducted the following analyses separately for mu and beta frequency bands. First, we examined mean power in the alternating task (self-13 and self-24 conditions) to test the replicability of agentive differences from Experiment 3. As in Experiment 3, we analyzed mean power in these conditions with a 2 (Condition: self-13 and self-24) x 4 (Tap: 1-4) x within-subjects ANOVA. We found evidence of a Condition by Tap interaction in both the mu and beta frequency bands and therefore conducted planned paired-samples *t*-tests in two steps. As in Experiment 3, we compared mean power between adjacent taps *within* each joint condition to check for differences between adjacent self- versus partner-produced taps, and we compared mean power at each tap *between* the two joint conditions to check for differences between self- versus partner-produced taps at each of taps 1-4.

Second, we examined mean power in the sequential task (self-12 and self-34 conditions) to explore agentive differences in the presence or absence of overlapping motor activity from preceding self-produced taps. We analyzed mean power in these conditions with a 2 (Condition: self-12, self-34) by 4 (Tap: 1-4) within-subjects ANOVA. We found evidence of a Condition by Tap interaction in both the mu and beta frequency bands and therefore conducted planned paired-samples *t*-tests in two steps. The first step that compared taps *within* sequences differed from our analyses of the alternating task. Here, we used the self-12 condition to compare a self-produced tap (tap 2) to a partner-produced tap that was adjacent and therefore preceded by a self-produced tap (tap 3) and to a partner-produced tap that was not adjacent and therefore not preceded by a self-produced tap (tap 4). We used the self-34 condition to conduct the reverse comparison: to compare self-produced taps that were (tap 3) or were not (tap 4) adjacent to and therefore preceded by a partner's preceding tap (tap 2). The second step remained the same as for our other analyses: we compared mean power at each tap *between* the two joint conditions to check for differences between self- vs. partner-produced taps at each of taps 1-4. For all ANOVAs, Greenhouse-Geisser corrections were applied to degrees of freedom and *p* values whenever Mauchly's test of sphericity indicated the assumption of sphericity was violated ($p < .05$). For all t-tests, *p* values were adjusted for multiple comparisons using the Holm-Bonferroni method with a family size of 3 for within sequence comparisons in the alternating task, 2 for within sequence comparisons in the sequential task, and 4 for between sequence comparisons in both tasks.

4.3.2 Results

4.3.2.1 Mu Band

4.3.2.1.1 Joint Sequence Production: Alternating Task (Self-13 and Self-24 Conditions).

The top left panel of Figure 4.4 shows the mean power in the mu frequency for each tap in the two alternating conditions.

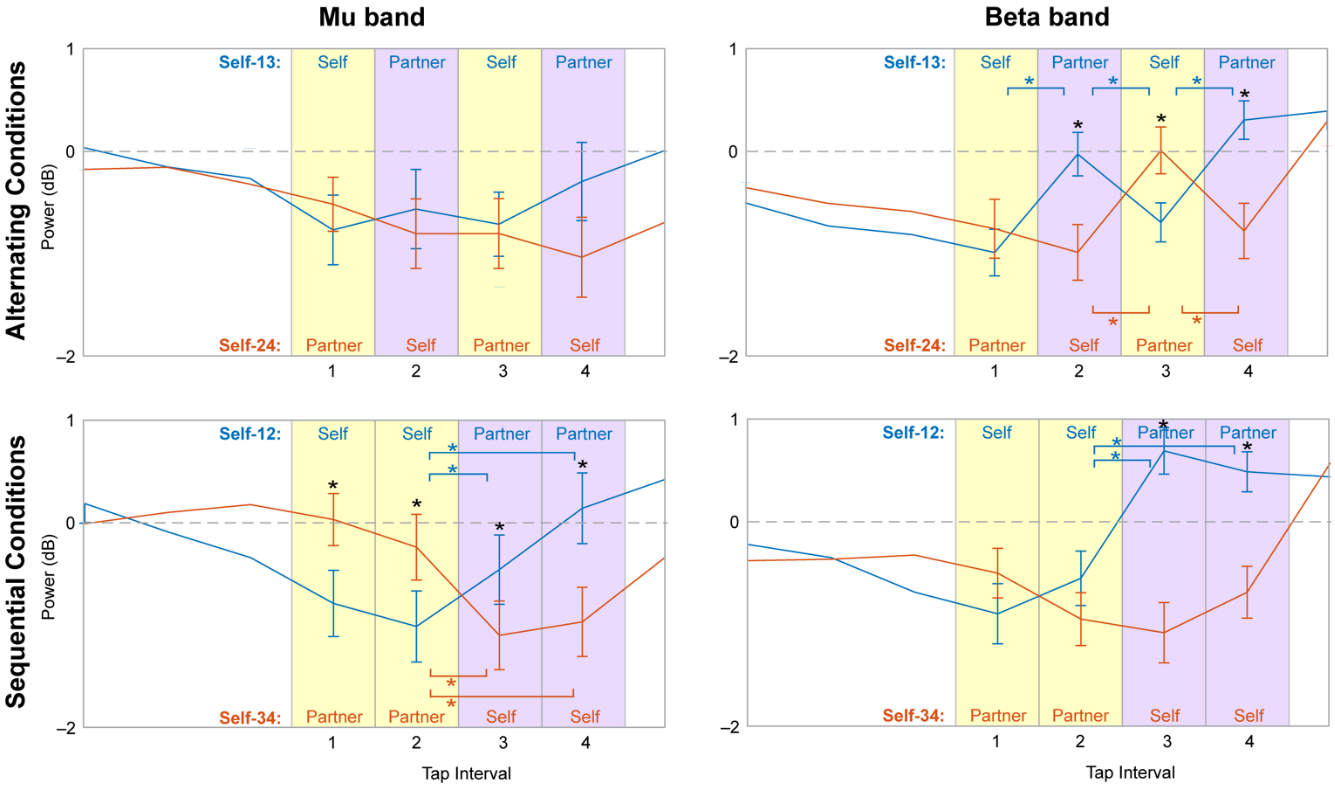

Figure 4.4. Mean power (± *SEM*) in the mu (left panels) and beta (right panels) frequency bands, during the alternating (top panels) and sequential tasks (bottom panels), at electrode C3, relative to the partner-solo condition (represented by the dotted horizontal line at 0 dB). Significant differences between taps 2, 3, and 4 *within* each joint condition are denoted with square brackets and an asterisk, at the top of the plot for conditions in which the participant led the sequence and at the bottom of the plot for conditions in which the partner led the sequence. Significant differences *between* joint conditions at each tap are denoted with an asterisk above the error bars.

Table 4.3. Power differences between adjacent taps *within* alternating joint conditions in mu (left) and beta (right) bands.

Joint Cond.	Taps Compared[a]	*mu*					*beta*				
		M_{diff}	95% CI	$t(20)$	p_{adj}	g_{av}	M_{diff}	95% CI	$t(20)$	p_{adj}	g_{av}
Self-13	1 vs. 2	−0.20	[−0.63, 0.22]	−1.00	.988	0.12	−0.96	[−1.44, −0.48]	−4.18	**<.001**	0.93
	3 vs. 2	–0.15	[–0.49, 0.20]	–0.90	1	0.09	–0.67	[–1.01, −0.32]	–4.01	**<.001**	0.71
	3 vs. 4	−0.42	[−0.95, 0.12]	−1.61	.367	0.26	−1.00	[−1.39, −0.60]	−5.29	**<.001**	0.26
Self-24	2 vs. 1	–0.29	[–0.71, 0.13]	–1.42	.517	0.20	–0.23	[–0.54, 0.08]	–1.53	.142	0.18
	2 vs. 3	−0.01	[−0.44, 0.44]	−0.01	.995	0.01	−0.99	[−1.39, −0.60]	−5.29	**<.001**	0.85
	4 vs. 3	–0.23	[–0.60, 0.14]	–1.29	.517	0.14	–0.78	[–1.11, −0.46]	–5.06	**<.001**	0.67

[a]Comparisons were ordered so that negative values indicate greater suppression for self- compared to partner-produced taps.

Table 4.4. Power differences *between* alternating joint conditions at each tap in mu (left) and beta (right) bands.

Tap	M_{diff}[a]	95% CI	$t(20)$	p_{adj}	g_{av}	M_{diff}	95% CI	$t(20)$	p_{adj}	g_{av}
Tap 1	−0.25	[−0.79, 0.29]	−1.00	.990	0.18	−0.23	[−0.66, 0.19]	−1.14	.267	0.19
Tap 2	−0.24	[−0.74, 0.26]	−1.00	.990	0.14	−0.96	[−1.48, −0.44]	−3.86	**.002**	0.85
Tap 3	0.09	[−0.31, 0.49]	0.48	.990	0.06	−0.70	[−1.07, −0.33]	−4.00	**.002**	0.72
Tap 4	−0.74	[−1.40, −0.08]	−2.34	.119	0.41	−1.08	[−1.61, −0.55]	−4.28	**.001**	1.01

[a]Comparisons were ordered so that negative values indicate greater suppression for self- compared to partner-produced taps.

Table 4.5. Power differences between selected taps *within* sequential joint conditions in mu (left) and beta (right) bands.

Joint Cond.	Taps Compared[a]	*mu*					*beta*				
		M_{diff}	95% CI	$t(20)$	p_{adj}	g_{av}	M_{diff}	95% CI	$t(20)$	p_{adj}	g_{av}
Self-12	2 vs. 3	−0.55	[−1.04, −0.07]	−2.37	**.028**	0.35	−1.24	[−1.69, −0.80]	−5.89	**<.001**	1.08
	2 vs. 4	−1.15	[−1.79, −0.51]	−3.77	**.002**	0.71	−1.04	[−1.54, −0.54]	−4.36	**<.001**	0.96
Self-34	3 vs. 2	−0.86	[−1.35, −0.37]	−3.64	**.003**	0.56	−0.13	[−0.45, 0.18]	−0.88	.390	0.10
	4 vs. 2	−0.73	[−1.22, −0.24]	−3.12	**.005**	0.47	0.26	[0, 0.52]	−2.08	.102	0.22

[a] Comparisons were ordered so that negative values indicate greater suppression for self- compared to partner-produced taps.

Table 4.6. Power differences *between* sequential joint conditions at each tap in mu (left) and beta (right) bands.

Tap	M_{diff}[a]	95% CI	$t(20)$	p_{adj}	g_{av}	M_{diff}	95% CI	$t(20)$	p_{adj}	g_{av}
Tap 1	−0.82	[−1.45, −0.19]	−2.70	**.027**	0.61	−0.40	[−0.88, 0.09]	−1.72	.101	0.32
Tap 2	−0.77	[−1.33, −0.22]	−2.92	**.026**	0.50	0.40	[−0.15, 0.94]	1.53	.142	0.33
Tap 3	−0.64	[−1.21, −0.07]	−2.34	**.030**	0.41	−1.78	[−2.35, −1.20]	−6.42	**<.001**	1.46
Tap 4	−1.11	[−1.74, −0.45]	−3.68	**.006**	0.70	−1.18	[−1.75, −0.61]	−4.30	**.001**	1.12

[a] Comparisons were ordered so that negative values indicate greater suppression for self- compared to partner-produced taps

Replicating Experiment 3, the ANOVA confirmed that there was a significant Condition by Tap interaction, $F(3, 60) = 4.45$, $p = .006$, $\eta^2_p = 0.18$, $\eta^2_G = 0.01$, and no main effect of Condition, $F(1, 20) = 1.14$, $p = .298$, $\eta^2_p = .05$, $\eta^2_G < .01$, or Tap, $F(1.94, 38.76) = 0.12$, $p = .883$, $\eta^2_p = .01$, $\eta^2_G < .01$. However, unlike in Experiment 3, planned comparisons indicated that mean mu power was not significantly different between any adjacent taps within either the self-13 or the self-24 condition (left half of Table 4.3), nor did it significantly differ between sequences at any of the four taps (left half of Table 4.4). The Condition by Tap interaction appeared to be driven by the difference between sequences at tap 4, which was significant at $p = .03$ before correcting for multiple comparisons.

4.3.2.1.2 Joint Sequence Production: Sequential Task (Self-12 and Self-34 Conditions).

The bottom left panel of Figure 4.4 shows the mean power in the mu frequency band for each tap in the two sequential conditions. The ANOVA confirmed that there was a significant Condition x Tap interaction, $F(1.76, 35.13) = 25.42$, $p < .001$, $\eta^2_p = .56$, $\eta^2_G = .08$. There was no main effect of Condition, $F(1, 20) = 0.03$, $p = .866$, $\eta^2_p < .01$, $\eta^2_G < .01$, or Tap, $F(3, 60) = 1.48$, $p = .173$, $\eta^2_p = .08$, $\eta^2_G = .01$. As the left half of Table 4.5 shows, mu power was more suppressed for self compared to partner-produced taps *within* both sequential conditions, regardless of whether or not partner-produced taps were preceded by self-taps or vice versa. Mean mu power also differed significantly *between* the two sequential conditions at all four taps, with self-produced taps again showing greater suppression than partner-produced taps (left half of Table 4.6). Thus, as expected, the sequential conditions revealed differences between self- and partner-produced taps in the mu band that were less evident (Experiment 3) or not evident (Experiment 4) in the alternating conditions.

4.3.2.2 Beta band

4.3.2.2.1 Joint Sequence Production: Alternating Task (Self-13 and Self-24 Conditions).

The top right panel of Figure 4.4 shows the mean power in the beta frequency band for each tap in the two alternating conditions. The ANOVA confirmed that there was a significant Condition x Tap interaction, $F(2.05, 41.04) = 27.05$, $p < .001$, $\eta^2_p = .57$, $\eta^2_G = .11$. In contrast to Experiment 3, there was no main effect of Condition, $F(1, 20) = 2.74$, $p = .114$, $\eta^2_p = .12$, $\eta^2_G = .02$. There was a significant effect of Tap, $F(1.81, 36.15) = 6.35$, $p = .006$, $\eta^2_p = .24$, $\eta^2_G = .05$;

similar to Experiment 3, mean power was more suppressed for tap 1 compared to taps 3 and 4, $t(20)$s > −2.93, ps > .05. None of the other taps differed from each other, all $t(20)$s < −2.17, ps > .167. More importantly, and replicating Experiment 3, planned comparisons confirmed that mean beta power differed between adjacent self and partner-produced taps *within* both the self-13 and self-24 conditions, with self-produced taps showing more suppression than partner-produced taps (right half of Table 4.5). The only exception was that in the self-24 condition, tap 2 (self tap) did not significantly differ from tap 1 (partner tap). Also replicating Experiment 3, mean beta power differed *between* the two alternating conditions at taps 2, 3, and 4, with self-produced taps showing greater suppression than partner-produced taps (right half of Table 4.6).

4.3.2.2.1 Joint Sequence Production: Sequential Task (Self-12 and Self-34 Conditions).

The bottom right panel of Figure 4.4 shows the mean power in the beta frequency at each tap in the two sequential conditions. The ANOVA confirmed that there was a significant Condition by Tap interaction, $F(1.74, 34.70) = 28.40$, $p < .001$, $\eta^2_p = .59$, $\eta^2_G = .11$. There was also a main effect of Condition, $F(1, 20) = 12.21$, $p = .002$, $\eta^2_p = .38$, $\eta^2_G = .09$, indicating that mean power was less suppressed overall in the self-12 condition (when the participant led the sequence) compared to the self-34 condition (when the partner led the sequence), $M_{diff} = 0.74$, 95% CI [0.30, 1.18]. Note that this pattern was also evident in the beta band in the alternating conditions in Experiment 3, but not in the alternating conditions in Experiment 4. There was also a significant main effect of Tap, $F(1.69, 33.85) = 9.47$, $p < .001$, $\eta^2_p = .32$, $\eta^2_G = .06$, whereby taps at the beginning of the sequence were more suppressed than later taps (tap 1 was more suppressed than tap 4, and tap 2 was more suppressed than taps 3 and 4, all ts > −3.27, all ps < .02). None of the other taps differed from each other, all ts < −2.43, all ps > 0.15. Similar patterns were evident in the beta band in the alternating conditions in both Experiments 1 and 2.

More importantly, beta power was more suppressed for self-produced taps compared to partner-produced taps *within* the self-12 condition, regardless of whether or not partner-produced taps were preceded by self-taps (right half of Table 4.5). However, the self-34 condition revealed an unexpected pattern: self-produced taps were not more suppressed than partner-produced taps in this condition. Inspection of the bottom right panel of Figure 4.4 suggests that this occurred because suppression was already evident at taps 1 and 2 (partner taps) and continued through taps 3 and 4 (self taps). This interpretation is further supported by our comparison of mean power *between* the two sequential conditions: mean power was more suppressed for self-produced taps compared to partner-produced taps at taps 3 and 4, but not at taps 1 and 2 (right half of Table 4.6). We return to this unexpected pattern of results in the General Discussion.

4.3.3 Discussion

The goals of Experiment 4 were twofold. First, we examined mu and beta suppression during alternating sequences to test the replicability of our findings from Experiment 3. Consistent with Experiment 3, we found agentive differences in beta suppression, with more suppression for self-produced taps compared to partner-produced taps in both the alternating and sequential task. Also as in Experiment 3, there were more agentive differences in the beta frequency band than the mu frequency band during the alternating task. The second goal of Experiment 4 was to examine whether agentive differences in mu suppression would be more evident during a sequential task, in which agents produced successive rather than alternating actions. Indeed, when agents produced successive actions, we found agentive differences in the mu frequency band across taps (i.e., within sequences) as well as across conditions (i.e., between sequences), indicating that agentive differences in the mu frequency band are more evident in the absence of overlapping suppression from a preceding self-produced tap. Together, the findings from Experiment 4 support social differentiation in both the mu and beta frequency bands.

4.4 Chapter 4 General Discussion

Experiment 3 and 4 investigated whether motor activity shows some degree of agent specificity for each person’s distinct contributions to a joint action. Specifically, we conducted novel analyses of data from two previously reported experiments to examine motor-related cortical oscillations while partners took turns producing taps to meet a joint timing goal. We examined both the mu and beta frequency bands because both are thought to underlie key processes that allow people to coordinate their actions with each other (Bolt & Loehr, 2021b; Wolpert & Flanagan, 2001). In both experiments, we found agentive differences in beta suppression, with more suppression occurring during one’s own actions compared to during a partner’s actions. Agentive differences in mu suppression became apparent when we removed the overlapping motor activity between agents’ actions by having agents produce their actions in succession. Together, both experiments provide support for social differentiation by showing distinct suppression for one’s own actions over the time course of a joint action.

This study is, to the best of our knowledge, the first to disentangle the motor activity that is associated with one's own vs. another person's actions as a joint action unfolds. Considerable evidence from solo action supports the idea that people display similar motor-related suppression during action execution and observation alike (for review see Fox et al., 2016). However, studies that examine motor-related suppression in joint action have typically done so by averaging across periods in which both people are contributing to the joint action simultaneously (e.g., Naeem et al., 2012), making it unclear how each partner's individual contribution is represented within one's own motor system. By examining motor activity during periods in which only one partner or the other was producing an action, we provide evidence that a certain degree of agent specificity does occur when interacting with others. Our findings are in line with those of Novembre et al. (2012), who found that the motor representations of self- and partner-related actions are not equivalent in the context of joint action, despite sharing resources at a neuroanatomical level. Importantly, Experiment 3 and 4 corroborates Novembre et al.'s (2012) findings by directly comparing motor activity during one's own versus a partner's actions, thus providing further evidence that distinct motor activity is associated with each person's actions. Our findings inform theories of joint action control, in which maintaining a distinction between one's own and partners' actions over the course of the joint action is thought to be crucial for generating online predictions about each person's respective contributions to the joint action (Keller et al., 2016; Pesquita et al., 2018; Wolpert et al., 2003).

Although mu and beta oscillations both showed evidence of social differentiation, there were also key differences between frequency bands. First, in the mu band, but not the beta band, we found evidence that overlapping motor activity from preceding self-produced taps contributed to reducing agentive differences across the joint action in Experiment 3. We provide evidence for this claim in Experiment 4 in two ways. First, differences between self- and partner-produced taps in the mu band were more evident when partners produced successive rather than alternating actions, the former of which reduced the number of times that a self-produced tap preceded a partner-produced tap. Second, when a partner-tap *did* precede a self-tap in the sequential task (i.e., tap 2 vs. tap 3 within the self-12 sequence), the difference in mu suppression between partner and self-produced taps was smaller ($M_{\text{diff}} = -0.55$) than when partner-produced taps were not preceded by a self-produced tap (all $M_{\text{diff}} > -0.73$). Thus, overlapping motor activity elicited by an immediately preceding self-produced tap obscured the difference between adjacent self and partner-produced taps within the self-12 sequential joint condition. Together, these two findings from Experiment 4 show that mu suppression from a previous action can contribute to suppression measured during a subsequent action, supporting the notion that mu and beta have different timelines for rebounding after the execution or observation of an action (Avanzini et al., 2012; Meyer, Hunnius, van Elk, van Ede, & Bekkering, 2011; Salmelin & Hari, 1994). Future research examining mu and beta suppression across a sequence of actions should take into consideration these timecourse differences between frequency bands prior to and/or following actions. This consideration is especially important for research investigating mu and beta suppression in the context of joint action because partners are often producing overlapping or even precisely synchronized actions (see also, Meyer, Hunnius, van Elk, van Ede, & Bekkering, 2011).

Agentive differences in mu suppression might also have been partially obscured in Experiment 4 by the subtraction of an auditory control condition comprised of listening to another person produce tones. This particular control condition likely elicited some degree of suppression compared to listening to a computer produce tones (i.e., the control condition used in Experiment 3). Although the difference between control conditions did not affect our findings in the beta band (i.e., agentive differences in beta suppression showed the same pattern regardless of which control condition was used), this difference could explain why agentive differences in mu suppression in the alternating task were even less pronounced in Experiment 4 compared to Experiment 3. The subtraction of our auditory control conditions in both experiments was critical to examining social differentiation in the *motor* activity related to each person's actions, rather than activity related to processing the sensory consequences of their actions. However, selection of our auditory control conditions was also limited by the design of our previous studies (Bolt & Loehr, 2021a, 2023). Thus, to be confident that agentive differences in mu suppression are not obscured by subtraction of a particular auditory control condition, future research should carefully consider the extent to which motor activity could be present in such a control condition. Our recommendation is consistent with recent work indicating that mu suppression should ideally be assessed relative to a non-biological control condition that is matched as closely as possible to the experimental conditions in all other regards (Hobson & Bishop, 2016, 2017).

Another difference between frequency bands was the unexpected finding that beta elicited increased suppression for *partner*-produced taps at the beginning of all joint sequences.

This pattern was particularly evident within the self-34 sequential condition, in which partner-produced taps 1 and 2 elicited a similar degree of suppression as self-produced taps 3 and 4. It seems unlikely that this was caused by reduced beta suppression during self-produced taps, because, as expected, self-produced taps 3 and 4 in the self-34 condition did show stronger suppression than partner-produced taps 3 and 4 in the self-12 condition. We speculate that suppression for partner-produced taps at the beginning of the sequence might have occurred because of the precise motor simulation required to adapt one's own subsequent action timing in light of the partner's initial action timing. That is, increased suppression for partner-produced taps reflected enhanced motor activity associated with simulating the partners' actions. Beta suppression is thought to be directly related to simulating movement parameters of observed actions (Brinkman et al., 2014). During joint action, people are thought to simulate their partners' actions to generate predictions about how their partners' actions will unfold (Wilson & Knoblich, 2005), and, in turn, to better coordinate their own actions with their partner to meet the joint goal (Keller et al., 2016). This explains why we saw the most noticeable suppression in the sequential task, with increased suppression for *both* initial partner-produced taps when the participant initiated their actions based on the timing of the partner's two taps (i.e., in the self-34 condition). In contrast, there was a remarkably large increase in power (i.e., release from suppression) during partner-produced taps at the end of the sequence when the participant did not have to adapt any subsequent actions, and thus did not need to simulate their partners' actions to the same extent (i.e., in the self-12 condition). Together, these findings support the idea that the dynamic coordination requirements of the joint action affect the degree to which people simulate their partners' action timing. More broadly, our findings speak to the idea that the two cortical oscillations might have distinct roles in joint action (Mustile, Kourtis, Edwards, Donaldson, & Ietswaart, 2022), since mu suppression does not appear to be affected by the coordination requirements of the joint action (Kourtis, Knoblich, et al., 2013).

Overall, the current findings demonstrate that periods of increased suppression for a partner's actions occur alongside distinct suppression for one's own actions, implying that *dynamic* patterns of motor activity might underpin successful interactions with others in the context of joint action. These findings align with the idea that successful joint action depends on a balance between self-other integration and differentiation (Keller et al., 2016; Liebermann-Jordanidis et al., 2021; Novembre et al., 2016). In other words, people need to integrate information about their partner’s part of the joint action with their own part of the joint action, while also maintaining a distinction between their respective parts to maintain autonomous control over their own actions. Studies that provide evidence of self-other integration and differentiation in joint action typically measure average motor activity across both parts of the joint action. For example, in naturalistic music performance, mu suppression is increased during periods that promote integration by requiring performers to act in congruent ways compared to periods that promote a self-other distinction by requiring performers to act in highly incongruent ways (Christensen, Slavik, Nicol, & Loehr, 2022). Our study suggests that self-other integration and differentiation are also evident in the dynamics of motor-related cortical oscillations as a joint action unfolds over time. Periods of increased suppression during a partner’s action could allow for the precise simulation of a partner’s action timing required to coordinate together over time, while distinct suppression for one’s own actions could serve to differentiate each person’s respective contributions to the joint action over time.

In sum, Experiment 3 and 4 provide evidence of distinct motor-related suppression for one’s own actions over the time course of a joint action, supporting sensorimotor social differentiation. Moreover, Experiment 3 and 4 showed that motor-related suppression during a joint action was also affected by the dynamic coordination requirements of the joint action; distinct beta suppression for one’s own actions coexisted with periods of increased beta suppression during a partner’s actions, potentially working together to facilitate successful interpersonal coordination. Together, Experiment 3 and 4 highlight the need to investigate dynamic, online joint action that is truly interactive to fully understand how cortical oscillations allow us to coordinate actions with others (Mustile et al., 2022).

CHAPTER 5

General Discussion

Portions of this chapter have been previously published or submitted for publication. Redundant information has been removed:

Bolt, N. K., & Loehr, J. D. (2023). The auditory P2 differentiates self- from partner-produced sounds during joint action: Contributions of self-specific attenuation and temporal orienting of attention. *Neuropsychologia, 182,* 108526.

Bolt, N. K., & Loehr, J. D. (2021a). Sensory attenuation of the auditory P2 differentiates self- from partner-produced sounds during joint action. *Journal of Cognitive Neuroscience, 33*(11), 2297-2310.

Bolt, N. K., & Loehr, J. D. (2021b). The motor-related brain activity that supports joint action: A review. *Acta Psychologica, 212*, 103218.

The goal of this dissertation was to directly investigate potential neural markers of self-other differentiation during joint action, and, by doing so, elucidate more about the processes that allow people to coordinate actions with each other. Converging neuroimaging research from both solo and joint action provides evidence that people represent their own and others' actions using the same neural resources (for reviews see, Bekkering et al., 2009; Bolt & Loehr, 2021; Rizzolatti & Fogassi, 2014). Furthermore, people make predictions about the sensory consequences of their own and others' actions using predictive processes that rely on similar motor representations for self and other (Novembre & Keller, 2014; Wilson & Knoblich, 2005). Together, these findings raise the question of how people differentiate between their own and others' actions and sensory consequences at a neural level. The sensorimotor differentiation hypothesis posits that, despite the activation of similar neural resources at an anatomical level, there is some degree of specificity in the sensorimotor activity associated with one's own and others' actions (Schütz-Bosbach et al., 2009, 2006). Moreover, sensorimotor differentiation becomes critical in the context of joint action because people must maintain autonomous control over their own actions, as well as generate predictions about each person's separate contributions to the joint action to facilitate interpersonal coordination (Keller et al., 2016; Pesquita et al., 2018). Despite the importance of self-other differentiation to joint action coordination, little research has investigated how the brain achieves this.

By examining potential neural markers of self-other differentiation, this dissertation assessed a) whether there is a *perceptual* differentiation in the processing of sensory consequences that result from one's own vs. others' actions and b) whether there is a differentiation in the *motor* activity associated with one's own and others' actions. Importantly, I addressed these questions with a joint action sequence production paradigm that required ongoing coordination, while each partner nevertheless produced independent actions and sensory consequences. This allowed me to disentangle the neural activity that was associated with each person's actions and their sensory consequences as they coordinated together over time. First, I examined whether *sensory attenuation* of auditory ERPs distinguishes self- from other-produced sensory consequences as partners coordinate their actions together over time. In Section 5.1, I summarize evidence that sensory attenuation provides a neural marker of perceptual self-other differentiation based on the findings from Experiment 1 (Chapter 2) and Experiment 2 (Chapter 3). Second, I examined whether the degree of suppression of *motor-related cortical oscillations* differentiates between the motor activity associated with one's own and others' actions as the joint action unfolds over time. In Section 5.2, I summarize evidence that the suppression of motor-related cortical oscillations provides a neural marker of motor self-other differentiation based on the findings from Experiment 3 and 4 (Chapter 4).

5.1 Evidence of Self-Other Differentiation in the Perception of Sensory Consequences

Chapter 2 and 3 investigated whether there is a *perceptual* differentiation in the processing of sensory consequences that result from one's own vs. others' actions. I hypothesized that *sensory attenuation* of auditory ERPs would differentiate self- from other-produced sensory consequences as partners coordinated their actions together over time (Weiss et al., 2011a). Experiment 1 (Chapter 2) and Experiment 2 (Chapter 3) assessed auditory ERPs in response to the first sequence tone and carefully controlled for differences in predictability between conditions, as predictability of tone onsets has been shown to affect ERP amplitudes during the processing of self-produced sensory consequences (Kaiser & Schütz-Bosbach, 2018;

Lange, 2009). Sensory attenuation was measured at both the auditory N1 and P2 ERPs, because both are considered potential neural markers of the differentiation between self- and externally-produced sensory consequences (e.g., Baess, Jacobsen, & Schröger, 2008; Ghio, Scharmach, & Bellebaum, 2018; Klaffehn, Baess, Kunde, & Pfister, 2019; Timm, Schönwiesner, Schröger, & SanMiguel, 2016). Both experiments provide evidence to support sensory attenuation of the auditory P2 as a neural marker of a perceptual self-other differentiation, as I discuss next.

Together, the findings from Experiment 1 and 2 support the hypothesis that sensory attenuation differentiates self- from other-produced sensory consequences during joint action. Experiment 1 provided evidence that during joint action, self-produced tones elicited an attenuated P2 amplitude relative to partner-produced tones. Further, Experiment 2 replicated the effect of self-specific P2 attenuation from Experiment 1, and additionally demonstrated that it occurred regardless of the coordination requirements between partners. The finding that self-specific processes attenuate the P2 furthers our understanding of auditory processing during joint action by showing that people display distinct neural activity for the perceptual consequences of their own and their partner's actions. This finding also complements other joint action studies that show that sensory attenuation differentiates between own and others' contributions to a single shared effect (Loehr, 2013; Weiss et al., 2011b) and corroborates action observation research that shows self vs. other differences in sensory attenuation (Ghio et al., 2018; Weiss et al., 2011a; Weiss & Schütz-Bosbach, 2012).

Furthermore, findings from Experiments 1 and 2 speak to the dissociation of the auditory P2 and N1 ERPs as independent processes that have distinct roles in auditory processing, despite many sensory attenuation studies grouping the two components together, or not acknowledging contributions of the P2 (for reviews see Horváth, 2015; Kiepe, Kraus, & Hesselmann, 2021). Both experiments provided evidence of P2 attenuation for self-produced tones relative to partner-produced tones as well as relative to tones produced by an external agent. On the contrary, there was no evidence to support N1 attenuation for self-produced tones in either experiment, in joint action, or relative to an external agent. The N1 has typically been interpreted as a mechanism that differentiates between self-produced and externally-produced sounds in solo action research (Baess et al., 2011, 2008; Mifsud et al., 2016; Schafer & Marcus, 1973; Timm et al., 2014). However, recent work challenges this idea and instead suggests that the N1 is attenuated when sounds are predictable, regardless of whether sounds are self-produced or not (Kaiser & Schütz-

Bosbach, 2018; Lange, 2009). In the joint action sequence production task used in all experiments in this dissertation, temporal predictability was carefully equated across all conditions by the isochronous tone timing required by the task, extensive practice of both solo and joint conditions, and the use of human-produced sequence timing in the computer condition. The fact that we replicated the lack of N1 attenuation for self-produced tones in both joint and solo action when predictability of tone timing was carefully controlled for provides strong evidence that the N1 does not differentiate self- from other-produced tones. Instead, our findings support the idea that self-other differentiation occurs later in sensory processing, at the auditory P2, which corroborates recent studies indicating that the P2 may be a better neural marker of self-other differentiation than the N1 (Ghio et al., 2018; Knolle et al., 2013; SanMiguel, Widmann, Bendixen, Trujillo-Barreto, & Schröger, 2013; Timm et al., 2016).

Finally, findings from Experiments 1 and 2 also suggest that sensory attenuation allows people to differentiate self- from partner-produced sensory consequences within joint action, while temporal orienting might concurrently facilitate the prediction of their partner's action timing relative to the joint goal. Experiment 1 found preliminary evidence that *partners'* tones received increased temporal orienting, resulting in *enhanced* P2 amplitude. Experiment 2 explicitly addressed this possibility and provided evidence that temporal orienting to partners' tones enhanced P2 amplitudes because of the coordination requirements of the joint action. Thus, people direct their attention to monitor deviations in a partner's action timing in accordance with the joint goal. The finding that temporal orienting affects auditory ERP amplitudes during the time window of self-other differentiation contributes to ongoing work investigating the separate, but overlapping, effects of sensory attenuation and temporal orienting during solo action (Lange, 2013; Saupe et al., 2013; Timm et al., 2013). Overall, the findings from Experiment 1 and 2 therefore provide evidence that sensory attenuation and temporal orienting both modulate auditory P2 ERP amplitudes during joint action and suggest that both processes play a role in facilitating precise interpersonal coordination between partners.

5.2 Evidence of Self-Other Differentiation in Motor-related Activity

Chapter 4 investigated whether there is a differentiation in the *motor activity* associated with one's own and others' actions. I hypothesized that *motor-related cortical oscillations* would show some degree of agent specificity for each person's distinct contributions to the joint action as it unfolds over time, with increased suppression (indicative of more sensorimotor activity) during one's own actions compared to during a partner's actions. Experiment 3 and 4 assessed this possibility by conducting novel analyses of data previously reported in Experiments 1 and 2 to examine *motor* activity across the joint action in separate intervals that were each associated with a single tap produced by one partner or the other. I analyzed motor-related suppression in the mu (i.e., 11-13 Hz) and beta (i.e., 20-26 Hz) frequency bands over left-lateralized frontocentral electrode sites, as both are suppressed during the execution and observation of actions alike (for a review see Fox et al., 2016), and both are thought to be involved in the representation and simulation of others' actions during joint action, respectively (Bolt & Loehr, 2021b; Wolpert & Flanagan, 2001). Experiment 3 and 4 provide evidence that motor-related suppression provides a neural marker of motor self-other differentiation, as I discuss next.

Together, the findings from Experiments 3 and 4 support the hypothesis that self-other differentiation occurs in motor-related activity, as indexed by increased motor-related suppression for one's own actions compared to a partner's actions. Experiment 3 provided evidence of increased mu and beta suppression during time periods that corresponded with one's own taps compared to time periods that corresponded with a partner's taps. Despite both mu and beta showing evidence of agentive differences, the findings of Experiment 3 also suggested that differences between agents in the mu frequency band were reduced because suppression from a previous action contributed to suppression measured during a subsequent action. Experiment 4 explicitly addressed this possibility and provided evidence that differences in mu suppression between agents were indeed more pronounced when not obscured by overlapping activity from previous taps. Further, Experiment 4 replicated the findings of agentive differences in the beta frequency band, providing further support for self-other differentiation in beta suppression. The finding of distinct mu and beta suppression for one's own actions relative to a partner's actions is consistent with research showing distinct corticospinal excitability for one's own vs. a partner's imagined actions during musical duet performance (Novembre et al., 2012), and further suggests a similar differentiation in motor activity can be measured in motor-related cortical oscillations over the time course of a joint action. Importantly, this finding further extends Novembre et al.'s (2012) findings by directly comparing motor activity during one's own versus a partner's actions, thus providing further evidence that there is qualitative difference in the motor activity that is associated with each person's actions, despite activation of the same neuroanatomical structures (Novembre et al., 2012; Schütz-Bosbach et al., 2009, 2006).

Furthermore, Experiments 3 and 4 also provide preliminary evidence that, instead of "mirroring" a partner's actions in one's own motor system, the degree of motor involvement for a partner's actions is dynamically modulated by the coordination requirements of the joint action. In both Experiments 3 and 4, beta suppression was increased for partners' taps that occurred at the beginning of the sequence when participants had to adapt their own timing in light of their partner's action timing. This finding suggests that motor simulation was selectively recruited when it benefited the planning of one's own actions (Kourtis, Knoblich, et al., 2013; Kourtis et al., 2014; Ménoret et al., 2013). This supports the idea that motor activity during a partner's actions reflects predictive action simulation that functions to facilitate coordination (Bekkering et al., 2009; Endedijk, Meyer, Bekkering, Cillessen, & Hunnius, 2017; Wilson & Knoblich, 2005). Further, this finding corroborates recent theoretical accounts of joint action (Vesper et al., 2010), according to which representing a partner's part of a joint action is not strictly necessary but may nevertheless prove advantageous in terms of predicting how others' actions will unfold and/or enabling modifications to one's own actions to smooth coordination. Finally, the fact that beta suppression during a partner's actions was dynamically modulated by the coordination requirements of the joint action but mu suppression was not further speaks to the idea that the two motor-related oscillations might have different roles in supporting joint action (Mustile et al., 2022), as mu suppression also did not appear to be affected by the coordination requirements of a joint action in previous research (e.g., Kourtis et al., 2013). Overall, then, findings from the current research indicate that periods of increased suppression for a partner's actions occur alongside distinct suppression for one's own actions, implying that *dynamic* patterns of motor activity might underpin successful interactions with others in the context of joint action.

5.3 Implications for Theoretical Accounts of Joint Action

Together, these experiments have several important implications for theoretical accounts of joint action. First, the current research extends our understanding of how people represent their partner's contributions to a joint action. Predictive models of joint action control posit that people form sensorimotor representations of their partner's actions through internal models, which allows them to predict the outcome of their partner's actions (Keller et al., 2016; Pesquita et al., 2018; Wolpert et al., 2003). The current research confirms that people represent both the motor and sensory aspects of their partner's tasks at a neural level, consistent with the hypothesis that people represent their partner's actions in an internal model. Further, this research delineates neurocognitive processes that are involved in maintaining and updating predictions about a partner's actions. Specifically, Experiments 3 and 4 provide evidence that people simulate their partner's actions in their own motor system, as indexed by increased beta suppression during their partner's actions, and Experiments 1 and 2 provide evidence that people monitor the consequences of their partner's actions, as indexed by increased orienting to partner's tone onsets. Previous work shows the advantage of motor simulation in facilitating predictions about others' actions (e.g., Kourtis, Sebanz, & Knoblich, 2013; Kourtis, Woźniak, Sebanz, & Knoblich, 2019). I propose that directed orienting towards the timing of a partner's sensory consequences (here tone onsets) also offers a similar advantage, by facilitating people's ability to detect small deviations in their partner's tone timing, in turn informing future predictions about their partner's action timing. Thus, motor simulation and temporal orienting may work together within a predictive model framework to compute motor predictions about a partner's actions and monitor deviations between these predictions and the resulting sensory consequences of their actions. Furthermore, the current research supports the idea that representing a partner's actions is a self-referential process, rather than an automatic process (Pesquita et al., 2018). Experiments 2, 3 and 4 provide evidence that the extent to which people simulate their partner's actions, and direct their orienting to their partner's tone timing, is dynamically modulated by the coordination requirements of the joint action, and more specifically, is selectively recruited when it benefits the planning of one's own actions (Kourtis, Knoblich, et al., 2013; Kourtis et al., 2014; Ménoret et al., 2013). This is in line with the recent proposal that people activate representations of their partner's actions that are most relevant to achieving the shared goal of a joint action, and implies that predictive representations about others' actions are dependent on predictions about one's own actions, supporting the idea that internal models for self and other are independent, and contingent on the ongoing interaction (Pesquita et al., 2018).

Second, the current research has important and direct implications for empirically validating the theoretical claim that people maintain a differentiation between each person's respective contributions to a joint action (Fairhurst et al., 2019; Keller et al., 2016; Novembre et al., 2012; Pesquita et al., 2018). These experiments show that, despite representing a partner's actions and sensory consequences in one's own sensorimotor system, there is a differentiation that occurs between one's own and a partner's contributions to the joint action. The current findings are consistent with the Predictive Joint Action Model (PJAM), which assumes that a differentiation occurs in the motor representation of each person's actions, allowing people to compute separate self and other sensory predictions (Pesquita et al., 2018). Furthermore, the findings from Experiments 1 and 2 suggest that sensory attenuation could provide a mechanism for routing each person's sensory consequences into their respective processing streams. According to PJAM, people monitor deviations between their motor predictions and the actual sensory consequences of each person's actions, which are routed back to internal models for self and other to train future predictions. Research in solo action supports this link between motor predictions and sensory attenuation, showing that increased motor activity preceding self-produced taps is correlated with greater sensory attenuation for tones that result from self-produced taps (Ford, Palzes, Roach, & Mathalon, 2014). However, the possibility that *motor-specific* predictions, rather than predictions derived from other sources such as temporal expectancies, lead directly to sensory attenuation is still highly debated (see, Dogge, Custers, & Aarts, 2019; Dogge, Hofman, Custers, & Aarts, 2018). Thus, future research is needed to examine the link between motor and perceptual levels of self-other differentiation to validate the assumption that these processes operate within internal models.

Lastly, these findings have implications for the idea that self-other differentiation is dynamically coupled with periods of self-other integration to facilitate successful interpersonal coordination (Christensen et al., 2022; Fairhurst et al., 2019; Keller et al., 2016; Liebermann-Jordanidis et al., 2021; Novembre et al., 2016). Joint action is thought to rely on a balance between integrating information related to one's own part, partners' parts, and the joint outcome, while also maintaining a differentiation between each person's respective part. However, studies investigating the neural markers of self-other integration and differentiation do not disentangle contributions from sensory and motor processes (e.g., Christensen et al., 2022; Novembre et al., 2016). The current research delineates neural markers of self-other integration and differentiation at *both* motor and perceptual levels. Experiments 3 and 4 provide evidence of self-other integration and differentiation in the motor activity associated with each partner's actions, in that distinct sensorimotor suppression differentiated between each person's actions, while periods of increased suppression allowed for the precise simulation and integration of a partner's action timing. Experiments 1 and 2 provide evidence for this claim in the perceptual processing of sensory consequences, in that sensory attenuation differentiated between self- and other-produced tones, while temporal orienting facilitated the integration of both partners' tone timing. Our findings therefore corroborate and extend previous research that had shown separate effects of motor and perceptual differentiation on interpersonal coordination at a behavioural level (Liebermann-Jordanidis et al., 2021). Moreover, in all experiments, shifts from periods of integration to differentiation occurred dynamically based on the coordination demands of the joint action, implying that continuous shifts between integration and differentiation are key to successful interpersonal coordination. Thus, I propose that the coordination demands of the joint action contribute to regulating the balance between self-other integration and differentiation by allocating attention to one's own or a partner's part of the joint action with respect to unfolding task demands. Together, the current findings demonstrate that investigating the dynamics of joint action may ultimately be crucial to understanding how self-other differentiation and integration facilitate interpersonal coordination.

5.4 Implications Beyond Joint Action

While this research contributes in several ways to advancing theoretical accounts of joint action, it also has important implications beyond joint action. First, this research contributes to our understanding of the neural processes that underlie agency within both joint and solo contexts. Self-agency refers to the ability to feel a sense of control, or authorship, over one's own actions and their resulting sensory consequences (Gallagher, 2000). Self-agency is important for maintaining control over one's own actions, as an impairment in self-agency can contribute to spurious feelings of control and deficits in self-other processing (discussed further in the next paragraph). The current research provides preliminary evidence that sensory attenuation and motor-related suppression underlie implicit feelings of self-agency during joint action, as both processes differentiate between one's own and a partner's individual contributions to a joint action. These findings align with recent evidence that sensory attenuation reflects self-agency over sensory consequences produced in joint action (Loehr, 2013; Weiss et al., 2011b; for a review see, Loehr, 2022). These findings further suggest that motor-related suppression could be another potential measure of self-agency over continuous actions, consistent with recent work in solo action contexts (Wen, Yamashita, & Asama, 2017). Thus, a potential avenue for future research is to explore to what extent motor-related suppression corresponds to people's explicit reports of agency over their continuous actions both within joint and solo contexts.

The current findings also have implications for neurodevelopmental and psychiatric disorders that are characterized by an impaired sense of agency. While these disorders all display different symptoms, they are thought to have overlapping difficulties in self-other processing that imply the disfunction of a common underlying neural mechanism (for review see, Eddy, 2022). For example, there is evidence that neural markers of self-other differentiation (i.e., motor activity and sensory attenuation) are reduced for individuals with schizophrenia, contributing to an impaired sense of agency (Ford et al., 2014; Randeniya, Oestreich, & Garrido, 2018). Thus, neural markers of self-other differentiation offer a potential diagnostic tool for identifying deficits in self-other processing. However, so far research has typically assessed these markers in a solo context, even though impairments in self-other processing indicate a *social* deficit. Furthermore, research on these disorders has not accounted for the balance between self-other integration and differentiation that occurs during normal social functioning, although there is evidence that both differentiation *and* integration could play a role these disorders (van der Weiden, Prikken, & van Haren, 2015). For example, there is evidence that the right temporal parietal junction (rTPJ) is involved in integration and differentiation during social interaction (Dumas, Moreau, Tognoli, & Kelso, 2020; Era, Aglioti, & Candidi, 2020; Fairhurst et al., 2019; Sowden & Catmur, 2015; Tsakiris, Costantini, & Haggard, 2008) and that its functioning is impaired in schizophrenia (Bitsch, Berger, Nagels, Falkenberg, & Straube, 2019; Eddy, 2022; Patel et al., 2021). The current findings suggest that the underlying neural markers of self-other differentiation and integration can only be fully understood within a truly interactive and dynamic context. Thus, future research examining self-other processing deficits, as well as the development of diagnostic criteria, should consider the benefit of employing online joint action paradigms to reveal more about the underlying disfunction in these disorders.

Furthermore, the current research provides insights that could be useful for motor training and rehabilitation following neurological impairment or physical injury. Motor training and rehabilitation commonly use motor imagery (MI) and action observation (AO) as intervention techniques used to simulate actions in one's own motor system and improve motor abilities when movement has been restricted (Eaves, Riach, Holmes, & Wright, 2016). For example, patients who have recently suffered a stroke resulting in impairment to motor-related brain areas are instructed to imagine themselves performing an action (MI) or watch a video of another person performing an action (AO) to elicit motor simulation in the absence of action execution. Recent findings show the benefit of simultaneously combining these approaches in a solo context to elicit more widespread motor activation (Bruton, Holmes, Eaves, Franklin, & Wright, 2020). A recent review on neurorehabilitation argues that including joint action contexts as part of the rehabilitation experience could improve motor outcomes, but as of yet this is a "missed opportunity" (Maier, Ballester, & Verschure, 2019). Based the current research, I propose that inducing coordination requirements between imagined and observed actions could further affect the degree to which people simulate actions in their own motor system. Previous research also shows that a virtual joint action context produces distinct motor activation compared to MI or OA in isolation (e.g., Bucchioni, Cavallo, Ippolito, Marton, & Castiello, 2013; Oberman, Pineda, & Ramachandran, 2007; Streltsova, Berchio, Gallese, & Umilta', 2010). We can therefore hypothesize that, by adding a virtual joint action context to a rehabilitation setting, patients might additionally a) represent observed actions to a greater extent dependent on the coordination requirements of the interaction and b) simulate the *differentiation and integration* of imagined and observed actions, which would not occur during MI or AO alone. Thus, creating a virtual joint action context that could be successfully implemented in a rehabilitation setting may dynamically activate one's own motor system, offering a potential advantage to the recovery process.

5.5 Limitations and Future Directions

The current research provides several avenues for future research. First, it will be important for future research to consider the extent to which perceptual and motor neural markers of self-other differentiation are affected by the control conditions used to isolate sensory and motor activity, respectively. In the current research, to isolate perceptual activity related to listening to tones (Experiment 1 and 2) and activity related to the degree of motor involvement for actions (Experiment 3 and 4), I subtracted a movement-only control condition and an auditory-only control condition, respectively. Because the timecourse of perceptual and motor activity overlaps, this approach was important to establish that *both* perceptual and motor neural markers of self-other differentiation exist in joint action. Notably, a growing body of evidence indicates perceptual and motor processes are intrinsically intertwined (Hommel, 2019; Hommel, Müsseler, Aschersleben, & Prinz, 2001; Prinz, 1990; van der Wel, Sebanz, & Knoblich, 2013), and that the close link between perception and action is used to generate predictions about others' actions in the same way that predictions are generated about one's own actions (Novembre & Keller, 2014; Wolpert et al., 2003). Based on this, the use of the respective control conditions to isolate sensory or motor activity might also have reduced the amount of differentiation that was observed in each process separately. This is especially relevant for mu-suppression (Experiments 3 and 4), as researchers have argued that mu suppression is related to perception-action integration and the mirror neuron system (for reviews see Fox et al., 2016; Kanakogi & Itakura, 2010), and that changes in mu suppression are related to sensory processing whereas changes in beta instead reflect motor activity (see, e.g., Coll, Bird, Catmur, & Press, 2015). Subtraction of auditory-related activity may therefore have contributed to reducing the amount of mu-suppression that was measured in these experiments because the resulting activity only reflected motor-related processes. The selection of an appropriate control condition to measure mu suppression is an issue highlighted in recent research (Hobson & Bishop, 2016), as it likely contributes to mixed findings in the literature (Hobson & Bishop, 2017). Thus, future research should replicate the findings of the current research using different control conditions, while also carefully considering how the selection of control conditions may affect measures of self-other differentiation.

Future research should also directly examine the relationship between perceptual and motor differentiation. As discussed above, I decided to separately examine these processes to establish that self-other differentiation occurs in neural activity at both levels. As also discussed above, there is a strong link between sensory and motor processes. For example, converging evidence indicates that for musicians, listening to a trained musical sequence results in activation of the same brain areas required to execute the performance of the sequence (Novembre & Keller, 2014). Furthermore, close links between perception and action are important for representing others' actions during joint action, allowing for predictions to be generated about others' actions via internal models, in the same way that predictions are generated for one's own actions (Wolpert et al., 2003). This implies that the degree of motor involvement for each person's actions may be directly related to the sensory processing of each person's respective sensory consequences. Research in schizophrenia further provides evidence for a correlation between anticipatory motor activity and sensory attenuation (Ford et al., 2014). However, the question of whether sensory attenuation directly results from motor predictions, or results from a separate, but parallel sensory predictive process, remains controversial (Stenner et al., 2015). Future research could begin to establish whether there is a link between sensory attenuation and motor activity by investigating the correlation between these processes at a trial level. Due to the spatial resolution limitations with EEG, other neuroimaging techniques should additionally be used to directly examine the source of these processes as they unfold over time. Such research could potentially use magnetoencephalography (MEG) to unravel the close link between these processes, as MEG provides simultaneous chronometric and source information. Such research would advance theoretical accounts of joint action and more broadly inform research on disorders associated with impairments in self-other processing.

Finally, future research needs to explore the relationship between self-other differentiation and interpersonal coordination. In the paradigm used here, the short sequence length (i.e., four tones) and separate isochronous tap intervals were both critical to disentangling neural activity that was associated with each person's distinct contributions to the joint action. However, these methodological decisions also limit the ability to explore the relationship between self-other differentiation and measures of behavioural coordination in this data. Mathematical measures of behavioural coordination for non-synchronous joint action can be calculated at a trial level (see Bolt, Poncelet, Schultz, & Loehr, 2016), but this requires longer sequence lengths (>24 tones per sequence). Furthermore, other measures of joint performance, such as the mean intertap interval (ITI) or standard deviation across the trial, do not capture the dynamic and mutual adjustments that partners engage in to match the overall pace. For example, one previous study that used the same sequence production paradigm showed that partners adjust their action timing in light of small fluctuations in their partner's previous tone timing, in order to coordinate with their partner to maintain the required metronome pace (Bolt & Loehr, 2017). So far, there is evidence that creating a perceptual differentiation between simultaneous parts of a joint action by having participants produce tones that are different pitches results in improved behavioural coordination (Liebermann-Jordanidis et al., 2021). However, research has yet to establish a link between neural markers of self-other differentiation and coordination performance. Future research could investigate this by increasing the sequence length in a similar joint tapping task, and/or by examining these neural markers during joint music performance, which requires more precise coordination than our isochronous tapping task. Together, this research would be key to confirming that self-other differentiation is critical to joint action success.

5.6 Conclusion

The experiments in this dissertation provide evidence that people differentiate between their own and their partner's distinct contributions to a joint action, supporting the social differentiation hypothesis. I show that people display a differentiation in the perceptual processing of sounds that result from their own vs. their partner's actions, as indexed by self-specific sensory attenuation. I also show that people display a differentiation in the motor involvement for their own vs. their partner's actions, as indexed by increased motor-related suppression for their own actions. Further, this distinct neural activity for one's own contributions to a joint action is dynamically coupled with periods of neural activity that reflect the integration of a partner's actions based on the coordination demands of the joint action. This research comprises a novel contribution to the field of joint action, as it uncovers neural markers of self-other differentiation that provide direct support for the theoretical claim that people represent their own and their partner's separate contributions to a joint action, informing theoretical models of joint action, and contributing to our understanding of disorders of self-other processing more broadly. Furthermore, by revealing more about how others' actions are dynamically represented in one's own motor system, this research provides potentially valuable insights for the development of effective paradigms for motor training and rehabilitation following injury or impairment. This research also underscores the importance of investigating online joint actions that are truly interactive and investigating the dynamic activity that occurs as a joint action unfolds, as the complex relationship between self-other differentiation and integration was only revealed by combining these methods. In conclusion, the experiments presented in this dissertation provide insight into how people differentiate and integrate their own and their partner's contributions to a joint action and broaden our understanding of how people coordinate their actions with each other, which is essential to daily life.

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