

Are You Ready to Jump? Predictive Mechanisms in Interpersonal Coordination

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When two or more individuals intend to achieve a joint outcome, they often need to time their own actions carefully with respect to those of their coactors. Online perceptual feedback supports coordination by allowing coactors to entrain with and predict each other's actions. However, joint actions are still possible when no or little online feedback is available. The current study investigated the interplay between higher-level planning processes and motor simulation in a joint action task where online feedback was not available. Pairs of participants performed forward jumps (hops) next to each other with the instruction to land at the same time. They could neither see nor hear each other, but were informed about their own and the partner's jumping distance beforehand. The analysis of basic movement parameters showed that participants adjusted the temporal and spatial properties of the movement preparation and execution phase of their jumps to the specific difference in distance between themselves and their partner. However, this adaptation was made exclusively by the person with the shorter distance to jump, indicating a distribution of coactors' efforts based on task characteristics. A comparison with an individual bipedal coordination condition suggests that joint coordination might rely on similar principles as interlimb coordination. These findings are interpreted within a framework of motor simulation.

Keywords: joint action, prediction, action simulation, coordination strategies, jumping

We are extraordinarily good at coordinating the movements of different effectors of our own body. For example, hitting a ketchup bottle with one hand, while the other hand is holding it upside down, we pour ketchup onto a plate without dropping the bottle (Wolpert & Flanagan, 2001). This is possible because predictive models in the motor system allow us to anticipate the consequences of motor commands (e.g., Wolpert & Flanagan, 2001; Wolpert & Ghahramani, 2000). In many situations, however, we do not only perform individual actions in which different effectors need to be coordinated, but we act together with other people to

bring about shared goals (Knoblich, Butterfill, & Sebanz, 2011). Examples of such joint actions are passing someone a bottle of water, playing a piano duet, or moving heavy furniture together. Joint actions require that the actions of two independent agents—and therefore of two independent motor systems—become coordinated. This is challenging because information about the other's actions can only be acquired from indirect sources rather than from the internal motor commands specifying an action (Wilson & Knoblich, 2005; Wolpert, Doya, & Kawato, 2003).

In many cases, receiving continuous visual, auditory, or haptic feedback about a task partner's actions allows people to achieve coordination (for a review, see Schmidt & Richardson, 2008). In rhythmic coordination tasks, people exhibit stable coordination patterns in the form of in-phase coordination when they can visually perceive each other's movements during activities such as swinging pendulums (Schmidt, Carello, & Turvey, 1990), rocking in rocking chairs (Richardson, Marsh, Isenhower, Goodman, & Schmidt, 2007), or performing a finger tapping task (Oullier, de Guzman, Jantzen, Lagarde, & Kelso, 2008). In these tasks, the degree of coordination is determined by how synchronously actions are performed.

Online feedback about others' actions also supports joint performance in cases where the degree of coordination depends on how well coactors adjust the timing of complementary actions to each other. For instance, van der Wel et al. found that continuous haptic feedback allowed dyads to achieve an equivalent degree of coordination as single individuals in a pole balancing task that required close coordination between pulling and releasing actions

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on two sides of a rope (van der Wel, Knoblich, & Sebanz, 2011). Using a computerized visual tracking task, Knoblich and Jordan (2003) investigated how dyads learn to coordinate the timing of independent actions resulting in deceleration or acceleration of a jointly controlled tracker. They found that given sufficient opportunity to practice, dyads achieved the same level of performance as individuals controlling the tracker bimanually. However, this was only true for dyads whose members received auditory feedback about the timing of each other's actions (a tone indicating when the other person acted). Dyads that were not provided with auditory feedback did not achieve an equivalent level of coordination.

In sum, a range of studies suggests that online sensory information about others' actions plays a crucial role in joint action coordination. Functionally speaking, online feedback may serve two roles. On the one hand, sensory information exchange is a necessary condition for direct perception–action coupling to occur, whereby two people's actions become aligned in time through coupled oscillations (Schmidt & Richardson, 2008). On the other hand, having more or less continuous information about someone else's actions may help to form predictive models that specify the consequences of the other's actions.

According to basic theories of motor control, interlimb coordination relies on the fine-tuning of internal forward models in the motor system that predict the sensorimotor consequences of to-be-performed actions (Wolpert & Flanagan, 2001; Wolpert & Ghahramani, 2000). These predictions are used to compute suitable motor programs and to monitor performance online. For example, when lifting a heavy suitcase with two hands, an individual's motor system predicts the likely outcome of an action based on the issued motor commands for the left and right arms. It has been suggested that interpersonal coordination relies on similar processes in which own internal models are used to form predictions about another person's actions by simulating the other's actions as if oneself would perform it (Wilson & Knoblich, 2005; Wolpert, Doya, & Kawato, 2003). Indeed, a lot of experimental evidence indicates that one's own motor system is active when observing another person act (e.g., Buccino et al., 2001; Cross, Hamilton, & Grafton, 2006; Cross, Kraemer, Hamilton, Kelly, & Grafton, 2009), as well as when imagining another's actions (Grèzes & Decety, 2001; Ramnani & Miall, 2004). Moreover, the strength of this motor resonance is modulated by familiarity with the action (Casile & Giese, 2006; Knoblich & Flach, 2001), by one's own expertise (e.g., Aglioti, Cesari, Romani, & Urgesi, 2008; Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005) and by the social relation to the actor (Kourtis, Sebanz, & Knoblich, 2010), supporting the idea that one's own motor system is involved in generating predictions for observed actions.

Although sensory information about others' actions is often available during joint action, this is not always the case. Experience tells us that joint action is possible when the availability of continuous perceptual information is greatly reduced, for example when handing over an object to someone in a dark room. How do people coordinate joint actions when they do not have direct information about when and how their task partner is acting? This case is important to consider for joint action research because it raises questions about the role of planning processes for coordination and the interplay between higher-level planning processes and predictive models in the motor system.

The less people can rely on online information about a partner's actions the more they may have to rely on general “heuristics” (Vesper, Butterfill, Knoblich, & Sebanz, 2010), beliefs about common knowledge (Clark, 1996), and knowledge about their partner's task (Sebanz, Knoblich, & Prinz, 2005). For instance, if two people would like to arrive at their friend's apartment on the 10th floor at exactly the same time but one of them is taking the stairs up and the other the elevator, it is obvious that the person in the elevator should wait for a while before pressing the “10.” An interesting question in this regard is how the coordination effort is distributed. Does the person with the physically less challenging task (the one in the elevator) take over the whole coordination effort? This would imply a distribution based on task characteristics. Or do both people make an effort, so that the one climbing the stairs is walking faster than usual while the one taking the elevator is waiting? This would imply a more balanced distribution of the coordination effort that may, however, result in poorer coordination performance due to overadaptation (Konvalinka, Vuust, Roepstorff, & Frith, 2010).

A second question of interest is how higher-level planning processes in the context of joint action interact with predictions about one's own and others' actions based on motor simulation. It is known that motor simulation processes can occur in the absence of perceptual input. For instance, Kilner and colleagues found evidence for motor activation in people who were expecting to observe someone performing an action, prior to seeing the action being carried out (Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004). A recent study showed that this anticipatory motor simulation is sensitive to the interaction context and occurs specifically when people expect that a joint action partner is going to act (Kourtis, Sebanz, & Knoblich, 2010). It is also known that imagining an action can trigger corresponding motor simulations (Grèzes & Decety, 2001). However, it remains to be explored whether motor simulation processes are recruited in a joint action without online feedback about the partner's actions. Combining general information about a partner's task with a motor simulation of the action to be performed is likely a more efficient way of achieving coordination than higher-level planning alone. To come back to our example, the person in the elevator may be able to improve her timing by engaging in a motor simulation of the stair climbing that allows her to predict her friend's progress.

The present study investigated the role of higher-level planning processes, the distribution of coordination efforts, and the interplay between planning and motor simulation processes in a joint jumping task. Pairs of participants were instructed to perform simple one-legged forward hops of variable length with the goal of landing at the same time (see Figure 1). Of critical importance, participants received precise spatial information about their own and their partner's jumping distances prior to jumping, but they could not see or hear each other before and during the jumps. Thus, participants knew what their partner's task was but they could not use perceptual information about the other's actions during the actual performance. Short feedback tones at the time of each person's landing indicated how well partners were coordinated.

The major challenge of our jumping task was that jumping is a ballistic movement. As a result, the time it takes to execute a jump largely depends on the distance of the jump (Juras, Slomka, & Latash, 2009) and cannot be easily controlled “on the fly.” In addition, ballistic movements take longer to prepare the farther the

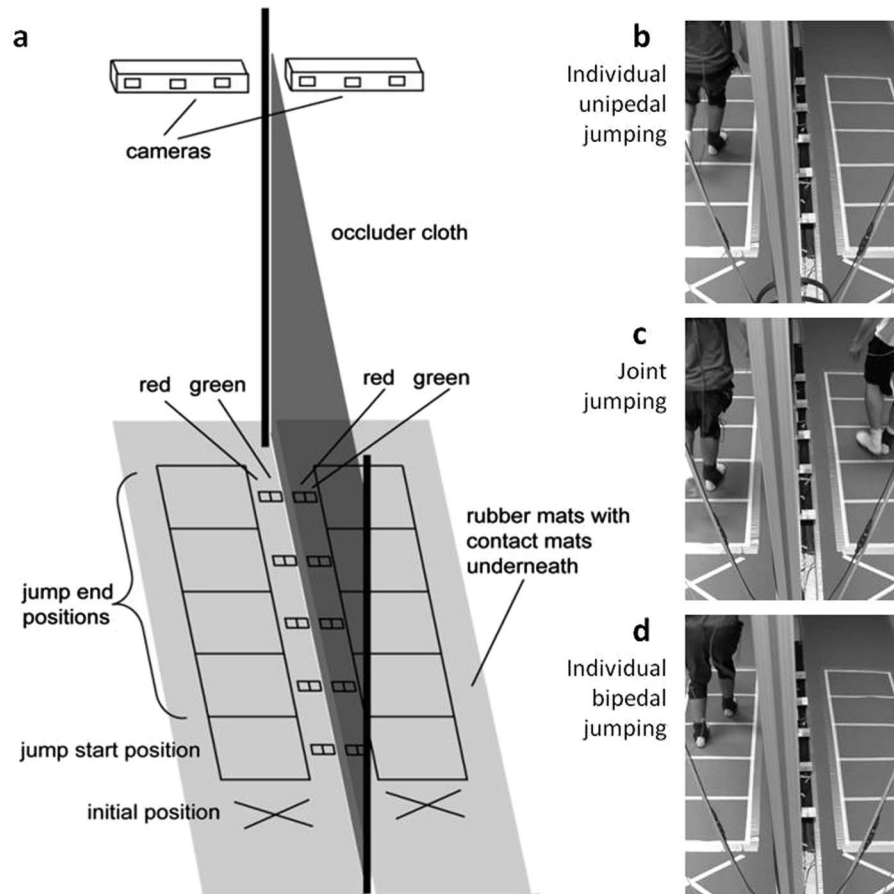


Figure 1. a) Schematic drawing of the experimental setup. b) Individual unipedal condition in which participants jumped alone on one leg. c) Joint condition in which participants jumped next to each other with the aim of landing at the same time. Like in the individual unipedal condition, each person jumped on one leg. d) Individual bipedal condition in which participants jumped individually on two legs with the instruction to synchronize the landing times of both legs.

jumping distance is (ibid.). In our task, the relation between preparation/execution time and jumping distance posed a challenge to coactors because their task was to land at the same time. If one person had to perform a relatively short jump, while the partner had to make a relatively long jump, their landings would not easily occur at the same time. Thus, successfully coordinating the landing times requires that coactors overcome the timing difference that will naturally occur when two people jump to targets at different distances.

We made use of a similar design as an earlier bimanual aiming study (Kelso, Southard, & Goodman, 1979). In Kelso et al.'s task, individual participants were instructed to aim for and reach to two targets simultaneously with their left and right hand. The distance and size of the two targets differed between the hands. Participants were not instructed to synchronize the endpoints of their two hands' movements, but it was observed that they did so anyway. In particular, participants slowed down the hand with the simpler task while keeping the movements to the more difficult target more or less constant (the experiment used a version of a Fitts' task in which the task difficulty was manipulated by either changing the distance and/or the target size [= index of difficulty]; Fitts, 1954).

Our study used a similar logic with the aim to investigate joint action coordination in the absence of online perceptual information. Consequently, the present study differs in important aspects from that of Kelso et al.: First, in the present study, the task was distributed between two people instead of two limbs (although we also included a bipedal coordination condition as described below). Second, to establish a shared goal for the joint action (Sebanz, Bekkering, & Knoblich, 2006; Vesper et al., 2010), we explicitly instructed participants to synchronize the endpoints of their movements. Third, we used jumping as a ballistic movement instead of aiming. Because recent findings by Juras and colleagues show that neither preparation nor movement time of jumping is affected by the target size (Juras et al., 2009), we only varied the movement distance.

Several prominent theories of action control make a clear distinction between action planning and action execution (e.g., Feldman & Latash, 2005; Flash & Hogan, 1985; Gomi & Kawato, 1996; Rosenbaum, Meulenbroek, Vaughan, & Jansen, 2001; Prinz, 1997). Jumping, in contrast to nonballistic movements such as aiming, is an action where, once the movement is initiated, control over its unfolding is given away. Thus, in jumping the two phases

have important differences in their characteristics. The preparation phase can be voluntarily controlled by participants because they decide at what time they will initiate their jump. In contrast, during the execution phase, participants cannot exert much influence on when they will land, besides for example, changing the angle of their feet during landing. In the present study, these distinct characteristics allow us to investigate different types of processes.

First, the preparation phase taps into higher-level planning processes and can be used to determine whether participants distribute the coordination effort equally between each other, or whether they distribute the coordination effort depending on task characteristics, such that the person with the easier task (i.e., the shorter jump) adjusts more to (i.e., waits longer for) the person with the more demanding task (i.e., the longer jump). This is interesting because it reveals strategic components of joint action coordination (Vesper et al., 2010).

Second, if participants engage in motor simulation to predict the timing of their partner's jump, then we expect to see effects of differences in jumping distance between coactors also in parameters that reflect how the actual movement is performed in the movement execution phase. Such parameters include for example the duration of the jump execution and the jump height. It is important that if participants simulate their partner's actions, one would expect effects both in the jump preparation and execution; however, only the movement execution phase can provide conclusive evidence for or against motor simulation.

The hypothesis that simulations of the other's jumping would influence one's own execution of the jumps is based on theories proposing a tight link between action observation/imagination and execution (Prinz, 1997). A variety of studies have shown that observing, executing, and imagining an action, or even reading words referring to that action activate common brain networks (Grèzes & Decety, 2001). The implication is that if two such processes occur at the same time, for example, observing an action and executing an action, they influence each other (e.g., Kilner, Paulignan, & Blakemore, 2003). In a similar way, we expected that simulating the partner's jump while at the same time preparing one's own jump would activate motor plans for both types of movement (Wolpert et al., 2003). Especially when coactors are instructed to jump different distances, the simulated motor plan of the partner's jump would influence the motor plan for one's own jump. Consequently, jumping performance would be different as compared with baseline jumping, leading, for example, to higher jumps than necessary when the partner has to jump farther than oneself. In line with earlier research revealing effects of action observation on execution (Kilner et al., 2003; Richardson, Campbell, & Schmidt, 2009), relatively small but systematic deviations toward the action to be performed by the partner are expected in our study.

In addition to the joint task, in which coactors were instructed to synchronize their landing times, two additional conditions were included (see Figure 1). In the individual unipedal condition, participants jumped individually by hopping on one leg without the need to coordinate with another person. We used this condition to obtain participants' baseline jumping performance because it required the exact same movements as the joint condition (i.e., jumping on one leg) and had the same task constraints (i.e., same jumping distances, same light cues) without the need to take someone else's jumping into account. As there was no one to

coordinate with, we expected jumping to be influenced only by the participant's own jumping distance. In the individual bipedal condition, participants jumped individually with both legs while instructed to synchronize the landing of their two legs. The jumping distance of each leg was independently varied in the same way as in the joint condition. In line with earlier findings on inter- and intrapersonal coordination (Schmidt & Richardson, 2008), we expected similar coordination patterns in the joint and in the individual bipedal condition. However, given that interlimb coordination naturally is a case where online prediction mechanisms are available within the motor system and where there is a mechanical coupling between the component parts of the system (e.g., the legs), we expected coordination performance to be better in the individual bipedal as compared with the joint condition.

Method

Participants

Twenty-four students of Radboud University Nijmegen participated in pairs of two (seven pairs all female, four pairs all male, one mixed-gender pair). The mean age of participants was 21.1 yr (standard deviation [*SD*] = 2.2 yr) and most had, according to self-report, a dominant right foot (three left-footed). Mean body height was 176.2 cm (*SD* = 10.5 cm) with a mean within-pair difference of 9.4 cm (*SD* = 8.2 cm). The two members of each pair were familiar with each other. The data of one pair of participants had to be removed from the analyses because one person had difficulties performing jumps with the farthest leg extension in the individual bipedal condition so that not enough trials could be completed in this condition. All participants were naïve as to the purpose of the study. They gave prior informed consent and were paid for their participation or received course credits. The experiment was conducted in conformance with the standards of the Declaration of Helsinki and local ethical guidelines.

Apparatus

The experimental setup (see Figure 1) consisted of two jumping areas divided by an occluder. On each side of an opaque black cloth (height 220 cm, length 400 cm), rubber mats on the floor were marked with two areas that indicated the jump starting and landing positions. These marked positions on each side formed a row of five rectangles with a rectangle size of 35 cm × 50 cm. On one end, a cross (also about 35 cm × 50 cm) outside the jumping area marked the initial position at which participants stood before each trial. Under the parts of the rubber mats with the markings, eight pressure-sensitive contact mats (Arun Electronics Ltd; size 55 cm × 70 cm) were placed that provided a binary signal whenever a person stepped on or off them. This signal was used to trigger the online auditory feedback for participants; it was not used for the data analysis.

On each side of the occluder cloth, five pairs of light-emitting diodes (LEDs) were positioned centrally next to each jump rectangle. A LED-pair consisted of one red and one green light covered by a transparent matted plastic cube (edge length 4 cm). Either the red light (on the left side) or the green light (on the right side) was next to the jumping area. Thus, on the left-hand side of the setup, one's own (left) side was associated with red lights and

the other (right) side with green lights, and on the right-hand side of the setup, one's own (right) side was associated with green lights and the other (left) side with red lights. All LEDs could be switched on and off independently. Two sets of headphones (Philips SHP1900) were used to provide participants with an auditory start signal as well as feedback about their own and their partners' landing times.

Data Acquisition

Movement data were recorded with two OPTOTRAK cameras (Optotrak 3020, Northern Digital, Inc.) connected to collect data in parallel. We recorded at a constant sampling rate of 100 Hz. The two OPTOTRAK cameras were positioned next to each other, facing participants from the front in the longitudinal axis. They were positioned 205 cm above and between 240 cm and 380 cm away from the jumping area (camera angle 56°). Because of the occluder cloth separating the field of view, we recorded each side of the setup with only one camera. The coordinate frame on each side was oriented such that the x, y, and z axes corresponded to the lateral, longitudinal, and vertical dimension, respectively, relative to the participants' jumping direction. Two infrared emitting diodes (IREDs) were used. Depending on the condition, markers were placed on participants' left and right big toe (on their right big toe in the individual unipedal and joint conditions and on both right and left toe in the individual bipedal condition). We used a customized DELPHI program (Borland Software Corporation, version 7.0 Professional) running on a standard PC (Intel Pentium 4, 1500 MHz; Microsoft Windows, 2000, Service Pack 4) to collect the OPTOTRAK data. A second computer (Intel Core 2 Duo, 3.00 GHz; Microsoft Windows XP Professional, Service Pack 3) with the experimental software Presentation (Neurobehavioral Systems Inc., version 14.0) controlled the trial procedure.

Procedure

The experiment consisted of three parts. Participants first performed the individual unipedal part separately while jumping on their right leg. The partner waited behind a room divider during this part of the experiment and could not see or hear the participant's jumping. In the joint part, the two participants of a pair performed the task together by jumping on their right legs. In the individual bipedal part, each participant performed the task individually with both legs while the partner was again seated out of sight. The order of the individual bipedal and the joint parts was counterbalanced, but the individual unipedal part was always performed first to acquire a baseline of participants' jumping and to familiarize participants with the task.

Participants received detailed written instructions at the start of the experiment as well as before each part. The experimenter instructed participants to land either at the same time as their partner (joint condition) or with both legs at the same time (individual bipedal condition). There was no additional coordination instruction for the individual unipedal condition; however, it was mentioned that the other light cues on the ground (those that were later used for indicating the jumping distance for the partner or the left leg) were not relevant in this part of the experiment.

Trials in each of the three parts followed the same general procedure: Participants stood in the initial position outside the

jumping area (marked by a cross). They then stepped forward to the jump start position, which was the first marked rectangle. At the same time, lights were switched on that indicated where the participant had to land (as well as where the partner/the other foot had to land). After a randomized foreperiod of either 1.7 s, 2.0 s, or 2.3 s, a short tone (440 Hz, 100 ms) was played as a start signal. Participants were instructed to initiate their jump at their own speed after the start signal. At the time of their landing, participants heard short tones (1320 Hz, 100 ms). These were triggered by the contact mats underneath the jumping area and provided feedback about their own landing time as well as their partner's landing time in the joint condition. After jumping, participants walked back to the initial position and waited for the next trial to begin (indicated by all lights being switched off).

Trials were self-paced by participants with the exception of the intertrial interval, which was controlled by an experimenter. The experimenter could also decide to repeat a trial if participants had not performed a trial correctly (e.g., jumping to the wrong position or not waiting for the auditory start signal) or if she noticed long occlusions of markers (e.g., because a cable was out of place). In such cases, the trial was repeated once immediately. On average, 6.1% of trials in the individual unipedal condition, 4.5% of trials in the joint condition and 1% of trials in the individual bipedal condition were repeated. The individual unipedal and individual bipedal conditions both consisted of 48 trials and lasted about 7 min. The joint condition included twice the amount of trials (96 trials, about 14 min). The experiment lasted for about 1.5 hr, including preparation for the movement recording and debriefing.

Data Preparation

Data analysis was based entirely on the signal from the OPTOTRAK system. Missing data points in the raw signal were filled in through a shape-preserving piecewise cubic interpolation function. The vertical and lateral dimensions were corrected with a simple linear equation because they were slightly distorted due to the large longitudinal distance the two cameras had to cover. The x-, y-, and z-velocity was computed on the interpolated, corrected data and low-pass filtered with a 4th-order Butterworth filter (cutoff 20 Hz).

Critical data points for each person's/leg's trajectory were determined by a customized semiautomatic Matlab (The MathWorks, version R2008b) analysis procedure and visually verified. These data points were the time of stepping into the jump start position (trial start), the time of leaving the ground for jumping (takeoff), and the time of landing on the ground after the jump (landing). All were determined based on the same velocity criterion of 0.1 cm/sec. From these data points, five dependent variables were calculated. First, movement onset (MO) is a parameter pertaining to the movement preparation phase and is the time between the start tone and takeoff. It therefore reflects the time people wait after the start signal until they perform the jump. Second, movement time (MT) is the time from takeoff to landing, thus representing the duration of the jump execution. Third, jump height (JH) is the maximum value of the vertical dimension in the time interval between takeoff and landing and constitutes an additional parameter pertaining to the movement execution phase. Fourth, landing position (POS) is the longitudinal (y) position at the point of landing and therefore provides a measure of spatial accuracy

during jump execution. Finally, asynchrony is the absolute difference between the landing times of the two participants in a pair (joint condition) or the two legs of one person (individual bipedal condition). It is a measure of coordination performance, thereby reflecting how well a pair/a person succeeds in following the task instructions to land at the same time. From all five dependent variables, difference scores were computed as described in the results section and Figure 2.

Trials in which more than half the data points in the critical time frame between jumping and landing were lost were excluded from additional analyses (2.8% of all trials: 0.4% in individual unipedal, 3.4% in joint, 4.6% in individual bipedal). Also trials in which participants made an error were removed from the analyses: location errors (trial start or landing not within the marked area ± 17.5 cm; 3.2% of all trials: 0.6% in individual unipedal, 3.6% in joint, 5.6% in individual bipedal) or if the timing of their jumps was outside ± 2 standard deviations of the mean of the respective condition (6.6% of all trials: 2.1% in individual unipedal, 8.3% in joint, 9.3% in individual bipedal). Based on these criteria, overall 7.4% of all trials had to be removed (2.2% in individual unipedal, 10.4% in joint, 9.5% in individual bipedal). Statistical analyses on the remaining trials were performed with SPSS for Windows (SPSS Inc., version 15.0).¹

Results

We first investigated whether the distance participants had to jump influenced the jump parameters as would be consistent with the literature on ballistic movement preparation and execution (e.g., Juras et al., 2009). For this purpose, separate analyses of variance (ANOVAs) with the single within-subject factor jumping distance (35 cm, 70 cm, 105 cm, 140 cm) were performed on the data with the same distance for both partners/legs. As expected, participants' MO (Figure 3a) and MT (Figure 4a) were longer, JH (Figure 5a) higher, and POS farther (Figure 6a) the larger participants' own jumping distance was, all $F > 23$, all $p < .001$. Linear regression analyses confirmed this relationship between increasing values of the jump parameters and increasing jump distances, all $\beta > .42$, all $t > 4.3$, all $p < .001$.

Based on these results, we computed difference scores of the MO, MT, JH, and POS data because this allowed us to analyze participants' jumps according to the difference in distance between them and their partner instead of their absolute jumping distances. For this purpose, the mean MO, MT, JH, and POS of trials with the same jumping distance (e.g., both persons/legs jumping 35 cm) was subtracted from the mean MO, MT, JH, and POS of trials with different jumping distances (e.g., one person/leg jumping 35 cm, the other person/leg jumping 105 cm). Figure 2 illustrates this procedure. The resulting relative parameters rMO, rMT, rJH, and rPOS provided measures of how much participants' own jumping was modulated by the relation (closer, farther) and the distance to their partner/second leg ($\Delta 35$ cm, $\Delta 70$ cm, $\Delta 105$ cm).

Adaptation of Jump Performance

The four relative jump parameters rMO, rMT, rJH, and rPOS were analyzed with within-subject ANOVAs with the factors context (individual unipedal, joint, individual bipedal), relation (closer, farther), and distance ($\Delta 35$ cm, $\Delta 70$ cm, $\Delta 105$ cm). The

overall results of this analysis are shown in Table 1. In order to investigate in detail under which conditions the distance of the partner or the second leg was taken into account, separate one-factorial ANOVAs with the factor distance ($\Delta 35$ cm, $\Delta 70$ cm, $\Delta 105$ cm) were used to determine in which cases the specific distance difference had an influence on one's own jumping. A significant result indicates that participants adapted their jumping depending on the difference in distance between their own and their partner's or other leg's jump or, in case of the individual unipedal condition, depending on the light cues on the ground. Whenever significant results were found in this analysis, an additional linear regression analysis tested the more specific hypothesis that adaptation was scaled to the distance difference. The outcome of this analysis is significant if participants adapted their jumping more the larger the distance difference to their partner/other leg was. Finally, to test whether participants generally slowed down or sped up, jumped higher or lower, and jumped closer or farther in trials involving different distances to be jumped, as compared with the baseline trials requiring the same distance to be jumped, we performed one-sample t tests on the average of the jump parameters in the three distance differences (i.e., the mean of rMO in $\Delta 35$ cm, $\Delta 70$ cm, and $\Delta 105$ cm). A significant result indicates that coactors' jumps were modulated in a general way, for example, overall faster as compared with the baseline.

Movement preparation. The results for the rMO, which is the time from the external start signal to participants' jump take-off in different distance trials relative to same-distance trials, are shown in Figure 3b. Participants modulated the rMO of closer jumps in the joint condition, $F(2, 42) = 21.01$, $p < .001$, and in the individual bipedal condition, $F(2, 42) = 13.24$, $p < .001$. This adaptation was specific to the distance difference such that, in the joint condition, coactors waited longer the farther their partner had to jump, $\beta = .484$, $t(64) = 4.42$, $p < .001$, and, in the individual bipedal condition, the right leg waited longer the farther the left leg had to jump, $\beta = .363$, $t(64) = 3.12$, $p < .01$. There were no significant effects in the joint or individual bipedal rMO of farther jumps or in the individual unipedal condition, all $F < 2.2$, all $p > .1$. Thus, participants adapted their movement preparation phase specifically to the distance difference, but only when coordination was required (i.e., not in the individual condition) and only when their own jump was shorter than their partner's or other leg's (i.e., not in farther trials).

In the joint and individual bipedal conditions, farther jumps were generally initiated faster than jumps in the same-distance baseline, $t(21) = -3.55$, $p < .01$ (joint) and $t(21) = -5.87$, $p < .001$ (individual bipedal). When their own jump was closer participants waited overall longer, $t(21) = 7.85$, $p < .001$ (joint) and $t(21) = 3.09$, $p < .01$ (individual bipedal). These general effects in joint and bipedal jumping indicate that in addition to the specific adaptation dependent on the distance difference, participants also sped up their jump preparation in farther trials, possibly to assist coordination. Consistent with this, jumping was not modulated in the individual unipedal condition, all $t < .3$, all $p > .7$.

Movement execution. For the movement execution phase, two parameters were of interest: The rMT reflects how long a

¹ For the results of analyses of variance, we report Greenhouse-Geisser corrected p -values and uncorrected degrees of freedom for F -values.

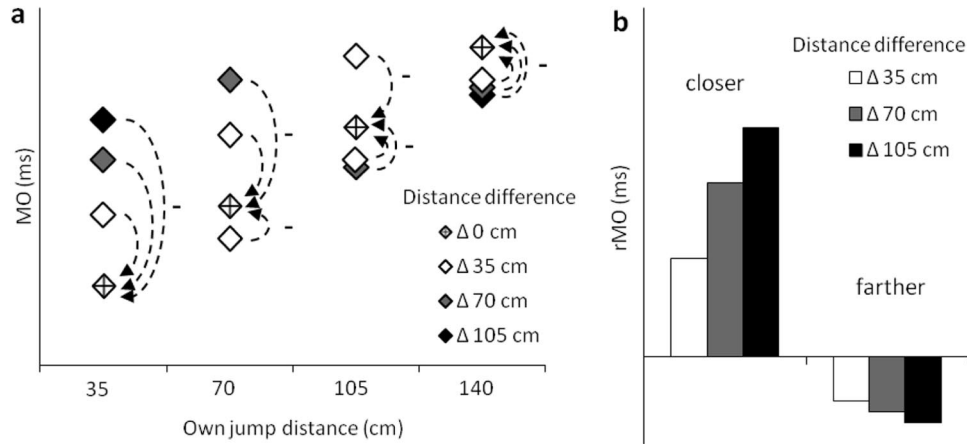


Figure 2. Computation of difference scores, exemplified by the movement onset (MO) in the joint condition. a) The original absolute MO values depending on own jump distance (35 cm, 70 cm, 105 cm, or 140 cm) and distance difference to the partner (0 cm, 35 cm, 70 cm, or 105 cm). b) The relative values (difference scores), computed from the original values in a) by subtracting from each MO in which partners jumped to different positions (distance difference of 35 cm, 70 cm, or 105 cm) the corresponding MO in which partners jumped to the same positions (distance difference of 0 cm). Cases in which one's own jump was closer than the partner's ("closer") and those in which one's own jump was farther than the partner's ("farther") were treated separately, but computed in the same way. The resulting parameter was called relative movement onset (rMO). The same procedure was used to calculate the other relative parameters (rMT, rJH, rPOS), as well as the respective parameters in the individual unipedal and individual bipedal conditions.

participant's jump lasted and the rJH is an indirect measure of how much force participants put into jumping. Participants modulated the rMT (Figure 4b) in closer jumps of the joint condition, $F(2, 42) = 8.95$, $p < .01$, such that the larger the distance difference between partners, the more time the jump of the person with the shorter distance took, $\beta = .261$, $t(64) = 2.17$, $p < .05$. In the individual bipedal condition, the distance to the left leg affected the rMT when the right leg had a closer jump, $F(2, 42) = 3.7$, $p < .05$, and also when the right leg's jump was farther, $F(2, 42) = 13.09$, $p < .001$. In both cases, jumping took more time the larger the distance between the two legs was, $\beta = .243$, $t(64) = 2.01$, $p = .05$ (closer relation) and $\beta = .38$, $t(64) = 3.29$, $p < .01$ (farther relation). The relative movement time in the individual unipedal

condition and in the joint condition for farther jumps was not significantly affected by the factor distance, all $F < .9$, all $p > .3$.

Overall, the relative movement time of the joint and the individual bipedal jumps of closer trials was slower, as compared with the baseline, $t(21) = 2.23$, $p < .05$ (joint) and $t(21) = 3.98$, $p < .01$ (individual bipedal). Movements were also slower in farther jumps of the individual bipedal condition, $t(21) = 5.57$, $p < .001$. Farther jumps of the joint condition, $t(21) = -1.85$, $p = .078$, and all jumps in the individual unipedal condition were not different from the baseline, all $t < 1.05$, all $p > .3$.

Thus, in the joint condition, the results of the movement execution time resemble those of the rMO such that the person with the closer jump adapted to the difference in distance, whereas the

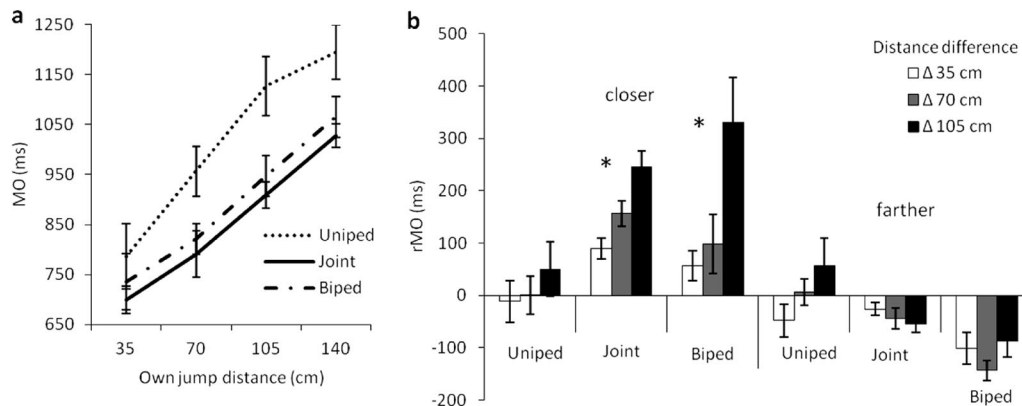


Figure 3. a) Movement onset (MO) for same-distance trials. b) Relative movement onset (rMO) depending on context, relation, and distance. * $p < .05$; error bars = standard error.

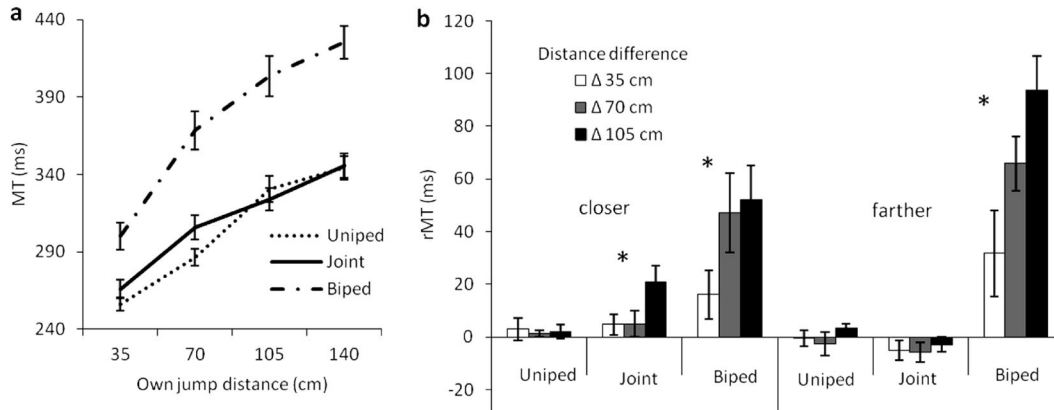


Figure 4. a) Movement time (MT) in same-distance trials. b) Relative movement time (rMT) depending on context, relation, and distance. * $p < .05$; error bars = standard error.

person with the farther jump adapted his or her jumping only in a more general way by decreasing the movement execution time. In the individual bipedal condition, the pattern was different. Here, both closer and farther jumps were influenced by the difference in jump distance between legs such that jumps took longer the larger the distance difference.

The results of the rJH reveal a similar pattern as the rMT. In the joint condition, rJH (Figures 5b and c) was adapted during closer jumps, $F(2, 42) = 17.46$, $p < .001$, such that participants jumped higher the larger the difference in distance between coactors was, $\beta = .389$, $t(64) = 3.38$, $p = .001$. In the individual bipedal condition, participants adapted the jump height of the right leg both in a closer relation, $F(2, 42) = 26.7$, $p < .001$, and a farther relation, $F(2, 42) = 25.77$, $p < .001$. Jumps were performed higher the larger the distance difference between legs was, $\beta = .465$, $t(64) = 4.2$, $p = .001$ (closer relation) and $\beta = .508$, $t(64) = 4.72$, $p < .001$ (farther relation). The rJH in the individual unipedal condition and in the joint condition for farther jumps were not significantly affected by the factor distance, all $F < .9$, all $p > .3$.

Closer jumps in the joint and individual bipedal conditions were generally higher than in the baseline in which both partners/legs jumped to the same positions, $t(21) = 4.01$, $p = .001$ (joint) and $t(21) = 5.79$, $p < .001$ (individual bipedal). Farther jumps were also higher in the individual bipedal condition, $t(21) = 6.77$, $p < .001$, but overall lower in the joint condition, $t(21) = -3.17$, $p < .01$. Jumps in the individual unipedal condition were not adapted, all $t < 1.06$, all $p > .3$. This suggests that participants in the joint condition purposefully jumped less high to support the partner's efforts in achieving coordination, whereas jumps in the bipedal jumping were generally higher the larger the difference in jumping distance of the two legs was.

Spatial accuracy. A parameter reflecting the nontemporal aspects of the jump execution is the spatial accuracy in the longitudinal dimension, the rPOS (Figure 6b). It reflects how far participants actually jumped within the boundaries of their own jumping target. The results show that the person with the closer jump in the joint condition specifically adapted the jump end point to the distance difference between partners, $F(2, 42) = 8.06$, $p = .001$.

She jumped farther (within her own target) the farther the partner had to jump, $\beta = .371$, $t(64) = 3.19$, $p < .01$. All other analyses (individual unipedal, individual bipedal, joint farther) were not significant, all $F < .6$, all $p > .5$. Thus, jumps were only spatially adapted to the distance difference in the joint condition when one's own jump was closer than the partner's. In the individual bipedal condition, spatial accuracy was not specifically influenced by the distance difference.

A comparison of the overall mean rPOS to the baseline of same-distance trials revealed a less clear pattern than the analyses of rMT and rJH. In particular, participants jumped overall a longer distance in closer jumps of the joint condition, $t(21) = 5.77$, $p < .001$, and overall a shorter distance in farther jumps of the individual bipedal condition, $t(21) = -5.22$, $p < .001$. The effects were not significant for farther jumps in the joint condition, $t(21) = -1.88$, $p = .074$, or closer jumps in the individual bipedal condition, $t(21) = -1.76$, $p = .093$, although there was a tendency in both such that jumps covered less distance than in the baseline. No general adaptation was found in jumps of the individual unipedal condition, all $t < .7$, all $p > .4$.

Coordination

As a parameter for coordination performance, the absolute asynchronies were computed for the landing times of the two partners (joint condition) or the two legs (individual bipedal condition). An independent samples t test on the asynchronies of trials where both people/legs jumped to the same position ($\Delta 0$ cm) revealed that the asynchronies in the joint condition were overall larger than in the individual bipedal condition (Figure 7a), $t(31) = 13.39$, $p < .001$. Thus, coordination performance was better when participants coordinated the landing of their two feet than when coordinating with another person.

To investigate the impact of the distance between partners/legs, difference scores for the absolute asynchronies were computed in the same way as for the MO, MT, JH, and POS by subtracting the means of trials where partners/legs jumped the same distance from the means in trials where partners/legs

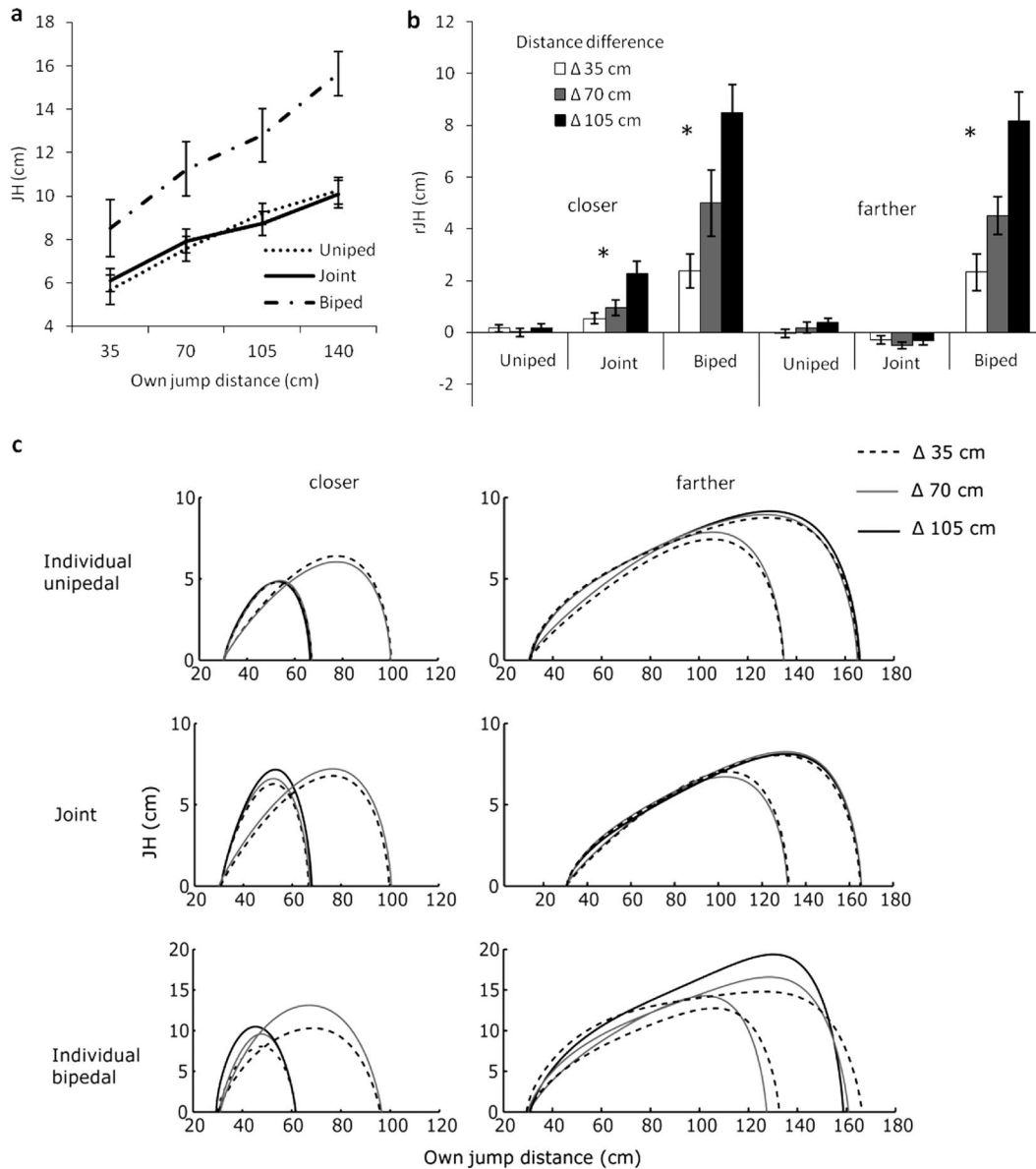


Figure 5. a) Jump height (JH) in same-distance trials. b) Relative jump height (rJH) depending on context, relation, and distance. * $p < .05$; error bars = standard error. c) Time-normalized trajectories showing how high participants jumped depending on their own distance as well as their partner's / the second leg's distance.

jumped different distances (relative asynchrony, rASYNC).² A within-subjects ANOVA with the factors context (joint, individual bipedal) and distance ($\Delta 35$ cm, $\Delta 70$ cm, $\Delta 105$ cm) on rASYNC (Figure 7b) revealed a significant main effect of context, $F(1, 21) = 6.52$, $p < .05$, a significant main effect of distance, $F(2, 42) = 7.58$, $p < .01$, and a significant interaction, $F(2, 42) = 4.43$, $p < .05$. This interaction suggests that the main effect of distance is based on only one of the two contexts. Separate post hoc ANOVAs with the single factor distance as well as a linear regression analysis confirmed this: Whereas the asynchronies in the individual bipedal condition depended strongly on the distance between the legs, $F(2, 42) = 11.01$, $p = .001$, such that larger distance differences lead to larger

asynchronies, $\beta = .359$, $t(64) = 3.08$, $p < .01$, the distance between partners in the joint condition did not have a significant impact on coordination performance, $F(2, 42) = 0.24$, $p > .7$. Overall, asynchronies were larger as compared with the baseline of same-distance jumps as confirmed by one-sample t

² To account for the different degrees of freedom of the asynchronies in the joint (12 pairs) and individual bipedal (24 persons) conditions, we computed the rASYNC from the perspective of the person with the closer jump only. Thus, in each trial, the asynchrony value was assigned to the person with the shorter jumping distance, providing asynchrony values for each individual participant.

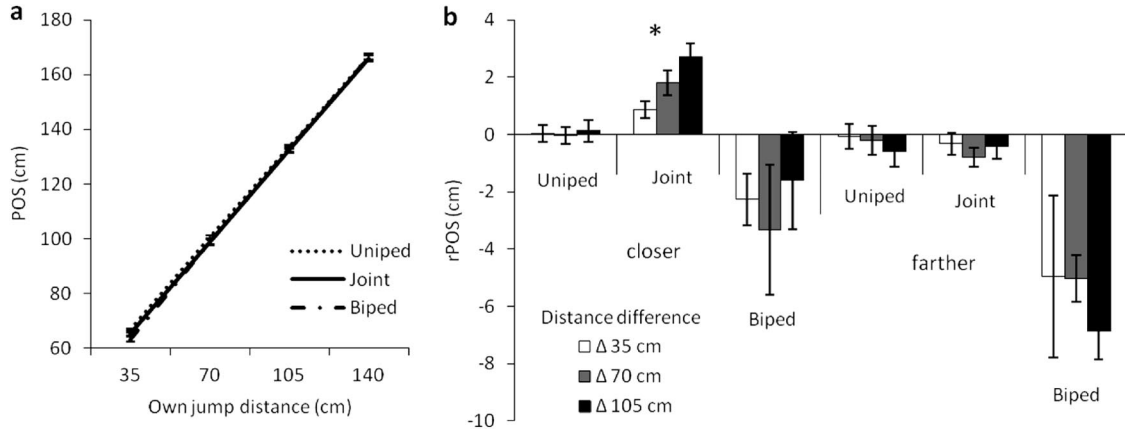


Figure 6. a) Jump position (POS) in same-distance trials. b) Normalized jump position (rPOS depending on context, relation, and distance). * $p < .05$; error bars = standard error.

tests, $t(21) = 5.74, p < .001$ (joint) and $t(21) = 6.77, p < .001$ (individual bipedal).

Relation of Preparation, Execution, and Performance in Joint Jumping

To investigate whether the effects observed in the movement execution phase in the joint condition were of a compensatory kind, we correlated the MO and MT of all trials with each other. If participants increased their jump execution time whenever their jump preparation time was too short given the distance difference to the partner, we should see a negative correlation between MO and MT. However, the two parameters were not significantly correlated, $r = -.009, p > .6$.

Finally, to further investigate the factors influencing coordination performance in joint jumping we correlated the slopes of the rMO of closer jumps, the rMO of farther jumps and the rASYNC with each other. The slope of rMO reflects how much participants adapted their jumping to the partner’s jumping distance. The slope of the rASYNC reflects the extent to which coordination is influenced by the difference in jumping distance between partners.

In the joint condition, the slope of the closer rMO was significantly correlated with the slope of the rASYNC, $r = -.43, p < .05$. The more participants adapted the MO when their jump was closer the less strongly coordination accuracy was influenced by the distance between partners. Farther rMO had no such influence

on coordination, $r = -.097, p > .6$. The slopes of closer rMO and farther rMO were significantly correlated, $r = -.469, p < .05$, such that participants who adapted their jumping a lot when they were closer than their partner were those who adapted only very little when their jump was farther, suggesting individual differences in the extent to which people engaged in role distribution.

Learning

We also investigated whether participants’ performance changed during the course of the interaction. For this purpose, the four jump parameters (MO, MT, JH, POS) were averaged (same-distance jumps $[\Delta 0 \text{ cm}]$ only) separately for each block of 24 trials (two blocks in the individual unipedal and individual bipedal conditions, four blocks in the joint condition). One factorial ANOVAs revealed that the jumping performance was not significantly modulated over time, all $F < 1.5$, all $p > .2$. The same analysis was done with the asynchronies of all trials in which pairs/legs jumped to the same positions ($\Delta 0 \text{ cm}$). It showed that, in the joint condition, coordination accuracy improved significantly over time, $F(3, 30) = 2.97, p < .05$, whereas the individual bipedal performance did not change from the first to the second block, $F(1, 21) = .93, p > .3$ (Figure 7a). Thus, only coordination performance in the joint condition was positively affected by the amount of training coactors had with the task.

Table 1

Results of the 3 Context (Individual Unipedal, Individual Bipedal, Joint) \times 2 Relation (Closer, Farther) \times 3 Distance ($\Delta 35 \text{ cm}$, $\Delta 70 \text{ cm}$, $\Delta 105 \text{ cm}$) Within-Subject ANOVAs for the Parameters rMO, rMT, rJH, and rPOS

	rMO	rMT	rJH	rPOS
Context (C)	$F(2, 42) = 1.34, p > .2$	$F(2, 42) = 37.26, p < .001$	$F(2, 42) = 48.39, p < .001$	$F(2, 42) = 18.13, p < .001$
Relation (R)	$F(1, 21) = 34.93, p < .001$	$F(1, 21) = 0.35, p > .5$	$F(1, 21) = 3.82, p = .064$	$F(1, 21) = 11.56, p < .01$
Distance (D)	$F(2, 42) = 28.58, p < .001$	$F(2, 42) = 15.73, p < .001$	$F(2, 42) = 54.79, p < .001$	$F(2, 42) = 0.05, p > .9$
C \times R	$F(2, 42) = 11.76, p < .001$	$F(2, 42) = 6.23, p < .05$	$F(2, 42) = 2.45, p > .1$	$F(2, 42) = 2.56, p > .1$
C \times D	$F(4, 84) = 2.08, p > .1$	$F(4, 84) = 7.91, p < .01$	$F(4, 84) = 36.51, p < .001$	$F(4, 84) = 0.33, p > .6$
R \times D	$F(2, 42) = 7.14, p < .01$	$F(2, 42) = 0.46, p > .6$	$F(2, 42) = .69, p > .5$	$F(2, 42) = 1.62, p > .2$
C \times R \times D	$F(4, 84) = 4.22, p < .05$	$F(4, 84) = 2.29, p > .1$	$F(4, 84) = 1.59, p > .2$	$F(4, 84) = 0.57, p > .5$

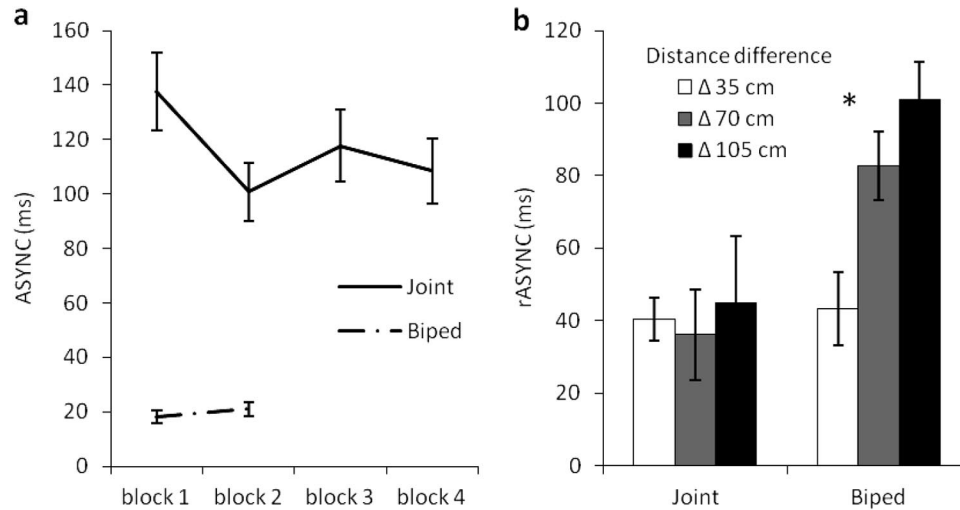


Figure 7. a) Absolute asynchronies (ASYNC) over blocks (2 blocks of 24 trials in the individual bipedal and 4 blocks in the joint condition). b) Relative asynchronies (rASYNC) in the joint and individual bipedal conditions. * $p < .05$; error bars = standard error.

Discussion

The present study investigated joint action coordination in the absence of online perceptual information about a coactor's actions. To address the interplay between higher-level action planning and motor simulation processes, we used a task that required pairs of participants to perform simple forward jumps of variable length with the goal of landing at the same time. Coactors could neither see nor hear each other, but received information about their own and their partners' required jumping distances prior to jumping as well as feedback when landing. Studying the coordination of ballistic movements allowed us to separate action planning processes during the preparation phase from subsequent effects on movement execution. In particular, movement onset, marking the end of the preparation phase, served to determine whether participants distribute the coordination effort equally between each other (regardless of the relative difference between their jumps), or whether they distribute the coordination effort depending on task characteristics, such that the person with the easier task (i.e., the shorter jump) adjusts more to (i.e., waits longer for) the person with the more demanding task (i.e., the longer jump). The movement execution phase served to determine whether participants engaged in motor simulation to predict the timing of their partner's jump, which should result in modulations of movement time, jump height, and landing position depending on the coactor's jump distance.

The present results provide evidence for a distribution of the coordination effort depending on task characteristics. Participants with the "easier" task on a given trial (individuals required to make a shorter jump than their partner) adapted their movement onset according to the distance between their own and their partner's jumps. The larger the distance difference between partners was, the longer they waited before initiating their jump. In contrast, participants with the more difficult task (required to make a long jump) did not adjust their movement onset to the partner's distance. These findings indicate that action planning is driven by the relative difficulty of the actions to be coordinated. The burden of coordination seems to be on task partners

whose actions require less effort and are more easily adjustable. Moreover, a correlation analysis showed that the more participants adjusted to the difference in distance when their own jump was the shorter one, the less they adjusted when their jump was the longer one, suggesting individual differences in the extent to which coactors engaged in role distribution.

Nevertheless, also coactors with the farther jump contributed to coordination by speeding up their movement preparation phase. In contrast to the adaptations of the person with the closer jump, however, this speeding was general, that is, not specific to the difference in distance between own and other's jumps. We have recently found similar evidence for general speeding in a joint coordination study in which pairs of participants were instructed to perform a visual two-choice reaction time task, either in synchrony or in close temporal succession (Vesper, van der Wel, Knoblich & Sebanz, 2011). In that study, speeding one's own button press responses supported coordination by increasing the predictability of subsequent actions. The same explanation is plausible in the present task. In particular, participants initiated their jumps faster in the farther relation, when coordination was more challenging, than baseline jumps with the same distance to jump, which were easier to coordinate.³ This suggests that speeding functioned as a coordination strategy that is particularly relevant for difficult coordination tasks (Vesper et al., 2010).

³ Another strong test of strategic speeding would be to compare the movement onset in the same-distance baseline of the joint condition to the corresponding trials in the individual unipedal condition. A significant difference would indicate that coactors made use of such a coordination strategy independent of the distance relation between them, i.e., for the general purpose of supporting joint coordination. However, this test would not be reliable in the present study because the individual unipedal condition was always performed first to acquire participants' individual baseline jumping and to familiarize them with the task. Therefore, the alternative explanation that speeding is a mere training effect could not be ruled out.

With respect to the movement execution phase, the important finding is that it was modulated in the same way as the movement preparation phase. The distance to the partner influenced each of the parameters reflecting jump execution. Participants with the shorter distance to cover jumped longer, higher, and farther, the longer the distance to be covered by their partner was. Again, participants who performed the longer, more effortful jump did not show any specific modulation by the distance difference to their partner's jump. These results suggest that participants performing the easier part that allowed for adjustments based on their partner's jump engaged in a motor simulation of the partner's jump at the same time as planning their own movement.

The modulation of one's own jump by the other's jump is in line with theories postulating common representations of imagined, perceived and planned actions (e.g., Prinz, 1997). Extending earlier evidence of motor simulation during action anticipation (Kilner et al., 2004; Kourtis et al., 2010) and imagination (Grèzes & Decety, 2001; Ramnani & Miall, 2005), our findings suggest that motor simulation during joint action planning takes place in the service of temporal prediction. In our task, engaging in motor simulation was possible because despite the lack of online perceptual information, participants had sufficient prior information about their partner's action to feed into their predictive forward models. Participants knew precisely which distance their partner had to cover and so they could initiate a simulation of their partner's jump that allowed them to time their own jump so as to minimize the asynchrony in landing times. Especially the fact that the final position of the jump was modulated is also consistent with the literature on individuals' decision-making processes reflected in manual aiming (e.g., Song & Nakayama, 2009; Spivey, Grosjean, & Knoblich, 2005). For example, one study showed that distracting reach locations influenced an individual's movement trajectory when reaching toward a goal location (Welsh & Elliott, 2004). In a similar way, in our study, simulating the partner's jump to a different target position conflicted with an individual's simulation for his or her own jump, thereby "leaking" into the motor plan before movement execution and altering jump performance.

One could argue that the modulations observed during the execution phase simply reflect participants' use of general heuristics rather than motor simulation processes. For instance, if participants reasoned that jumping higher could be a useful means to compensate for the difference in jumping distance to their partner, they could have altered their jumps intentionally. Although this may be a possibility, several aspects of our findings speak against it. First of all, a correlation analysis with MO and MT showed that these two parameters were not related. Participants did not seem to adapt their movement preparation and execution time on a trial-by-trial basis which would be expected if they intentionally jumped higher on trials where they did not wait long enough to make up for the distance difference to their partner. Second, given the large number of combinations of different jump distances for the two participants (16 in total) it seems challenging, if not impossible, to apply a cognitive strategy that leads to the consistent and fine grained adaptations on a timescale of tens of milliseconds that we have observed. Third, none of the jump parameters changed over the course of the experiment. This implies that coactors did not need to learn the partner's temporal jump characteristics based on the feedback at landing. Instead, they could immediately do the task, possibly by relying on existing internal

models for their own jumping (Repp & Knoblich, 2004). Finally, participants never mentioned the active modulation of jump execution parameters in postexperiment debriefing interviews, although most reported that they intentionally delayed the time of initiating their movements. Thus, the effects observed in the jump execution phase are most likely not brought about intentionally, but occur because of the active simulation of the partner's jump during movement planning.

An additional aim of the current study was to investigate similarities and differences between joint and individual bipedal jumping. In the individual bipedal condition, participants' task was to jump to different positions with their two legs and to synchronize the landing of both feet. Therefore, the two legs of one individual had the same task as the two partners of a pair in the joint condition, allowing for a direct comparison of participants' performance in both conditions. With respect to movement preparation, the results of the individual bipedal condition closely resemble those of the joint condition. The movement onset of the leg covering the shorter distance was adapted to the distance difference between the two legs. This result is consistent with earlier findings on movement preparation in bimanual aiming (Kelso et al., 1979). In bimanual aiming, individuals synchronized their movements by modulating the timing of the hand with the shorter path, whereas the hand with the longer path was not influenced by the distance difference between the hands. This distribution of tasks made perfect sense for an individual given that both hands are controlled by a single motor system. By distributing the coordination effort like this, only one hand's movements needed to be carefully controlled with respect to timing. If both hands would adapt to each other, this would likely require more computational effort (Konvalinka et al., 2010). The same is true for our individual bipedal condition, where delaying the movement onset of the leg that jumped the shorter distance was likely more efficient than distributing the coordination effort over both legs.

Whereas the similarity between joint and interlimb coordination is striking with regard to the movement preparation phase, there was a profound difference in the coordination pattern during the movement execution phase. In the joint condition, coactors showed the same distribution of the coordination effort in preparing and executing their jumps, so that the individual with the shorter jump adjusted to the distance to be covered by the individual with the longer jump, but not vice versa. However, in the execution phase of the individual bipedal jumping condition, movement times and jump heights of both legs were affected by the distance difference such that they jumped slower, higher, and farther the larger the difference in distance between them. How can this finding, which is inconsistent with the findings from bimanual aiming (Kelso et al., 1979), be explained? The answer lies in the difference between ballistic and nonballistic movement. As the two legs of one individual are biomechanically coupled, they are not as independent from each other during a ballistic jumping movement as one individual's two hands or two separate persons. Therefore, interlimb coordination of ballistic movements is a case where distributing the coordination effort asymmetrically across effectors would actually be very effortful or even impossible because individuals would need to overcome the natural biomechanical constraints of their body.

Given the availability of motor commands within one system in the individual bipedal condition and the biomechanical linkages

within the system, we expected that individual bipedal jumping would be better in terms of coordination performance than joint jumping, where coactors needed to overcome the difficulties of coordinating two independent motor systems. This hypothesis was supported by the current results because the absolute asynchrony between the landing times of the two legs in the individual bipedal condition was lower than that of the landing of the two partners in the joint condition. Moreover, although there was a learning effect in early trials of the joint condition, coordination remained relatively stable afterward. This is consistent with earlier findings highlighting the importance of feedback about a task partner's actions for improving interpersonal coordination (Knoblich & Jordan, 2003).

It is interesting, however, that despite the overall poorer coordination performance in the joint condition, as compared with the individual bipedal condition, participants succeeded better in compensating for the distance difference between each other. In fact, joint coordination performance was equally good, independent of how much farther one partner had to jump as compared with the other one. In the individual bipedal condition, in contrast, the distance difference had a big impact on asynchronies which were larger the farther one leg had to jump, as compared with the other. This dependence between the two legs of one individual could again be explained by the biomechanical coupling that constrains individual bipedal jumping.

The finding that pairs of people coordinated their movement onsets in a highly similar way as single individuals coordinating two limbs extends previous research on the relation of intra- and interpersonal coordination (see Schmidt & Richardson, 2008). So far, similarities between intra- and interpersonal coordination have mainly been found in the context of tasks where online feedback about a partner's actions was available during interpersonal coordination (e.g., Richardson, Marsh, & Baron, 2007; Schmidt, Bienenven, Fitzpatrick, & Amazeen, 1998). The present study indicates that interpersonal coordination resembles intrapersonal coordination even when online feedback about a partner's actions is not available. On the one hand, this could be taken to imply that principles of individual motor coordination structure dyadic performance. When people simulate a partner's actions to coordinate their actions with him or her they may be relying on internal models that govern the coordination of an individual's own limbs.

On the other hand, there may be a more strategic component guiding joint action coordination in our task. In the joint condition, both coactors are independent from each other, which would make mutual adaptation possible. Previous research has shown that when people try to synchronize identical actions (tapping) they both keep trying to adjust to each other on a trial-by-trial basis, which results in overadaptation (Konvalinka et al., 2010). Task distribution could be an effective coordination strategy that facilitates joint action coordination (Vesper et al., 2010) and serves to prevent impairments in synchronization due to overadaptation. By assigning the coordination effort to one individual, depending on the relative difficulty of the actions to be coordinated, the problem of mutual adaptation is effectively solved. Evidence for a strategic component in the joint jumping condition is provided by the observation that participants who adapted a lot when they jumped a lesser distance than their partner hardly adapted when they jumped a greater distance.

Taken together, the current study extends prior knowledge in mainly three areas of interest. First, the results add to the action prediction literature (e.g., Wolpert et al., 2003) by suggesting that, in situations in which no online perceptual information about the coactor is available, general task information can provide a basis for forming motor simulations about a partner's subsequent actions. Second, similarities between a joint and an individual bipedal jumping condition extend prior findings from studies on inter- and intrapersonal coordination (Schmidt & Richardson, 2008) that propose common mechanisms underlying both. Finally, the finding of a clear task distribution between the person with the easier task and the person with the more difficult task supports recent suggestions about a strategic component to joint action coordination (Vesper et al., 2010).

References

- Aglioti, S. M., Cesari, P., Romani, M., & Urgesi, C. (2008). Action anticipation and motor resonance in elite basketball players. *Nature Neuroscience*, *11*, 1109–1116. doi:10.1038/nn.2182
- Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., & Freund, H.-J. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. *European Journal of Neuroscience*, *13*, 400–404.
- Calvo-Merino, B., Glaser, D., Grèzes, J., Passingham, R., & Haggard, P. (2005). Action observation and acquired motor skills: An fMRI study with expert dancers. *Cerebral Cortex*, *15*, 1243–1249. doi:10.1093/cercor/bhi007
- Casile, A., & Giese, M. A. (2006). Nonvisual motor training influences biological motion perception. *Current Biology*, *16*, 69–74. doi:10.1016/j.cub.2005.10.071
- Clark, H. (1996). *Using language*. Cambridge, U.K.: Cambridge University Press.
- Cross, E. S., de C. Hamilton, A. F., & Grafton, S. T. (2006). Building a motor simulation de novo: Observation of dance by dancers. *NeuroImage*, *31*, 1257–1267. doi:10.1016/j.neuroimage.2006.01.033
- Cross, E. S., Kraemer, D. J. M., de C. Hamilton, A. F., Kelley, W. M., & Grafton, S. T. (2009). Sensitivity of the action observation network to physical and observational learning. *Cerebral Cortex*, *19*, 315–326. doi:10.1093/cercor/bhn083
- Feldman, A. G., & Latash, M. L. (2005). Testing hypotheses and the advancement of science: Recent attempts to falsify the equilibrium point hypothesis. *Experimental Brain Research*, *161*, 91–103. doi:10.1007/s00221-004-2049-0
- Fitts, P. M. (1954). The information capacity of the human motor system in controlling the amplitude of movement. *Journal of Experimental Psychology*, *47*, 381–391. doi:10.1037/h0055392
- Flash, T., & Hogan, N. (1985). The coordination of arm movements: An experimentally confirmed mathematical model. *The Journal of Neuroscience*, *5*, 1688–1703.
- Gomi, H., & Kawato, M. (1996). Equilibrium-point control hypothesis examined by measured arm-stiffness during multi-joint movement. *Science*, *272*, 117–120. doi:10.1126/science.272.5258.117
- Grèzes, J., & Decety, J. (2001). Functional anatomy of execution, mental simulation, observation, and verb generation of actions: A meta-analysis. *Human Brain Mapping*, *12*, 1–19. doi:10.1002/1097-0193(200101)12:1<1::AID-HBM10>3.0.CO;2-V
- Juras, G., Slomka, K., & Latash, M. (2009). Violations of Fitts' law in a ballistic task. *Journal of Motor Behaviour*, *41*, 525–528. doi:10.3200/35-08-015
- Kelso, J. A. S., Southard, D. L., & Goodman, D. (1979). On the nature of human interlimb coordination. *Science*, *203*, 1029–1031. doi:10.1126/science.424729

- Kilner, J. M., Paulignan, Y., & Blakemore, S. J. (2003). An interference effect of observed biological movement on action. *Current Biology, 13*, 522–525. doi:10.1016/S0960-9822(03)00165-9
- Kilner, J. M., Vargas, C., Duval, S., Blakemore, S. J., & Sirigu, A. (2004). Motor activation prior to observation of a predicted movement. *Nature Neuroscience, 7*, 1299–1301. doi:10.1038/nn1355
- Knoblich, G., Butterfill, S., & Sebanz, N. (2011). Psychological research on joint action: Theory and data. In B. Ross (Ed.), *The psychology of learning and motivation, 54* (pp. 59–101), Burlington, MA: Academic Press.
- Knoblich, G., & Flach, R. (2001). Predicting the effects of actions: Interactions of perception and action. *Psychological Science, 12*, 467–472. doi:10.1111/1467-9280.00387
- Knoblich, G., & Jordan, J. S. (2003). Action coordination in groups and individuals: Learning anticipatory control. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 29*, 1006–1016. doi:10.1037/0278-7393.29.5.1006
- Konvalinka, I., Vuust, P., Roepstorff, A., & Frith, C. D. (2010). Follow you, follow me: Continuous mutual prediction and adaptation in joint tapping. *Quarterly Journal of Experimental Psychology, 63*, 2220–2230. doi:10.1080/17470218.2010.497843
- Kourtis, D., Sebanz, N., & Knoblich, G. (2010). Favouritism in the motor system: Social interaction modulates action simulation. *Biology Letters, 6*, 758–761. doi:10.1098/rsbl.2010.0478
- Oullier, O., de Guzman, G. C., Jantzen, K. J., Lagarde, J., & Kelso, J. A. S. (2008). Social coordination dynamics: Measuring human bonding. *Social Neuroscience, 3*, 178–192. doi:10.1080/17470910701563392
- Prinz, W. (1997). Perception and action planning. *European Journal of Cognitive Psychology, 9*, 129–154. doi:10.1080/713752551
- Rammani, N., & Miall, R. C. (2004). A system in the human brain for predicting the actions of others. *Nature Neuroscience, 7*, 85–90. doi:10.1038/nn1168
- Repp, B. H., & Knoblich, G. (2004). Perceiving action identity: How pianists recognize their own performances. *Psychological Science, 15*, 604–609. doi:10.1111/j.0956-7976.2004.00727.x
- Richardson, M. J., Campbell, W. L., & Schmidt, R. (2009). Movement interference during action observation as emergent coordination. *Neuroscience Letters, 449*, 117–122. doi:10.1016/j.neulet.2008.10.092
- Richardson, M. J., Marsh, K. L., & Baron, R. M. (2007). Judging and actualizing Intrapersonal and interpersonal affordances. *Journal of Experimental Psychology: Human Perception and Performance, 33*, 845–859. doi:10.1037/0096-1523.33.4.845
- Richardson, M. J., Marsh, K. L., Isenhowe, R. W., Goodman, J. R., & Schmidt, R. (2007). Rocking together: Dynamics of intentional and unintentional interpersonal coordination. *Human Movement Science, 26*, 867–891. doi:10.1016/j.humov.2007.07.002
- Rosenbaum, D. A., Meulenbroek, R. G., Vaughan, J., & Jansen, C. (2001). Posture-based motion planning: Applications to grasping. *Psychological Review, 108*, 709–734. doi:10.1037/0033-295X.108.4.709
- Schmidt, R. C., Bienvenu, M., Fitzpatrick, P. A., & Amazeen, E. G. (1998). A comparison of intra- and interpersonal interlimb coordination: Coordination breakdowns and coupling strength. *Journal of Experimental Psychology: Human Perception and Performance, 24*, 884–900. doi:10.1037/0096-1523.24.3.884
- Schmidt, R. C., Carello, C., & Turvey, M. T. (1990). Phase transitions and critical fluctuations in the visual coordination of rhythmic movements between people. *Journal of Experimental Psychology: Human Perception and Performance, 16*, 227–247. doi:10.1037/0096-1523.16.2.227
- Schmidt, R. C., & Richardson, M. J. (2008). Coordination: Neural, behavioral and social dynamics. In: A. Fuchs & V. K. Jirsa (Eds.) *Dynamics of interpersonal coordination* (pp. 281–308). Berlin / Heidelberg, Germany: Springer.
- Sebanz, N., Bekkering, H., & Knoblich, G. (2006). Joint action: Bodies and minds moving together. *Trends in Cognitive Sciences, 10*, 71–76. doi:10.1016/j.tics.2005.12.009
- Sebanz, N., Knoblich, G., & Prinz, W. (2005). How two share a task: Corepresenting stimulus–response mappings. *Journal of Experimental Psychology: Human Perception and Performance, 31*, 1234–1246. doi:10.1037/0096-1523.31.6.1234
- Song, J.-H., & Nakayama, K. (2009). Hidden cognitive states revealed in choice reaching tasks. *Trends in Cognitive Sciences, 13*, 360–366. doi:10.1016/j.tics.2009.04.009
- Spivey, M. J., Grosjean, M., & Knoblich, G. (2005). Continuous attraction toward phonological competitors. *PNAS Proceedings of the National Academy of Sciences of the United States of America, 102*, 10393–10398. doi:10.1073/pnas.0503903102
- van der Wel, R. P. R. D., Knoblich, G., & Sebanz, N. (2011). Let the force be with us: Dyads exploit haptic coupling for coordination. *Journal of Experimental Psychology: Human Perception and Performance, 37*, 1420–1431. doi:10.1037/a0022337
- Vesper, C., Butterfill, S., Knoblich, G., & Sebanz, N. (2010). A minimal architecture for joint action. *Neural Networks, 23*, 998–1003. doi:10.1016/j.neunet.2010.06.002
- Vesper, C., van der Wel, R. P. R. D., Knoblich, G., & Sebanz, N. (2011). Making oneself predictable: Reduced temporal variability facilitates joint action coordination. *Experimental Brain Research, 211*, 517–530. doi:10.1007/s00221-011-2706-z
- Welsh, T. N., & Elliott, D. (2004). Movement trajectories in the presence of a distracting stimulus: Evidence for a response activation model of selective reaching. *The Quarterly Journal of Experimental Psychology, 57*, 1031–1057.
- Wilson, M., & Knoblich, G. (2005). The case for motor involvement in perceiving conspecifics. *Psychonomic Bulletin, 131*, 460–473. doi:10.1037/0033-2909.131.3.460
- Wolpert, D. M., Doya, K., & Kawato, M. (2003). A unifying computational framework for motor control and interaction. *Philosophical Transactions of the Royal Society of London, 358*, 593–602. doi:10.1098/rstb.2002.1238
- Wolpert, D. M., & Flanagan, J. R. (2001). Motor prediction. *Current Biology, 11*, R729–R732. doi:10.1016/S0960-9822(01)00432-8
- Wolpert, D. M., & Ghahramani, Z. (2000). Computational principles of movement neuroscience. *Nature Neuroscience, 3*, 1212–1217. doi:10.1038/81497

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