

The effect of movement kinematics on predicting the timing of observed actions

Lincoln J. Colling · William F. Thompson · John Sutton

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Abstract The ability to predict the actions of other agents is vital for joint action tasks. Recent theory suggests that action prediction relies on an emulator system that permits observers to use a model of their own movement kinematics to predict the actions of other agents. If this is the case, then people should be more accurate at generating predictions about actions that are similar to their own. We tested this hypothesis in two experiments in which participants were required to predict the occurrence and timing of particular critical points in an observed action. In Experiment 1, we employed a self/other prediction paradigm in which prediction accuracy for recordings of self-generated movements was compared with prediction accuracy for recordings of other-generated movements. As expected, prediction was more accurate for recordings of self-generated actions because in this case the movement kinematics of the observer and observed stimuli are maximally similar. In Experiment 1, people were able to produce actions at their own tempo and, therefore, the results might be explained in terms of self-similarity in action production tempo rather than in terms of movement kinematics. To control for this possibility in Experiment 2, we compared prediction accuracy for stimuli that were matched in tempo but differed

only in terms of kinematics. The results showed that participants were more accurate when predicting actions with a human kinematic profile than tempo-matched stimuli that moved with non-human kinematics. Finally, in Experiment 3, we confirmed that the results of Experiment 2 cannot be explained by human-like stimuli containing a slowing down phase before the critical points. Taken together, these findings provide further support for the role of motor emulation in action prediction, and they suggest that the action prediction mechanism produces output that is available rapidly and available to drive action control suggesting that it can plausibly support joint action coordination.

Keywords Perception–action · Joint action · Embodied cognition · Action prediction

General introduction

Humans possess an astonishing ability for highly accurate temporal coordination of action. The ability to engage in temporally coordinated action is evident in pursuits such as music and dance where two or more co-actors might be required to produce actions that are temporally aligned. That humans can coordinate their actions with a high degree of temporal precision is not in doubt; what is less clear is the mechanism that underlies this ability. Coordination tasks that impose heavy demands on accurate timing of action execution require an agent to plan their actions early so that the execution of their actions can be temporally aligned with the actions of their co-actor. Therefore, it is unlikely that actions are planned based on the incoming sensory input because sensory transduction would introduce disruptive time delays. Therefore, to achieve the temporal precision that is evident in many cases of coordinated

L. J. Colling
School of Psychology, Australian Catholic University,
Brisbane, Australia

L. J. Colling (✉)
Donders Institute for Brain, Cognition and Behaviour,
Radboud University Nijmegen, Nijmegen, The Netherlands
e-mail: lincoln@colling.net.nz
URL: <http://research.colling.net.nz>

W. F. Thompson · J. Sutton
ARC Centre of Excellence in Cognition and Its Disorders,
Macquarie University, Sydney, Australia

joint action, it is necessary for actors to predict the movements of their co-actors (Sebanz and Knoblich 2009). If these predictions are available to the agent's action control system before incoming sensory information about their co-actor's actions, then they could serve as the basis for early, or anticipatory, motor planning.

Recent theoretical accounts have suggested that the motor system of an agent might play a crucial role in generating predictions about the actions of their co-actors (Colling et al. 2013; Csibra 2008; Wilson and Knoblich 2005). In particular, *mirror neurons*, originally discovered in the monkey premotor cortex, which have been shown to code for both performed and perceived actions (for a review, see Rizzolatti and Craighero 2004). This property provides a neurophysiological basis for shared representations for perception and action, as argued for by theories of common coding (Prinz 1997). Colling et al. (2013) suggest that this perception–action matching, or “mirroring”, mechanism plays a crucial role in joint action, specifically in predicting the actions of other agents. This idea follows from a model developed by Wilson and Knoblich (2005) that suggests that mirror mechanisms form part of an *emulator*—a term they borrow from Grush (1997; 2004)—that is used for predicting the actions of other agents (Wilson and Knoblich 2005). According to Grush (1997), an emulator, or forward model, is a system that replicates the input–output relations of a target system, and it can, therefore, be used to predict the behaviour of that system. Grush (1997) has suggested that emulators might be useful during action control where an emulator of the body could be used to generate predictions about the feedback that would result during the execution of specific actions. This predicted feedback could then stand in for actual feedback and be used for real-time updating of the motor plans used to drive those actions without having to wait for actual feedback from the periphery, which would arrive too late to be useful (Wolpert 1997). Wilson and Knoblich (2005), in their *emulator hypothesis* of action prediction, argue that emulators might not only be useful during intrapersonal action prediction—generating predictions of one's own actions during action control—but that they might also be used during interpersonal action prediction by replicating the input–output relations of a co-actor's action control system. That is, agents might be able to use their own model of how their body moves to predict the movements of others.

Several approaches have been used to investigate the role of the motor system in interpersonal action prediction. One approach has been to examine whether predictions are influenced by a participant's motor knowledge. This can be done by comparing the predictions generated by observers with specific motor expertise with the predictions generated by observers lacking that expertise. For example, Aglioti et al. (2008) compared expert and novice basketball players

on a task where they were required to predict whether a free throw would be successful. The general findings of these paradigms are that experts are able to generate more accurate predictions than novices (Abernethy 1990; Aglioti et al. 2008; Isaacs and Finch 1983; Sebanz and Shiffrar 2009). However, it can be difficult to infer causal relationships from these paradigms because it may be the case that elite athletes become elite athletes because they already possess superior prediction abilities rather than the superior prediction abilities arising from their motor expertise.

Another approach has been to examine whether concurrent action production interferes with action prediction. The logic of this approach is that if a common system is responsible for both action production and action prediction, then occupying the system with one task should disrupt the other task (e.g. see Springer et al. 2011). However, while these studies provide evidence for motor system involvement in action prediction, they still do not provide evidence for the emulator hypothesis of action prediction. The emulator hypothesis holds that action prediction is performed using the observers' kinematics to model the actions of the observed agent. Therefore, it might be the case that although action prediction is mediated by the motor system, it is done without the observer using their kinematic model as an emulator. One way to examine whether observers use knowledge of their own kinematics to generate predictions is to examine whether prediction accuracy is modulated by the degree of similarity between the kinematics of the observer and the observed agent.

Several studies have examined the role of kinematic information, or other motor knowledge, in self-recognition (e.g. see Jokisch et al. 2006; Repp and Knoblich 2004; Sevdalis and Keller 2010; Wöllner 2012); however, these studies have not examined the question of prediction. Therefore, Knoblich and Flach (2001) explicitly asked participants to generate predictions about recordings of their own actions and compared the accuracy of these predictions to the predictions participants generated about the actions of other people. The logic of this paradigm is that if people use their own kinematic model to generate predictions about observed actions, then their predictions will be more accurate when an observed agent moves similarly to the observer—the observer and the observed agent are maximally similar when observing recordings of self-produced action. Knoblich and Flach's (2001) task involved predicting the landing position of a dart that was thrown at a dartboard from a series of video recordings. The recordings were stopped at the point where the dart was released from the hand so that the videos contained no information about the dart's flight path. Observers were significantly better at predicting the dart landing position for their own throws compared with the throws of other people. Similar results, where participants predicted whether a pen stroke

was produced in isolation or as part of a character, have also been reported by Knoblich et al. (2002).

While the results from these self/other prediction tasks are consistent with the emulator hypothesis of action prediction, for researchers interested in mechanisms supporting joint action two related questions remain unaddressed. First, if the emulator system is to plausibly support joint action coordination, then its output must be available to drive action production; and second, the predictions must be available rapidly. Both these issues arise in paradigms where verbal report measures, or untimed decision tasks, are used. Recent work by Mann et al. (2010) highlights the problem of using such measures by showing that prediction accuracy is different depending on whether participants verbally report their predictions or act on their predictions (at least in experts, no differences were found for novices). Based on this dissociation between predictions available for action control and predictions available for verbal report, verbal report measures or choice decision tasks may not be suitable for assessing whether the emulator hypothesis provides a plausible account of the mechanisms that underlie joint action coordination (for some examples using these measures, see Graf et al. 2007; Knoblich and Flach 2001; Knoblich et al. 2002; Sparenberg et al. 2012; Springer et al. 2011; Stadler et al. 2012). Similarly, without placing temporal constraints on the responses by, for example, requiring participants to produce responses that are temporally aligned, or coordinated, with the observed actions, it is difficult to assess how rapidly output from the emulator is available.

One method that has traditionally been used to study whether participants can align their responses with an external stimulus is the sensorimotor synchronisation (SMS) task. SMS tasks often take the form of finger tapping in time with a regular beat (for a review, see Repp 2005; Repp and Su 2013). In order to achieve synchronisation in this type of task, it is necessary to form a representation of the temporal structure of the stimulus so that action production can be aligned with this temporal structure. However, it is unlikely that these types of tasks are probing into the same predictive mechanisms that underlie tasks such as predicting the landing position of a dart (Knoblich and Flach 2001), handwriting strokes (Knoblich et al. 2002), or the fate of a basketball free throw (Aglioti et al. 2008).¹ That is, rather than probing motor emulation mechanisms, these experiments may instead probe timing mechanisms and entrainment governed by the dynamics of

¹ Where tapping studies examined human pacing signals and compared them with non-human pacing signals the pacing signal have either had non-human dynamics in both conditions or the stimulus dynamics have not been reported (Hove and Keller 2010; Hove et al. 2010; Kirschner and Tomasello 2009). Therefore, these studies do not provide a test of the emulator hypothesis, which makes predictions about role of stimulus dynamics not visual form.

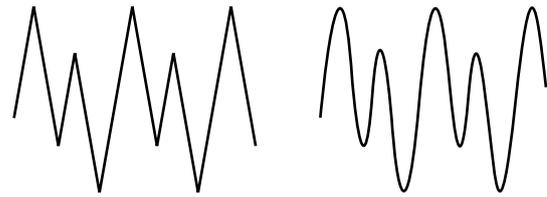


Fig. 1 The zigzag (*left*) and wave (*right*) patterns used as stimuli during the recording session

coupled oscillators found when two rhythmic units interact, such as flashing fireflies, interacting pendulums, or limbs (Large 2000; Schmidt et al. 1990, 2011). Therefore, a more suitable way to address how rapidly information from the emulator system is available to drive motor planning is simply to modify the paradigms that have been used to assess action prediction so that a time constraint is put on the responses.

To date, only one study using visual stimuli has attempted to assess how rapidly output from the emulator is available to drive action control. Flach et al. (2003) employed a self/other prediction task where, rather than providing a verbal response or performing a choice decision task, participants were asked to align a button press with a particular critical point in the observed action. To do this, participants observed a moving dot corresponding to the endpoint of a pen as it traced a zigzag or wave pattern (cf. Fig. 1) and pressed a button when the moving dot changed direction at the apex of each upstroke. These trajectories had been generated earlier by asking participants to draw patterns on a digitiser tablet. During the test session, participants were presented with trajectories that they had produced themselves as well as trajectories that had been produced by another person. Any advantage in prediction accuracy for self-produced recordings relative to other-produced recordings could be taken as evidence of an emulator mechanism. The results of this experiment were, however, not entirely consistent with the predictions of the emulator hypothesis. In particular, while some evidence of a self-prediction advantage was found, this difference only emerged in the later experimental blocks (blocks 3 and 4) with the initial experimental blocks showing no difference. Thus, if the self/other difference is taken as evidence of the emulator hypothesis, then the absence of this evidence in the initial phase of the experiment suggests that another mechanism might underlie performance on this task, at least initially. Therefore, on the basis of this finding, it is difficult to make the case that an emulator mechanism supports action coordination during joint action tasks.

A subsequent study by Keller et al. (2007) examined the same question in the auditory domain. In their study, trained pianists were asked to play duets with either recordings of themselves or another person. The results showed

superior timing accuracy when pianists played duets with themselves, as predicted by the emulator hypothesis. While this study may provide clearer evidence for the emulator hypothesis, there are two issues of concern. First, pianists are highly trained in auditory-motor synchronisation and, therefore, it is not clear how generalizable these findings are to non-experts. And, second, this experiment used auditory stimuli with relatively long running trials (between 66 s and 98 s) and, therefore, it is not clear whether the findings would be generalizable to “one-shot” encounters during visually guided joint action—for example, a football player passing a ball to a teammate.

While the results of Flach et al. (2003) are problematic for the emulator hypothesis, and many possible causes may account for their finding, one plausible reason for their problematic results may be the stimuli they used. In particular, the stimuli employed by Flach et al. (2003) provide no information about the actual action being performed. By only showing the endpoint of a pen held by the actor, the observer is left with the task of inferring the action from this limited information. This is the equivalent of, for example, inferring the movements of a basketball player when only being presented with the movements of the ball. Not only does this lack ecological validity, but also it adds task complexity because many different actions might be able to produce the same pattern of ball movements, or pen movements. This added task complexity may account for the finding in Flach et al. (2003) if it takes time to infer an action from the movements of a manipulated object; thus, only in the later experimental blocks, once the inference process is complete, will observers be able to properly engage in motor emulation. Given the concerns with the findings of Flach et al. (2003) and concerns about the generalizability of findings in Keller et al. (2007), we have sought to improve upon methodology employed by Flach et al. (2003) in an attempt to perform a better test of the emulator hypothesis. To this end, we have designed stimuli that directly depict actions thereby increasing ecological validity and bypassing any requirement to infer the actions from their effects.

In two experiments (Experiment 1 and Experiment 2), we tested the emulator hypothesis by examining whether observers are more accurate at generating predictions about actions when the kinematics of the observed action more closely match their own kinematics. In Experiment 1, we test this prediction by comparing prediction accuracy for basic human-like avatars whose movements are controlled by motion capture recordings of either self-produced or other-produced actions. In Experiment 1, participants were free to produce the actions at whatever tempo was comfortable and, as a result, inter-individual differences in the tempo of action production might be able to account for the differences in prediction accuracy. Therefore, in

Experiment 2, we held the tempo of the actions constant and varied only kinematics, so that they were either similar to the observer’s kinematics (human movements) or dissimilar to the observer’s kinematics (constant velocity movements). Finally, in Experiment 3, we rule out an alternative explanation for the data presented in Experiment 2, and we show that superior prediction accuracy for human movements cannot simply be explained by the presence of a deceleration phase in the movements before the critical points (found only in the human movements) acting as a cue.

Experiment 1

In Experiment 1, we sought to test the emulator hypothesis by modifying the paradigm of Flach et al. (2003) so that participants viewed animations of 3-D humanoid characters as stimuli. We anticipate that prediction accuracy will be enhanced when observers view 3-D characters constructed from self-generated movements compared with characters constructed from other-generated movements.

Methods

Participants

Twenty-two participants (18 females), with an average age of 24 years (18–49 years), took part in the experiment. Twenty-one participants were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield 1971). All participants had normal or corrected-to-normal vision and were free of movement difficulties. All procedures were approved by the Macquarie University Human Subjects Ethics Committee.

Motion capture

Motion data were recorded using an 8-camera 3-D passive optical motion capture system (Vicon MX+ with 4 Vicon MX-F20 and 4 Vicon MX13+ cameras) at a sampling rate of 200 Hz. A total of 11 spherical markers measuring 9 mm in diameter were placed on the shoulders, right arm, right hand, and waist of the participant (see Fig. 2). The shoulder markers were placed on the top of the left shoulder (LSHO) and right shoulder (RSHO) and on the lateral side of the right shoulder (RLSH). Right arm markers were placed on the lateral side of the right upper arm (RUPA) and on the inside (RMEL) and outside (RLEL) elbow. Right-hand markers were placed on the medial wrist (RMWR) and lateral wrist (RLWR) and at the base of the right middle finger (RFIN). Waist markers were placed between the iliac crest and the rib cage on the left (LFWT) and right (RFWT) side.

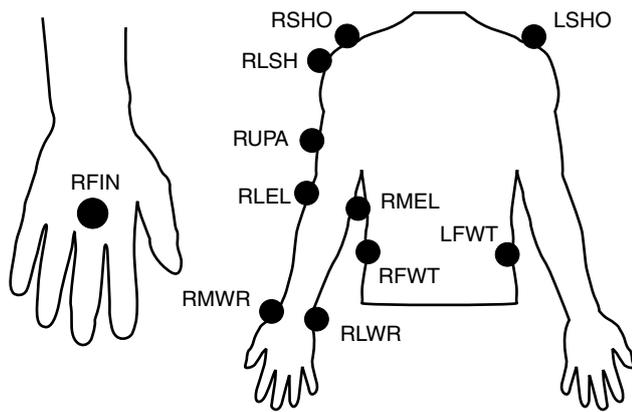


Fig. 2 Marker positions for the 11 reflective markers used during the recording session

This configuration of markers was used because it defines the joints and limb segments required to generate the mannequin. Participants were instructed to keep their left arm rested by their side to ensure that it did not obscure the left waist marker. Participants were also instructed to clench their fist to ensure that the fingers did not move independently of the rest of the hand.

Stimuli

During the recording session, participants reproduced two movement patterns (see Fig. 1). These movement patterns were chosen so that the results of the present study would be directly comparable to those of previous studies (i.e. Flach et al. 2003). Both patterns consisted of five peaks and five troughs with the peaks alternating in height. The fact that the peaks alternate in height is important because if the peaks were of equal height, then this would create an isochronous stimulus with peaks of equal temporal spacing, and participants may be able to predict the timing of the upcoming peak solely on the basis of the temporal gap between the current peak and the previous peak without any need to predict the observed actions. Such a stimulus would tap into timing mechanisms rather than prediction mechanisms.² The two patterns differed in the nature of the direction change at the apex of the peaks. The zigzag pattern had a sharp direction change while the wave pattern had a smooth, flowing, direction change. Participants viewed the patterns on large sheets of cardboard measuring 0.594 m × 0.841 m. For the zigzag pattern, the first up-stroke was 0.3 m long, with the remaining short up-strokes measuring 0.25 m and the long up-strokes measuring

² When Flach et al. (2003, Experiment 1) used an isochronous stimulus they failed to find a self/other prediction difference; therefore, we have avoided the use of isochronous stimuli.

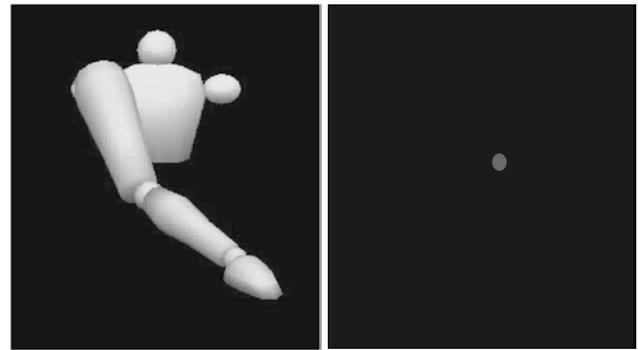


Fig. 3 Sample of the stimuli used during the test session for Experiment 1 and 2 (left) and Experiment 3 (right)

0.5 m. All the down-strokes were 0.375 m long. The angles enclosed by the strokes measured 0.35 radians. The wave pattern was based on the zigzag pattern and the stroke lengths were closely matched. The eccentricity of the curve at the apex was approximately 0.95 for all peaks.

To create the stimuli for the test session, raw motion capture data were first resampled to 25 Hz. Animated characters were constructed with C-Motion Visual 3D (C-Motion INC, Rockville, MD) using the resampled motion data. The characters consisted of an upper torso and right arm and hand. The torso was constructed using the shoulder markers (RSHO and LSHO) and waist markers (RFWT and LFWT). The upper arm was constructed using the shoulder markers and elbow markers (RMEL and RLEL), and the right lower arm was constructed using the elbow and wrist markers (RMWR and RLWR). The hand was constructed using the wrist markers as the proximal endpoint and the right finger marker (RFIN) as the mid-point. The size of the torso was not accurately modelled for each participant; however, the limb lengths were modelled using measurements acquired from the captured marker positions. Thus, limb lengths appeared relatively longer for animations constructed from taller participants and shorter for animations constructed from shorter participants. All animated characters were presented from a frontal view so that the action appeared as if viewed from the front (Fig. 3 left).

Procedure

The experiment was split over two sessions separated by approximately 2–6 weeks ($M = 18$ days, $SD = 7$). The delay was introduced in an attempt to reduce any effects that might result from participants recalling how they performed the actions. During the recording session, participants sat on a chair in the middle of the capture volume. At the start of each trial, they were shown the appropriate pattern (using the stimulus card held at their arm's length; see Stimuli) and they were told to produce either a wave or a zigzag. To

generate the movements, participants were asked to pretend that they were drawing the patterns on a large blackboard with their right hand. (Participants were not given constraints on how to produce this movement by, for example, being told that they had to keep their elbow straight or that they could only move their shoulder—although they may have chosen to do this if that is how they would naturally produce the movement). This resulted in participants making a series of up-and-down arm movements. Participants practised each pattern once with their eyes open and then reproduced each pattern 15 times with their eyes closed to limit visual familiarity with the movement. The movements were produced in three blocks containing five repetitions of each pattern in a randomized order. Participants reproduced the patterns at their own pace.

In the test session, participants observed a series of animated 3-D characters (see Fig. 3, left). Animations were used to control for the possible effects of overt recognition cues, while mannequins were chosen instead of point-light displays because point-light displays generated from motion capture do not preserve occlusion. The movement of the characters was controlled by the motion capture data recorded during the recording session; however, participants were not informed that this was the case. To ensure that stimulus factors did not influence prediction accuracy, participants were grouped into pairs (by randomly selecting two available participants), and each participant in the pair observed a series of animated characters controlled by their own movement data as well as a series of animated characters controlled by the movement data of the other person in the pair. Both participants in the pair viewed the same set of stimuli in identical order. The task in the test session was to press the response button when the hand of the mannequin reached the peak of each upward movement. Participants were instructed to press the button *at the exact time* that the hand of the mannequin reached the peak of each upward movement, and they were told that this may require them to anticipate when the peaks will occur. Before continuing, participants confirmed that they had understood the instructions, and they were given the opportunity to ask for clarification. Each participant performed four blocks containing 40 unique stimuli (20 trials of self-generated movements and 20 trials of other-generated movements). The stimuli were presented in a pseudo-random order so that self-generated movements and other-generated movements were evenly distributed through the block.

Data analysis

The peak of each upward movement was determined using the raw motion capture data. Absolute timing error was used as a measure of prediction accuracy and was calculated as the absolute difference between the timing of the peak in the motion capture data (the critical points) and the

timing of the button press. Absolute timing error was used because it provides a good proxy for accuracy of hitting a target (Spray 1986). Button presses with a timing error that was greater than 600 ms were excluded from analysis. This was done to ensure that participants were anticipating the peak rather than merely responding to the peak once it had appeared on screen. A relatively long cut-off was used to ensure that only rare extreme values were rejected while ensuring that the maximum number of values were included. Data analysis was performed on absolute timing error using a 2×4 repeated measures ANOVA with the factors Authorship (self and other) and Block (1, 2, 3, and 4). The Greenhouse–Geisser procedure was used to correct for violations of sphericity, where appropriate (we report uncorrected *dfs* along with the ε value).

Results and discussion

The movement leading up to the first peak was often contaminated with motion capture artefacts such as missing samples and, therefore, the first peak was dropped from analysis. Additionally, less than 1 % of button presses were dropped from analysis because their timing error exceeded 600 ms. We found a significant main effect of Authorship ($F_{1,21} = 6.290$, $p = .020$, $\eta_p^2 = .230$), indicating that timing error was significantly lower when generating predictions about recordings of self-generated actions ($M = 110.8$ ms, $SD = 28.15$) compared with other-generated actions ($M = 125.67$ ms, $SD = 33.68$; $M_\Delta = 14.87$, 95 % CI [2.54] [27.20]). This pattern of data held for 10 of the 11 participant pairs. The main effect for Block ($F_{3,63} = 0.645$, $p = .509$, $\varepsilon = .577$, $\eta_p^2 = .030$) and the Block \times Authorship interaction did not reach significance ($F_{3,63} = 0.727$, $p = .488$, $\varepsilon = .659$, $\eta_p^2 = .033$), indicating that both timing error and the effect of action authorship did not vary systematically across the four experimental blocks. These data are shown in Fig. 4a.

Consistent with the emulator hypothesis, predictions were more accurate when participants viewed recordings of self-generated actions compared with recordings of other-generated actions. This is consistent with the idea that observers use their own motor dynamics as the basis for action prediction. Importantly, unlike previous studies (Flach et al. 2003), we found no evidence that the self-prediction advantage took time to emerge. Rather, our results show a self-prediction advantage evident from the first experimental block and the size of this advantage remained consistent in size throughout the task. This finding suggests that the output from the emulator system is available to action control rapidly enough to provide a plausible basis for joint action coordination.

Because we did not control for differences in limb length between participants, we examined the relationship

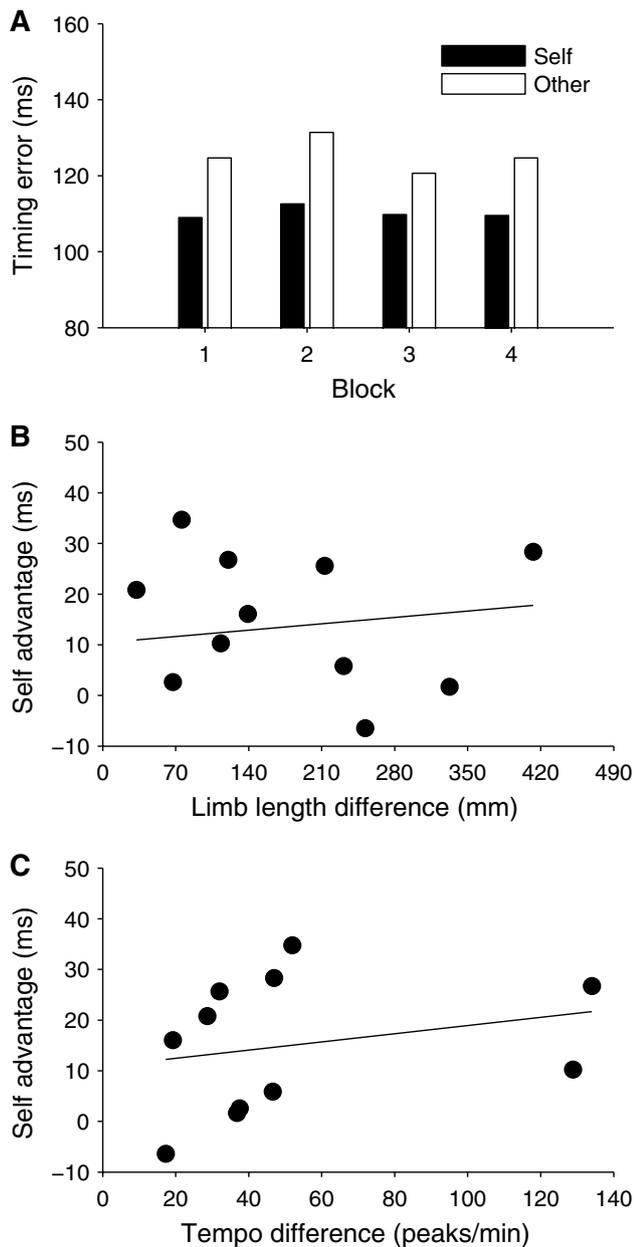


Fig. 4 Mean timing error for self-generated and other-generated actions (a), the relationship between the size of the self-prediction advantage and limb length difference (b), and the relationship between the size of the self-prediction advantage and tempo difference (c)

between differences in limb length and the size of the self-prediction advantage. The results of this analysis showed that there was no reliable relationship between difference in limb length and the size of the self-prediction advantage ($r = -0.161$, $p = 0.637$), suggesting that mere physical dissimilarity cannot explain the self-prediction advantage. These data are displayed in Fig. 4b.

While the results of Experiment 1 provide support for the emulator hypothesis by showing that prediction accuracy

is modulated by the match between the kinematics of the observed agent and the observers, it should be noted that there is another factor that may be influencing this result. It may be that, rather than using the kinematics of the observed actions as the basis for their prediction, participants may have simply used the temporal spacing between the critical points in the stimulus to predict the timing of subsequent points (as is done in an SMS task) and what appears as a prediction advantage for self-produced actions is a result of the critical points being spaced at intervals that the participant finds comfortable for producing button presses. Several studies (for a review, see Fraisse 1982) have suggested that people do indeed have a preferred tempo for spontaneous rhythmic movements and, therefore, if participants' preferred tempo for producing arm movements coincided with their preferred tempo for producing button presses, then this may account for the greater degree of temporal alignment between the produced and observed actions.

We attempted to rule out this possibility by examining the relationship between the size of the self-prediction advantage and the similarity between arm movement tempos for the two participants in the pair. Tempo similarity was measured as the absolute difference in the temporal spacing of the critical points (measured in peaks per minute) between the two participants in the pair. No reliable relationship was found between the size of the self-prediction advantage and tempo similarity ($r = 0.247$, $p = 0.465$).³ These data are shown in Fig. 4c. If these results could be explained by a coincidence of preferred tempo, then we would expect to find that the self-prediction advantage increased as the difference in arm movement tempo increased. Although these data suggest that similarity in action production tempo cannot adequately explain the self-prediction advantage without a design that controls for stimulus tempo, it is not possible to explicitly rule this out. Therefore, Experiment 2 was conducted for this purpose.

Experiment 2

The aim of Experiment 2 was to examine the effect of movement kinematics on action prediction while holding all other factors, including the temporal spacing between the critical points, constant between conditions. To do this, we created two sets of stimuli that were matched in terms of tempo and differed only in terms of kinematics. In order to create the stimuli, we employed the same procedure described in Experiment 1. A group of participants, who only took part in the movement task, were asked to perform a series

³ In addition, we calculated the Spearman's rank correlation coefficient, as this is less sensitive to outliers, and the same result was obtained ($r_s = 0.491$, $p = 0.129$).

of up-and-down arm movements tracing out the shape of a zigzag or wave while motion capture data were recorded. The recorded data was duplicated to create two sets, and for one set, the dynamics of the movement between the critical points were altered. The recorded trajectories were modified so that rather than the movements exhibiting a typical natural velocity profile—for example, as described by the two-thirds power law (Viviani and Stucchi 1992) or minimum jerk model (Flash and Hogan 1985)—the movements exhibited a constant velocity profile.

Directly altering the trajectories is preferable to the alternative of using an external pacing signal for two reasons: First, because the peaks are not equally spaced (due to the alternating peak heights) it would not be possible to use an isochronous pacing signal, and the use of a poly-rhythmic pacing signal is problematic because learning to produce actions in time with a polyrhythm may require extensive training (see also, footnote 2 on the problems of using isochronous stimuli). Second, placing constraints on how people produce an action can destroy inter-individual kinematic variability (Knoblich et al. 2002). If inter-individual kinematic variability is reduced along with timing variability, then there would be no sources of inter-stimulus variability to drive the self-prediction advantage. However, by directly modifying the movement kinematics, we are able to isolate a single parameter while holding all other parameters constant. If the self-prediction advantage is due to a better match between the movement kinematics of the observer and the observed action, then we should similarly find a prediction advantage for natural velocity stimuli over constant velocity stimuli because they more closely resemble the movement kinematics of the observer. If, however, observers only use the temporal spacing of the critical points as a cue, and enhanced prediction is a result of a similarity between the temporal spacing of the critical points and the participants preferred tempo for producing button presses, then we should expect to find no difference in prediction accuracy for the two sets of stimuli, because the temporal spacing of the two stimulus sets is identical.

Methods

Participants

Eighteen undergraduate psychology students (14 females) volunteered for the experiment. All were right-handed ($M = 1.67$; 1.11–2). The participants had an average age of 24 years (18–46 years).

Stimuli

To create the stimuli for the test session, five individuals performed the movement task while their movements were

recorded using motion capture. Four movements per individual (two of each pattern) were selected for the final stimuli. All of the participants used for the stimulus creation were female and right-handed ($M = 1.9$; 1.6–2). They had an average age of 24.8 years (21–31 years) and were free from movement difficulties. To create the natural velocity stimuli, we employed the same procedure described in Experiment 1. For the constant velocity stimuli, an additional step was added to create modified trajectories. Modified trajectories were created by using linear interpolation between the points of zero velocity in each of the three spatial dimensions in the trajectories recorded for each marker.

Procedure

The procedures for data analysis were identical to those described in Experiment 1.

Results

All five peaks were analysed and less than 1 % of button presses were eliminated for having a timing error greater than 600 ms. The results showed a significant main effect of Block ($F_{3,51} = 6.125$, $p = .009$, $\varepsilon = .549$, $\eta_p^2 = .272$), suggesting that overall timing error decreased as the experiment progressed. In addition, there was a significant main effect of Velocity Profile ($F_{1,17} = 107.850$, $p < .001$, $\eta_p^2 = .978$), suggesting that timing error for the constant velocity stimuli ($M = 169.81$ ms, $SD = 47.76$) was significantly higher than the timing error for the natural velocity stimuli ($M = 128.52$ ms, $SD = 40.51$; $M_{\Delta} = 41.28$, 95 % CI [32.89][49.67]). Finally, the Velocity Profile \times Block interaction was significant ($F_{3,51} = 3.267$, $p = .029$, $\eta_p^2 = .161$), suggesting that the effect of Velocity Profile decreased as the experiment progressed (see Fig. 5a).

Taken together, these data demonstrate that prediction accuracy is not equal for stimuli with equal tempo. Rather, they suggest that the kinematics of the observed movement (characterised by velocity profile) is the primary determinant of prediction accuracy. This finding is consistent with the emulator hypothesis of action prediction because the natural velocity stimuli more closely match the observer's kinematics. There is, however, an alternative explanation for these data. Rather than the kinematics of the observed action being an important cue for predicting the timing of the critical points, the mere presence of a deceleration phase before the occurrence of a critical point,⁴ as is found in the natural velocity stimuli, might explain the enhanced prediction accuracy for these

⁴ This deceleration occurs because human movements conform to the minimum jerk model (Flash and Hogan 1985).

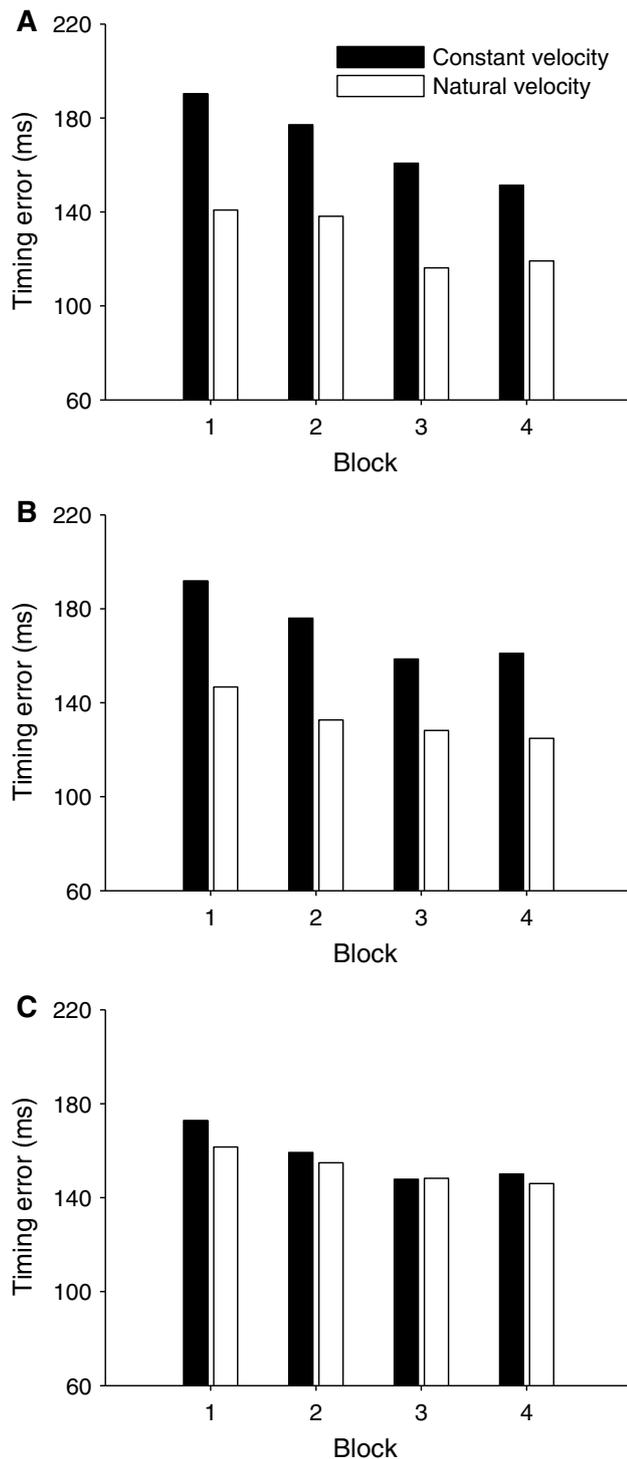


Fig. 5 Absolute timing error for natural velocity stimuli and constant velocity stimuli for each of the four experimental blocks for Experiment 2 (a), Experiment 3a (b), and Experiment 3b (c)

stimuli. Therefore, Experiment 3a and 3b was designed to test whether deceleration before the critical points is sufficient to explain the difference in prediction accuracy between the natural and constant velocity stimuli.

Experiment 3a and 3b

The aim of Experiment 3a and 3b was to address the question of whether the mere presence of a deceleration phase can act as a reliable predictor for the timing of the critical points. That is, Experiment 3a and 3b was designed to test whether the presence of a deceleration phase can account for the difference in prediction accuracy between the constant velocity stimuli and the natural velocity stimuli observed in Experiment 2.

If the results of Experiment 2 can be trivially explained by the mere presence of a deceleration cue, then we should expect to find a prediction advantage whenever this cue is present. However, if this cue is not sufficient to explain the difference observed in Experiment 2, then it may be possible to modulate prediction accuracy while leaving the presence or absence of this cue unchanged. One idea for a parameter that may modulate prediction accuracy is suggested by the emulator hypothesis. According to the emulator hypothesis, prediction of observed action relies on observers using a model of their own kinematics to model the kinematics of the observed action. However, before the model can be used to generate predictions about the observed action, the observer must map the observed action onto their own action system in a manner that makes it possible to adequately replicate the dynamics of the stimulus. That is, the observer must internally replicate the action so that it is appropriately matched with what is observed. When observing actions performed by other people, the observer's internal model of the observed action may not be adequately matched to the observed action in the first instance; however, if the same action is viewed multiple times, then the observer may be able to make adjustments to their internal model so that it better replicates the observed action. Prediction errors may be fed back into the emulator system so that the system can select the best model which produces the smallest errors. Selecting the correct model would take time and, therefore, it may be possible to exploit this to test between the two alternative explanations for Experiment 2: an account, which suggests that the difference in prediction accuracy is merely due to the natural velocity stimuli containing a deceleration phase prior to the critical points; and an account consistent with the emulator hypothesis.

To adjudicate between these accounts, we altered the amount of variability in the stimulus sets. The two explanations predict different patterns of results for this manipulation. The trivial account predicts that this manipulation will make no difference as the presence or absence of the critical cue is not changed. However, the account consistent with the emulator hypothesis would predict that this manipulation will reduce any prediction advantage for the natural velocity stimuli because increasing inter-stimulus

variability means that more time is needed to select the appropriate internal model that can account for the dynamics of the stimuli. This would reduce the effectiveness of the prediction process and this should, in turn, disrupt the observer's ability to accurately predict the natural velocity stimuli.

Following this logic, we designed two further experiments where we changed the amount of variability in the stimulus set. Experiment 3a contained a low level of variability (the same amount as Experiment 2), while the variability was increased for Experiment 3b. Additionally, changes were made to the stimuli so that they were composed of only a single moving point. This was done to isolate the effect of the deceleration cues in the stimulus (our parameter of interest) while removing any other factors that may influence prediction accuracy. Similarly, we were only interested in stimulus-related effects so we removed the movement task that preceded the observation task in Experiment 1 and 2, because movement experience has been shown to influence action prediction.⁵ Note that these changes were made because this creates the minimum necessary design to test the hypothesis that the presence or absence of a deceleration phase in the stimulus is sufficient to explain the difference observed in Experiment 2. Because of the changes made to the paradigm, Experiment 3a was used to determine whether the findings of Experiment 2 could be replicated with the modified paradigm.

Method

Participants

For Experiment 3a, a total of 15 participants (12 females) volunteered to take part. All were right-handed ($M = 1.5$; 0.4–2), and they had an average age of 20.18 years (19–23 years). For Experiment 3b, 23 participants (18 females) volunteered to take part. All were right-handed ($M = 1.7$; 0.6–2), and they had an average age of 21.49 years (19–28 years).

Stimuli

The movements used to create the stimuli for Experiment 3a were identical to those used in Experiment 2. However, rather than using animated mannequins, the stimuli consisted of a single moving point-light (see Fig. 3, right) that tracked the movement of the right-hand marker (RFIN). For Experiment 3b, the same procedure was used to create the single moving point-light, but instead of using movements from five different individuals, we used movements from 20 different individuals to increase stimulus variability. As only

one movement from each person was used in Experiment 3b, only exemplars of the wave movements were selected. Constant velocity stimuli were also created using the procedure described in Experiment 2. The 20 individuals (15 female) used for stimulus creation had an average age of 25.35 years (19–50 years), and 19 were right-handed ($M = 1.2$; –1.2–2).

Results

Experiment 3a

The results showed a significant main effect for Velocity Profile ($F_{1,14} = 57.934$, $p < .001$, $\eta_p^2 = .805$), suggesting that overall timing error for constant velocity stimuli ($M = 171.83$ ms, $SD = 23.98$) was significantly higher than timing error for the natural velocity stimuli ($M = 133.09$ ms, $SD = 21.64$; $M_{\Delta} = 38.74$, 95 % CI [27.82][49.66]). Additionally, a significant main effect of Block ($F_{3,42} = 7.670$, $p = .007$, $\varepsilon = .454$, $\eta_p^2 = .354$) was found, suggesting that overall timing error decreased over the course of the experiment. Finally, the Block \times Velocity Profile interaction ($F_{3,42} = 3.968$, $p = .014$, $\eta_p^2 = .221$) was also significant, suggesting that the effect of Velocity Profile was not consistent throughout the experiment, and instead decreased as the experiment progressed (see Fig. 5b). As Experiment 3b only used wave stimuli, we repeated the analysis selecting only exemplars of the wave pattern. This did not change the pattern of results.

Experiment 3b

The analysis revealed a significant main effect of Block, suggesting that overall timing error decreased as the experiment progressed ($F_{3,66} = 5.536$, $p = .010$, $\varepsilon = .580$, $\eta_p^2 = .201$). However, neither the main effect for Velocity Profile ($F_{1,22} = 1.296$, $p = .267$, $\eta_p^2 = .056$) nor the Block \times Velocity Profile interaction ($F_{3,66} = 2.242$, $p = .092$, $\eta_p^2 = .092$) were significant. This suggests that there was no difference in prediction accuracy between the constant velocity stimuli ($M = 157.42$ ms, $SD = 32.41$) and the natural velocity stimuli ($M = 152.39$ ms, $SD = 41.16$; $M_{\Delta} = 5.03$ 95 % CI [–4.13][14.19]). These data are displayed in Fig. 5c. Furthermore, a direct comparison of the size of the prediction advantage for the natural velocity stimuli showed that this advantage was significantly greater in Experiment 3a ($M = 38.739$ ms, $SD = 19.712$) compared with Experiment 3b ($M = 5.028$ ms, $SD = 21.179$; $M_{\Delta} = 33.71$, 95 % CI [19.83][47.59]; $t_{36} = 4.926$, $p < .001$).

Discussion

The primary aim of Experiment 3a and 3b was to determine whether the mere presence of a deceleration phase in the

⁵ Subsequent testing revealed that the addition of a movement task did not alter the pattern of data.

stimulus before the critical points is sufficient to explain the difference observed in Experiment 2. The results of Experiment 2 suggest that tempo alone does not determine synchronisation accuracy. Rather, prediction accuracy is determined, in part, by the dynamic properties of the stimulus. While this finding is consistent with the emulator hypothesis, the results are also consistent with participants merely responding to the deceleration that occurs before the critical points. Experiment 3a and 3b was designed to test the plausibility of this alternative explanation.

The results of Experiment 3b show that deceleration is not sufficient to explain the results of Experiment 2. While participants were still able to more accurately predict the timing of the critical points in the natural velocity stimuli when there was little inter-stimulus variability (Experiment 3a), increasing the variability (Experiment 3b) resulted in the natural velocity stimuli being no more predictable than the constant velocity stimuli. This suggests that the results of Experiment 2 cannot be explained by participants merely responding to the presence of deceleration in the stimuli.

General discussion

The primary aim of the present set of experiments was to investigate the mechanisms that underlie interpersonal action prediction. In particular, our aim was to investigate whether people are able to use knowledge of their own movement kinematics to generate predictions about the actions of other agents. Importantly, our aim was also to investigate whether this mechanism allows people to predict the timing of observed actions and to plan and execute actions on the basis of these predictions. Previous studies of action prediction have either relied on paradigms where participants generate predictions about the nature of action outcomes—for example, whether a free throw would be successful or not (for examples, see Aglioti et al. 2008; Knoblich and Flach 2001; Sebanz and Shiffrar 2009)—or perform choice decision tasks—for example, deciding whether a test pose is a continuation of a previously observed action (e.g. see Graf et al. 2007; Knoblich et al. 2002; Springer et al. 2011). Therefore, these paradigms have been unable to test whether the mechanisms that support performance on these tasks can also plausibly underlie joint action coordination in temporally constrained situations because they do not test whether people can predict when actions will occur (or when particular features in an action will occur) or whether people can generate actions on the basis of these predictions. Furthermore, one previous study that has directly addressed these questions within the visual domain has produced results that are not entirely consistent with the hypothesis that people use their own kinematics as the basis for generating predictions about

observed actions (Flach et al. 2003). Our study sought to improve on the methodology of this previous work, and in two experiments, we tested the hypothesis that observers use kinematic knowledge embodied in their action systems in order to generate predictions about the movement of observed agents. In Experiment 1, we found that observers are more accurate at generating predictions about observed actions when the actions are performed in the same way that the observers would themselves perform them—that is, when observing recordings of their own actions. This finding is consistent with the hypothesis that observers use their own kinematic knowledge to generate predictions about observed actions because a better match between the observed kinematics and the observer's kinematics results superior prediction accuracy. In Experiment 1, we did not control the tempo of action production; therefore, in Experiment 2, we held stimulus tempo constant across conditions, and we again found that predictions were more accurate when observers viewed actions that were kinematically similar to their own (natural velocity stimuli) relative to kinematically dissimilar actions (constant velocity stimuli). Finally, in Experiment 3a and 3b, we ruled out an alternative explanation for the results of Experiment 2, that superior prediction accuracy for natural velocity stimuli is a result of the movement slowing down before the critical points, and we confirmed that the presence of slowing down alone is not sufficient to explain the difference observed in Experiment 2.

The only other attempt to examine whether people use knowledge of their own kinematics to generate predictions about observed actions have produced results that are not entirely consistent with this hypothesis. In particular, Flach et al. (2003) found no difference in prediction accuracy for self-generated and other-generated actions during the first two blocks of their experiment. A prediction advantage for self-generated actions is taken as evidence that observers use their knowledge of their own kinematics to generate predictions, because a better match between the observed kinematics and the observer's kinematics should result in superior prediction accuracy. Therefore, the results of Flach et al. (2003) provide no evidence for this hypothesis during the initial stages of the experiment and instead suggest that a different mechanism is initially used to generate predictions. In the present study, however, there was no systematic change in the size of the self-prediction advantage across the four experimental blocks. The most salient difference between Flach et al. (2003) and the present study is that Flach et al. (2003) did not present participants with actual human movement. The pen traces used as stimuli in their study were representations of the results or consequences of human movement. The present study, however, presented participants with actual limb movements by using 3-D animated characters composed of a torso

and right arm. Stimuli of this type are isomorphic with the observer and, therefore, may be more easily mapped onto the observer's body. Before the emulator system can be used for action prediction, the emulator needs information about which effectors to model and providing this information in the stimulus may facilitate building an appropriate model. When only using pen traces, the observer might first have to attempt to infer the action behind the effect before the action can be modelled, and this added task complexity may account for the difference in results between our study and Flach et al. (2003).

In Experiment 2, we again sought to investigate whether people use knowledge of their own movement kinematics to generate predictions about observed actions. However, in Experiment 2, we sought to control for the effect of stimulus tempo. In Experiment 1, we placed no restrictions on the rate at which participants produced their actions during the action production phase of the experiment. Therefore, it is possible that rather than being a result using knowledge of their own kinematics, the self-prediction advantage might result only from the temporal properties of the stimulus. That is, the self-prediction advantage might result from a coincidence of preferred tempo for action production in the movement and prediction phases of the experiment. It has been found that people have a preferred tempo for producing rhythmic actions (Fraisse 1982) and, therefore, participants may find it easier to produce button presses that align with the critical points in the stimulus if their preferred tempo for producing button presses is similar to the tempo of the observed action. If people have a similar preferred tempo for producing the arm movements in the movement phase and button presses in the test phase, then this could manifest as a self-prediction advantage. By holding stimulus tempo constant across conditions in Experiment 2, we were able to control for this possibility.

As with Experiment 1, the aim of Experiment 2 was to examine whether kinematic similarity between the observer and the observed agent leads to superior prediction accuracy; however, unlike Experiment 1, we held stimulus tempo constant across the kinematically similar and kinematically dissimilar conditions. To do this, we compared prediction accuracy for two sets of stimuli that were matched for tempo and differed only in terms of the kinematic properties. The kinematically similar stimuli were recordings of human movements with unaltered velocity profiles while the kinematically dissimilar stimuli were created by altering the velocity profiles of the movements so that they no longer obeyed the laws that govern human action production and instead exhibited a constant velocity profile. If tempo is a primary determinant of prediction accuracy, rather than the degree of kinematic similarity between the observer and observed agent, then we should expect to find no difference in prediction accuracy

for tempo-matched stimuli. The results show that this is not the case. Instead, predictions were more accurate for the stimuli with human kinematic properties—that is, kinematically more similar to the observer, as would be expected if observers use knowledge of their own kinematics to generate predictions about observed actions.

While the results of Experiment 2 are consistent with the emulator hypothesis of action prediction, it could be argued that the results are trivial and that the difference between conditions is a consequence of participants merely starting the process of response execution when they observed the stimulus begin to slow before the critical points. To rule out this explanation, Experiment 3a and 3b examined whether the mere presence of deceleration before the critical points, which occurs only in stimuli with a natural velocity profile, was sufficient for enhanced prediction accuracy.

The results of Experiment 3a and 3b suggest that prediction accuracy is only better for natural velocity stimuli when stimulus variability is low (Experiment 3a). When stimulus variability is increased (Experiment 3b), prediction of natural velocity stimuli is no more accurate than prediction of constant velocity stimuli. This suggests that the mere presence or absence of a deceleration phase in the stimuli used in Experiment 2 is not sufficient to explain the difference in prediction accuracy between conditions. That is, the trivial explanation for the results of Experiment 2 can be ruled out on the basis of Experiment 3a and 3b suggesting that the emulator hypothesis of action prediction provides a more plausible account of the results of Experiment 2.

However, it should be noted that our failure to find a difference in prediction accuracy between stimuli that do and do not have a deceleration cue in the high variability experiment (Experiment 3b) does not rule out the importance of the deceleration cue as a primary driver of the self-prediction advantage reported in Experiment 1. Indeed, it may be that action emulation allows observers to use their kinematic knowledge to predict the timing of the critical point from the timing of the deceleration, because these two features will be related in a systematic way, that is determined by the observed kinematic properties that are modelled by the emulator. Therefore, our results suggest that before deceleration can be used as a cue, participants need an opportunity to select the correct internal model for the observed action, which can accurately replicate the dynamics of the stimulus, and accurately relate the deceleration to the timing of the critical points. In Experiment 3a and 3b, all participants viewed actions performed by other people and, therefore, selecting the correct internal model would need to be achieved through repeated exposure to the stimulus over the course of the experiment. When examining the self/other prediction difference, there is an additional source of information that participants have access to that

can help them select the correct internal model—they have access to their own action dynamics that already provide a good match for the stimulus without the need for fine tuning. Therefore, it may be the difference in this source of information that drives the self-prediction advantage.

Taken together, the results of the present study provide further support for the role of motor emulation in action prediction and joint action. Consistent with the hypothesis that observers use a model of their own kinematics to generate predictions about observed actions, the results of Experiment 1 demonstrate that observers are more accurate at generating predictions about recordings of their own actions. Furthermore, the results of Experiment 1 suggest that information generated by motor emulation is available rapidly, and available to drive action production, thereby suggesting that motor emulation could plausibly support temporally constrained joint action. The results of Experiment 2 also provided support for this hypothesis by showing that prediction accuracy is modulated by the degree of similarity between the kinematics of the observer and the observed action even when the tempo of the observed actions is held constant across conditions. Therefore, the results of Experiment 2 also ruled out an alternative explanation for the results of Experiment 1, that superior prediction accuracy for recordings of self-generated actions is due to a coincidence of action production tempo during the test phase and stimulus tempo. Finally, the results of Experiment 3a and 3b ruled out an alternative explanation for the results of Experiment 2, that participants merely responded to the deceleration cues present in the natural velocity stimuli (kinematically similar condition). The results show that the difference in the presence of deceleration cues between conditions is not sufficient to explain the difference in prediction accuracy between conditions.

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