Mechanisms for action prediction operate differently in observers with motor experience

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Abstract

Recent theoretical and empirical work has suggested an important role for the motor system in generating predictions about the timing of external events. We tested the hypothesis that motor experience with an observed action changes how observers generated predictions about these actions by comparing the performance of naïve and experienced observers on a task that required participants to predict the timing of particular critical points in a ongoing observed action. Crucially, we employed action and non-action stimuli with identical temporal dynamics, and we predicted that motor experience would enhance prediction accuracy specifically for actions and would have a reduced or negligible effect on enhancing prediction accuracy for non-action stimuli. Our results showed that motor experience did modulate prediction accuracy for action stimuli relative to non-action stimuli. No difference between conditions was observed for the naïve observers.

Keywords: action prediction, perception–action

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Introduction

Many types of joint action require two actors to coordinate their actions in time. For example, in joint actions such as ensemble music and dance performance, successful completion of the joint action might require the actions of two people to be precisely temporally aligned, or synchronised. If people were to observe and then react to the actions of their co-actors this would introduce disruptive delays. Instead, individuals must anticipate the actions of their co-actors so that they can plan actions early. Consequently, researchers have emphasised the role of prediction in recent theoretical accounts of joint action coordination (Colling & Williamson, 2014; Csibra, 2008; Wilson & Knoblich, 2005; Knoblich, Butterfill, & Sebanz, 2011; Colling, Knoblich, & Sebanz, 2013). Furthermore, as many cases of joint action, such as music, dance, or sport performance, also involve cases of *expert* performance, researchers have also turned their attention to how these predictive processes might be modulated by motor experience (e.g., Sebanz & Shiffrar, 2009; Aglioti, Cesari, Romani, & Urgesi, 2008). It is the influence of motor experience on action prediction that is the primary concern of the present study.

Neural mechanisms for action observation and prediction

There is a rich literature examining the influence of motor experience on neural networks that are preferentially activated during action observation (for seminal examples, see Calvo-Merino, Glaser, Grézes, Passingham, & Haggard, 2005; Calvo-Merino, Grézes, Glaser, Passingham, & Haggard, 2006; Cross, Hamilton, & Grafton, 2006). The initial work on this action observation network began with the discovery of *mirror neurons* in premotor regions of the monkey brain. Mirror neurons are active when the monkey performs an action and also when the monkey observes the same, or a similar, action performed by another (Rizzolatti, Fadiga, Gallese, and Fogassi, 1996; Gallese, Fadiga, Fogassi, and Rizzolatti, 1996; and for a recent review see Giese and Rizzolatti, 2015). The literature on mirror neurons, or more precisely, the *mirror system*, provide a rich trove of data linking various manipulations to changes in the pattern of activity in these neural systems. The seminal work of Calvo-Merino and colleagues (e.g., Calvo-Merino et al., 2005; Calvo-Merino et al., 2006) and Cross and

colleagues (e.g., Cross et al., 2006) are particularly relevant to the present study. To take just

one example, Calvo-Merino et al. (2006) examined activity in the action observation network

when dancers viewed dance moves that they either had experience performing themselves or

dance moves that they did not have experience performing. This was done by showing male

and female expert ballet dancers examples of dance moves that were either specific to their

gender (and thus were part of their repertoire), specific to the opposite gender (which they

would be visually familiar with but have no experience performing), or gender common. The

results showed that neural regions that responded to observed actions were sensitive to motor

familiarity, being more responsive to dance moves that fell within the observer's repertoire.

While this work provides important insights into how responses in the mirror system can be

changed by the observers' motor experience they don't provide much information about the

functional consequences of these changes.

Many theories about the functional role of the mirror system have focused on how the

mirror system might play a role in action recognition or action understanding (e.g., Sartori &

Betti, 2015; Giese & Rizzolatti, 2015). Other accounts, however, suggest that this system

might also, or even primarily, be involved in generating predictions about ongoing observed

actions (e.g., Wilson and Knoblich, 2005; Csibra, 2008; Colling et al., 2013; and see Kilner,

Friston, and Frith, 2007, for an account of the role of the mirror system in action prediction in

the context of action understanding). Accounts linking the mirror system to action prediction

have relied on the fact that the mirror system is partially co-extensive with the action control

system and, therefore, observed actions might be processed by some of the same neural

machinery involved in planning and executing actions. This link to planning and executing

actions is important, because work on computational models of action control highlight a

fundamental role for *prediction* in action control (Wolpert, 1997).

Computational models of action control

Concepts borrowed from control theory have been particularly useful for understanding

how prediction, during both action observation and action control, might be achieved (for an

introduction to control theory, see Golnaraghi, 2010). Specifically, *inverse models* and

forward models have proven theoretically useful. Inverse models perform an *inverse mapping*

58 from an output or goal state to the sequence of control commands necessary to produce that

59 output. And forward models perform a *forward mapping* from the control commands to the

60 output. That is, they model the dynamics of the system being controlled.

61 Inverse and forward models—together known as *internal models*—have a central role in

62 theoretical accounts of action control (for example, see Wolpert, Miall, & Kawato, 1998).

63 Inverse models act as controllers that transform a desired limb trajectory into the motor

64 commands that would produce that trajectory. And forward models replicate the dynamics of

65 the limb and can, therefore, be used to predict how the limb will respond to motor commands

66 (Wolpert & Kawato, 1998). Running the forward model *offline*—that is, without producing

67 any actual motor output—can be used to internally simulate limb movements. Grush (1997;

68 2004) refers to this process as *emulation* and to the forward model as an *emulator*.

Predicting observed actions

70 Grush's (1997; 2004) ideas about emulation have been developed into an account of

71 action prediction that has been termed the *emulator theory of action prediction* (Colling &

72 Williamson, 2014; Colling, Thompson, & Sutton, 2014). While many slightly varying

73 formulations exist (see also Colling et al., 2013; Csibra, 2008; Keller, 2012; Wilson &

74 Knoblich, 2005; Wolpert, Doya, & Kawato, 2003; Vesper, Butterfill, Knoblich, & Sebanz,

75 2010), the basic idea is that prediction of observed actions relies on the same internal

76 mechanisms that support action production. The basic claim is that the observer's action

77 control system acts as an emulator enabling the observed action to be internally simulated in

78 real-time. These real-time simulations can then be used as the basis for anticipatory action

79 planning. However, in order to internally simulate the observed action using an emulator, a

80 motor command, which ordinarily drives the forward model during action production, is

81 needed. One way to generate this motor command might be to formulate a conjecture about

82 what action the observed agent is producing (Kilner et al., 2007) or by visual analysis of the

83 observed action (Csibra, 2008). Visual analysis can be coupled with an inverse model to

84 simulate the motor commands driving the observed action.

85 **Prediction and motor experience.** A key claim of the emulator theory of action

86 prediction, at least as formulated by Wilson and Knoblich (2005) and Colling and colleagues

87 (Colling et al., 2013; Colling & Williamson, 2014), is that the observed action is mapped onto

88 the observer's body in a part-by-part manner. That is, prediction occurs by internally

89 simulating the action *as if the observer was performing it*. Because prediction is tied to the

90 observer's own action control system, predictions should carry traces of this system.

91   One way to test this claim is to compare action prediction in experts and novices[1]. For

92 example, Aglioti et al. (2008) employed a basketball free throw prediction task to compare the

93 performance of novice and expert basketball players. The general finding from these

94 paradigms is that experts generate more accurate predictions than novices (Abernethy, 1990;

95 Isaacs & Finch, 1983; Aglioti et al., 2008; Sebanz & Shiffrar, 2009). Although studies

96 comparing action prediction in experts and novices appear to demonstrate that predictive

97 processes are enhanced by motor experience at least one concern can be raised. Specifically,

98 the causal relationship between expertise and prediction is not clear. It may be the case that

99 expertise causes superior predictive abilities; however, it is also possible that those who

100 become experts do so because they already possess superior predictive abilities. To uncover

101 the direction of causality it may be preferable to train people on an action rather than use

102 experts. This approach was adopted by Casile and Giese (2006). However, this study only

103 examined whether motor training led to enhanced performance on a visual action

104 discrimination task, and it did not examine the question of action prediction.

105   In addition to concerns about the direction of causality, a second concern can also be

106 raised about previous studies. In previous work by, for example, Aglioti et al. (2008), Sebanz

107 and Shiffrar (2009), Ikegami and Ganesh (2014), Mulligan and Hodges (2013), and others[2],

108 participants were asked to generate a prediction about the outcome of an action. For example,

109 whether a basketball free-throw would be successful or not. While these tasks do test

110 predictive mechanisms, it is not clear whether they test the same predictive mechanisms that

111 underlie joint performance in music, dance, and sport. The predictive mechanisms that

112 underlie joint action must have two features, neither of which are tested by these kinds of

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[1]Related to these studies are those that examine expertise-related changes in motor cortex activity during action observation tasks (e.g., see Calvo-Merino et al., 2005; Calvo-Merino et al., 2006). While the results of these studies are consistent with the emulator hypothesis, they do not provide a test of the theory because they do not involve prediction tasks.

[2]For neuroimaging studies that involve outcome prediction see, for example, Abreu et al. (2012) and Diersch et al. (2013).

113 tasks. First, predictions must be generated rapidly and in real-time and, second, it must be

114 possible to use these predictions as the basis for anticipatory action planning. This second

115 concern is highlighted by recent work from Mann, Abernethy, and Farrow (2010). In this

116 study, participants were required to generate a prediction about an action and then report their

117 prediction in different ways. This could either be by verbal report or by producing the

118 appropriate action in response to the prediction (in this case, performing the correct cricket

119 shot in response to the predicted trajectory of a ball delivered by a bowler). The results

120 showed that the accuracy of predictions was modulated by response modality, suggesting that

121 predictions generated for verbal report and action planning might reside in different

122 (sub)systems. Therefore, in order to examine the action prediction mechanisms that might

123 underlie joint action, it is necessary to employ tasks that replicate (at least some) of the

124 coordination demands found in joint action. One example of this can be found in temporal

125 alignment tasks.

126 **Temporal alignment tasks.** Temporal alignment tasks are tasks requiring observers to

127 perform an action on the basis of their prediction, rather than make a decision. Performing an

128 action on the basis of a prediction is indeed the response modality chosen by Cross, Stadler,

129 Parkinson, Schütz-Bosbach, and Prinz (2013). In this study, participants were asked to

130 generate a prediction about when a gymnast or a toy, which was moving across the screen,

131 would reappear after moving behind an occluder. Participants were required to press a button

132 at the point in time that they believed the person or toy would reappear. The primary finding

133 of this study was that repeated visual exposure to the stimuli resulted in more accurate

134 predictions about when the gymnast or toy would reappear. Importantly, however, it is not

135 clear whether this task actually taps into action prediction mechanisms. Rather, this task could

136 be performed using mechanisms that allow people to judge the duration of intervals. As the

137 gymnast or toy moves across the screen, accurate perception of how long it takes to move a

138 fixed distance would allow the observer to accurately predict when it will reappear from

139 behind the occluder.

140 A different task, developed by Colling et al. (2014)[3], was designed to tap into

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[3]See Keller, Knoblich, and Repp (2007) and Flach, Knoblich, and Prinz (2003) for similar tasks.

mechanisms specifically related to action prediction, and to test the claim of the emulator hypothesis that traces of the observer's action control system should be evident in the predictions that they generate. In this temporal alignment task, participants viewed mannequins performing up-and-down arm movements while attempting to align a button press with the apex of each upward movement (when it changed from upward to downward). Importantly, the spacing between the points of direction change was irregular thus preventing the observer from relying on interval timing mechanisms (see Colling et al., 2014, Experiment 2–3). Mannequins were viewed under two conditions. In the *self* condition, participants viewed mannequins created from motion capture recordings of their own movements produced at an earlier time. In the *other* condition, participants viewed mannequins created from recordings of another person's movements. The logic of this manipulation was that if people generate predictions using their own action control system, with forward models that replicate their own action dynamics, then predictions in the self condition should be more accurate, because in the self condition the dynamics of the predictor and the dynamics of the predicted action are matched.

The results confirmed this and people were significantly more accurate at aligning button press responses with recordings of their own actions. Importantly, these tasks require participants to not only generate predictions quickly and in real-time but also to plan and execute actions on the basis of these predictions. By employing a paradigm such as this, it should be possible to examine the influence of motor experience on prediction in tasks that more closely match the coordination demands found in joint action.

How does motor experience modify action prediction?

While we have highlighted some concerns about the previous literature, there is a more fundamental concern about this work that motivates the present study. The studies cited above (e.g., Aglioti et al., 2008) suggest that motor experience enables more accurate predictions (at least for action outcome tasks); however, these studies do not answer the question of *how* the prediction process changes in order to achieve this. For instance, it might just be that experts and novices employ the same strategy [4] or mechanisms and that experts are just able to

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[4]The word *strategy* is not meant to imply a high-level cognitive function or something that is conscious or deliberative.

169   employ this strategy with greater efficiency or accuracy. However, it might also be the case

170   that novices and experts employ distinct mechanisms, or use distinct strategies, with the

171   consequence of this being superior prediction accuracy for the experts. The suggestion that

172   distinct processes or strategies might underlie action prediction in experienced and naïve

173   observers is found in an extension of the emulator hypothesis, developed by Schubotz (2007).

174   Based on results from fMRI (e.g., Schubotz & von Cramon, 2004) and lesion studies (e.g.,

175   Schubotz, Sakreida, Tittgemeyer, & von Cramon, 2004), which implicate premotor regions in

176   sequence prediction, Schubotz (2007) suggests that motor simulation is a general purpose

177   predictive mechanism for predicting not only human actions but all manner of external events.

178   In the case of *reproducible events* (e.g., human actions) it is possible to internally simulate the

179   observed action using the same mechanisms used to produced them, as claimed by the

180   emulator theory (e.g., see Colling et al., 2013; Wilson & Knoblich, 2005; Colling &

181   Williamson, 2014). In the terminology of Schubotz (2007, p. 213), observers use their "motor

182   memories to run a simulation of the observed movement". In the absence of these motor

183   memories, Schubotz (2007) suggests that predictions might be generated by mapping the

184   observed event onto an effector that best matches the general dynamics of the observed

185   stimuli. This suggests that experienced and naïve observers might actually engage different

186   mechanisms or employ distinct strategies during action prediction, with experienced observers

187   internally replicating the observed action *as it was performed* and naïve observers just

188   replicating the stimulus dynamics with whatever effector does the best job. This generic

189   simulation (as opposed to *action specific* simulation) might not only occur in the absence of

190   motor experience. It might also occur when the observed stimuli cannot be easily mapped onto

191   the observer's body. For example, when the action stimuli are impoverished so that it is not

192   clear *how* the action is being produced—that is, when the observed actions are not amenable to

193   visual analysis (Csibra, 2008)—it might not be clear which action, out of all possible actions,

194   to internally simulate. In this case, observers might again internally replicate the dynamics of

195   the stimulus using whatever effector does the best job rather than simulating the actual action.

Aims of the present study

The aim of the present study is to investigate *how* predictive processes change when observers have experience producing observed actions. Previous studies have reported that action prediction becomes more accurate when observers possess motor experience; however, it is not clear how the process changes to enable this. Indeed, measuring prediction accuracy alone may not be sufficient to do this. Furthermore, previous studies on action prediction have generally tended to focus on predicting action outcomes, with relatively few studies (e.g., Colling et al., 2014; Keller et al., 2007; Flach et al., 2003) employing the kind of tasks that replicate the temporal demands found in joint action.

The work of Schubotz (2007) suggests that experienced and naïve observers employ distinct mechanisms for action prediction. It might be possible to test whether experienced and naïve observers engage distinct predictive mechanisms, or employ different predictive strategies, by designing a manipulation that should effect only one strategy and not the other. Schubotz (2007) suggests that generic, non-action specific, simulation should occur not only when observers have little or no experience producing the observed action, but it should also occur when the stimulus is impoverished, so that is cannot easily be mapped on to the body in a part-by-part manner or when the stimulus does not clearly depict an action. Therefore, we can expect these two factors—the motor experience of the observer and the nature of the stimulus—to interact. That is, if an observer is engaged in generic, or approximate, simulation of the observed action, such as when they have no experience producing the action, then diminishing stimulus detail, so that the stimulus cannot be mapped onto the body, should be of little consequence, because generic simulation does not require the stimulus to be mapped onto the body. However, if the observer is engaged in a detailed part-by-part simulation then decreasing the stimulus detail, so that it is not clear how the action is being produced, should interfere with the predictive process. That is, changing the nature of the stimulus, so that action specific but not the critical dynamic information is reduced, should only have an effect on experienced observers.

To test this hypothesis, we examined the influence of motor experience on prediction during a temporal alignment task similar to that used by Colling et al. (2014). Two groups of

participants, those with experience producing the observed action and naïve participants,

viewed actions under two conditions. In the full information condition, the stimuli depicted

the actions in full, including information about the arrangement of the limbs and joints during

the production of the action. In the point information condition, participants were required to

align a response with the same dynamic information; however, the displays were impoverished

so that they did not depict an action. We predict that naïve observers, who only engage an

approximate, rather than an action specific, predictive solution, which replicates the dynamic

information of the stimulus but without internally replicating the action itself, should display

little, or no, difference between the two conditions. In experienced observers, however,

decreasing stimulus information should hamper the process of internal replication. This

should result in a difference in prediction accuracy between stimulus conditions as a function

of motor experience—that is stimulus condition and motor experience should interact. Using

this procedure has an advantage over simply comparing prediction accuracy for a single

stimulus type (e.g., as typically done in studies of sports expertise such as, for example,

Aglioti et al., 2008) because the stimulus manipulation is predicted to have a different effect

on alignment accuracy depending on the strategy employed by the observer. Thus it may be

possible to examine whether the naïve and experienced group employ distinct strategies.

Typical sports expertise studies are blind to whether experts employ a different, more accurate,

strategy relative to novices or whether experts just employ the same strategy as novices but

with greater precision. It is important to note here that, unlike previous studies, our prediction

is not that experienced observers will be more accurate. Indeed, we are agnostic about whether

experienced or naïve observers will be more accurate. We only aim to test whether naïve and

experienced observes rely on distinct strategies, and our stimulus manipulation is designed to

influence one strategy and not the other. Therefore, the key comparison is whether the effect

of stimulus is different between the two groups (that is, whether group and stimulus interact).

It may be the case the the experienced observers' strategy will be more accurate—for

example, as shown in previous work. However, it does not follow from this work that this will

necessarily be the case. This is because whether a one strategy or another is more successful,

253   less successful or equally successful is dependent on the context in which they are employed [5].

Methods

Participants

256   There were 13 participants (11 females, mean age of 27.5 years) in the experienced

257   group, and 12 participants (8 females, mean age of 20.1 years) in the naïve group. All

258   participants were right-handed (Oldfield, 1971), and all procedures were approved by the

259   Macquarie University Human Subjects Ethics committee.

Stimuli

261   To create the stimuli for the test session, five right-handed females (mean age of 24.8

262   years) performed a movement task while their movements were recorded with motion capture.

263   The movement task involved tracing out wave and zigzag patterns as if drawing them on a

264   blackboard (the patterns measured 0.584 m × 0.841 m; see Figure 1). Each pattern contained

265   five peaks, alternating in height from large to small; however, they differed in the nature of the

266   direction change at the apex of the peaks. The zigzag pattern contained an abrupt change

267   while the wave pattern had a smooth direction change. We had no predictions about how

268   pattern would influence performance; therefore, the data were collapsed over pattern during
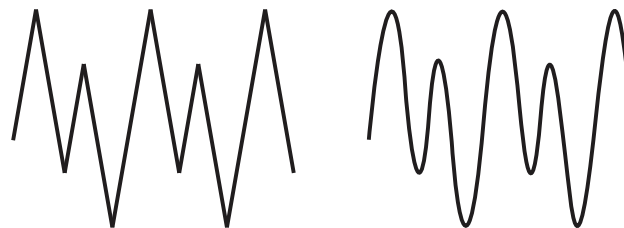
269   data analysis.

Figure 1. The zigzag (left) and wave (right) patterns used as stimuli during the movement task

270   Movements were recorded using an 8-camera 3-D passive optical motion capture system

271   (Vicon MX with 4 MX-F20 and 4 MX13+ cameras; 200 Hz sampling rate). To define the limb

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[5]If this claim seems initially implausible consider the, admittedly extreme, example in which somebody could employ two strategies to catch a ball. The expert strategy involves moving just so and so in response to the movement of the ball and anticipating the flight of the ball. The dumb strategy involves simply placing ones hand in a particular spot. In a context where the ball, with a high degree of regularity, can be expected to land in a specific spot, the dumb strategy will be just as good as, and possibly even better than, the expert strategy. However, in a context with more variability, only the expert strategy will be successful. Therefore, paradigms that rely solely on gross accuracy or success differences between groups cannot fully answer the question of how action prediction is modulated by experience.

272 segments, and the position of the torso, markers were placed on the shoulders, the right elbow,

273 wrist, waist, and the top of the right hand (See Figure 2). For the full information condition,

274 the motion capture data was rendered as an animated character consisting of an upper torso,

275 right arm and right hand. For the point information condition, only a single point tracking the

276 movement of the RFIN marker was displayed (See Figure 3). Mannequins were preferred over

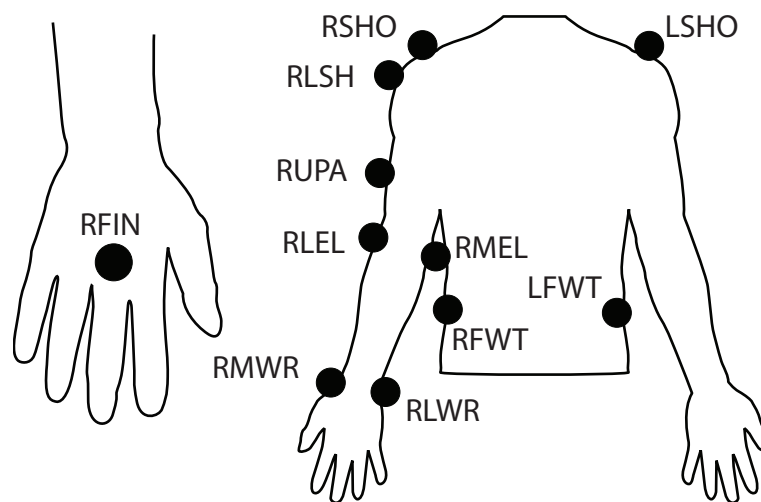277 point-light displays because they preserve occlusion.

Figure 2. Marker positions for the 11 reflective markers used during the movement task

Procedure

279   Participants in the experienced group undertook a movement session that was identical

280 to the task employed during stimulus creation. Participants performed 3 blocks containing 5

281 repetitions of each pattern (in random order) with their eyes closed to limit visual experience.

282 The movement session and the test session were on average separated by 16.69 days (7 to 28

283 days).

284   The task in the test session, which was conducted in a different lab to the movement

285 task, was to press the response button when the hand of the mannequin, or the marker tracking

286 the hand, reached the apex of each upward movement. That is, on each trial participants were

287 required to press the button *five* times. They were instructed to synchronise the button-press

288 with the display as accurately as possible and were told that this may require them to

289 anticipate when the peak will occur. Each participant performed 4 blocks containing 40 unique

290 stimuli (composed of 20 trials for the full information condition and 20 trials for the point
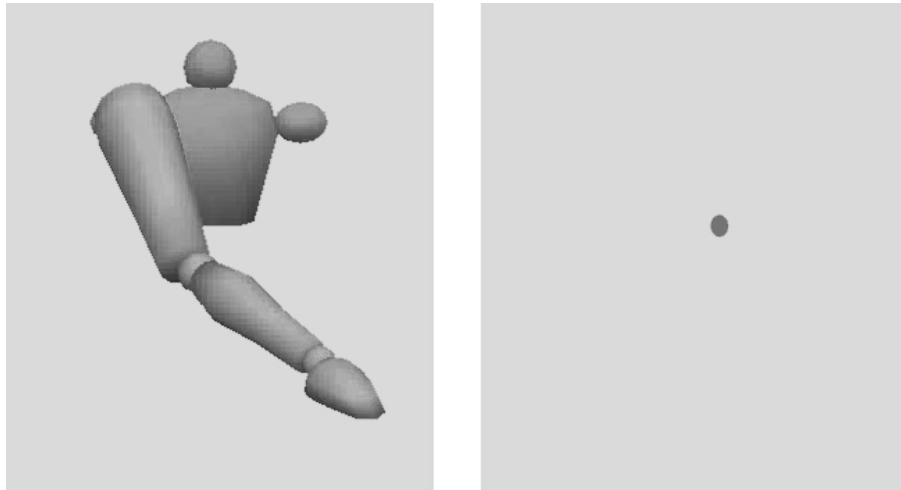
Figure 3. Example stimuli from the full information condition (left) and the point information condition (right)

information condition) with equal numbers of wave and zigzag stimuli. Participants that did not undergo the movement session were given a brief verbal description of the movement task.

Statistical analyses

To measure alignment accuracy, we calculated the absolute timing difference between the occurrence of the peak in the motion capture trajectory and the occurrence of the button presses performed by the participant. Only the last four button presses were analysed because several stimuli contained missing frames leading up to the first peak. Absolute timing error was analysed by means of a 2×2 mixed ANOVA with the factors stimulus condition (full information, point information) and group (experienced, naïve). The primary comparison of interest was the interaction term— that is, whether the difference between the stimulus conditions was different between the two groups. Therefore, we report the effect size in the form of Hedges g (with bootstrapped confidence intervals), because our predictions, and thus our interpretation of the data, are focused on the magnitude of the difference between the groups and conditions. Conventional interpretations of the Hedges g, a unbiased estimate of Cohens d, places the boundaries for small, medium, large effects at 0.2, 0.5, and 0.8 (Cohen, 1969).

In addition to the standard null hypothesis significant tests, we also include confidence intervals, as recommended by Cumming (2013). Furthermore, we provide bayesian parameter estimates for all the comparisons reported in the primary analysis. We adopt the approach

310 outlined by Kruschke (2013), which involves fitting a t-distribution to the data by estimating

311 the three parameters of the t-distribution: a mean (μ), a standard deviation (σ), and a shape

312 parameter (ν)—the addition of the shape parameter (ν) allows the model to account for

313 outliers in the data[6]. We report the 95% highest density intervals (HDI) for the parameter μ, as

314 well as the 95% HDI for the effect size estimates, designated as d, which are calculated as μ/σ

315 for the one sample comparisons and as $(\mu_1 - \mu_2)/(\sqrt{(\sigma_1^2 N_1 - 1 + \sigma_2^2 N_2 - 1)/(N_1 + N_2 - 2)}$

316 for two sample comparisons. These effect sizes can be interpreted using the same conventions

317 as for Hedges g.

318   In an exploratory follow-up analysis, we report the effect size η_G^2, which provides a

319 measure of the proportion of variance in the measured variable that is explained by the level of

320 the factor (see Olejnik & Algina, 2003). The boundaries for small, medium, and large effects

321 are usually placed at 0.01, 0.06, 0.14 (Cohen, 1969)[7]. For violations of sphericity we report

322 Greenhouse-Geisser ϵ, uncorrected dfs, and corrected ps.

Results

324   The results showed that there were no systematic differences in alignment accuracy

325 between the experienced group (M = 126.42, SD = 48.40) and the naïve group (M = 114.46,

326 SD = 33.22), $F_{1,23} = 0.51$, $p = .482$, Hedges $g = 0.28$, 95% CI [-0.52, 1.02], $M_D = 11.11$, 95%

327 HDI [-26.45, 49.89], $d = 0.26$, 95% HDI [-0.56, 1.06]. The group main effect, and 95%

328 confidence intervals, are shown in Figure 4A.

329   Furthermore, there were no systematic differences in the alignment accuracy between

330 the point information condition (M = 121.84, SD = 40.83) and the full information condition

331 (M = 119.52, SD = 42.44), $F_{1,23} = 1.867$, $p = .185$, Hedges $g = 0.25$, 95% CI [-0.11, 0.63],

332 $M_D = 2.19$, 95% HDI [-1.54, 5.98], $d = 0.25$, 95% HDI [-0.16, 0.67]. The condition main

333 effect, and 95% confidence intervals, are shown in Figure 4B.

334   Our primary comparison of interest was whether the effect of stimulus condition was

335 modulated by group. This is examined by the interaction in the ANOVA, which compares the

336 difference in alignment accuracy between the Point information and the Full information

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[6]For more details on the prior distributions for each parameter, see Kruschke (2013).

[7]Note, however, that Cohen (1969) provides definitions for small, medium, and large effects in terms of f. Here we have converted from f to the equivalent values of η_G^2.
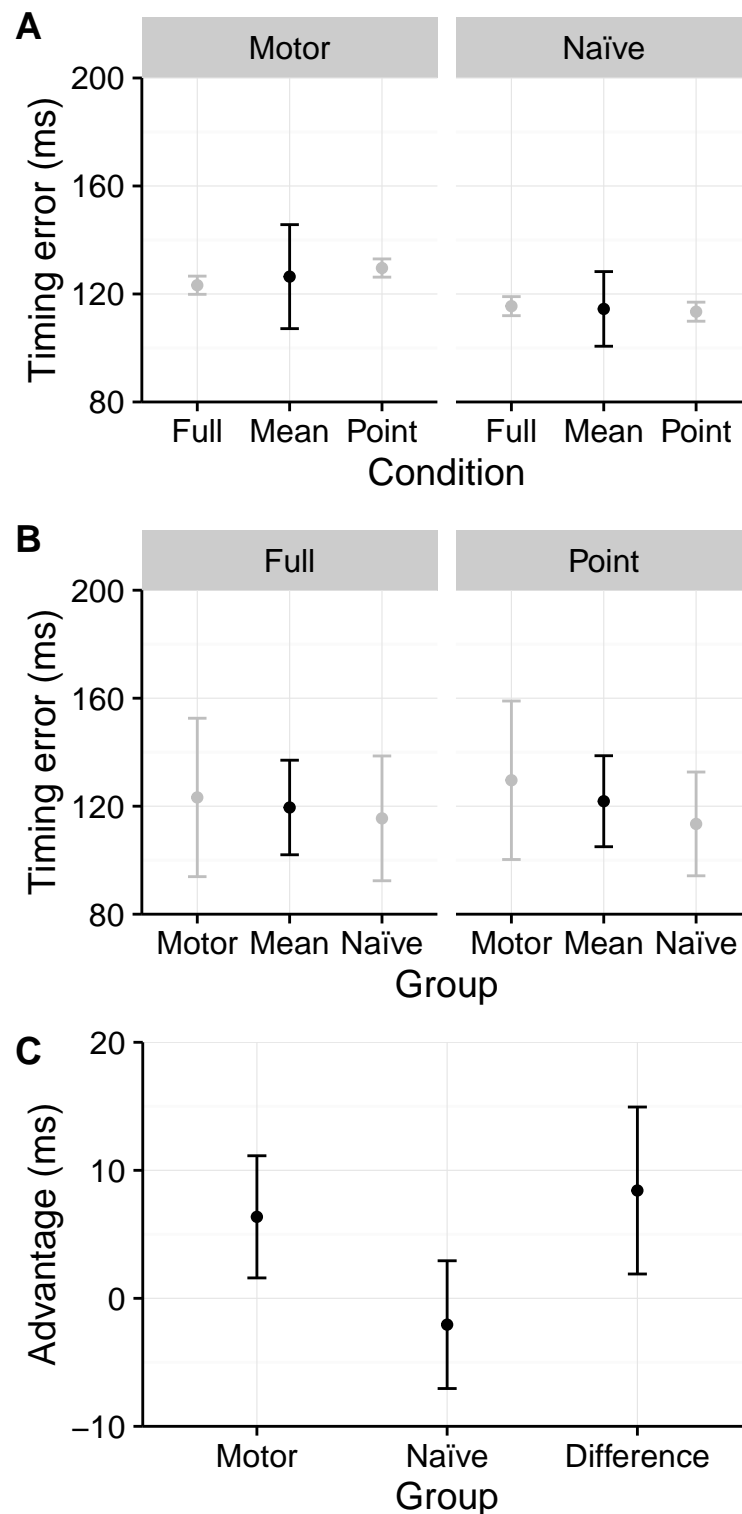
Figure 4. (A) Plot of the Group main effect. Black bars show the two group means and 95% confidence interval, while the grey bars show the cell means and the within-subject confidence intervals. (B) Plot of the Condition main effect. Black bars show the two condition means and the 95% confidence intervals, while the grey bars show the cell means and the between subject confidence intervals. (C) Plot of the Group × Condition interaction, showing the full information advantage for each group together with the difference between the two groups.

condition in the experienced group with this difference in the naïve group. This difference,

which we term the *full information advantage* was larger in the experienced group (M = 6.15,

95% HDI [1.22, 11.28], $d = 0.77$, 95% HDI [0.12, 1.44]) than in the naïve group (M = -2.26,

95% HDI [-7.58, 3.18], $d = -0.28$, 95% HDI [-0.91, 0.36]), $F_{1,23} = 7.135$, $p = .014$, Hedges $g =$

1.03, 95% CI [0.22, 1.87], $M_D = 8.41$, 95% HDI [1.24, 15.76], $d = 0.94$, 95% HDI [0.09,

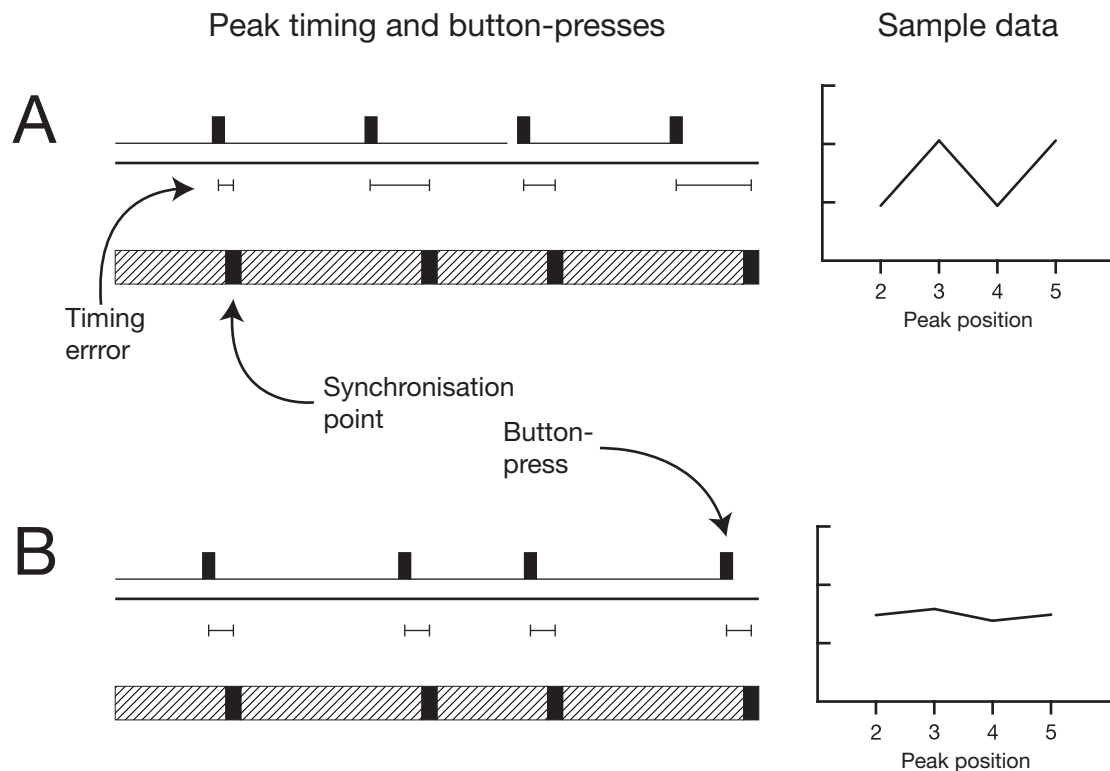1.88]. This interaction is shown in Figure 4C.

Figure 5. (A) Evenly spaced button-presses results in timing errors that vary as a function of peak number. (B) Button presses that vary according to peak position results in timing errors that do not vary according to peak position

Exploratory analysis of group differences

A further attempt was made to explore differences in task performance between the experienced and naïve group. To do this, we examined whether there were any differences in task performance related to whether participants primarily responded to the local or the global dynamics of the stimulus. In the stimulus, the duration of each upward movement alternated from long to short leading to local variations in the timing of the peaks. That is, the timing of the peaks was not evenly spaced across the trial with peaks being separated by alternating long and short gaps. If participants based their responses on the global dynamics of the

351 stimulus—for example, the average inter-peak interval—and produced evenly spaced button

352 presses that matched these global dynamics then the magnitude of the timing error would

353 fluctuate from peak to peak. That is, if participants just tapped at a regular isochronous rhythm

354 then timing error would vary as a function of peak position because the stimulus itself is not

355 isochronous. If, on the other hand, participants adjusted their responses according to the local

356 variations in the stimulus—that is, the local peak to peak timing variations—then timing error

357 should be relatively constant across the trial. (The logic of this analysis is shown in Figure 5).

358   In order to examine which of the two strategies was adopted by each of the groups, we

359 analysed timing error as a function of peak position using two seperate one-way ANOVAs. If

360 participants adopted the strategy of responding to the global dynamics of the stimulus, then

361 this should be evident as a significant effect of peak position on timing error. However, if

362 participants adopted the strategy of responding to the local dynamics of the stimulus then we

363 should not find a significant effect of peak position ofntiming error. The results of the analysis

364 showed a significant effect of peak position on timing error for the naïve group, $F_{3,33} =$

365 11.148, $p = .005$, $\eta_G^2 = 0.216$, $\epsilon = 0.369$, but not for the experienced group, $F_{3,36} = 2.745$, $p =$

366 $.117$, $\eta_G^2 = 0.036$, $\epsilon = 0.386$. This is consistent with the experienced group and the naïve group

367 adopting different strategies, with the naïve group responding to the global dynamics of the

368 stimulus and the experienced group responding to the local dynamics. These data are shown in

369 Figure 6.

Discussion

370

371   The primary aim of the present study was to investigate how online prediction of action

372 is changed by motor experience. Previous studies have shown that observers who have

373 experience performing an action are able to generate more accurate predictions about that

374 action (e.g., Aglioti et al., 2008; Sebanz & Shiffrar, 2009). This increase in prediction

375 accuracy could be achieved in at least two ways. It might be that increased accuracy is

376 achieved through motor experience fine-tuning or otherwise enhancing the operation of a

377 predictive mechanism that is common to both naïve and experience observers. However, it

378 might also be the case that motor experience allows observers to engage different predictive

379 mechanisms or apply distinct predictive strategies to the problem of action prediction,
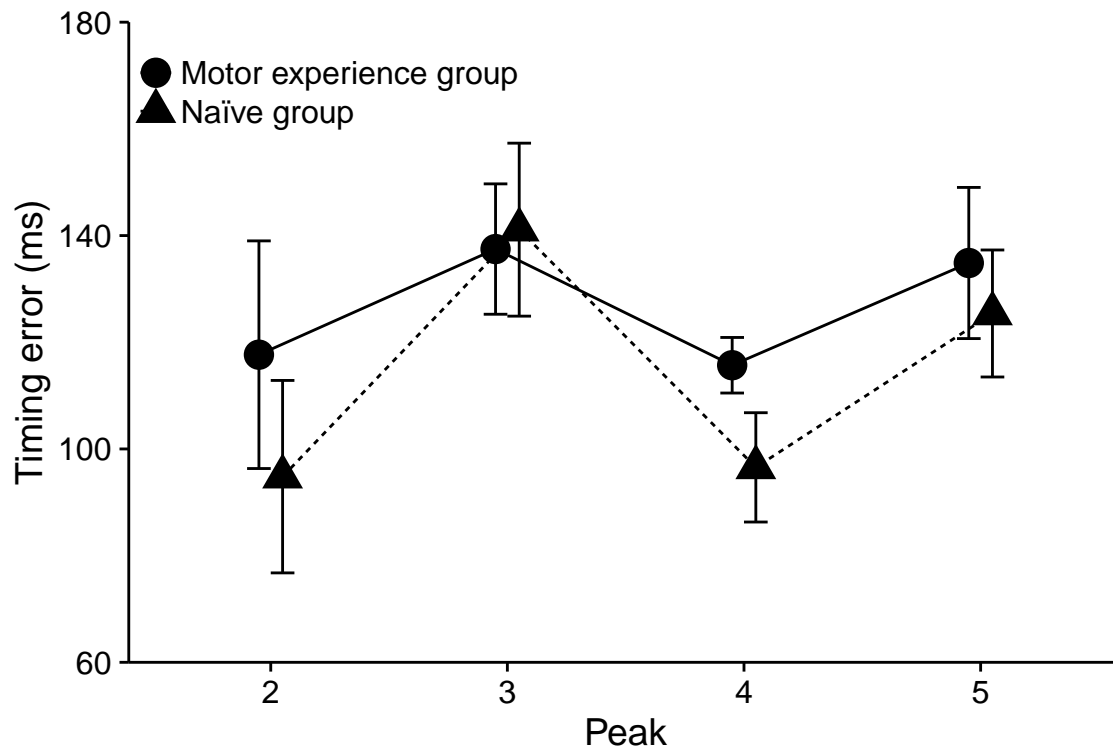
Figure 6. Timing error as a function of peak position for the experienced and naïve group. Error bars show the within-subjects 95% confidence intervals.

380 strategies or mechanisms that naïve observers are not able to call upon. By only measuring

381 overall prediction accuracy, these studies only show *that* prediction is altered by motor

382 experience but not *how* it is altered. Addressing this question was the aim of the present study.

383   Based on work by Schubotz (2007), we hypothesised that motor experience may allow

384 observers to engage in a different kind of prediction to naïve observers. Specifically, we

385 predicted that observers with motor experience would be capable of reactivating "motor

386 memories" from previous performances, which would enable them to internally simulate the

387 same action that was being observed. Naïve observers, on the other hand, would only be able

388 to engage in a non-specific simulation of the stimulus dynamics using the motor dynamics of

389 the effector that most closely replicated the dynamics of the stimulus.

390   To test this hypothesis, we compared prediction accuracy for experienced and naïve

391 participants under two stimulus conditions, which were designed to have an differential effect

392 depending on whether the observer performed a non-specific or action specific simulation of

393 the observed action. In the full information condition, participants viewed stimuli that fully

394 depicted the action being performed, including information about the limbs and joints used to

produce the action. In the point information condition, participants viewed stimuli that did not depict an action but did replicate the stimulus dynamics of the full information condition. The logic of this manipulation is that if observers are engaged in a non-specific simulation of the stimulus dynamics then altering the *action-related* properties of the stimulus—for example, the depiction of which effectors were used to produce the action—while holding the critical dynamic properties of the stimulus constant should have little or no effect on prediction accuracy, because the critical information—the stimulus dynamics—do not change between conditions. If, however, observers engaged in an action-specific simulation of the stimulus then changing *action-related* properties should have an effect on prediction accuracy. Therefore, by comparing the difference between the two conditions between the experienced and naïve observers it should be possible to examine whether the underlying predictive process is different between the two groups.

The effect of stimulus condition

The results showed that overall there was no difference in alignment accuracy between the full information and the point information condition. This result may initially appear surprising. However, the stimulus manipulation was designed to only affect one prediction strategy—namely, the strategy that involves mapping the observed action onto the body and simulating the action as it was produced; therefore, this finding is consistent with our prediction that stimulus information should only increase alignment accuracy in participants with motor experience.

The effect of motor experience

The primary aim of the present study was to examine the influence of motor experience on action prediction. Contrary to previous work by, for example, Aglioti et al. (2008) and Sebanz and Shiffrar (2009), the results of the present study did not show that motor experience results in an overall increase in prediction accuracy. This may initially appear strange or counterintuitive; however, this finding is consistent with our hypothesis that naïve and experienced observers employ different predictive strategies or engage distinct mechanisms for action prediction. This is agnostic to the question of whether one or the other predictive strategy results in superior prediction. While a null finding is difficult to interpret, it may be

424 the case that, within the context of our experiment, overall performance accuracy is no

425 different; furthermore, if our hypothesis is correct, then our results are not in conflict with

426 other findings that show that in other contexts, such as those examined by Aglioti et al. (2008)

427 and Sebanz and Shiffrar (2009), motor experience results in superior prediction. Indeed, we

428 might even expect to find that in some contexts experienced observers perform worse than

429 naïve observers. This is because prediction accuracy alone cannot distinguish one prediction

430 strategy from the other. This can only be done by manipulations designed to have an influence

431 on one prediction strategy and not another, such as, for example, our stimulus manipulation.

432   Although not part of our initial hypothesis, we did conduct an exploratory secondary

433 analysis to examine whether there was any information in the pattern of alignment accuracy

434 data that would suggest that experienced and naïve observers were performing the task in

435 different ways. In particular, if naïve participants generated their predictions by means of a

436 generic, non-specific, simulation then we might expect these predictions to be less sensitive to

437 fine-grained timing changes in the stimulus relative to the full-blown internal action

438 replication that we hypothesised would be performed by the experienced observers.

439   To test this possibility we compared the intra-trial differences in alignment accuracy for

440 the two groups. The results showed that for the naïve group, alignment accuracy differed

441 significantly as a function of peak position. This was not the case for the experienced group.

442 This result could be produced by naïve participants merely responding to the global dynamics

443 of the stimulus instead of responding to the fine-grained timing variations in the stimulus, as

444 seen in the experienced participants. This result is consistent with the notion that experienced

445 observers generate predictions about observed actions by employing an internal model of that

446 action that is acquired through motor experience. By mapping the observed action onto their

447 internal model for that action they are better able to capture the fine-grained timing variations

448 in the stimulus because their predictive model more completely captures the constraints

449 specific to the effectors used to produce the action. If naïve observers do not internally

450 simulate the observed action then this generic model may be less capable of capturing these

451 fine-grained details while still being able to capture the global dynamics.

452   Recent work using transcranial magnetic stimulation may also be relevant to the current

453 work. Agosta, Battelli, and Casile (2016) examined cortico-spinal excitability during

454 observation of action and non-action motion stimuli. While Agosta et al. (2016) found no

455 difference in overall motor evoked potential (MEP) amplitude between the action and the

456 non-action condition, with mean MEP amplitude only being sensitive to stimulus kinematics

457 rather than stimulus form, differences in the temporal dynamics of cortico-spinal excitability

458 were observed. In particular, it was found that the amplitude of the MEP correlated with the

459 instantaneous velocity of the movement stimulus but not the abstract stimulus. This suggests

460 that while non-action stimuli might, via mirror neurons, activate the motor system (consistent

461 with the claims of Schubotz et al. (2004)), this activation might be different in nature to the

462 activation produced by action stimuli. Indeed, Agosta et al. (2016, p. 190) suggest that

463 "observation of abstract motion [produce] a 'coarser' activation of the observer's motor

464 system". This "coarser" activation, which less accurately tracks the fine-grained dynamics of

465 the stimulus, might underlie the difference in prediction accuracy between the full information

466 stimuli and point information stimuli reported in the present work. However, since Agosta

467 et al. (2016) did not examine action prediction all that can be said is that their finding is

468 consistent with the claims advanced here and not that they support our claims. An interesting

469 avenue for future work, which may allow a further bridge to be built between the mirror

470 neuron system and action prediction literatures, would be to examine how the difference in the

471 temporal dynamics of MEPs (reported by Agosta et al., 2016) are modulated by motor

472 experience, perhaps using a task similar to the present or on an outcome prediction task such

473 as that used by Aglioti et al. (2008).

Motor experience modulates stimulus effects

475   The key to testing our hypothesis that experienced and naïve observers engage distinct

476 predictive mechanisms was our examination of how motor experience modulated the effect of

477 stimulus condition. This is because our stimulus manipulation was designed to only have an

478 influence on one predictive strategy—mapping the observed stimulus onto the body—and not

479 the other—simulating the observed action by non-action-specific means. We hypothesised that

480 motor experience would allow participants to engage in a different type of action prediction

481 compared with naïve participants. In particular, we hypothesised that experienced participants

would be able to activate an internal representation of the observed action that had been laid down by earlier performance of the action while naïve participants would just engage general purpose predictive mechanisms that are not specific to the action. This difference in the nature of prediction between the two groups should result in differences in how the two groups respond under the two stimulus conditions. For the experienced group, the full information condition should allow observers to more accurately select the correct internal action representation that corresponds to the observed action and this should result in an enhancement in alignment accuracy relative to the case where this information is absent. In the naïve group, however, the observers do not activate an internal representation of the observed action and, therefore, the addition of information that helps select the appropriate internal action representation should be of no benefit. As hypothesised, we found that alignment accuracy was enhanced in response to the full information stimuli only for participants who had experience producing the observed action.

Two mechanisms for action prediction in experience and naïve observers

While previous studies have been able to demonstrate *that* motor experience changes processes involved in action prediction by, for example, enhancing prediction accuracy (Aglioti et al., 2008), the results presented here go further to demonstrate *how* these predictive processes are changed. Specifically, these results are consistent with the idea that experienced and naïve participants rely on different mechanisms or strategies for action prediction. This distinction between internally replicating the action itself and merely simulating the stimulus dynamics with in the motor system is similar to the distinction between *emulation* and *simulation*, respectively, put forward by Grush (2004). By internally replicating the action itself, observers might not only (in certain circumstances) generate more accurate predictions but may also generate predictions that more accurately replicate the fine-grained timing details of the observed action. These differences in fine-grained details may not appear in tests of gross performance, such as predicting binary action outcomes (e.g., Aglioti et al., 2008; Sebanz & Shiffrar, 2009).

The findings of the present study are also consistent with recent TMS work by Novembre, Ticini, Schütz-Bosbach, and Keller (2014) and Hadley, Novembre, Keller, and

Pickering (2015). Both these studies involved applying TMS over motor regions while participants' were engaged in temporal coordination with stimuli that they either did or did not have experience with. For example, Novembre et al. (2014) had pianists play a duet along with a recording of a piece that they had also be trained to perform or with a untrained piece. The results showed the TMS was able to disrupt temporal coordination only when participants were playing along with a piece on which they had been trained. Similarly, in a musical turn-taking task, Hadley et al. (2015) found that TMS was able to disrupt the temporal precision of the participants' entry into a joint performance only in trained but not untrained contexts. Taken together, these studies, as well as the results of the present study, show that temporal coordination with unfamiliar stimuli relies on different mechanisms or brain networks compared with temporal coordination with familiar stimuli.

Conclusions

Taken together, the results presented here suggest that observers with and without experience performing an action rely on different mechanisms or strategies when asked to generate predictions about that action. Observers who have experience actually performing the observed action generate predictions by internally replicating the actual observed action, possibly through reactivating motor representations laid down by earlier performance. Observers without this experience, however, engage general purpose predictive mechanisms that do not necessarily replicate the actual action nor the fine-grained details of the observed action. Furthermore, when stimulus dynamics are held constant, only experienced observers are able to take advantage of action-related information (information about the limbs and joints used to produce the action) while this action-related information has no influence on the predictions generated by naïve observers. Thus, the findings of this study show not only *that* motor experience changes action prediction but also *how* motor experience changes the operation of these predictive processes. Furthermore, the results of the present study suggest the future work examining how experience modulates action prediction should, rather than employing a single task that cannot distinguish between different strategies for action prediction, employ manipulations that specifically tap into the predictive strategy of observers so that any differences in predictive strategy between experienced and naïve observers is

540   evident.

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544

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