Accepted as a Full Length Article in Cognition on 10th December, 2017

Sensory predictions during action support perception of imitative reactions across suprasecond delays

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Word count (excl. abstract, references, figure legends): 4661

Abstract

Perception during action is optimized by sensory predictions about the likely consequences of our movements. Influential theories in social cognition propose that we use the same predictions during *interaction,* supporting perception of similar reactions in our social partners. However, while our own action outcomes typically occur at short, predictable delays after movement execution, the reactions of others occur at longer, variable delays in the order of seconds. To examine whether we use sensorimotor predictions to support perception of imitative reactions, we therefore investigated the temporal profile of sensory prediction during action in two psychophysical experiments. We took advantage of an influence of prediction on apparent intensity, whereby predicted visual stimuli appear brighter (more intense). Participants performed actions (e.g., index finger lift) and rated the brightness of observed outcomes congruent (index finger lift) or incongruent (middle finger lift) with their movements. Observed action outcomes could occur immediately after execution, or at longer delays likely reflective of those in natural social interaction (1800 or 3600 ms). Consistent with the previous literature, Experiment 1 revealed that congruent action outcomes were rated as brighter than incongruent outcomes. Importantly, this facilitatory perceptual effect was found irrespective of whether outcomes occurred immediately or at delay. Experiment 2 replicated this finding and demonstrated that it was not the result of response bias. These findings therefore suggest that visual predictions generated during action are sufficiently general across time to support our perception of imitative reactions in others, likely generating a range of benefits during social interaction.

Keywords: Prediction; Action: Social Interaction; Perception; Imitation; Sensorimotor Integration.

1. Introduction

Behavioural success for humans and other animals often depends on effectively navigating the social world – on accurately anticipating and interpreting the actions of conspecifics (Happé, Cook, & Bird, 2017). An influential hypothesis in recent decades has been that we use our motor system to generate predictions about how others will behave while we observe them during interaction (Schütz-Bosbach & Prinz, 2007; Wolpert, Doya, & Kawato, 2003). Specifically, processes for anticipating the sensory consequences of our own actions during selection and execution (e.g., we predict that we will see our hand waving when we send a motor command to wave; Greenwald, 1970) are repurposed to support perception of similar reactions in others (e.g., when we wave to a friend and they return the gesture). These processes are proposed to support the perception of imitation given that the sensory consequences generated by our own movements closely resemble those generated by our imitative partner. This generalized predictive process would increase our sensitivity to imitative responses in others, promoting fluent social interactions by facilitating rapid and appropriate responses to our partner's behaviour (see Schütz-Bosbach & Prinz, 2007 for a discussion).

However, it remains unknown whether sensorimotor predictions have the temporal profile needed to support perception of imitative reactions. Typically, when we produce an action (e.g., a wave) the direct outcome of visual stimulation relating to our own action is perceived at reliable and short delays after action execution, whereas the imitative responses of others are observed across variable delays in the order of seconds. While a number of influences of sensorimotor prediction on visual processing have previously been reported with no action-outcome delays (Deschrijver, Wiersema, Brass, 2017; Stanley & Miall, 2007, Yon & Press, 2017), no empirical work has investigated whether sensorimotor predictions operate across the suprasecond delays between action and reaction that characterize natural social interaction. In fact in contrast with theories of social interaction, it has been argued by action control researchers that sensorimotor prediction operate with subsecond precision (e.g., Frith, Blakemore, & Wolpert, 2000) and therefore the temporal variability with which others imitate our actions may preclude prediction.

The experiments presented here therefore considered the time-course of visual sensorimotor prediction. To measure influences of prediction on perception of observed actions, we exploited the fact that predicted stimuli appear more intense (brighter) than unpredicted stimuli. For example, Han and VanRullen (2016) report that predictable gray shapes are perceived as brighter than the same gray hues displayed in the unpredictable context of random lines. These brightness effects are consistent with models where predictions increase the 'gain' on (or activation of) expected sensory units, enhancing the effective signal strength of predicted events (Summerfield & de Lange, 2014). Specifically, physically more intense signals are associated with increased activation in populations of sensory neurons, and therefore manipulations which increase apparent intensity are reasoned to reflect gain enhancements of underlying sensory populations (see Carrasco, Ling, & Read, 2004; Cutrone, Heeger & Carrasco, 2014, for a discussion). These schemes are consistent with suggestions from ideomotor theory that action execution involves activating representations of anticipated sensory outcomes (Greenwald, 1970). They are argued to be an adaptive use of sensory systems given that they will bias perceptual processes towards events that are by definition more likely to occur, leading to (on average) more veridical percepts (Yuille & Kersten, 2006; Summerfield & de Lange, 2014; see General Discussion).

We have recently demonstrated these influences of expectation on apparent brightness in an action context (Yon & Press, 2017). In these previous experiments, participants executed finger movements (index or middle lifts) and observed synchronized congruent or incongruent finger movements (same or opposite finger, i.e., expected or unexpected action outcome) performed by an avatar hand. The perceived brightness of these outcomes was measured by briefly increasing the brightness of the observed avatar finger shortly after movement, and asking participants to compare its apparent brightness to a reference stimulus. Results revealed that participants perceived congruent action outcomes probed shortly after action (50 ms delay) as brighter than incongruent ones. This effect was absent for non-action control stimuli (squares) presented at equivalent locations, suggesting that the underlying predictive process is sensitive to the identity of action outcomes rather than simple spatial features.

In the present study we adapted our previous task, but varied the delay between action execution and the presentation of action outcomes. In Experiment 1, participants executed finger movements (e.g., index finger lift) and judged the brightness of resulting congruent (index lift) or incongruent (middle lift) outcomes made by an onscreen avatar. Observed actions occurred at different delays after the participant's own movement (0, 1800, 3600 ms). The suprasecond (> 1 s) delays employed in the 1800 ms and 3600 ms conditions mirror the natural delay with which our actions are likely to be imitated, given reports that prosocial effects of being imitated arise with 2-4 s delays (Bailenson & Yee, 2005; see Catmur & Heyes, 2013). If sensorimotor predictions influence perception across variable action-outcome delays in a manner that would support social interaction, signatures of perceptual prediction should be found across delays, with participants rating congruent action outcomes as more intense (brighter) than incongruent outcomes regardless of action-outcome delay. Alternatively, if sensorimotor predictions are temporally-specific, congruency would interact with the action-outcome delay, such that congruent action outcomes are not judged as more intense when delays are imposed. In Experiment 2, a near identical procedure was used, though the nature of the judgment was altered to determine whether effects reflected predictive influences on perception or response bias (Firestone & Scholl, 2016).

2. Experiment 1

2.1. Methods

Participants: Twenty-four participants (16 female, mean age = 25.1 years, SD= 6.9) were recruited from Birkbeck, University of London and given a small honorarium for their participation. Two of these were replacements for participants who did not follow task instructions or where points of subjective equivalence (PSEs – see below) modelled to their responses were beyond the range of presented stimuli. Participants in both experiments reported normal or corrected to normal vision, no history of neurological or psychiatric illness and were naïve to the purpose of the study. Both experiments were performed with local ethical committee approval and in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Stimuli and Procedure: The experiment was conducted in MATLAB using the Cogent toolbox (developed by the Cogent 2000 team at the FIL and the ICN and Cogent Graphics developed by John Romaya at the LON at the Wellcome Trust Centre for Neuroimaging). Each trial began with the presentation of an avatar hand (see Figure 1), in a resting position on a CRT monitor (32 x 24cm, 85Hz, 21 DPI). Participants held down two keys on a keypad with their right hand. To control for spatial compatibility (Catmur & Heyes, 2011), this key pad was rotated 90 °, such that their forearm lay in a horizontal position across their body, parallel with the stimulus monitor, and their response hand was visually occluded.

Participants were instructed to lift either their index or middle finger, and were free to make either movement on a given trial. They were told to perform roughly equal numbers of each movement across the experiment, and that they should make large, punctate, up-down finger movements, moving directly from the apex of the lift back to the starting position (see Figure 1). When participants lifted a finger, the resting hand image was replaced by one depicting the avatar performing either an index or middle finger lift for 600 ms. This sequence resulted in apparent motion of the avatar's finger. Importantly, the observed finger lift occurred at one of three delays after the participant's own movement (0, 1800 or 3600 ms from key release). Irrespective of the action-outcome delay, 50 ms after the observed lift the finger would flash for

100 ms at one of seven intensities (increased brightness by 10-70%, in 10% steps[1]). These events allowed us to measure the perceived brightness of the observed congruent and incongruent outcomes. Following an inter-stimulus interval of 1000 ms, a square reference stimulus was presented for 100 ms, equivalent in mean hue and brightness to the midpoint of the test continuum (i.e. 40 % increased brightness).

After 400-500 ms participants were asked whether the target or reference stimulus was brighter, pressing one of two buttons with their left thumb to indicate their choice. The next trial started after 1000 ms.

There were at least 420 trials; 70 at each of the three delays where test stimuli were congruent with the lifted finger (i.e. execute index lift, observe index lift) and 70 where test stimuli were incongruent with the lifted finger (i.e. execute index lift, observe middle lift). The experiment was divided into five blocks. The first four blocks comprised 84 trials each, while the fifth ran until participants had completed 210 of each finger lift (i.e. index or middle). In breaks between blocks participants were given on screen feedback regarding the percentage of index and middle finger lifts executed across the experiment. Responses beyond the 210th trial for each movement were not recorded. Trial type was randomized and participants completed eight practice trials.

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[1] The luminance of the brightest point on the finger was ~17 cd/m^2 before it flashed, rising to a maximum of ~37 cd/m^2, with stepsizes of ~3 cd/m^2. Luminance was measured with a Konica Minolta Chromometer CS1000A

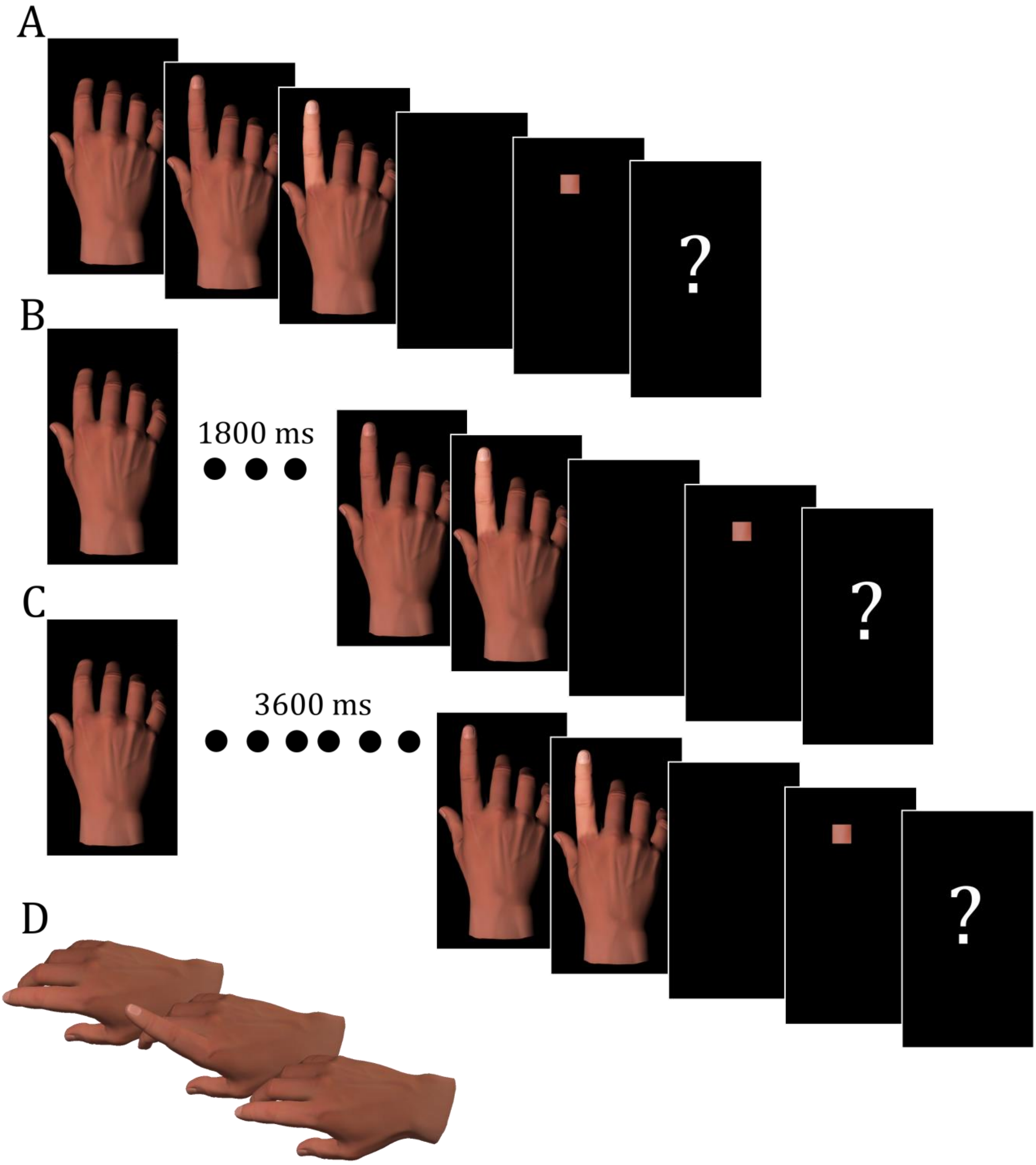

Figure 1. The timecourse of stimulus presentation on a single trial in both Experiments 1 and 2. Sensory outcomes were presented at a 0ms (A), 1800 ms (B) or 3600 ms delay (C) relative to the participant's own executed action (D). In the above figure the observed outcome (index lift) is congruent with the executed action. Note that in Experiment 1 participants were required to report which event (target or reference) was brighter, while in Experiment 2 participants were required to report whether the target and reference events were the same brightness or not. Hand stimuli were generated using Poser 7.0 (Smith Micro Software).

To estimate psychometric functions, the responses for each individual were modelled by fitting cumulative Gaussians, and associated pDev statistics were calculated to establish the goodness-of-fit of each function (Palamedes toolbox, Kingdom & Prins, 2009). This procedure was performed separately for congruent and incongruent response data for each action-outcome delay level. In each condition, bias was inferred from the PSE and precision from the difference threshold. The PSE describes the point where participants judge the target and reference events to have equal brightness, with lower values indicative of brighter percepts. Judgment precision was inferred from the standard deviation of the Gaussian distribution which best fits the data; it pertains to the inverse of the slope, with lower thresholds reflecting more consistent categorizations, thereby indicating better performance.

2.2. Results

Participants successfully followed the instruction to perform roughly equal numbers of each movement type, with a mean of 49.66 % (SEM = .005 %) index finger movements across the experiment. This ratio led to a mean number of 434 trials (SEM = 3.45), which represents a small difference compared to the minimum of 420 that would be achieved by perfectly balanced action selection. There were no outliers.

PSE and precision values were analyzed with a 2 x 3 repeated measures ANOVA, with factors of Action Congruency (congruent, incongruent) and Delay (0, 1800, 3600 ms). Where appropriate, Greenhouse-Geisser corrections were applied. The precision analysis found no effect of Action Congruency (p=.264) or Delay (p=.086) and no interaction between these factors (p=.423). However, importantly, the PSE analysis revealed a significant main effect of Action Congruency ($F(1,23) = 7.96$, p=.010, η_p^2 =.257) reflecting the fact that participants had lower PSEs (i.e., brighter target percepts) for congruent (mean = 36.7%, SEM =1.6) compared to incongruent stimuli (mean = 39.4%, SEM =1.9; see Figure 2). No main effect of Delay (p=.067) or importantly, any interaction between Congruency and Delay (p=.807) was observed.

To examine whether the non-significant interaction between Congruency and Delay reflects the absence of an effect or a lack of statistical power, we calculated a Bayes Factor (BF_{10}) which represents the ratio of evidence for the alternative model over evidence for the null model. It is assumed that $BF_{10}<.33$ provide good evidence to support the null (Jeffreys, 1939; Lee & Wagenmakers, 2014). We conducted a repeated measures Bayesian ANOVA in JASP (Love et al, 2015) with the same factorial structure. This analysis revealed evidence for the null hypothesis over an interaction effect ($BF_{10} = 0.145$).

2.3. Discussion

The effect of Action Congruency, and the absence of its interaction with Delay, therefore provides evidence that sensorimotor predictions exhibit the requisite generality to predict imitative responses across action-outcome delays comparable to those found in natural social settings.

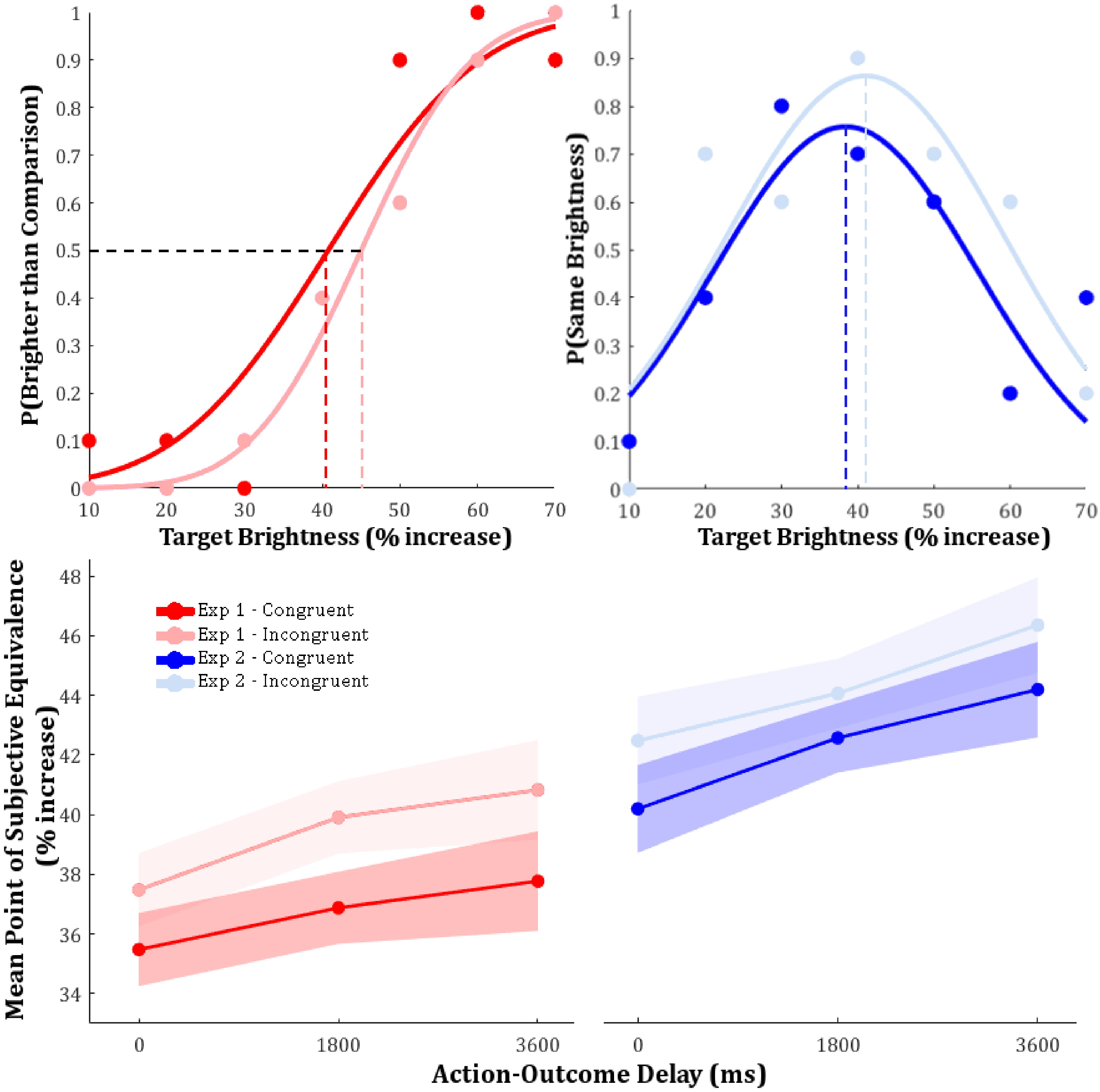

Figure 2. Top panel: Demonstration of how the point of subjective equivalence (PSE) was calculated in Experiment 1 (left) and Experiment 2 (right) with psychometric functions from example participants for stimuli congruent (solid) and incongruent (faded) with executed actions. The PSE describes the point where participants judge the target and comparison events to have equal brightness. When target stimuli are perceived as brighter PSEs tend towards *lower* values. Bottom panel: Mean PSEs for stimuli congruent and incongruent with action, across all action-outcome delays across both experiments. Error bars represent 95% within-participant confidence intervals (Cousineau, 2005).

3. Experiment 2

The results from Experiment 1 provide evidence that congruent action outcomes are judged to be more intense than incongruent action outcomes regardless of whether these outcomes occur immediately after action execution (0 ms condition: replicating Yon & Press, 2017) or delays in the order of seconds are imposed between actions and outcomes (1800 and 3600 ms conditions). This result is consistent with the hypothesis that sensorimotor predictions may influence perceptual processing of imitative reactions, increasing their apparent intensity via increases in sensory gain that result from prediction (Han & VanRullen, 2016; Summerfield & de Lange, 2014; Yon & Press, 2017).

Our PSE measure was chosen to index perceptual biases that may be induced by sensorimotor predictions. However, PSE measures of perceptual biasing can also be influenced by response biasing. For example, in Experiment 1 all action outcomes may have been perceived with equivalent brightness, but participants may have been biased to select the interval where the congruent action outcome occurred. Such biases could occur given previous reports that activity in decision making circuits can be biased towards responding for expected events even before a stimulus has been presented (Hanks, Mazurek, Kiani, Hopp & Shadlen, 2011; Summerfield & de Lange, 2014). A particular concern is the possibility that sensorimotor predictions generated perceptual biases when action outcomes were simultaneous (in line with previous work – Yon & Press, 2017, where effects were not due to response bias), but generated response biases at later delays – giving the impression of a temporally-general perceptual prediction.

To address this concern we designed a version of the task which dissociates response biases from perceptual biases (cf. Experiment 3; Yon & Press, 2017). Experiment 2 was identical to Experiment 1, though the nature of the question asked was altered. Rather than eliciting a comparative judgment (was the first or second event brighter?) participants were asked to complete an equality judgment (were the two events the same or different brightness?).

Gaussians were fitted to responses rather than Cumulative Gaussians (see Figure 2). The PSE was therefore derived as the mean of the function and the precision as the standard deviation. The advantage of an equality judgment is that it no longer requires participants to select a particular stimulus as more intense on a given trial, and ensures that biases to opt for one response alternative (i.e. same or different) no longer influence the PSE value (Han & VanRullen, 2016; Schneider & Komlos, 2008). Therefore, if any of the effects seen in Experiment 1 reflect a bias to select the congruent event they should not be found in Experiment 2. Alternatively, PSE effects determined by perceptual biases will remain.

3.1. Methods

Participants: Twenty-four new participants (21 female, mean age = 21.4 years, SD= 2.5) were recruited from Birkbeck, University of London and given a small honorarium for their participation. Fourteen of these were replacements for participants who did not follow task instructions or where points of subjective equivalence modelled to their responses were beyond the range of presented stimuli. This relatively high exclusion rate in comparison to Experiment 1 most likely reflects the fact that equality judgments are much more difficult and generate noisier estimates of underlying psychometric functions than do comparative judgments with equivalent stimuli (Anton-Erxleben, Abrams, & Carrasco, 2010).

Stimuli and Procedure: Stimuli and procedure used were identical to Experiment 1. However, participants were not asked to judge whether the target or reference stimulus was brighter, but whether the two events were the same or different brightness. Psychometric functions were therefore modelled as standard (not cumulative) Gaussians, with the mean of the modelled function taken as the PSE and judgment precision was inferred from the standard deviation.

3.2. Results

Participants successfully followed the instruction to perform roughly equal numbers of each movement type, with a mean of 50.61 % (SEM = .003 %) index finger movements across the experiment. This ratio led to a mean number of 430 trials (SEM = 2.25), again representing a small difference compared to the minimum of 420. There was one outlier (468 trials), but removal of this outlier did not alter the statistical pattern of results.

PSE and precision values were analyzed with a 2 x 3 repeated measures ANOVA, with factors of Action Congruency (congruent, incongruent) and Delay (0, 1800, 3600 ms). Where appropriate, Greenhouse-Geisser corrections were applied. The precision analysis revealed a main effect of Delay - $F(2,46) = 4.843$, p=.023, η_p^2 =.174 – which followed a significant quadratic trend, $F(1,23) = 6.139$, p=.021, η_p^2 =.211. This effect reflected that fact that judgment precision was significantly lower for events presented at the 1800 ms action-outcome delay (mean = 29.9 %, SEM =2.08) than events presented at either the 0 ms delay (mean =25.9 %, SEM = 1.88; $t(23) = 2.373$, p=.026) or the 3600 ms delay (mean = 26.8 %, SEM = 1.50; $t(23) = 2.366$, p=.027; precision at the 0 ms and 3600 ms delays did not differ, p=.330). No other significant effects were obtained in the precision data (all $p \geq .530$).

The PSE analysis also revealed a significant effect of Delay - $F(2,46) = 4.152$, p=.022, η_p^2 =.153. This main effect of Delay followed a linear trend – $F(1,23) = 7.22$, p=.013, η_p^2 =.239 – and reflected lower PSEs (i.e. brighter percepts) for events presented at the 0 ms delay (mean = 42.1 %, SEM = 2.31) relative to the 3600 ms delay (mean = 45.7 %, SEM = 1.78; $t(23) = 2.69$, p=.013), with the PSEs lying intermediate at the 1800 ms delay (mean = 43.8%, SEM = 2.19) although not differing significantly from 0 ms (p = .211) or 3600 ms (p =.079) conditions.

Crucially, the PSE analysis again demonstrated a significant effect of Action Congruency - $F(1,23) = 7.313$, p=.013, η_p^2 =.241 – which did not interact with Delay (p=.928). This main effect reflected lower PSEs for congruent action events (mean = 42.9 %, SEM = 2.06) than incongruent events (mean = 44.8 %, SEM = 1.96) – suggesting that predicted action outcomes were perceived as brighter than unpredicted ones, and that this pattern does not reflect a response bias caused by expectation (Hanks et al, 2011). The non-significant Action Congruency x Delay result was again shown through a Bayesian ANOVA in JASP to reflect the absence of an effect ($BF_{10} = .126$).

3.3. Discussion

The effect of Delay on judgment precision was unpredicted. A speculative explanation for this effect is that the timing of the event is perhaps least expected at 1800 ms (see Rohenkohl, Cravo, Wyart & Nobre, 2012), relative to the timepoint at which action outcomes typically occur (0 ms) and the timepoint which is the latest employed in this paradigm (3600 ms; i.e., if an event has not been presented by this point in the epoch then its arrival is certain). One could further speculate that such an effect is more pronounced in more difficult tasks (see Ratcliff, 2014), explaining why it was obtained with the harder equality judgment in Experiment 2 but not the easier comparative judgment in Experiment 1 (Anton-Erxleben, Abrams, & Carrasco, 2010). The main effect of Delay on PSEs may similarly reflect greater processing of events occurring at the earliest timepoint, given the typically strong likelihood that outcomes are simultaneous with action.

Most importantly, the main effect of Action Congruency and the convincing absence of an Action Congruency x Delay interaction suggest that the results of Experiment 1 were not due to participants being more likely to select the congruent event through response bias. Instead, they provide further support for the hypothesis that sensorimotor predictions exhibit generality across action-outcome delays.

4. Cross-experiment analysis

Experiments 1 and 2 tested the hypothesis that we repurpose the sensorimotor processes for predicting the immediate direct consequences of our own movements to support perception of similar – but delayed – reactions in others. To this end they were designed to establish whether an effect of prediction on perception (greater apparent brightness of congruent relative to incongruent sensory events) interacted with Delay between action and perceived outcome. Consistent with the hypothesis, these experiments revealed a main effect of Action Congruency on PSEs, with evidence against an interaction with Delay. The experiments and associated power analyses were designed to test the hypothesis via these analyses (Gelman & Stern, 2006) but we were interested post-hoc in whether the Congruency effect could be shown independently at each of the three tested delays. We therefore combined samples from both experiments for maximum sensitivity and conducted 2 x 2 mixed ANOVAs with factors of Action Congruency (congruent, incongruent) and Experiment (1,2) separately for PSE values at each delay. These analyses revealed a significant effect of Action Congruency at the 0 ms ($F(1,46) = 4.845$, $p=.033$. $\eta_p^2= .095$), 1800 ms ($F(1,46) = 6.95$, $p=.011$, $\eta_p^2 = .131$) and 3600 ms ($F(1,46) = 4.764$, $p=.034$. $\eta_p^2 = .094$) delays – with no interactions between Action Congruency and Experiment at any delay (all $p \geq .373$, all $BF_{10} \leq .318$). These results therefore tentatively suggest that predictions of our own action consequences could support perception of others' imitative reactions regardless of the specific suprasecond delay before the reaction.

5. General Discussion

It is widely assumed that the sensorimotor predictive processes we use for controlling our own actions are useful for supporting perception of the imitative reactions of others (e.g., Schütz-Bosbach & Prinz, 2007). However, it has been unclear whether sensory predictions generated during action have the requisite generality across time to be useful for perceiving imitation in others. In both experiments reported here we found evidence consistent with the hypothesis that such generality is indeed present - signatures of predictive processing, i.e., more intense percepts for action-congruent relative to -incongruent sensory events, were found regardless of whether outcomes were observed immediately or at suprasecond delays.

The finding of greater apparent intensity for action-congruent than –incongruent events is consistent with a number of previous demonstrations that predicted sensory events are perceived with greater phenomenal intensity (e.g., Han & VanRullen, 2016) and accord with computational models which hypothesise that prediction increases the gain on expected sensory units. Under these accounts, 'gain modulations' are akin to increasing the activation in these units, which enhances the effective strength of associated sensory signals (Wyart, Nobre & Summerfield, 2012; see also Tsetsos & Summerfield, 2015; Carrasco, Ling & Read, 2004). These brightness effects are thereby considered to be part of a wider phenomenon whereby predictive processes facilitate perception through enhancing effective signal strength – increasing detectability (Yuille & Kersten, 2006) and speeding the entry of stimuli into awareness (Pinto, van Gaal, de Lange, Lamme, & Seth, 2015), as well as increasing phenomenal intensity (NB. detection and intensity judgments are thought to depend on identical computational quantities and a detection 'threshold' is simply considered the weakest perceptible intensity; Brown et al., 2013). These schemes are likely to be an adaptive use of our perceptual systems in the face of a natural environment containing high levels of sensory noise and a large number of sensory events (Summerfield & de Lange, 2014; Yuille & Kersten, 2006). Namely, they will bias perceptual processing towards events that are more likely to occur, leading to the rapid construction of (on average) more veridical percepts.

The present findings crucially demonstrate that visual predictions during action operate with a temporal profile that allows them to influence imitative reactions. The resulting increased sensitivity to these reactions is proposed to promote fluent social interactions by facilitating rapid and appropriate responses to our partner's behaviour (e.g., Schütz-Bosbach & Prinz, 2007). It has also been suggested that it may facilitate pro-social effects that result from perceiving imitation in others, e.g., increased social motivation and rapport (e.g., Bailenson & Yee, 2005; Neufeld & Chakrabarti, 2016; van Baaren, Holland, Steenaert, & van Knippenberg, 2003) given that the signal on which these effects depend is enhanced. Furthermore, one could speculate that – by comparison between predictions and sampled inputs - these predictive processes could also assist the detection of unexpected *absences* of imitation (e.g., when a friend does not return a wave). Sensitivity to such prediction errors could be useful in highlighting the need for further learning (e.g. to infer whether they are upset with are us) or the need for a novel response (e.g. to call their name).

Interestingly, this generalization appears inconsistent with a handful of studies in the tactile domain which suggest that sensorimotor predictions show precise temporal tuning[2]. For example, signatures of sensorimotor prediction on tactile perception are seen when action execution and sensory outcomes are synchronous, but these influences are not seen when delays of ~300 ms are imposed between action and outcome (Bays, Wolpert, & Flanagan, 2005; Blakemore, Frith & Wolpert, 1999). These findings have been argued to reflect adaptive processes for action control, given that subsecond tuning will allow the predictive processes to contribute to rapid error correction (Wolpert et al., 1995) and the agentive labelling of self-produced events (Frith, Blakemore, & Wolpert, 2000). However, the present experiments present the first investigation of the temporal properties of *visual* prediction during action (NB: the only visual work of relevance has not dissociated between temporal and spatial elements of prediction, see Christensen et al., 2011), and these discrepant findings can therefore be integrated if it is assumed that visual predictions exhibit broader temporal tuning than tactile predictions. Given that imitative reactions are typically perceived visually, such a separation

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[2] The experiments supporting this assumption have been designed to examine action control theories. To this end they have compared predictive effects for simultaneous outcomes and those following subsecond delays and consistently find the largest effects in simultaneous conditions. Given that our primary aim was to test theories from social cognition, it was more appropriate to compare simultaneous conditions against those employing suprasecond delays given that imitative reactions occur in the order of seconds, not milliseconds (see Catmur & Heyes, 2013).

between modalities may be most adaptive in balancing temporal sensitivity to optimize action control with the temporal generality required to optimize perception of others.

The hypothesis tested in these experiments proposes that predictions we generate about the consequences of our own actions also influence perceptual processing of imitative reactions of others (Wolpert et al., 2003; Schutz-Bosbach & Prinz, 2007). This hypothesis would appear to assume that the learning we acquire through sensorimotor experience with our own direct action effects at subsecond delays (e.g., observing our own index finger tapping; de Wit & Dickinson, 2009; Elsner & Hommel, 2004; Wolpert, Diedrichsen, & Flanagan, 2011) generalizes over suprasecond action-outcome delays (Pearce, 1987). Under this assumption, these processes may only operate for the prediction of *imitative* reactions in others. However, an alternative possibility is that predictions at delay may be derived by specific experience of others imitating our actions at delay. This account is consistent with the idea that the socio-cultural environment is responsible for furnishing the mechanisms needed for social interaction (Brass & Heyes, 2005; Heyes, 2012). This latter possibility is easier to reconcile with reports of temporal precision in touch (Bays et al., 2005), as we have little opportunity to learn that tactile outcomes follow our actions at delay. Importantly, this hypothesis assumes that the predictive process is not dependent on the fact that imitative reactions match our actions but only that they are typically the most probable reaction (see Ray & Heyes, 2011). The same process could therefore in principle facilitate perception of non-matching reactions in settings where these are more likely. For instance, expressions of aggression and dominance (e.g., expansive postures) tend to elicit expressions of submission (e.g., constricted postures) rather than mirrored aggression (Tiedens & Fragale, 2003). Under this account, any predicted reaction would benefit from the same facilitated processing, hence further contributing to smooth and appropriate responses to others during social interaction.

In conclusion, the present study provides support for the hypothesis that sensorimotor predictive processes show a temporal profile which can support the perceptual processing of imitative reactions in others, with a host of potential benefits in social settings.

Acknowledgements: This work was funded by an ESRC studentship (DY) and a Leverhulme Trust project grant (CP, DY; RPG-2016-105).

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