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Predicted action consequences are perceptually facilitated before cancellation

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Running head: Sensory prediction during action

Abstract

Models of action control suggest that predicted action outcomes are 'cancelled' from perception, allowing agents to devote resources to more behaviorally-relevant unexpected events. These models are supported by a range of findings demonstrating that expected consequences of action are perceived less intensely than unexpected events. A key assumption of these models is that the prediction is subtracted from the sensory input. This early subtraction allows preferential processing of unexpected events from the outset of movement, thereby promoting rapid initiation of corrective actions and updating of predictive models. We tested this assumption in three psychophysical experiments. Participants rated the intensity (brightness) of observed finger movements congruent or incongruent with their own movements at different timepoints after action. Across Experiments 1 and 2, evidence of cancellation – whereby congruent events appeared less bright than incongruent events – was only found 200 ms after action, whereas an opposite effect of brighter congruent percepts was observed in earlier time ranges (50 ms after action). Experiment 3 demonstrated that this interaction was not a result of response bias. These findings suggest that 'cancellation' may not be the rapid process assumed in the literature, and that perception of predicted action outcomes is initially 'facilitated'. We speculate that the representation of our environment may in fact be optimized via two opposing processes: The primary process facilitates perception of events consistent with predictions and thereby helps us to perceive what is more likely, but a later process aids the perception of any detected events generating prediction errors to assist model updating.

Keywords: Motor Processes; Prediction; Perception; Cancellation; Sensorimotor Integration.

Public significance statement: When we perform an action we can usually predict the effects it will have on the environment. For example, when pressing a doorbell we expect to see a moving hand, to feel touch on our fingertips and to hear the bell ring. Previously it has been suggested that we are worse at perceiving sensations we produce because of processes in the brain that remove what was predicted from the sensations that we experience. These processes are thought to explain why we cannot tickle ourselves. However, the present study suggests that these processes are unlikely to work in the way that is commonly thought. We find evidence that we in fact have stronger perceptual experiences for expected effects very soon after we begin to move. We suggest that this finding could reflect the existence of two complementary processes that influence how we perceive the outcomes of our actions.

Introduction

It has long been appreciated that action control depends on predicting the sensory consequences of our movements (James, 1890). We select actions based on their predicted outcomes (Hommel, Müsseler, Aschersleben, & Prinz, 2001; Shin, Proctor, & Capaldi, 2010) and can use these predictions to generate rapid corrective actions when we experience deviant sensory input (Wolpert, Ghahramani, & Jordan, 1995). In recent decades, interest has developed in the functional mechanisms via which these predictions may also alter the perception of action outcomes. Prompted by anecdotal observations that it is difficult to tickle oneself (Weiskrantz, Elliott, & Darlington, 1971), researchers have reported numerous experiments where events expected on the basis of action are perceptually attenuated. For instance, self-generated tactile forces and auditory tones are perceived as less intense than externally-generated events (Bays, Wolpert, & Flanagan, 2005; Weiss, Herwig, & Schütz-Bosbach, 2011), and it is harder to detect masked arrows or low-contrast gabor patches when their orientation is congruent with an executed action (Cardoso-Leite, Mamassian, Schütz-Bosbach, & Waszak, 2010; Müsseler & Hommel, 1997a; 1997b). Interestingly, signals predictable on the basis of action are also associated with reduced activity in early sensory brain regions (Blakemore et al., 1998; Shergill et al., 2013; Stanley & Miall, 2007). Therefore, it has been concluded that expected visual, tactile and auditory consequences of action are perceptually attenuated relative to their unexpected counterparts.

These perceptual and neural effects have largely been interpreted under the Cancellation framework (Wolpert et al., 1995; see also 'Code Occupation Hypothesis'; Stoet & Hommel, 1999; Hommel, 2004). The Cancellation model suggests that during

action execution a forward model predicts the likely sensory consequences that will arise as a result of movement. When experienced inputs closely match those predicted by the motor system, they are 'cancelled' from perception. Such a mechanism is thought to enable preferential processing of unexpected events that are more likely to require learning or a novel response, supporting adaptive interaction with the physical and social world. For example, when picking up a cup of tea agents will reduce processing of expected sensory events (e.g., sight of grasping, pressure on the fingertips) relative to unexpected ones (e.g., the sight of spillage) to enable rapid initiation of corrective actions and updating of predictive models. Similarly, when interacting with others, greater processing of unexpected reactions (e.g., a frown after a wave) may facilitate social exchanges (Wolpert, Doya, & Kawato, 2003). In recent decades it has also been suggested that this mechanism plays a fundamental role in constructing our sense of agency during action (Frith, Blakemore, & Wolpert, 2000) and that its malfunction may contribute to delusions of control experienced in schizophrenia and the healthy population (Shergill, Samson, Bays, Frith, & Wolpert, 2005; Teufel, Kingdon, Ingram, Wolpert, & Fletcher, 2010).

A key assumption of these models is that the prediction is subtracted from the sensory input (Bays & Wolpert, 2007). This early subtraction allows resources to be devoted to unexpected events from the outset of movement, thereby promoting rapid initiation of corrective actions and updating of predictive models. Such an early perceptual attenuation of expected events therefore supports smooth and finely-timed interactions with our physical and social environments (Wolpert et al., 1995). However, the timecourse of cancellation effects has not been examined. Specifically, while we know that imposing a delay between action and effect reduces cancellation effects (Bays et al.,

2005; Blakemore, Frith, & Wolpert, 1999) – suggesting that temporal features of the outcome may constitute part of the action prediction – we do not know whether cancellation effects reflect immediate or later influences on perception.

The present experiments were conducted to assess systematically the timecourse of influences of action on perception. Participants abducted either their index or middle finger, while observing synchronized abduction of the same or opposite finger of an onscreen hand (constituting outcomes congruent and incongruent with expectation, respectively). To mirror the measure typically used in the literature testing the Cancellation model, we required participants to judge the intensity (brightness) of these congruent and incongruent outcomes at different timepoints after action (50 ms, 200 ms, 350 ms). It should be noted that the field typically studies perceived intensity of tactile outcomes (e.g., ticklishness or force), but that models hypothesize comparable influences across all modalities where sensation can be predicted on the basis of action (Brown, Adams, Parees, Edwards, & Friston, 2013; Wolpert et al., 2003). The use of visual stimuli allowed us to isolate easily those effects due to prediction, relative to those due to generalized suppression of any tactile sensation on a moving effector regardless of whether it was predicted or not (likely mediated by spinal mechanisms; Seki & Fetz, 2012).

We probed the perceived brightness at specific timepoints by temporarily altering the luminance of the outcome and requiring participants to judge its brightness relative to a subsequently presented reference stimulus. Brighter perception of incongruent relative to congruent outcomes would be predicted under the Cancellation account. Specifically, all models of Cancellation of which we are aware predict effects on low level attributes

such as tactile force and visual brightness. For example, formulations based on predictive coding equate phenomenal intensity (e.g., brightness contrast) with the precision of a sensory estimate (Brown & Friston, 2012) and suggest that cancellation mechanisms reduce the precision on expected sensory channels during action (Brown et al., 2013). If predictive attenuation occurs from the outset of an executed action, congruent outcomes should be perceived as less bright than incongruent outcomes as soon as an action has been initiated, i.e., at the earliest timepoint of 50 ms. However, if cancellation is in fact reflective of a later process, this effect will only be found at a delay after action, i.e., not at 50 ms, but at 200 ms or 350 ms.

Experiment 1

In Experiment 1, participants performed finger movements while observing synchronized congruent and incongruent effects, and judged the brightness of these effects at different delays after action (50 ms, 200 ms and 350 ms).

Methods

Participants: Twenty-six participants (17 female, mean age = 27.5 years [SD = 9.14]) were recruited from Birkbeck, University of London and paid a small honorarium for their participation. These included ten replacements for participants who could not perform the necessarily challenging perceptual discrimination (Points of Subjective Equivalence [PSEs] were beyond the range of presented stimuli and/or acceptable psychometric functions could not be modelled to their responses – see below). The

sample size was determined a priori on the basis of pilot testing to estimate effect size. The experiment was performed with local ethical committee approval and in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Design: A within-participants design was used with factors of Action Congruency (congruent, incongruent) and Delay (50, 200, 350 ms).

Procedure: The experiment was conducted in MATLAB using the Cogent toolbox[i]. At the start of the trial, a hand at rest was presented on a computer monitor (Fig. 1; LCD monitor, 153 x 32 cm, 60 Hz, 82 DPI). Participants held down two keys on a keypad until an imperative cue instructed them to abduct either their index ('1') or middle ('2') finger. They were instructed to make large, rapid, single-movement abductions and their hand was visually occluded (NB. hands were not occluded during training to verify that participants were executing the actions as instructed). When participants abducted the cued finger, the neutral hand image was immediately replaced by one depicting the hand performing either an index or middle finger abduction for 600 ms (given the screen refresh rate, the effect was presented within ~16.6 ms of the action). This sequence resulted in apparent motion of the observed finger approximately synchronized with the participant's action. At a variable time after the observed and executed abduction (50 ms, 200 ms, or 350 ms), the finger flashed for 100 ms at one of seven intensities (increased brightness by 10-70 %, in 10 % steps[ii]). Following an inter-stimulus interval (ISI) of 1000 ms a reference stimulus (the abducted finger at a central position between the index and middle finger locations) was presented at 40 % increased brightness of the observed hand for 100 ms.

After 400-500 ms participants judged whether the target or reference event was brighter, responding with a keypress made with their left thumb. They subsequently returned their right abducted finger to the start key, with their finger abducted throughout the trial until this point. The next trial started after 1000 ms. There were 420 trials; 70 at each of the three delays in the congruent condition and 70 at each delay in the incongruent condition. For each combination of congruency and delay, each of the seven intensities (10-70 %, 10 % steps) was presented ten times. As such, for the first three intensity steps the target flash was less bright than the reference event, for the middle intensity it was of equal brightness and for the last three steps it was brighter. Trial type was randomized and participants completed eight practice trials.

To estimate psychometric functions, responses for each individual were modelled by fitting cumulative Gaussians, and associated pDev statistics were calculated to establish each function's goodness-of-fit (Palamedes toolbox, Kingdom & Prins, 2009). Participants with unacceptably poor fits (pDev < 0.05 for any function) were not analyzed further. This procedure was performed separately for congruent and incongruent response data for each 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. Judgement 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 (see Fig. 2).

Results

PSE and precision values were analyzed with separate ANOVAs. No significant effects were found in the precision data (all $p \geq .595$). However, the PSE analysis revealed a significant main effect of Delay, $F(2,50) = 32.830$, $p < .001$, $\eta_p^2 = .568$, alongside a significant interaction between Delay and Action Congruency, $F(2,50) = 5.530$, $p = .007$, $\eta_p^2 = .181$. This interaction was driven by lower PSEs for congruent (mean = 30.7 %, SEM = 2.14 %) than incongruent (mean = 34.0 %, SEM = 2.11%) action outcomes at 50 ms delay ($t(25) = 2.236$, $p = .035$, $d = .301$), higher PSEs for congruent outcomes at 200 ms (congruent mean = 39.5%, SEM = 1.74 %; incongruent mean = 37.2 %, SEM = 1.75 %; $t(25) = 2.875$, $p = .008$, $d = .260$), and no effect of congruency at the 350 ms delay ($t(25) = .383$, $p = .705$, $d = .042$; see Fig. 2).

Reaction times (RTs) for the unspeeded perceptual judgements were also analyzed using a repeated measures ANOVA. There were no significant effects (all $p \geq .219$).

Discussion

These findings demonstrate that congruent outcomes are perceived to be brighter at 50 ms delay (lower PSE = brighter target percept), but this effect switches to brighter perception of incongruent outcomes at 200 ms. Strikingly, this result contrasts with assumptions made by the Cancellation model, whereby brighter perception of incongruent outcomes would be expected at all time-ranges.

Experiment 2

The findings of Experiment 1 are difficult to reconcile with current formulations of the Cancellation model, given that cancellation effects are not observed at early timepoints (50 ms). However, this switching from a facilitatory to attenuating influence on perception is reminiscent of 'inhibition of return' effects observed in the spatial attention literature (Posner & Cohen, 1984). Unsurprisingly, attending towards a spatial location facilitates perception of events presented nearby. However, spatially localized perceptual decrements are observed shortly after facilitatory effects. In Experiment 1, when participants abducted their index finger, an observed 'congruent' event both matched the digit moved (e.g., index finger) and spatial location (e.g., both stimulus and response events were on the left of fixation). Given that attention is known to modulate perceived brightness (Carrasco, Ling, & Read, 2004), it is possible that the effects in Experiment 1 reflect the spatial location of action effects rather than their action (effector) congruency. Experiment 2 removed simple spatial congruency first by rotating the response hand 90° with respect to the observed hand, such that both index and middle finger movements were at body midline. Second, half of participants judged the brightness of non-action rather than action stimuli presented at the same spatial locations. If effects were equivalent in Action and No Action conditions, spatial locations would appear to drive effects, but if they were only present in the Action condition, they would appear dependent on observation of a predicted action outcome (observation of finger abduction rather than an arbitrary event at the same location).

The 350 ms delay was also removed given that effects were not observed at this delay in Experiment 1, and the task was modified such that action type was self-selected rather than cued by an imperative, thus removing any congruency between imperative cues

and the observed movement. Finally, an arbitrary square was used as the reference stimulus, removing any potential congruency between responses and the reference event.

Methods

Participants: Twenty-six new participants (21 female, mean age = 24 years [SD = 5.67]) were recruited. Three were replacements for participants who could not complete the perceptual discrimination. Participants were randomly allocated to either the Action or No Action condition (see below), creating two groups of thirteen. The sample size was determined a priori on the basis of the effect size in Experiment 1. Inclusion criteria, as well as ethical support, were the same as in Experiment 1.

Design: A mixed design was used, with the between-participants factor of Stimulus (Action, No Action) and the within-participants factors of Action Congruency (congruent, incongruent) and Delay (50, 200 ms).

Procedure: The stimuli and procedure used in Experiment 2 were identical to that of Experiment 1 with the following changes. The keypad was rotated 90°, such that both index and middle finger movements were at body midline, and participants were free to execute either an index or middle finger lift on each trial rather than responding to an imperative. Participants were instructed to perform roughly equal numbers of each movement in a random sequence. When participants lifted their finger, the neutral hand image (CRT monitor; 32 x 24 cm, 85 Hz, 21 DPI) was immediately (within ~11.8 ms, given the screen refresh rate) replaced by the target stimulus. For participants in the

Action condition, this image was identical to Experiment 1. In contrast, participants in the No Action condition saw a square overlaid on either the index or middle finger (neutral hand image), matching the action event for hue and luminance. At 50 or 200 ms after the participant's action the abducted finger/square would flash [iii] for 100 ms before returning to its original brightness level for a further 300 ms. Following a 1000 ms ISI, a reference square was presented for 100 ms (see Fig. 1).

Participants completed at least 280 trials; 70 at each of the two delays in the congruent and incongruent conditions. The experiment was divided into four blocks. The first three blocks each comprised 70 trials, while the fourth ran until participants had completed 140 trials of each lift. In breaks between blocks participants were given feedback on-screen regarding the distribution of their responses. Responses beyond the 140th trial for each movement were not recorded.

Results

PSE and precision values were analyzed via separate ANOVAs. No significant effects were found in the precision data (all $p \geq .078$). However, the PSE analysis revealed a significant main effect of Delay, $F(1,24) = 37.077$, $p < .001$, $\eta_p^2 = .607$, alongside a significant interaction between Delay and Action Congruency, $F(1,24) = 6.497$, $p = .018$, $\eta_p^2 = .213$ and a three-way interaction between Delay, Action Congruency and Stimulus, $F(1,24) = 4.840$, $p = .038$, $\eta_p^2 = .168$.

To clarify the nature of this three-way interaction we conducted separate two-way ANOVAs looking at the effects of Action Congruency and Delay in each Stimulus

condition (Action, No Action). These analyses revealed that while an interaction between Action Congruency and Delay was found in the Action condition, $F(1,12) = 9.924$, $p=.008$, $\eta_p^2 = .453$, this interaction was absent in the No Action condition, $F(1,12) = .070$, $p = .795$. Simple effects analyses found that the effects obtained in Experiment 1 were replicated in the Action condition - at the 50 ms delay PSEs were lower for congruent (mean = 30.03 %, SEM = 2.35 %) than incongruent (mean = 33.31 %, SEM = 1.89 %) outcomes ($t(12) = 2.395$, $p = .034$, $d = .350$), while PSEs were higher for congruent (mean = 38.7 %, SEM = 2.4 %) than incongruent (mean = 35.7 %, SEM = 2.69 %) action outcomes at the 200 ms delay ($t(12) = 2.470$, $p = .029$, $d = .311$; see Fig. 2). Like Experiment 1, these findings demonstrate that congruent outcomes are perceived to be brighter at 50 ms delay, but the effect switches to brighter perception of incongruent outcomes at 200 ms. In contrast, and in line with the non-significant interaction, no effects of Action Congruency were detected in the No Action condition at either the 50 ms ($p = .747$) or 200 ms delays ($p = .949$).

RTs for the unspeeded perceptual judgements were also analyzed with a mixed model ANOVA. This analysis revealed a significant effect of Action Congruency - $F(1,24) = 5.132$, $p = .033$, $\eta_p^2 = .176$ – with faster judgments for incongruent (mean = 641.1 ms, SEM = 62.6 ms) relative to congruent (mean = 667.2 ms, SEM = 65.0 ms) outcomes [iv]. There were no other main effects and no interactions (all $p \geq .103$). We repeated the PSE analysis including the congruent-incongruent difference in mean RT for each participant as a covariate. The key three-way interaction between Action Congruency, Delay and Stimulus was also significant when this covariate was included, $F(1,23) = 6.982$, $p =.015$, $\eta_p^2 = .233$, as was the two-way interaction between Action Congruency

and Delay in the Action condition, $F(1,11) = 6.406$, $p=.028$, $\eta_p^2 = .368$. The same two-way interaction remained non-significant in the No Action condition ($p=.919$).

Discussion

These findings in the Action condition provide further support for the idea that predictive attenuation of expected action outcomes does not occur immediately after action execution, but at a delay. Interestingly, the results provide further evidence for an early facilitation of expected outcomes, contrary to the predictions of the Cancellation model. Moreover, the persistence of both effects having controlled for simple spatial features of stimuli, and their absence in the No Action condition, suggests that the underlying mechanisms are sensitive to the expected identity of action effects, rather than simply where in space they occur.

Experiment 3

Experiments 1 and 2 provide evidence of early increased intensity judgements for congruent stimuli, followed by increased intensity judgements for incongruent stimuli at delay. The PSE measure was chosen because Cancellation theories predict that action should bias perceived intensity, such that you are biased to perceive events as less intense when congruent with action. However, PSE measures of perceptual biasing can also be influenced by response biasing. For example, in Experiments 1 and 2, event types may be always perceived with equivalent intensity, but the PSEs may differ if participants are biased to select the first interval when the event is congruent with

expectations at 50 ms and the second interval when the event is congruent with expectations at 200 ms.

Therefore, we designed a version of the task where response biases could be dissociated from perceptual biasing. To this end, Experiment 3 presented a similar set-up to Experiment 2 (Action condition) but changed the nature of the question asked. Rather than performing a comparative judgment (was the first or second event brighter?), participants performed an equality judgment (were the two events the same or different brightness?). Gaussians were now fitted to their responses rather than Cumulative Gaussians (see Figure 2). The PSE was derived as the mean of the function and the precision was the standard deviation. This task has the important advantage that it precludes selection of a particular stimulus as more intense on a given trial, and ensures that biases to select a particular response alternative no longer influence the PSE value (Han & VanRullen, 2016; Schneider & Komlos, 2008). Therefore, if effects in Experiments 1 and 2 are a function of response bias they will not be found in this experiment. In contrast, PSE effects determined by perceptual biases will remain.

Methods

Participants: Twenty-six new participants (19 female, mean age = 24.7 years [SD = 4.1]) were recruited. Four were replacements for participants who could not complete the perceptual discrimination. Sample size was determined a priori on the basis of the effect size in Experiments 1 and 2. Inclusion criteria, as well as ethical support, were the same as in Experiments 1 and 2.

Design: A within-participants design was used with factors of Action Congruency (congruent, incongruent) and Delay (50, 200 ms).

Procedure: The procedure used was identical to the Action condition in Experiment 2. However, participants were not asked to report which stimulus was brighter (first or second) but whether the presented stimuli had the same brightness or different brightness. The stimuli shown were the same as those in Experiments 1 and 2. Responses were again recorded via keypresses with the participant's left thumb.

Results

PSE and precision values were analyzed via separate ANOVAs. No significant effects were found in the precision data (all $p \geq .165$). However, the PSE analysis revealed a significant main effect of Delay, $F(1,25) = 18.911$, $p<.001$, $\eta_p^2 = .431$, alongside a significant interaction between Delay and Action Congruency, $F(1,24) = 7.125$, $p = .013$, $\eta_p^2 = .222$. This interaction reflected the same pattern as observed in Experiments 1 and 2. At the 50 ms delay PSEs were lower for congruent outcomes (mean = 34.0 %, SEM = 2.44 %) than incongruent outcomes (36.3 %, SEM =2.62 %; $t(25) = 2.326$, $p = .028$, $d = .174$). The opposite pattern was seen at the 200 ms delay, with lower PSEs for incongruent outcomes (mean = 39.2 %, SEM = 2.39 %) than congruent outcomes (mean = 40.2 %, SEM = 2.37 %), although the difference at this delay did not reach statistical significance – $t(25) = 1.613$, $p = .119$.

RTs to make the unspeeded perceptual judgements were also analyzed with a repeated measures ANOVA. This analysis revealed no significant main effects or interactions (all $p \geq .418$).

Discussion

In summary, the same broad pattern of results was found as that in Experiments 1 and 2. Crucially, the effects of congruency once again varied as a function of timecourse, confirming that the equivalent effects in Experiments 1 and 2 are not driven by response bias. At the early interval we replicated the enhancement effect. However, we did not observe such convincing evidence of a later 'cancellation' effect. We propose that a likely reason for this difference with respect to Experiments 1 and 2 is that the task used in Experiment 3 was more difficult, producing noisier PSE estimates and resulting in a signal that was less reliably detected. It is worth noting that the cancellation effect has been found multiple times in previous experiments (i.e., it is the early effect / interaction with respect to timecourse that represents the novelty relative to previous studies) and that previous work explicitly comparing judgment types in similar psychophysical tasks suggests that equality judgments have reduced sensitivity to effects on perceived intensity when compared to comparative judgments (Anton-Erxleben, Abrams & Carrasco, 2010). This explanation is consistent with the observation that modelled functions were less precise relative to Experiments 1 and 2 (mean in Experiments 1 and 2 = 19.6 %; mean in Experiment 3 = 23.1 %; see also [v]).

Nevertheless, importantly this experiment conclusively supports the finding of Experiments 1 and 2 that predictive attenuation of expected action outcomes does not

occur immediately after action execution - that the influence of action on perception interacts with delay, and that in these early timeranges there is in fact a facilitatory influence.

Cross-experiment analysis: Response selection-perception relationship

In Experiment 1, responses were cued and therefore there was a random relationship between the responses on trial N and trial N-1 as well as between the responses on trial N and the stimuli on trial N-1 (note also that reaction times to execute these unspeeded responses were equivalent when responses were the same and alternating with respect to the previous trial, $t(25) = .042$, $p = .967$, and when they were imitative or counter-imitative with respect to the preceding stimuli, $t(25) = .987$, $p = .333$). In Experiments 2 and 3 participants chose voluntarily which actions to execute to remove any potential confounds related to imperative stimuli. In both experiments additional analyses demonstrated that participants showed a tendency to select actions which differed from the executed action on the preceding trial (to 'alternate'; Experiment 2: mean = 57.5 %, $t(25) = 2.676$, $p = .013$; Experiment 3: mean = 59.1 %, $t(25) = 3.236$, $p = .003$) and from the observed action on the preceding trial (to 'counter-imitate'; Experiment 2: mean = 52.6 %, $t(25) = 2.136$, $p = .043$; Experiment 3: mean = 55.1 %, $t(25) = 5.280$, $p = .003$). In principle, despite the lengthy temporal separation between the trials, these biases could provide additional sources of expectation that are confounded with action-effect congruency and which could therefore contribute to our observed perceptual effects.

To investigate this possibility, for each participant we analyzed the proportion of alternation choices and counter-imitative choices using a binomial test. This analysis allowed us to classify participants as either 'alternators' or 'non-alternators' (19 and 20 participants, respectively) and 'counter-imitators' or 'non-counter-imitators' (15 and 24 participants, respectively). We then conducted an additional factorial ANOVA on our PSE data, collapsed across Experiments 2 and 3 for maximal power (participants in the No Action condition of Experiment 2 were excluded as this group showed no perceptual effects). We included the same within-participants factors as in our main analyses (Action Congruency and Delay), and added the between-participants factors of Alternation (alternator, non-alternator) and Counter-imitation (counter-imitator, non-counter-imitator). This analysis found that the interaction between Action Congruency and Delay identified in our experiments did not significantly differ between the groups defined according to Alternation ($F(1,35) = .994$, $p=.326$) or Counter-imitation ($F(1,35)=1.638$, $p=.209$), and the four-way interaction between Action Congruency, Delay, Alternation and Counter-imitation was also found to be non-significant ($F(1,35) = .236$, $p=.630$). Therefore, these analyses suggest that the relationships between responses on trial N and responses / stimuli presented on trial N-1 did not contribute to the perceptual effects observed.

General Discussion

These experiments find evidence that congruent action outcomes are perceived with greater brightness 50 ms after action execution, while incongruent action outcomes

appeared brighter at a 200 ms delay. Importantly, both effects demonstrate specificity to perceived actions rather than spatial locations.

These results are inconsistent with current formulations of the Cancellation model. First, our results suggest that predictive attenuation does not emerge immediately after action, but at delay. This finding conflicts with the traditional assumption that the prediction is subtracted from the sensory input (Bays & Wolpert, 2007), promoting rapid initiation of corrective actions and updating of predictive models. Therefore, although forward models may allow rapid initiation of corrective action, it is perhaps unlikely that any perceptual cancellation aids the rapid corrections. However, perceptual 'cancellation' may still support a range of other functions hypothesized in the literature. For example, ideomotor theorists have appreciated that the tendency of actual and anticipated sensory effects to prime responses (Brass, Bekkering, & Prinz, 2001; Elsner & Hommel, 2001; Kunde, Koch, & Hoffmann, 2004) may generate a 'perseveration loop' – with agents performing actions, producing effects, and having the same actions subsequently primed by the effects they have produced (Mackay, 1986). Attenuated processing of self-produced action effects could act to prevent such perseverative loops (Müsseler & Hommel, 1997a); even if such attenuations are generated at delay. Similarly, a later cancellation process may still be suitable for the agentive labelling of self-generated events (Frith et al., 2000).

Second, our results reveal an early 'facilitating' influence of prediction on perception, such that events congruent with expectation are perceived to be brighter than incongruent events. While this effect is not predicted under the Cancellation model, it in fact appears consistent with some other observations within the action literature. For

instance, agents are sometimes better at detecting visual motion congruent with action (Christensen et al., 2011;2014; Desantis, Roussel, & Waszak, 2014), and computational models of perception consider detection to be related to perceived intensity such that the detection threshold reflects the lower bound of perceptible intensities (Brown et al., 2013). Additionally, and likely relatedly, ambiguous inputs (e.g. illusions, binocular rivalry) are typically resolved in line with executed movements (Di Pace & Saracini, 2014; Maruya, Yang, & Blake, 2007; Wohlschläger, 2000).

Interestingly, these 'facilitatory' influences of prediction are also consistent with observations outside of the action literature. It is a common finding in visual cognition that events predictable on the basis of other environmental information are *more* readily detectable (e.g., a loaf of bread is identified more accurately in the context of a kitchen; Palmer, 1975), and perceived with *greater* intensity and contrast than unexpected events (Bar, 2004; Han & VanRullen, 2016; Floris de Lange, personal communication). These findings are taken as support for Bayesian models of perception, whereby accurate percepts within our noisy environment are generated by using prior expectations to constrain sensory evidence such that we perceive more readily what we expect (Yuille & Kersten, 2006), rather than what we do *not* expect ('Cancellation' model). These processes are argued to aid the generation of veridical percepts, given that expected events are (by definition) more likely to occur. Notably, these adaptive arguments would seem to apply equivalently regardless of whether sensation is predicted on the basis of action or another environmental cue. While these arguments relate to the adaptive nature of *detecting* predicted over unpredicted events, current computational models require that any mechanism acting to facilitate detection

of predicted events will also increase the apparent intensity of suprathreshold stimuli (Brown et al., 2013).

Several current theoretical frameworks examine mechanisms for generating both attenuation and facilitation effects but cannot explain our observed interaction across time. For instance, Lally, Frendo and Diedrichsen (2011) suggest that the nervous system may be able to attenuate or facilitate self-generated stimuli on the basis of task demands, while Desantis et al. (2014) suggest that opposite effects may be found in intensity judgement and identification tasks (see also Kok, Jehee, & de Lange, 2012, for a demonstration of how neural attenuation may be related to behavioural facilitation). However, such explanations are difficult to apply to our findings given that task-demands and dependent variables were identical at short and long delays.

Our findings are potentially consistent with the Code Occupation hypothesis (Stoet & Hommel, 1999). Under this account, preparation of an action initially activates codes associated with that action. This activation facilitates responses which require these codes (Stoet & Hommel, 1999; 2002) and may also enhance perception of associated events. However, activating codes does not form an action plan; a stage which involves binding feature codes in a manner akin to feature integration theory for object representation (Kahneman & Treisman, 1984). When features are bound into a single event representation – as required for completion of the action plan – the codes are 'occupied', generating attenuated perception of events activating them (Müsseler & Hommel, 1997a; 1997b). Given that these mechanisms generating perceptual facilitation followed by attenuation are proposed to operate in order to generate action plans, one might expect that this framework would hypothesize the perceptual shift to occur prior to action execution, and therefore that it could only explain the attenuating

influences observed in the present study. However, in principle one might speculate that our interaction could be incorporated within this account if assuming that the codes are not fully bound by the time of action initiation or that the binding required for initiation does not generate perceptual attenuation immediately.

Alternatively, we speculate that a viable model may reconcile reasoning from Cancellation action models and facilitatory visual cognition models. A primary process enhances perception of expected events and a later process facilitates perception of events generating prediction errors. A primary facilitatory process may more typically lead to veridical percepts within our inherently noisy sensory environment, increasing detection of expected events that are more likely, and via the same mechanism (Brown et al., 2013), increasing the perceived intensity of suprathreshold stimulation. The mechanism generating these effects may be the same as the expectation-based process thought to facilitate expected percepts within visual cognition (Yuille & Kersten, 2006; Summerfield & de Lange, 2014). However, if we still perceive unexpected information despite these biases – as will be the case with suprathreshold sensory events as presented here – later processes may enhance the processing of unexpected events. Enhanced processing of events generating prediction errors will help the updating of models of the world and the preparation of novel responses – the functional role presently assigned to 'cancellation' under existing models. Under this speculative account, the apparent paradox in the literature where expected events are cancelled in action contexts, and facilitated outside of action contexts, may be only apparent – in fact largely generated by the different measures typically used in the two fields (intensity judgements of suprathreshold stimulation and detection of at-threshold events,

respectively). Future work must importantly address whether both processes operate similarly in both contexts.

We propose that spatial attention mechanisms may generate these later cancellation effects. For example, eye-tracking paradigms demonstrate that we overtly attend towards events which are unexpected in either spatial or temporal dimensions (Itti & Baldi, 2009). Attention is known to increase perceived contrast (Carrasco, Ling & Read, 2004; Liu, Abrams & Carrasco, 2009), and therefore could generate the observed effects. Importantly such a process is consistent with the emergence of cancellation at later timepoints, given that we may assume we perceive a surprising event before reallocating attentional resources towards it (see Figure 3).

Our dual-process model assumes that prediction lies at the heart of the observed effects, but of course it must be noted that sensory events were not predictable on the basis of action in the present experiment. A motor command to lift one's index finger was followed on 50 % of trials by observation of an index finger movement and on the other 50 % by a middle finger movement. Our logic assumes that prior experience has established predictive relationships – a prior contingent relationship has existed between executed and observed actions (Cook, Bird, Catmur, Press & Heyes, 2014; Hommel et al., 2001) – and that the non-contingent experience present in the experiment is insufficient to extinguish these predictions (Baeyens et al., 2005). Under this assumption, the effects observed here would also be predicted in paradigms where contingent relationships are present within the context of the experiment (see Badets et al., 2016 for a review).

In conclusion, while the cancellation concept has had a significant impact on research programmes in motor control, computational psychiatry, social cognition and the study of agentive awareness, our data question a key assumption of the cancellation account – that the prediction is subtracted from the sensory input, generating immediate cancellation effects. Here we have presented evidence that prediction initially facilitates, rather than attenuates, perception of expected sensory events, and that evidence of 'cancellation' can only be found in later time ranges. These findings suggest that influences of action prediction on perception may be more similar than appreciated to those outside of action contexts.

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Figure 1. The timecourse for the action-related events (created using Smith Micro Software's Poser 7.0) in the three experiments.

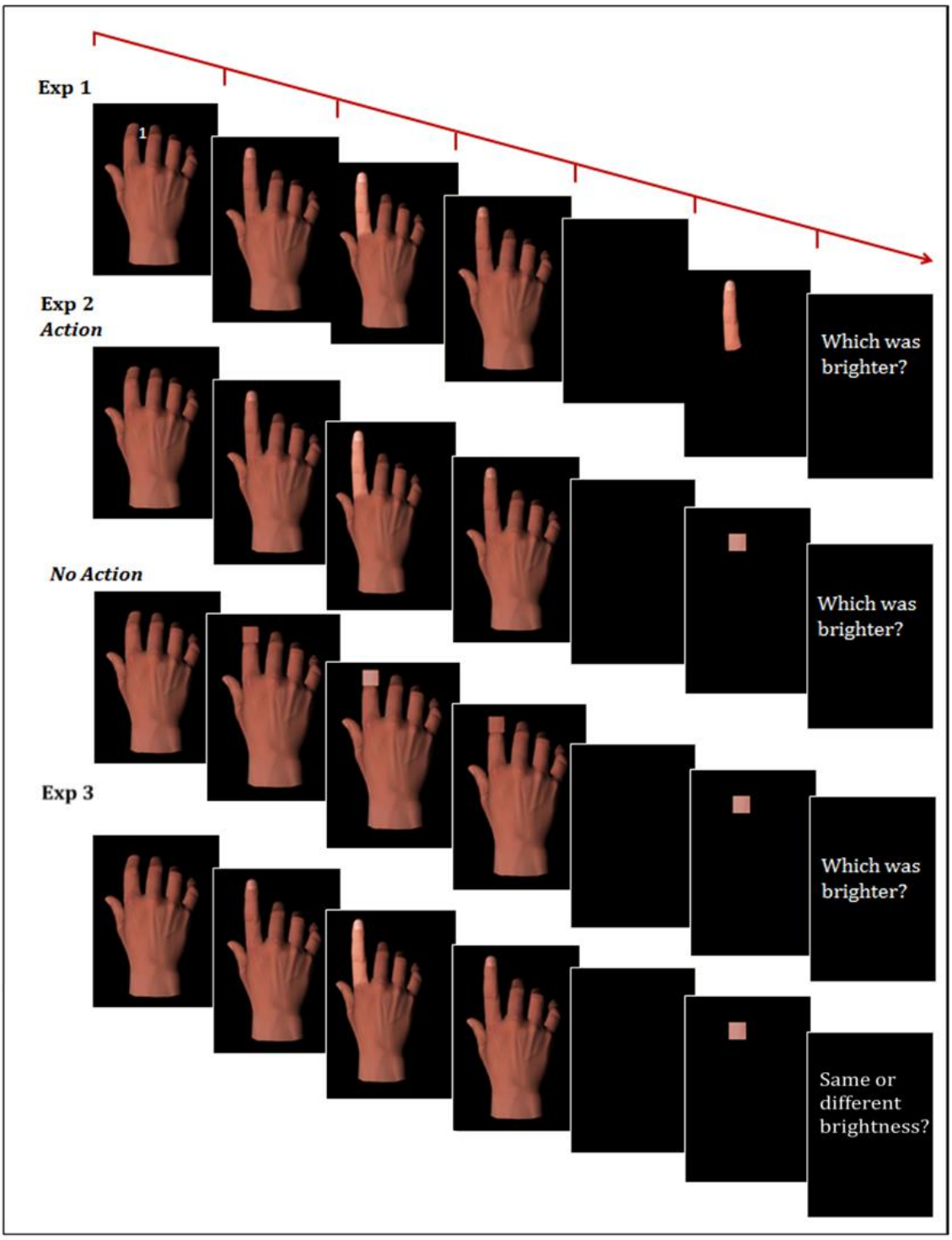


Figure 2. Top panel, Left: Demonstration of how the PSE was calculated in Experiments 1 and 2 with psychometric functions for an example participant, for stimuli congruent (saturated) and incongruent (faded) with action. The PSE describes the point where participants judge the target and reference events to have equal brightness. When observers overestimate the physical brightness of the target stimulus PSEs tend towards *lower* values. Top panel, Right: Demonstration of how the PSE was calculated in Experiment 3 for an example participant. Middle panel: PSEs for stimuli congruent and incongruent with action, for all experiments and conditions. Solid colours indicate PSEs for action congruent events, faded colours for incongruent events. Bottom panel: Congruency effects, calculated as incongruent PSE – congruent PSE, for each delay in all experiments and conditions. Positive values indicate that congruent effects were perceived more brightly than incongruent effects, negative values indicate that congruent effects were perceived less brightly than incongruent effects, and zero values (black dashed line) indicate no difference. Error bars represent the standard error of the mean.

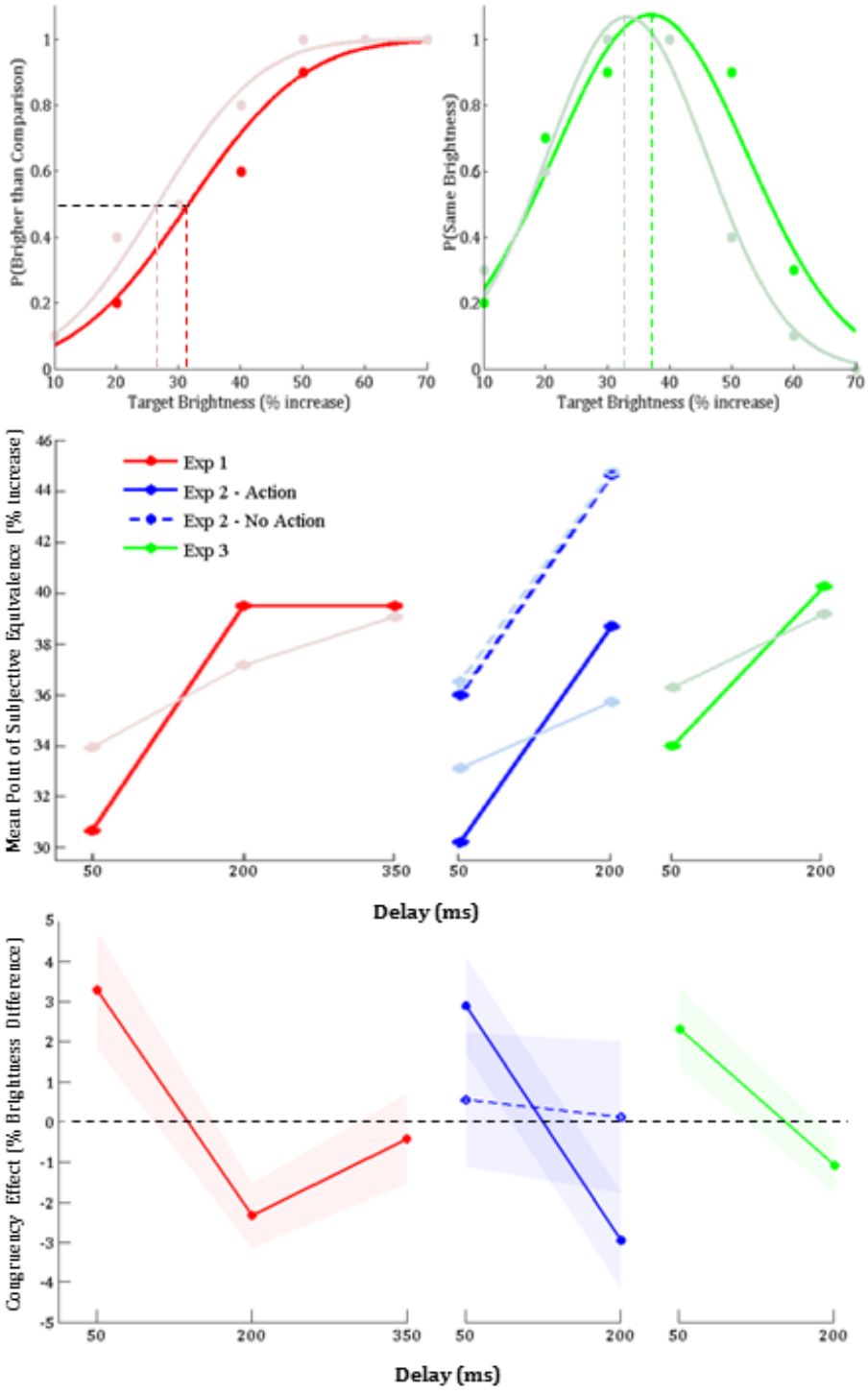
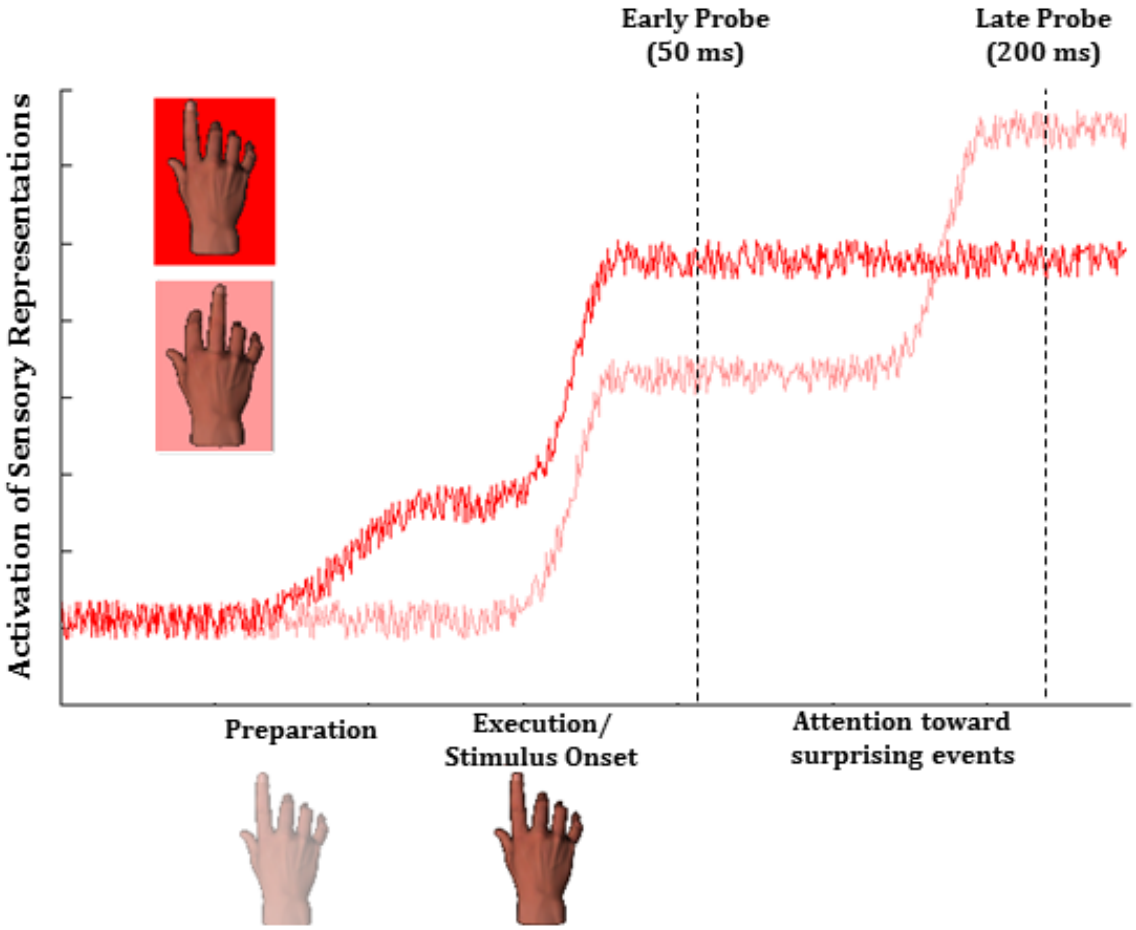


Figure 3. A schematic of our speculative model. Before action initiation, the activation of congruent sensory event representations increases via prediction mechanisms. When congruent events are presented, the activation of these representations increases further. When incongruent events are presented, the activation of incongruent representations is initially lower, as they have not been activated via prediction mechanisms. Therefore, at early probes after presentation (50 ms) congruent events will be associated with greater activation of underlying sensory representations than incongruent events. However, once incongruent – surprising – events have been detected, evidence suggests that we shift our attention towards these events. This attentional shift would increase the activation of the sensory representations associated with the surprising events. Therefore, at later probes (200 ms) incongruent events can be associated with greater activation of underlying sensory representations than congruent events. However, it should be noted that these 'cancellation' effects – where incongruent activation is relatively higher than congruent activation rather than simply equivalent – require at least one of two conditions to be met. First, the increase in activation according to later attentional shifts must exceed that generated by initial predictive activation. Second, the activation of the (unsurprising) predicted representation has already started to decay. (NB. This model does not assume that a 'sensory representation' is singular per se. At minimum, each representation will likely be encoded at a population level, and furthermore, under predictive coding schemes these would refer to the sum of activation in 'prediction' and 'input' units).



Footnotes

[i] 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

[ii] The luminance of the brightest point on the finger was ~36 cd/m^2 before it flashed, rising to a maximum of ~75 cd/m^2, with stepsizes of ~5.5 cd/m^2. Luminance was measured with a Konica Minolta Chromometer CS1000A in both experiments.

[iii] 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. The square's luminance was ~13 cd/m^2 before it flashed, rising to a maximum of ~33 cd/m^2 with stepsizes of ~3 cd/m^2 (note that the luminance of the square was matched to the mean luminance of the finger rather than the brightest point).

[iv] We speculate that this advantage in RTs for judgments on incongruent trials is driven by the fact that, by the point in the trial where responses are given, observers will have entered the later perceptual stage where incongruent events receive a relative processing advantage (see General Discussion and Figure 3).

[v] Also note that the flip in effect with one minor stimulus manipulation (50 ms vs 200 ms delay), along with its disappearance with another (No Action condition; Experiment 2) and the nature of the response in Experiments 1 and 2 (unrelated to the nature of expected events – participants reported whether a certain stimulus attribute applied to a first or second event – and about which participants are unlikely to have had any pre-conceived notions about how expectation would have related to this attribute – brightness) are all features that have been proposed to render response bias accounts less likely (Firestone & Scholl, 2015).