Susceptibility to the fusion illusion is modulated during both action execution and action observation

Timothy N. Welsh[1,2], Connor Reid[1], Gerome Manson, Merryn D. Constable, Luc Tremblay

[1]Faculty of Kinesiology & Physical Education, University of Toronto
[2]Centre for Motor Control, University of Toronto
[3]Department of Neurosurgery, Houston Methodist Research Institute
[4]Department of Psychology, Northumbria University

Corresponding Author
Timothy N. Welsh, Faculty of Kinesiology & Physical Education, University of Toronto, 55 Harbord St, Toronto, Ontario, Canada, M5S 2W6 E-mail: t.welsh@utoronto.ca

Shortened Title
Action Observation and the Fusion Illusion

Highlights
- The weighting of visual information changes during the execution of movement
- Changed weighting of visual information alters susceptibility to audio-visual illusion
- Susceptibility to audio-visual illusion also changes during action observation
- Action observation may involve the real-time simulation of the observed action

Abstract

Many researchers have proposed that when an individual observes the actions of another individual, the observer simulates the action using many of the same neural areas that are involved in action production. The present study was designed to test this simulation hypothesis by comparing the perception of multisensory stimuli during both the execution and observation of an aiming action. The present work used the fusion illusion - an audio-visual illusion in which two visual stimuli presented with one auditory stimulus are erroneously perceived as being one visual stimulus. Previous research has shown that, during action execution, susceptibly to this illusion is reduced early in the execution of the movement when visual information may be more highly weighted than other sensory information. We sought to determine whether or not a non-acting observer of an action showed a similar reduction in susceptibility to the fusion illusion. Participants fixated a target and either executed or observed a manual aiming movement to that target. Audiovisual stimuli were presented at 0, 100, or 200 ms relative to movement onset and participants reported the number of perceived flashes after the movement was completed. Analysis of perceived flashes revealed that participants were less susceptible to the fusion illusion when the stimuli were presented early (100 ms) relative to later in the movement (200 ms). Critically, this pattern emerged in both execution and observation tasks. These findings support the hypothesis that observers simulate the performance of the actor and experience comparable real-time alterations in multisensory processing.

Keywords

action observation; multisensory integration; motor control; fusion illusion

1. Introduction

Many of our daily tasks are dependent upon our ability to understand, predict, and coordinate our movements with the actions of others. As an example, if three individuals are pushing a car out of the snow, each person must effectively observe the actions of their co-actors, predict what they are going to do and when they are going to do it, and coordinate their movements with each other to achieve their common spatio-temporal goal. It has been suggested that action understanding and prediction, and subsequent coordination, is facilitated by a network of cortical regions that become active when an individual observes another person act (e.g., Jeannerod, 2001). This action observation system seems to involve many of the same cortical areas that are active when an individual actually performs an action, such as posterior parietal cortex and dorsal premotor cortex, and may even consist of a specific subset of neurons that are active during both the observation and execution of action (see Rizzolatti & Craighero, 2004 for a review).

Although the proposed functions and origins of such an action observation system are still very much under debate (e.g., Campbell & Cunnington, 2017; Cook, Bird, Catmur, Press & Heyes, 2014; Hickok, 2013), much of the discussion currently focuses on the potential for both direct and complementary sensorimotor mappings that allow for a dynamic malleable action observation and understanding system that activates appropriate context specific responses (e.g., Catmur, Walsh & Heyes, 2007; Constable et al., 2017; Roberts et al., 2016a, 2016b; Roberts, Constable, Burgess, Lyons, & Welsh, 2018; Sartori, Bucchioni & Castiello, 2013; Sebanz, & Knoblich, 2009). That is, although it is clear that a system of motor-related areas becomes active during the observation of action, and that this system is sensitive to the goals of the action, the nature of the sensorimotor representations activated during action observation and of any possible associated sensorimotor simulation is less clear. If it is the case that the observation of an action involves the simulation of the observed action in real-time (i.e., as the movement unfolds) or in a predictive manner (e.g., Flanagan & Johansson, 2003; Wolpert & Ghahramani, 2000), then the observer may engage sensorimotor mechanisms that are activated when the observer actually performs the action. If so, then the same sensorimotor experiences that occur when an individual executes a task may arise when the individual observes that task being performed by another individual, even when there is no reciprocal or coordinated action (Constable, Pratt, Gozli, & Welsh, 2015; Welsh et al., 2005). The present study was designed to test these predictions by investigating whether or not changes in multisensory integration that occur during action execution also arise during the observation of the same actions.

1.1 Action Observation and Simulation

There is a large and growing body of evidence for motor system activation and action simulation during action observation. For example, neurophysiological studies have revealed that the observation of an action alters the activity of the motor system in a task- and muscle-specific manner (e.g., Fadiga et al., 1995) and that the repeated observation of an action can cause short-term changes in the neural representation of actions in the motor systems in a manner similar to that of physical action execution (e.g., Stefan et al., 2005; Ray, Dewey, Kooistra, & Welsh. 2013). In addition, behavioural studies have revealed that psychological phenomena, such as inhibition of return and the Simon effect, are observed when individuals act alone and also when individuals perform the task as a pair (e.g., Sebanz, Knoblich, & Prinz, 2003; Welsh et al., 2005, 2007). Overall, the results of these studies indicate that sensorimotor systems respond similarly when an individual executes and observes an action.

In a set of recent behavioral studies that are particularly relevant to the present study, it was reported that observers have more difficulty predicting the outcome of an observed action when the observers perform a secondary motor task that is incongruent with the action which they are observing as compared to when they perform a congruent secondary motor task (Mulligan et al., 2016a, 2016b). For example, in the study by Mulligan et al. (2016b), skilled and non-skilled dart-throwers observed another person throwing a dart towards a dartboard and were asked to judge the location at which the dart landed on the board. While completing this judgement and prediction task, participants also engaged in one of three secondary tasks: 1) an incongruent motor task that required participants to generate an isometric force with the arm that the participant uses when throwing a dart; 2) a congruent motor task that required the participant to imitate the throwing of a dart with the arm they use when throwing a dart; and, 3) an attentional control task in which the participant had to monitor a constant tone and determine if the tone changed frequency or not. The authors reported that the accuracy of the predictions of the non-skilled throwers were not affected by any of the secondary tasks. For skilled throwers, however, the accuracy of the predictions decreased when they executed the incongruent motor task. Performance of the congruent movements or the tone monitoring task did not interfere with predictions for the skilled throwers. The secondary-task specific nature of the interference effect was taken as evidence for motor simulation during action observation and prediction. That is, the authors suggested that this interference effect was restricted to the incongruent motor task in the skilled throwing group because the motor system is actively involved in the simulation of the observed action. Incongruent activation of the motor system generated by the secondary task created noise and/or response competition within the motor system that interfered with the simulation process that enabled the prediction. In contrast, congruent motor activation or a tone-monitoring task did not create noise or interference with the motor simulation and, as such, the prediction process was not affected.

If, as suggested by others (e.g., Jeannerod, 2001; Rizzolatti & Craighero, 2004), the responses codes associated with the observed action are involved in a simulation of the observed actions within the sensorimotor system of the observer, then sensorimotor effects that arise during execution may also emerge when one individual observes the action of another individual. The purpose of the present study was to test this prediction and the simulation hypothesis by determining if the real-time alterations in multisensory integration that occur when an individual executes an action also emerge when that same individual observes that same action being executed by another individual.

1.2 Multisensory Integration

During perception and action, humans combine and integrate multiple sources of sensory (afferent) information to form accurate representations of their surroundings and the location of their body in their surroundings. One particularly useful method for understanding the processes leading to multisensory integration involves studying the interference or perceptual illusions that emerge following the presentation of conflicting stimuli across different modalities. In particular, perceptual illusions that arise from conflicting information reveal how the central nervous system (CNS) prioritizes the different sources of sensory information. The ventriloquist illusion (Bonath et al., 2007) and the McGurk effect (McGurk & MacDonald, 1976) are classic examples of perceptual effects that arise from the presentation of conflicting audio and visual information. The current study focused on a well known audiovisual illusion known as the "fusion" illusion (e.g., Shams, Kamitani, & Shimojo, 2000; 2002; Andersen, Tiipana, & Sams, 2004).

In the fusion/fission illusion paradigm, participants are presented with a series of brief visual and auditory stimuli (referred to as “flashes” and “beeps”, respectively) in close temporal proximity. The same number of flashes and beeps are presented on some trials and different numbers of flashes and beeps are presented on other trials. For example, Shams et al. (2000) presented 1-4 brief flashes with 1-4 brief beeps to participants on a given trial, with the stimuli being presented approximately 50 ms apart. When individuals were asked to report the number of flashes, they were influenced by the number of beeps and experienced what are known as the fusion and fission illusions (Andersen et al., 2004; Shams et al., 2000; 2002). In the fission illusion, a single flash presented with two or more beeps is erroneously reported as more than one flash - the single visual stimulus is perceptually “split” into multiple visual stimuli. In the fusion illusion, two flashes presented with a single beep can be erroneously reported as one flash - the two visual stimuli are perceptually “merged” into a single visual stimulus. Andersen et al. (2004) suggested that the fission and fusion illusions were due to multisensory integration mechanisms in which the CNS prioritizes or more heavily weights auditory stimuli over visual stimuli (see also: Mishra, Martinez, Sejnowski & Hillyard, 2007; Mishra, Martinez & Hillyard, 2008).

In typical studies of multisensory integration, the participants rest or perform movements of small amplitudes (i.e., keypresses). More recent research, however, has revealed that the perception of the fusion illusion can be modulated depending on when the stimuli are presented during goal-directed actions. In a study by Tremblay and Nguyen (2010), participants executed manual aiming movements with their index finger toward a 30 cm target within a movement time bandwidth of 290-350 ms. Audiovisual stimuli that would elicit the fusion or the fission illusion were also presented, spatially just below the target on the aiming board, at 0, 50, 100, 150, and 200 ms relative to movement onset. Participants were instructed to report the number of flashes they perceived after each trial. For the stimulus onset conditions that corresponded to the higher limb velocities (i.e., 50 and 100 ms) during the early and middle stages of the movement, the susceptibility to the fusion illusion was significantly lower than when the stimuli were presented at lower limb velocities very early or late in the movement trajectory. That is, accuracy at reporting the number of flashes was better (i.e., the participant more often correctly reported seeing 2 flashes, rather than the illusory fused single flash) when stimuli were presented when the limb was moving faster as compared to when the limb was moving slower. Also, the participants' accuracy in reporting the number of flashes when the number of audiovisual stimuli were congruent did not change as a function of the timing of stimulus presentation during the movement. Hence, it was not just the case that participants generally reported seeing *more* visual stimuli during certain stages of the movement. The finding that the number of perceived stimuli on congruent trials did not change is also important because it indicates that the perception of the visual stimuli were not impacted overall by the movement. Instead, the movement-based modulation of the perception of visual stimuli was restricted to the condition in which the fusion illusion emerges.

Tremblay and Nguyen (2010) hypothesized that the susceptibility to the fusion illusion may change throughout a goal-directed movement because visual information at the early and middle portions of the limb trajectory is more important than visual information obtained in later portions of the trajectory for the implementation of online control processes that work to ensure accurate movement termination (see Elliott et al., 2010; Kennedy et al., 2015; Tremblay et al., 2017; see also Manson et al., 2018). That is, the CNS might more highly weight visual information during high velocity stages in early- to mid-stages of the movement because these stages of the movement are critical to detecting and predicting errors in the movement trajectory that may need to be changed to ensure endpoint accuracy. In contrast, visual information regarding the limb late in the trajectory may not be used as effectively to correct and control movement trajectories. This relatively higher weighting of visual information has the effect of increasing the accuracy of visual perception more generally during the early and mid-stages of the movement. This altering of the weighting of vision as a function of the movement enables the actor to more accurately report seeing 2 visual stimuli (a decrease in the fusion illusion) at those early and mid-stages of the movement relative to other later stages when the relative importance (and hence weighting) of visual information is lower (Kennedy et al., 2015, Tremblay et al., 2017). That is, with a lower weighting of the visual information in the late stages, the auditory stimuli would have a larger influence on multisensory integration and increase the susceptibility of the individual to experience the illusion (as evidenced by a larger proportion of trials on which the fusion illusion occurred and only a single flash was perceived, see also Manson et al., 2018)

1.3 Research Aims

The purpose of the present study was to test the hypothesis that action observation involves the real-time simulation of the observed action. To test this hypothesis, it was investigated whether or not similar alterations in sensory/perceptual processes occur during action execution **and** observation (e.g., Tremblay & Nguyen, 2010). If observers engage in real-time simulation of the observed action as the observed movement unfolds, then the observer should experience an altered relative weighting of visual information during different stages of the observed goal-directed action. As a result, susceptibility to the fusion illusion should change as a function of the stage of the observed movement (see Tremblay & Nguyen, 2010).

Consistent with the study by Tremblay and Nguyen (2010), the key trials were those with 2 flashes presented with 1 beep (i.e., trials leading to the fusion illusion in which only 1 flash is erroneously perceived when 2 are actually presented). In different blocks of trials, the participants executed or observed aiming movements. Based on the results of Tremblay and Nguyen (2010), it was predicted that participants would experience a modulation of the fusion illusion during action execution. A decreased susceptibility to the illusion (i.e., an increase in the number instances in which two flashes were correctly perceived) was expected earlier in the movement on execution trials when the actor's limb was travelling at higher velocities (when visual feedback is important for online limb-target regulation processes; Tremblay et al., 2017), compared to later in the movement when the limb is decelerating (Tremblay & Nguyen, 2010). Because two flashes of visual stimuli were actually presented when only one auditory stimulus is presented on the critical trials, a higher average number of perceived flashes should be reported earlier than later in the movement during execution trials.

With respect to the main purpose of the study, if observers actively simulate the observed action, then similar modulations of the fusion illusion should occur during action observation and action execution. Specifically, there should be a decreased susceptibility to the audiovisual fusion illusion (i.e., larger number of flashes perceived) earlier in the observed movement compared to later in the observed movement (i.e., a larger number of flashes perceived when the stimuli are presented early in the observed movement and a lower number of flashes perceived in the later stages of the observed movement). Conversely, if observers do not simulate the observed performance in real-time or if the simulation of the observed action does not influence sensory/perceptual processing, then the alterations in susceptibility to the audiovisual illusion should not emerge during observation. That is, perceived flashes in the trials on which two flashes and one beep were presented should not differ across presentation times during the observed action.

2.0 Methods

2.1 Participants

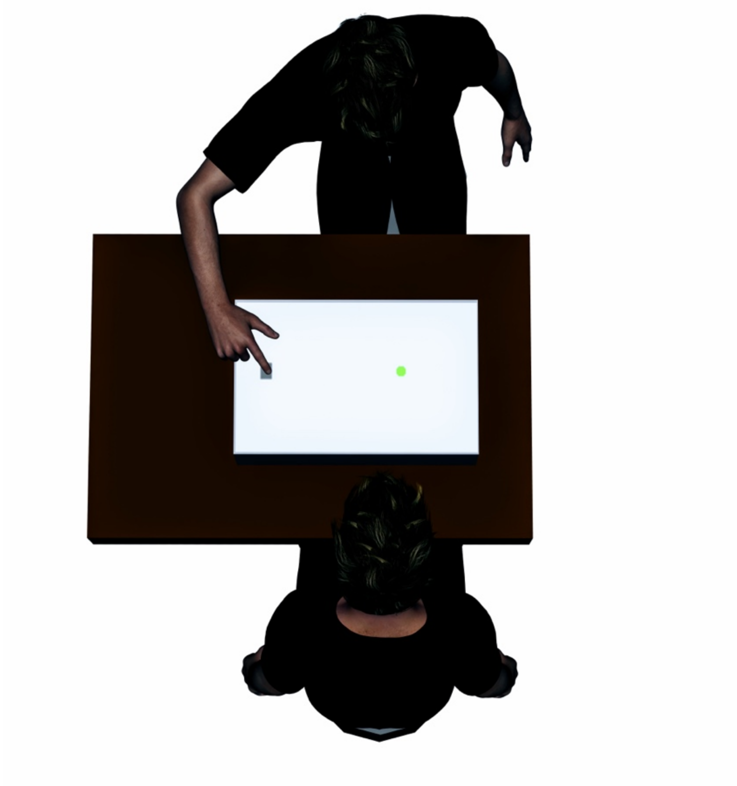
Twelve volunteers (6 male; aged 18-25 years) from the University of Toronto participated in the experiment. Testing sessions lasted approximately 60 minutes, and subjects were compensated $10 CAD for their time. All participants were right-hand dominant. Prior to the experiment, participants gave written consent to the procedures. All procedures complied with the ethical standards of the 1964 Declaration of Helsinki regarding the treatment of human participants in research and were approved by the Ethics Review Office at the University of Toronto.

2.2 Equipment

In all experimental trials, a single actor executed an aiming movement toward a target on an aiming board (50 cm x 27.5 cm x 8.5 cm; see Figure 1). The aiming board lay flat (horizontal) on the surface of a table. The home position for all movements was a 4 cm x 4 cm piece of translucent polymer with an indentation in its center. The target was a green light emitting diode (LED: 0.3 cm in diameter) positioned 30 cm from the home position. The devices used in the audiovisual task were a red LED (0.3 cm in diameter) and a piezoelectric sound generator placed in-line with each other under the surface of the board, 6 cm from the target position (see Figure 1B). The surface of the aiming board was a translucent white polymer sheet. The LEDs were clearly visible through the sheet when they were illuminated, but the translucent surface masked the LEDs when they were turned off. The sheet also hid the underlying wiring, piezoelectric sound generating device, and internal structure of the board.

During action execution (AE) trials, the participant sat alone in front of the aiming board. During action observation (AO) trials, the experimenter and participant sat across from one another, with the aiming board between them (see Figure 1A). The participant sat in the same seat throughout testing so that the location of the target and of the audiovisual stimuli were consistent throughout both conditions. An infrared light emitting diode (IRED) was placed on the index finger of the participant during AE trials and on the index finger of the experimenter on AO trials. The IRED location was recorded (at a rate of 250 Hz) by an Optotrak Certus motion tracking system (Northern Digital, Waterloo, Ontario, Canada). A custom Matlab (The Mathworks Inc. Natick, MA) program controlled the stimulus events, and recorded the 3D coordinates of the IRED. Participants verbally reported their responses for the perceptual task and the experimenter input the responses manually into the computer at the end of each trial.

A)



B)

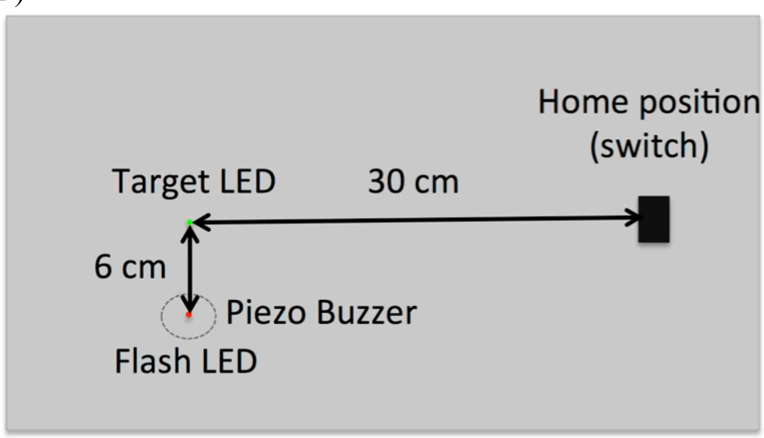


Figure 1: Diagrams of the experimental environment. A) Diagram of the seating arrangement during the action observation condition. B) Diagram and measurements of the display board from the perspective of the participant during both action execution and observation trials. Note that the hand of the acting individual never obscured the location of the "Flash" LED used in the audiovisual illusion task.

2.3Procedure

The experimental session consisted of two main phases: a perception only pre-test phase, and an experimental phase in which the AO and AE conditions were completed. The key differences between the tasks were the timing of the stimuli and the absence or presence of an action.

Trials in all conditions began with the illumination of a green target (0.003 lux) LED located 30 cm away from a home position. After the target was illuminated, a combination of beeps (1 or 2) and red flashes (1 or 2) were presented just below (6 cm) the target location. The beeps (20 ms in duration at 65 dB- measured with ambient noise) were presented via a piezoelectric buzzer (2900 Hz; Model SC628: Mallory Sonalert Products Inc., Indianapolis, IN). The red flashes (20 ms in duration) were presented via a red LED (0.013 lux). The duration of the stimulus presentation on unimodal trials on which only 1 beep or 1 flash were presented was always 20 ms because there was only 1 stimulus. For trials on which 1 beep and 1 flash were presented together, the total presentation duration was also 20 ms because the two stimuli were presented simultaneously. For 2 flash/1 beep and 1 flash/2 beep trials (i.e., illusion trials), the single stimulus was presented between the other 2 stimuli (e.g., the 1 flash was presented in between the 2 beeps). Although the exact timing of the stimuli was different for each individual (see staircase procedure described below), an example of a total stimulus presentation duration on these trials was 60 ms (e.g., 20 ms flash + 20 ms beep + 20 ms flash with no delay or overlap between the stimuli). However, to account for the individual differences in the efficiency of processing auditory and visual information, and hence illusion sensitivity, a staircase procedure was used to identify the most appropriate total stimulus presentation time for each individual. This staircase procedure involved varying the time between the two stimuli of the same modality (inter-stimulus interval or ISI; see below for details). Similar to the 1 flash/1 beep trials, individual flashes and beeps in the 2 flash/2 beep trial were presented simultaneously. The paired flash/beep stimuli were separated by the same ISI identified in the staircase procedure. In all trials, participants were instructed to maintain fixation on the target location and verbally report how many red flashes they saw below the target after the trial was completed.

Because of individual differences in the efficiency of processing visual and auditory information and the resulting window over which the fusion illusion occurs, a unique ISI duration was determined for each participant. That is, the beeps and flashes were always 20 ms in duration, but the timing between the stimuli was different for each participant. These individualized presentation timings were identified via a staircase-like procedure completed during the perception-only pre-test phase. During that perception-only procedure, participants were seated comfortably in front of the aiming console with their mid-sagittal plane aligned with the target. In the first two trials of the procedure, the participant was presented with trials with just 2 beeps or 1 flash/1 beep to familiarize participants with both sound and the light stimuli. All subsequent trials of the staircase procedure were either 1 flash/2 beep trials or 2 flash/1 beep trials.

The stimulus condition of interest of the staircase procedure was the one in which the “fusion” stimulus would emerge (i.e., 2 flash/1 beep). The starting duration of the series of stimuli for the staircase procedure was always 74 ms (20 ms for each of the two auditory or visual stimuli plus a 34 ms ISI). The 34 ms ISI consisted of the 20 ms beep stimulus and 7 ms without any stimulus on either side of the beep stimulus). If the participant could accurately perceive the correct number of visual stimuli with an ISI of 34 ms, the experimenter decreased the ISI by 10 ms (5 ms on each side of the middle singular stimulus). The experimenter continued to decrease the total ISI by 10 ms on subsequent trials until the participant could not accurately perceive the correct number of flashes. At this point, the ISI was increased by 5 ms until a correct report was obtained. After this correct report, the experimenter adjusted the ISI by 1 ms until the lowest duration whereby the participant could perceive the correct number of stimuli was found. If the participant could not perceive the correct number of flashes at an ISI of 34 ms, then the ISI was increased by 10 ms until the participant could accurately identify the correct number of flashes. The experimenter then decreased the ISI by 5 ms until the participant could not accurately identify the correct number of flashes. The experimenter then increased the ISI by 1 ms until the lowest duration whereby the participant could correctly identify the number of flashes was found. The goal of the staircase procedure was to identify a unique presentation duration (i.e., ISI plus the 2 x 20 ms stimulus duration) for each participant to ensure that there were no ceiling or floor effects on the fusion illusion during action execution or observation. This individually-determined presentation timing was then used during all subsequent familiarization and experimental trials for the given participant. On average, the duration of the stimulus presentation for trials on which 2 stimuli were presented was 92.3 ms (an average ISI of 43.2 ms plus the 2 stimuli which lasted 20 ms each), with values ranging from a minimum of 70 ms to a maximum of 130 ms. Trials on which only 1 flash, 1 beep, or when 1 flash and 1 beep were presented, had a total stimulus duration of 20 ms because there was no ISI on these trials.

Following the completion of the staircase procedure, the familiarization, control and experimental trials that involved action were completed. Prior to control and experimental trials, there were 10 familiarization trials where the participant practiced aiming movements toward the target. The purpose of these trials was to familiarize the participant with the movement component and the specified movement time bandwidth of 290-350 ms. Participants were told to reach to and touch the target LED '*as quickly and as accurately as possible within the movement time bandwidth*'. The custom motion capture algorithm (see below for details) determined and displayed movement time feedback at the end of each trial, and the experimenter instructed the participant to adjust their movement speed up or down when movement times were outside of this bandwidth for two consecutive trials. Following the familiarization trials, the two sets of experimental conditions were completed. The order of AE and AO blocks was counterbalanced between participants to control for effects of order.

The actor (the experimenter in AO blocks; the participant in AE blocks) began every trial with their right index finger on the home position. On control trials, the actor's index finger remained on the home position throughout the duration of the trial, whereas on experimental trials, the actor performed an aiming movement with their right index finger to the target location. At the beginning of all trials, the green target was illuminated for one second, was extinguished for 50 ms, and then illuminated again to signal the actor to start moving. On all trials, the target remained illuminated for the duration of the movement and participants were instructed to maintain fixation on the target at all times. Participants were instructed to report whether they deviated from fixating on the target at any point during trials and were given reminders every 40 trials to emphasize fixation.

During the experimental trials, participants were instructed to monitor the location of the red LED and detect the number of times the red LED flashed while maintaining fixation on the target location. The location of the LED was never obscured from view by the moving hand (as evinced by the accurate and consistent performance in the congruent 2 flash/2 beep condition;

see Results). At the location of the red LED, a series of 1 or 2 flashes of the LED with 1 or 2 beeps from the sound generator were presented (at the presentation duration determined during the staircase procedure) at 0, 100, or 200 ms relative to movement onset[1]. Movement onset was defined by the movement kinematics as the first instant in which movement velocity in the primary axis was more than 30 mm/s for 2 consecutive samples [8 ms]). Velocity was identified in real time by computing a two-point differentiation based on the immediate position data (the position at point "n" was subtracted from the position at point "n-1" to obtain an instantaneous velocity value). Although there was some between-participant and between-condition variability in movement time (MT), the average MT was 310 ms for the AE condition and was 312 ms for the AO condition. Based on these MTs and the individualized nature of timing of the presentations of the audiovisual stimuli due to the staircase, there were instances in the presentation of the last stimuli ended after movement end of the movement. Considering the results from Tremblay and Nguyen (2010) and Manson et al. (2018), it was thus expected that the 200 ms condition likely yield differences in the perception of audio-visual events, as compared to the other experimental conditions.

Upon movement completion, the participant verbally reported the number of flashes they perceived. There were 28 control trials (7 trials x 4 stimulus conditions) and 144 experimental trials (12 trials x 3 presentation times x 4 stimulus conditions) in both the AE and AO blocks.

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[1] **Note that there was a delay of less than 10 ms between movement onset (the first occurrence of the 30 mm/s in the limb trajectory) and the onset of the first audio-visual stimulus. This delay occurred because a limb velocity above 30 mm/s had to be detected over two samples (4 ms between samples). In addition, one needs to consider the transmission delay between the Optotrak and the Matlab computer (approximately 2 ms), the Matlab processing time (less than 1 ms), the activation of the digital board (less than 2 ms), and the activation of the LED and/or piezoelectric buzzer (less than 1 ms). Such a total delay of less than 10 ms was thus carried over for all experimental conditions (i.e., 0, 100, and 200 ms relative to the detection of movement onset).**

2.4 Dependent Variables and Analysis

MT was calculated as the time between movement initiation and termination (the first frame on which the velocity of the finger surpassed 30 mm/s and fell below 30 mm/s, respectively, and remained there for 8 ms). To determine if MTs changed as a result of the stimuli, mean MTs for each participant in the AE condition were submitted to a 2 (Flash: 1, 2) by 2 (Beep: 1, 2) by 4 (Stimulus Timing: 0 ms, 100 ms, 200 ms) repeated measures ANOVA.

The main measure of interest was the number of flashes the observer perceived. The mean number of perceived flashes was calculated for each participant and these mean values were submitted to a 2 (Task: AO, AE) 2 (Flash: 1, 2) by 2 (Beep: 1, 2) by 4 (Stimulus Timing: Control, 0 ms, 100 ms, 200 ms) repeated measures ANOVA. Post hoc analysis of the perceived flash data included a series of planned comparisons that focused on *a priori* predictions regarding the change in the susceptibility of the individual to the fusion illusion during movement execution and observation. To test these *a priori* predictions, a series of paired-samples *t*-tests were conducted to compare mean reported flashes in the fusion condition (2 flash/1 beep) presented during the movement (i.e., control vs. 200 ms, 0 ms vs. 200 ms, and 100ms vs. 200ms, with the last comparison being of critical focus). More accurate perception of the visual stimuli (less susceptibility to the fusion illusion) was indicated by a higher number of flashes reported on the 2 flash/1 beep condition, whereas less accurate perception of the visual stimuli (greater susceptibility to the fusion illusion) was indicated by a lower number of flashes reported in the 2 flash/1 beep condition. Alpha was set to $p<.05$ for all analyses.

3.0 Results

The repeated measures ANOVA for MTs revealed that the different timing and combination of the visual and auditory stimuli did not significantly affect the execution of the movements (*p*s>0.11). Further, the range of MTs of the observed movements in the AO (i.e., executed by the experimenter) was comparable to those that were executed by the participants (AE: mean 310 ms, SD = 30 ms, range 239-388 ms; AO: mean 312 ms, SD = 18 ms, range 247-351 ms).

The repeated measures ANOVA for the perceived number of flashes revealed a main effect of Flash, $F(1,11)=35.21$, $p<.001$, $\eta_p^2 = 0.762$. As expected, fewer flashes were perceived on trials with 1 flash (M=1.33; SD=0.12) than on trials with 2 flashes (M=1.70; SD=0.15). A main effect for Beep, $F(1,11)=49.46$, $p<.001$, $\eta_p^2 = 0.818$, also revealed that there were fewer flashes perceived on trials with 1 beep (M=1.28; SD=0.14) than trials with 2 beeps (M=1.75; SD=0.13). The main effect of Time was also significant, $F(3,33)=3.67$, $p<.05$, $\eta_p^2 = 0.25$. Post hoc analysis using a series of paired sample *t*-tests revealed that fewer flashes were perceived when the stimuli were presented 200 ms after movement onset (M=1.47; SD=0.09) than when the stimuli were presented at 0 ms (M=1.54; SD=0.09), $t(11)=3.13$, $p<0.01$, and 100 ms (M=1.53; SD=0.10), $t(11)=3.16$, $p<0.01$, after movement onset. The difference between the 200 ms condition and the control condition without movement (M=1.52; SD=0.09) approached, but did not cross the threshold of conventional levels of statistical significance, $t(11)=1.84$, $p>0.05$.

In addition to these main effects, there were significant interactions between Flash and Beep, $F(1,11)=10.88$, $p<.05$, $\eta_p^2 = 0.497$, and, critically, between Flash, Beep, and Time, $F(3,33)=4.75$, $p<.01$, $\eta_p^2 = 0.301$. Post hoc analysis of this three-way interaction was consistent with the findings of Tremblay and Nguyen (2010) by revealing that participants were less susceptible to the fusion illusion (i.e., they accurately perceived 2 flashes on 2 flash/1 beep trials) when the stimuli were presented 100 ms into the movement (M=1.57; SD=0.09) than 200 ms into the movement (M=1.41; SD=0.08), $t(11)=6.24$, $p<0.001$. Performance on the perception task was not statistically different across all other presentation time conditions. Notably, the 4-way interaction between Observation Condition, Flash, Beep, and Time was not significant, $F(3,30)<0.48$, $p>.63$, $\eta_p^2 = 0.042$.

Although the 4-way interaction was not statistically significant, we conducted a further analysis of a subset of the values involved in the interaction to test the *a priori* predictions that significant changes in the susceptibility to the illusion would emerge in both execution and observation conditions. To test these predictions, a series of paired-samples *t*-tests were conducted on the mean number of perceived flashes in the fusion illusion condition (2 flash/1 beep) separately for both the AE and AO conditions. Consistent with the findings of Tremblay and Nguyen (2010), when participants executed the movements (AE condition), participants were less susceptible to the illusion (i.e., more flashes were correctly perceived) when the series of stimuli were presented 100 ms into the movement (M=1.56; SD=0.31) than when the stimuli were presented 200 ms into the movement (M=1.38; SD=0.30), $t(11)=2.94$, $p<0.05$ (Figure 2a). Eleven of the twelve (92%) participants had perceived more flashes at the 100 ms than at the 200 ms presentation condition when the action was executed (Figure 2b). No other conditions were statistically different from one another. Interestingly, this same pattern emerged in the observation (AO) condition – more flashes were correctly perceived when presented 100 ms into the movement (M=1.58; SD=0.32) than when presented 200 ms into the movement (M=1.44; SD=0.35) $t(11)=3.41$, $p<0.01$. All twelve participants reported more (n=9) or an equivalent number (n=3) of perceived flashes in the 100 ms than at the 200 ms presentation condition when the action was observed. The perceived number of flashes in any of the other time conditions were not statistically different from one another. While the absence of the statistically significant 4-way interaction suggests that the patterns of modulations were not statistically different in AE and AO conditions, the results of these *t*-tests confirm the experimental predictions that the modulation of illusion susceptibility would occur in both action execution and observation.

Although the results of the analyses presented thus far are consistent with the predicted changes in the susceptibility to the visual illusion as function of the stage of the movement, it is also possible that processing at the 200 ms was simply negatively affected and participants perceived less visual stimuli overall 200 ms into the movement. That is, because the visual stimuli were presented near the end of the movement and near the target location, the stimuli at the “flashing” LED may have been obscured by the hand and/or the processing of these stimuli might have been hindered in some way (perhaps by a change in the location or relative distribution of attention). If so, then the lower number of perceived stimuli at the 200 ms presentation time in the key 2 flash/1 beep condition could have occurred because of these other factors and not because of the change in the weighting of the processing of the visual stimuli throughout the movement. To test this possibility, a sub-analysis was conducted on only the data in the congruent 2 flash/2 beep condition. If participants simply perceived less visual stimuli 200 ms into the movement than in any other condition, then performance in this congruent condition would also be poorer at the 200 ms presentation time condition than any other time interval. In contrast to this prediction, the 2 (Task: AO, AE) X 4 (Stimulus Timing: Control, 0 ms, 100 ms, 200 ms) repeated measures ANOVA did not indicate a statistically significant effect for Time, $F(3, 33) = 2.15$, $p>0.1$, nor a statistically significant interaction between Task and Time, $F(3, 33) <1.0$, $p>0.7$. Hence, this sub-analysis indicates that the perception of the visual stimuli in the 2 flash/2 beep condition was not significantly affected by the Stimulus Timing for both Task conditions (Figure 2a).

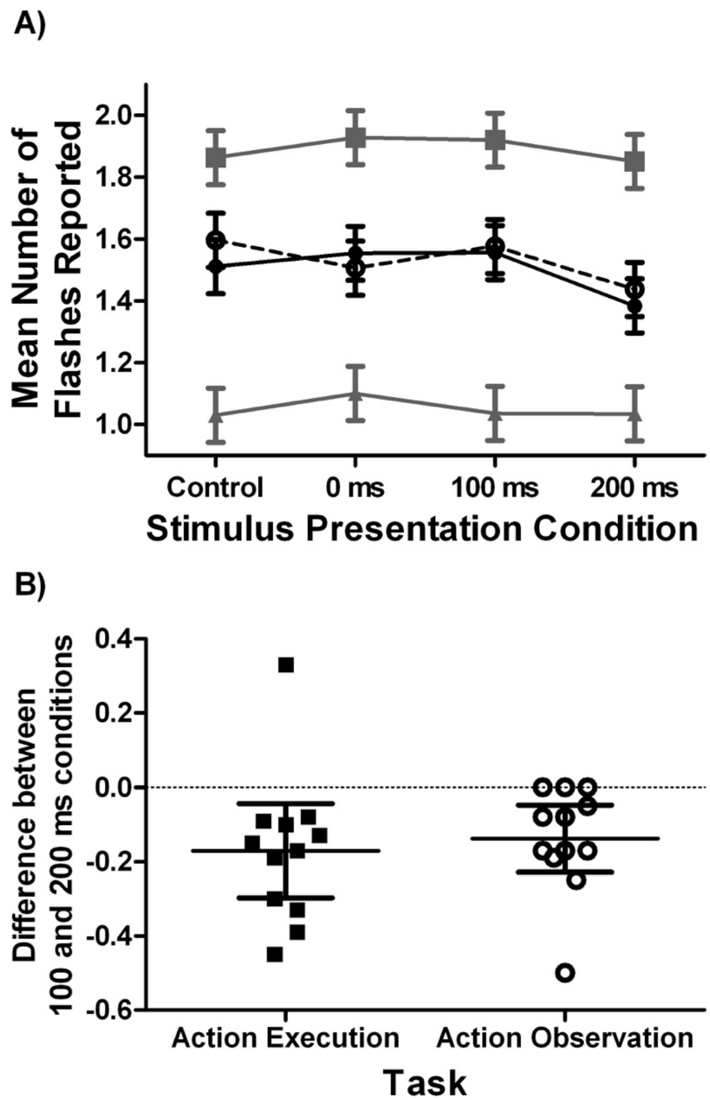

Figure 2: A) Mean number of perceived flashes for each presentation time. Performance in the key 2 flash/1 beep (fusion) conditions are represented by the black lines. The solid circle markers and connecting lines represent values for the 2 flash/1 beep condition in the action execution task. The open circle markers and dashed connecting lines represent values for the 2 flash/1 beep condition in the action observation task. For reference, performance in the congruent 2 flash/2 beep and 1 flash/1 beep conditions (averaged across action execution and observation tasks) are plotted in grey. Solid grey square markers and connecting lines represent values for the 2 flash/2 beep conditions and solid grey triangle markers and connecting lines represent values for the 1 flash/1 beep conditions. Error bars represent the 95% confidence

intervals for repeated measures designs calculated following Masson and Loftus (1994). B) The difference in the number of perceived flashes on each task when fusion (2 flash/1 beep) stimuli were presented 100 ms and 200 ms into the movement. Markers represent each individual participant's performance, the longer central line represents the mean, and error bars are conventional 95% confidence intervals.

4.0 Discussion

The purpose of the present study was to test the hypothesis that observers simulate the performance of the observed action in their own sensorimotor systems. To test this hypothesis, an assessment was made of the modulation of the fusion illusion during the execution and the observation of an aiming action. Tremblay and Nguyen (2010) reported that participants were less susceptible to the fusion illusion when the audiovisual stimuli were presented 100 ms than 200 ms after the onset of their own goal-directed movement. This pattern of findings was replicated in the present study. Specifically, participants were more likely to accurately report 2 flashes for the 2 flash/1beep condition when audiovisual stimuli were presented at 100 ms than at 200 ms relative to movement onset; in other words, the participants were less susceptible to the fusion illusion earlier in the movement than later in the movement (Figure 2). Of greater empirical and theoretical relevance to the current study, the same pattern of changes in susceptibility to the illusion emerged when participants observed a movement. This finding is consistent with the experimental hypothesis that observers simulate the performance of the observed action and, as a result, experience comparable alterations in multisensory processing during the observation and execution of a movement. Notably, the accuracy of reporting the number of visual stimuli on the compatible 2 flash/2 beep trials did not change across the presentation times. This consistency in perception in the compatible trials indicates that the decrease in the number of flashes reported in the 2 flash/1 beep condition was not a general decrease in perceiving 2 flashes at that later stage of the movement due to increased attentional demands at the end of the movement or to the hand obscuring the flashing stimuli. The remainder of the discussion will address the change in susceptibility of the participants to the illusion during action execution and subsequently the mechanisms of action observation.

Although several mechanisms could explain the increased susceptibility to the fusion illusion during action execution at 200 ms, the most likely explanation is that there is a shift in the relative weighting of the sensory information towards visual information during the higher-velocity portion of a goal-directed movement (Kennedy et al., 2015; Tremblay et al., 2013; Tremblay et al., 2017). That is, because vision is important for the early detection and correction of errors in the trajectory to ensure an accurate movement, the weighting of visual information is likely increased in the early stages of the movement. This increase in the weighting of visual information for corrections early in the movement may have the secondary consequence of increasing the efficiency and/or resolution of the processing of other visual stimuli in the environment – the flashing of the non-target LED in the present case. In contrast, there would be a decreased weighting of visual information later in the trajectory, in part because the system prioritizes movement stopping processes over feedback-based corrections (see Todorov & Jordan, 2002; Tremblay et al., 2017). As a result of the decreased weighting of visual information later in the movement, other visual stimuli are not processed as efficiently or with the same resolution and there is an increased potential for the auditory information to have a relatively greater weighting and influence on perception. This relative weighting of the auditory information may increase potential for the audiovisual illusion to emerge later in the movement trajectory than earlier in the trajectory. This presumed alteration of the weighting of the visual information relative to other sources of information (i.e., auditory which is less or not important to the ongoing movement: e.g., Manson et al., 2018) can explain the altered susceptibility to the illusion during action execution.

Why did the same change in susceptibility to the illusion occur during action observation? There is substantial evidence that the observation of a movement activates the same motor representations that are activated when people execute actions (e.g., Mulligan et al., 2016a, 2016b; Rizzolatti & Craighero, 2004; Wong et al., 2013). Further, perceptual states associated with a co-actor may also be represented in dyadic tasks (Constable et al., 2015). These activated cognitive states are thought to result from the activation of cortical networks that represent the perceptual, motor, and goal codes associated with the observed and executed actions of other people. If such matched activation of perceptual and action states occurs and the observed actions are simulated in the sensorimotor systems of the observers in real-time, then it follows that the observer should experience the same change in weighting of visual information within their own CNS that occur when the action is actually executed. Because of these relative changes in weighting of visual information during the observation of action, as seen in the present study, comparable changes in the susceptibility to the fusion illusion can emerge during both action observation and action execution.

An alternative non-motor related explanation for the effects observed here is that the mere presence and/or motion of an extra visual stimulus, such as the hand of the actor or the partner, led to changes in the susceptibility to the illusion. In other words, it could be that there was nothing special about the presence of human movement per se, but instead it was simply the presence of another visual stimulus that altered the processing of the audiovisual stimuli in a manner that enhanced the processing of the visual stimuli and decreased the susceptibility to the illusion early relative to late in the movement. Although this alternative explanation cannot be ruled out at present, data from other experiments would suggest that this account is unlikely. For example, previous studies looking at audiovisual integration have demonstrated that the ability to judge the temporal onset of unimodal stimuli (temporal order judgement tasks) in a multisensory stimulus is negatively impacted by the presence of an auditory or visual dual task (see Dean et al., 2017). That is, the temporal discrimination of visual stimuli is worse in the presence of additional auditory and visual stimuli. Based on this work, one would have predicted that the illusion would have been enhanced, not reduced, by the additional visual stimulus. Such was not the case. Further, there was no change in the number of flashes reported in the congruent conditions where the number of flashes and beeps were the same (see the sub-analysis of the 2 flash/2 beep condition) suggesting that there does not appear to be a distraction effect in the 200 ms overall or that the hand obscured the flash LED. As such, the lower number of flashes reported in the 200ms condition is interpreted as a relatively larger fusion illusion later in the movement than in the early stages of the movement. This interpretation is consistent with the notion that visual information is processed more efficiently in the early stages of the movement because visual information regarding the movement trajectory is critical to control/correction processes during the earlier stages of the movement (e.g., Tremblay et al., 2017). Nonetheless future work could directly address and contrast these potential accounts.

It should be noted that similar concerns regarding the mere presence of other visual stimuli have been raised by other researchers who have critically evaluated the accounts of other social phenomena like the joint Simon effect (Sebanz et al., 2003 vs. Dolk, Hommel, Prinz, & Liepelt, 2013) and the social inhibition of return effect (Welsh et al., 2005 vs. Atkinson, Simpson, Skarratt, & Cole, 2014). It is the case that an experimental design which can effectively distinguish between the mere effects of motion alone and movement of a limb remain elusive due to the overlapping nature of the characteristics of the two categories of stimuli and potential influence of top-down influences of belief in the animacy of the stimulus (see Chandler-Mather, Welsh, Sparks, & Kritikos, in press). Nonetheless, given the substantial behavioural and neurophysiological evidence that cortical regions that are activated during the execution of action are also activated during the observation of movement (e.g., Mulligan et al., 2016a, 2016b; Rizzolatti & Craighero, 2004) and that some social effects met the minimum criteria to be considered social (e.g., Atkinson, Millett, Donveva, Simpson, & Cole, 2018), it remains our contention that it is the sensorimotor activation during the execution and observation of goal-direct human movement Future research will need to be conducted to definitively distinguish these possibilities.

Overall, the present results are consistent with the hypothesis that the observed action is simulated in the sensorimotor systems of the observer. Such simulation effects have been observed across a variety of techniques and methods including neuroimaging (e.g., Avikainen, Forss, & Hari, 2002; Buccino et al., 2004; Gazzola, Rizzolatti, Wicker, & Keysers, 2007; Grèzes, Armony, Rowe, & Passingham 2003;

Iacoboni et al., 1999), corticospinal stimulation (Catmur et al., 2007; Fadiga et al., 1995; Strafella & Paus, 2000), and imitation (Cracco, De Coster, Andres & Brass, 2015). The present study is the first study, however, to reveal how multisensory integration is impacted during the observation of action and to provide a possible real-time index of the sensorimotor simulation process.

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