

Sensorimotor contingency modulates breakthrough of virtual 3D objects during a breaking continuous flash suppression paradigm

Keisuke Suzuki^{1,2}, David J. Schwartzman^{1,2}, Rafael Augusto³, Anil K. Seth^{1,2}

¹ Department of Informatics, University of Sussex, Brighton BN1 9QJ, United Kingdom

² Sackler Centre for Consciousness Science, University of Sussex, Brighton BN1 9QJ, United Kingdom

³ Universidade de Lisboa, Alameda da Universidade, Lisboa 1649-004, Portugal

Corresponding Author: K.Suzuki@sussex.ac.uk

Number of pages: 52

Number of figures: 6

Word Count: Abstract: 247, Introduction: 955, Experiment1 Methods: 2038, Experiment 1 Results: 1391, Experiment2 Methods: 1940, Experiment 2 Results: 1278, Discussion: 2148, Conclusions: 94.

Conflict of interests: The authors declare no competing financial interests

Abstract

To investigate how embodied sensorimotor interactions shape subjective visual experience, we developed a novel combination of Virtual Reality (VR) and Augmented Reality (AR) within an adapted breaking continuous flash suppression (bCFS) paradigm. In a first experiment, participants manipulated novel virtual 3D objects, viewed through a head-mounted display, using three interlocking cogs. This setup allowed us to manipulate the sensorimotor contingencies governing interactions with virtual objects, while characterising the effects on subjective visual experience by measuring breakthrough times from bCFS. We contrasted the effects of the *congruency* (veridical versus reversed sensorimotor coupling) and *contingency* (live versus replayed interactions) using a motion discrimination task. The results showed that the contingency but not congruency of sensorimotor coupling affected breakthrough times, with live interactions displaying faster breakthrough times. In a second experiment, we investigated how the contingency of sensorimotor interactions affected object category discrimination within a more naturalistic setting, using a motion tracker that allowed object interactions with increased degrees of freedom. We again found that breakthrough times were faster for live compared to replayed interactions (contingency effect). Together, these data demonstrate that bCFS breakthrough times for unfamiliar 3D virtual objects are modulated by the contingency of the dynamic causal coupling between actions and their visual consequences, in line with theories of perception that emphasise the influence of sensorimotor contingencies on visual experience. The combination of VR/AR and motion tracking technologies with bCFS provides a novel methodology extending the use of binocular suppression paradigms into more dynamic and realistic sensorimotor environments.

Keywords: Sensorimotor Coupling; Affordance; Visual Awareness; Continuous Flash
Suppression; Virtual Reality; Augmented Reality

1.0 Introduction

The human brain engages with the environment through the body, instantiating a closed loop between perception and action. The relevance of these interactions for perceptual phenomenology is emphasized by the Sensorimotor Theory of Consciousness (STC) (Noë, 2004; O'Regan & Noë, 2001). In STC, perceptual phenomenology is shaped by “mastery” of the sensorimotor contingencies governing how sensory signals respond to actions. STC has been applied, conceptually, to many aspects of perceptual phenomenology. One prominent application has been to the phenomenology of “objecthood” in vision. In STC, objecthood depends on the brain’s encoding knowledge about how afferent visual signals change given motor actions, such as eye movements. For example, when I experience the coffee cup in front of me as a three-dimensional object with a back-and-sides, it is because my brain “knows about” the sensory consequences of moving my eyes, or rotating the mug. In this sense, I perceive that the mug has a back even though I cannot directly see it (Noë, 2004; O'Regan & Noë, 2001).

The original formulation of STC, as expressed by O'Regan and Noe, lacks a clear implementation in neural circuits. Addressing this, (Seth, 2014) incorporated sensorimotor contingencies into a ‘predictive processing’ account of perception in which perceptual content is constituted by neurally-encoded predictions about the hidden causes of sensory signals (Clark, 2013; Friston, 2010; Hohwy, 2013). In this Predictive Processing Theory of SensoriMotor Contingencies (PPSMC), perceived objecthood arises when the brain encodes a rich repertoire of predictions about how sensory signals would change given specific actions (Seth, 2014, 2015). Both STC and PPSMC predict that visual

phenomenology, including the phenomenology of objecthood, will be systematically shaped by how a perceptual system masters, or encodes, sensorimotor contingencies.

Accompanying these theoretical developments, a growing body of empirical research has investigated embodied approaches to cognition and perception (Bekkering & Neggers, 2002; Brunel, Carvalho, & Goldstone, 2015; Chan, Peterson, Barense, & Pratt, 2013; Fagioli, Hommel, & Schubotz, 2007; Hannus, Cornelissen, Lindemann, & Bekkering, 2005; Lindemann & Bekkering, 2009). In one striking example, Dieter et al. (2014) found that blindfolded participants who waved their hands in front of their faces reported experiencing visual sensations, demonstrating that actions may not only shape visual perception but may even possess a generative effect on visual experience. Of particular relevance are studies that examine the perceptual consequences of disruptions to normal sensorimotor contingencies. For example, during binocular rivalry, visual stimuli whose movements are contingent on a participant's voluntary actions show longer ocular dominance durations, and shorter suppression times, compared to stimuli that move independently from a participant's actions (Maruya, Yang, & Blake, 2007), indicating that disruption of veridical sensorimotor contingencies can affect the formation of a visual percept even outside of awareness. However, the simple visual stimuli (dot stereogram) and trained stereotypical movements used by Maruya et al., (2007) did not address how naturalistic sensorimotor interactions with real-world objects shape subjective visual experience. To achieve this aim an experimental setup that allows naturalistic embodied interactions with realistic objects is needed. Such a setup could better address the

dependence of visual experience on the dynamic causal coupling between actions and their sensory consequences within a real-world setting.

So far, studies have not distinguished between two aspects of sensorimotor contingencies when addressing such questions: *contingency* and *congruency*. For *contingency*, it is sufficient to have a tightly (temporally) coupled relationship between changes in action and changes in sensory consequences. *Congruency* refers to whether these sensory changes are in line with what would be expected for a particular action (congruent) or not in line (incongruent). For example, moving an object to the left and seeing it move to the right (with the same timing and speed) would be contingent but incongruent. In addition, empirical tests of the influence of sensorimotor contingencies on perception using realistic or real objects have yet to be achieved, mainly due to the technical challenges of real-time manipulation of sensorimotor contingencies in such contexts.

Here we address both these challenges by leveraging recent developments in virtual reality (VR) and augmented reality (AR) that allow flexible manipulations of the sensorimotor coupling of morphologically complex virtual 3D objects. To investigate how sensorimotor interactions shape subjective visual experience, we combined these technologies with a variant of the binocular rivalry paradigm, known as breaking continuous flash suppression (bCFS) (Jiang, Costello, & He, 2007; Stein, Hebart, & Sterzer, 2011; Tsuchiya & Koch, 2005). During bCFS, perception of a target stimulus presented to one eye is suppressed by a series

of rapidly changing, high contrast, Mondrian patterns presented to the other eye, and the time it takes the target to 'break through' into awareness is measured.

In two experiments, we asked whether altering the dynamic causal coupling between a person's actions and their visual consequences would modulate breakthrough times during bCFS, for realistic virtual 3D objects and naturalistic embodied interactions. Based on previous investigations into the effects of multisensory integration during binocular suppression paradigms (Salomon, Kaliuzhna, Herbelin, & Blanke, 2015; Salomon, Lim, Herbelin, Hesselmann, & Blanke, 2013) we predicted that altered sensorimotor coupling would lead to increased breakthrough times, compared to veridical coupling.

Experiment 1 compared the effects of contingency and congruency on breakthrough times of target objects under bCFS, as assessed by judgements of rotation direction, while participants made rotating actions. Here, contingency reflected whether the object's motion was either directly linked to the participant's on-going actions, or whether it was driven by a replay of actions from an earlier trial. Congruency was determined by whether the apparent motion direction of the object was congruent or incongruent with the participant's actions. Experiment 2 further investigated the effects of contingency, employing a more naturalistic setup which allowed object interactions with greater degrees of freedom and used a category discrimination task, rather than a motion discrimination task.

2.0 Experiment 1: Comparing sensorimotor contingency and congruency

Using an adapted bCFS paradigm, participants were asked to report the rotation direction of a virtual 3D object as soon as it entered visual awareness. Participants manually rotated the virtual object using a novel AR setup with interlocking cogs (Figure 1A). This setup was designed to prevent participants obscuring the AR marker with their hand during a trial, and to allow them to rotate an object in a single direction while maintaining continuous contact with the apparatus. Using this setup, we compared the effects of two aspects of sensorimotor coupling on breakthrough times to visual awareness: (i) contingency: object movements were directly coupled to the participant's actions (Live), or they were based on a replay of previous actions recorded during a practice trial (Replay), and (ii) congruency: object movements were congruent with (same direction) or incongruent with (opposite direction) the participant's actions.

2.1. Materials and Methods

2.1.1 Participants

32 participants completed Experiment 1 (mean age = 23.18, SD = 5.57; 27 females, 2 left-handed, see section 2.1.3). Participants provided informed consent before taking part and received £5 or course credits as compensation for their time. The experiment was approved by the University of Sussex ethics committee.

2.1.2 Experiment Setup

Participants were seated approximately 50cm from a set of three interlocking cardboard cogs and wore a head mounted display (HMD) (Oculus Rift CV1, Oculus VR, California, US; resolution: 2160 x 1200, 1080 x 1200 per eye, diagonal field of view: 110°, refresh rate: 90 Hz) with an AR stereo camera (OVRVision Pro, Shinobiya.com Co., Ltd, Osaka, Japan; resolutions: 1280 x 800 per camera, 60 frame per sec, visual angle: H115° V90°) attached to the front of the HMD. The experiment setup was developed in a game development engine Unity (Unity Technologies, San Francisco, CA). In both experiments, the actual refresh rate was determined by the amount of time it took to process motion data and render the virtual object for a single frame in Unity. The frame rate within Unity for Experiment 1 was 47.07 frames per second (SE = 0.38). Additionally, we tested the latency of the hardware, measured as the time for a signal from the AR stereo camera to trigger a visual change on the HMD, which was approximately 84 milliseconds. An augmented reality (AR) marker, on the right cog was used to locate a virtual 3D object, which was superimposed on the real world through the HMD (Figure 1A, 1B). The AR camera live video feed was used to project virtual 3D objects onto the location of the AR marker. The distance between the AR camera and the AR marker was approximately 50cm. Each cog had a 17cm diameter (19.3° degrees of visual angle). The AR marker was 7.5 x 7.5cm (8.6° degrees of visual angle). The 3D object was spherically shaped, approximately 5 cm diameter (5.7° degrees of visual angle). The Mondrian mask was approximately 17 x 17cm (19.3° degrees of visual angle) and was centred on the object. Manual rotation of the left cog caused the right cog to rotate in the same direction. In each trial, participants rotated

the cogs smoothly in a single direction (clockwise, CW, or counterclockwise, CCW), while maintaining their hand on the cog at all times.

During bCFS, the virtual 3D object was presented through the HMD to the non-dominant eye of the participant, while a dynamic Mondrian mask was presented to the dominant eye. The object and the mask were seen by participants as being located directly over the AR marker printed on the right-most cog (Figure 1A). The visual rotation of the object was controlled by in-house software developed in Unity. The two conditions *contingency* (Live vs. Replay) and *congruency* (congruent vs. incongruent) were organised in a 2x2 design. In the 'Live' condition, the virtual object responded directly to the participant's movements and rotated either in the same (50% of trials, congruent) direction or in the opposite (50% of trials, incongruent) direction to the manual rotation of the cog. In the 'Replay' condition, the virtual object rotated according to the movements of a pre-recorded practice trial. Replay trials were randomly selected from 20 practice trials, subject to the constraint that 50% were congruent (same rotation direction as the current trial) and 50% were incongruent (opposite direction) (see Section 2.1.3).

Virtual 3D objects were designed using Blender (The Blender Foundation, Amsterdam, the Netherlands). All objects were designed to be novel abstract 3D objects (Figure 1B). All objects had a roughly spherical shape, but with slight asymmetry so that rotation direction would be easy to detect. For both Experiments we chose to use novel rather than familiar objects in order to exclude any potential influence of inter-subject differences in

sensorimotor knowledge for differing familiar object categories – these objects however remained highly realistic in their rendering during sensorimotor interactions.

A matt grayscale texture (saturation: 0.5) was applied to each object with natural shading from a directional light located directly above the object. Rotational movements of the object were updated at 47 frame per second, the refresh rate of our setup. The virtual object was introduced 500ms following onset of the mask and gradually increased in opacity from 0% to 100%, reaching 100% opacity after 2000ms (Figure 1C, see also Supplemental Video 1).

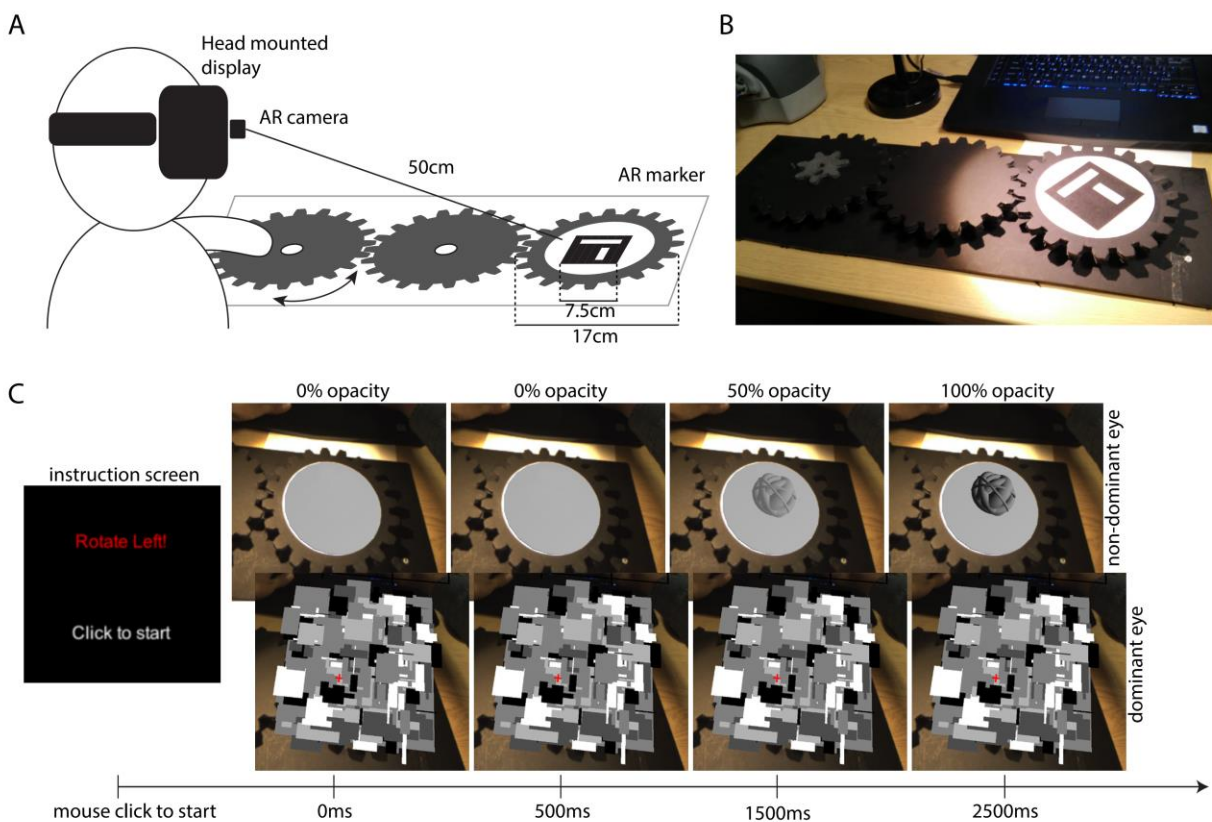


Figure 1. Experiment 1. **A.** A schematic illustration of the experimental setup. The participant freely rotated the leftmost cog either clockwise or counter-clockwise, according

to an instruction screen presented at the beginning of each trial (rotation direction was counterbalanced across the trials). Rotating the leftmost cog causes the rightmost cog to rotate in the same direction. An AR marker was placed on the rightmost cog over which a virtual 3D object and the dynamic Mondrian mask were projected via HMD. **B.** An image of the experimental setup. **C. Left:** Instruction screen. **Right-top:** images presented to the non-dominant eye. The grey disc underneath the virtual object was used in order to hide the rotation of the physical AR marker. The object appeared 500ms after the beginning of each trial. The opacity of the virtual object increased from 0% to 100%, reaching 100% opacity after 2000ms. **Right-bottom:** The CFS mask presented to the dominant eye.

The Mondrian mask consisted of 200 rectangles moving continuously in 6 different directions (two horizontal, two vertical, and two diagonal), which were uniformly assigned and consistent to each rectangle. The width and the height of the rectangles were randomly chosen from 176 different lengths from 0.03cm (0.03° degrees of visual angle) to 1.39cm (1.6° degrees of visual angle), in increments of 0.08cm (1.0° degrees of visual angle). The colour of each rectangle was randomly assigned from 5 possible grayscale values (saturation 0, 0.3, 0.5, 0.7, and 1.0). The size of the Mondrian mask (17 x 17cm, 19.3° degrees of visual angle) was such that it obscured the first cog with the AR marker in order to hide the rotation direction of the cog, as well as the virtual object. All rectangles moved at a constant speed of 1.75cm (2° degrees of visual angle) per second (Moors, Wagemans, & De-Wit, 2014). The average frame rate of the Mondrian mask was 25 frames per second.

The speed of the rectangles was chosen to optimize suppression based on the outcome of a pilot study. A red cross was projected onto the middle of the Mondrian mask as a fixation point, to help reduce eye-movements during the experiment.

2.1.3 Procedure

Before the experiment, ocular dominance for each participant was determined using the Miles test (Miles, 1930). Participants were then fitted with the HMD and completed a practice session to familiarize them with the task. All participants (including the 2 left-handers) held a standard computer mouse with their right hand and maintained continuous contact with the left cog with their left hand throughout the experiment. The practice session consisted of 20 trials of the Live condition (10 congruent, 10 incongruent, each consisting of 5 CW and 5 CCW rotations). At the beginning of each trial an instruction screen informed the participant to rotate the cog either to the left (CCW) or to the right (CW). The instructed rotation direction was randomized across trials (Figure 1C Left). Each trial started with the participant viewing their immediate environment through the AR camera. The Mondrian mask was then presented to the dominant eye superimposed over the AR marker, which was followed by a virtual 3D object gradually appearing to the non-dominant eye. Participants were instructed as follows: “As soon as you identify the direction the virtual 3D object is rotating, click the associated mouse button”. Participants indicated rotation direction by clicking the left mouse button if the object was rotating CCW, and the right mouse button if the object was rotating CW. The timing of this response determined the *breakthrough time*, the main dependent variable. Participants were also instructed to fixate on the red cross in the centre of the Mondrian mask, and were asked to

try to avoid blinking during each trial, as blink rate has been shown to affect breakthrough times in bCFS (Stein et al., 2011; Tsuchiya & Koch, 2005). During the practice session, the movements of the object were recorded for later use in 'Replay' trials. In order to train participants to maintain a consistent rotation speed during the experiment, we included a rotational 'speed indicator' bar in the practice trials, which was located above the Mondrian mask. This bar changed colour from blue (when the rotation speed was in the desired range, see below) to red, (when the rotation speed was either too fast or too slow). Rotation speeds were computed as a rolling average across 5 frames. The desired range used, had a lower limit of 0.5 degree/frame and an upper limit of 2.5 degree/frame. The speed indicator bar was not shown in the main experiment.

The main experiment used the same trial structure as the practice session. It consisted of 4 blocks, each with 24 trials (total of 96 trials, note that the duration of each trial varied according to individual differences in breakthrough times). Participants were encouraged to take a short break at the end of each block during which they could remove the HMD. Trial types followed the same 2x2 design, with factors contingency (Live, Replay) and congruency (congruent, incongruent rotation), leading to a total of 4 trial types with each type being presented a total of 24 times. The whole experiment took approximately 45 minutes to complete, including the practice and breaks in-between blocks.

2.1.4 Analysis

In the remainder of this paper, we distinguish two types of rotation speed: the *apparent* rotation speed of an object, which refers to the rotation speeds of (virtual) objects as viewed by participants, and the *manual* rotation speed, which refers to the participant's physical movement of the cog (or stylus, in Experiment 2). The manual and apparent rotational speeds were derived by measuring changes in the orientation of the corresponding AR marker from one frame to the next. The accumulated angles across frames for each trial were divided by the number of frames within the trial to provide the average rotation speed (manual and apparent) in degrees-per-frame, for each participant, and for each trial. For Live trials, apparent and manual rotation speeds were by construction identical. For Replay trials, apparent speeds depended on the rotation speeds of earlier practice trials, from which virtual object movements were drawn.

Exclusion criteria were as follows. We calculated the difference in average apparent rotation speed between for Replay and Live trials, for each participant. Participants with an average difference of more than 2 standard deviations (SDs) from the group average were excluded from all further analyses. This criterion was applied to guard against the possibility that large differences in apparent visual rotation speed between conditions might affect breakthrough times. For the remaining participants, trials where breakthrough times were >30 sec or were more than 2.5 SDs from the mean breakthrough time across participants were excluded. Finally, incorrect trials were removed from all further analyses, and error rates were calculated for each condition (see Section 2.2 for results of exclusion criteria). All further analyses and plots used the above exclusion criteria.

A two-factorial repeated measures ANOVA consisting of the factors contingency (Live/Replay) and congruency (Congruent/Incongruent) was applied to assess how these factors affected breakthrough time. Additional Bayesian two-factorial repeated measures ANOVAs were applied to the same data. Following this primary analysis, we conducted a number of follow-up analyses to investigate whether disparities in either manual or apparent rotation speeds between conditions may have affected breakthrough times. In these analyses we compared, using standard and Bayesian two-factorial repeated measure ANOVAs, average manual and apparent rotation speeds across conditions. All ANOVA results also included the Eta Squared effect size denoted by η^2 . We also applied a Bayesian Pearson's correlation analysis to assess evidence of a correlation between manual and apparent rotation speed and breakthrough time in the Live and Replay conditions. Finally, for each participant we ran a within-subjects multiple linear regression (i.e. at the single-trial level) to model breakthrough time as a function of (i) contingency (Live/Replay), (ii) congruency (congruent/incongruent), (iii) interaction between contingency and congruency, (iv) manual rotation speed, (v) apparent rotation speed.

2.2 Results

Based on the exclusion criteria, three participants were excluded due to excessive differences in apparent rotation speed between Live and Replay trials (> 2.0 SDs; $M = -0.415$ degree/frame, $SD = 0.43$ degree/frame). For the remaining 29 participants, the following trials were excluded from further analysis: incorrect trials (133 out of 2784,

4.8%), trials with breakthrough time >30 sec (1 out of 2651, 0.04%) and outliers (>2.5 SDs of mean breakthrough time across all participants; 68 out of 2650 trials, 2.6%).

The remaining data, consisting of 2582 trials out of 2784, was submitted to a two-factorial repeated measures ANOVA consisting of the factors contingency (Live/Replay) and congruency (congruent/incongruent). The results revealed a significant main effect of contingency ($F(28,1) = 14.972, p < 0.01, \eta^2 = 0.348$), with Live sensorimotor coupling breaking through faster ($M = 3.57$ s, $SE = 0.20$ s) than Replay ($M = 3.81$ s, $SE = 0.20$ s). Congruency did not reach significance ($F(28,1) = 0.499, p = 0.486, \eta^2 = 0.017$) (congruent trials: $M = 3.67, SE = 0.20$, incongruent trials: $M = 3.71, SE = 0.20$) and there was no interaction between the two factors ($F(28,1) = 0.262, p = 0.612, \eta^2 = 0.009$) (Figure 2A). Additional two-way Bayesian repeated measures ANOVA consisting of the same factors provided the strongest evidence for an effect of contingency only ($BF_{10} = 482.016$). Post-hoc Bayesian t-tests, investigating individual factors further, revealed that there was no evidence in support of an effect of congruency ($BF_{10} = 0.190$), whereas there was strong evidence in support of an effect of contingency ($BF_{10} = 403.9$). These analyses indicate that breakthrough into awareness of visual rotation direction was faster for interactions that were directly coupled to (i.e., contingent upon) participants' movements, while the congruency of the coupling did not affect breakthrough times.

There were very few incorrect responses: 4.6% ($SE = 1.00$) across all participants. A 2-way repeated measures ANOVA revealed significant no differences in correct responses for

either contingency ($F(28,1) = 0.239$, $p = 0.629$, $\eta^2 = 0.008$), or *congruency* ($F(28,1) = 2.060$, $p = 0.162$, $\eta^2 = 0.069$), or an interaction between these factors ($F(28,1) = 0.2085$, $p = 0.160$, $\eta^2 = 0.069$) (Figure 2B). Additional Bayesian repeated measures ANOVA showed strong evidence for the null model, indicating no differences across conditions in response accuracy (contingency: $BF_{10} = 0.239$, congruency: $BF_{10} = 0.316$).

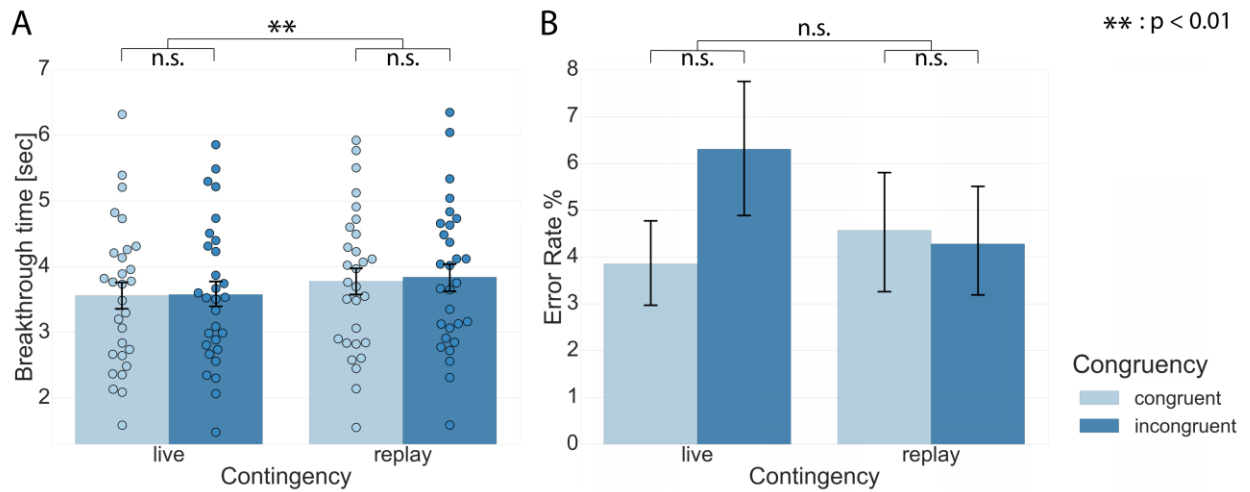


Figure 2. Experiment 1. **A.** Breakthrough time by contingency (Live/Replay) and congruency (congruent/incongruent). Significantly shorter breakthrough times were found for the Live compared to the Replay condition. **B.** Error rate by condition. No significant differences in error rate were found. Error bars indicate standard errors. Dots in panel A show individual participant results.

We next investigated, at the group-level, if differences in the manual or apparent object rotation speed could account for condition-specific differences in breakthrough time. For the group-level analysis, we averaged breakthrough times and rotation speeds (manual and

apparent) across trials for each participant and condition (Live/Replay, congruent/incongruent).

We first investigated if there were differences in the average manual rotation speed between conditions (Live/Replay, congruent/incongruent, Figure 3A). A two-factorial repeated measures ANOVA found no significant differences in manual rotation speed either for contingency ($F(28,1) = 3,090, p = 0.090, \eta^2 = 0.099$) (Live trials: $M = 3.34$ degree/frame, $SE = 0.20$ degree/frame, Replay trials: $M = 3.38$ degree/frame, $SE = 0.21$ degree/frame) or congruency ($F(28,1) = 1.133, p = 0.296, \eta^2 = 0.039$) (congruent trials: $M = 3.35$ degree/frame, $SE = 0.20$ degree/frame, incongruent trials: $M = 3.37$ degree/frame, $SE = 0.20$ degree/frame) and there was no interaction between these two factors ($F(28,1) = 3.503, p = 0.072, \eta^2 = 0.111$). An additional Bayesian repeated measures ANOVA did not provide evidence in support of either the null or alternative hypothesis for contingency ($BF_{10} = 1.044$), whereas congruency showed evidence in support of the null hypothesis ($BF_{10} = 0.324$) i.e. no difference in manual rotation speed between congruent and incongruent trials.

We next investigated, still at the group-level, if there were differences in the apparent (not manual) rotation speed between conditions (Figure 3B). A two-factorial repeated measures ANOVA revealed a significant main effect of contingency ($F(28,1) = 33.456, p < 0.01, \eta^2 = 0.544$), with faster apparent rotation speeds during Live sensorimotor coupling ($M = 3.34$ degree/frame, $SE = 0.19$ degree/frame) compared to Replay trials ($M = 2.90$ degree/frame,

$SE = 0.18$ degree/frame). Congruency did not reach significance ($F(28,1) = 1.780, p = 0.193, \eta^2 = 0.060$) (congruent trials: $M = 3.12$ degree/frame, $SE = 0.19$ degree/frame, incongruent trials: $M = 3.13$ degree/frame, $SE = 0.19$ degree/frame). There was no interaction between these two factors ($F(28,1) = 0.2484, p = 0.126, \eta^2 = 0.081$). An additional two-way Bayesian repeated measures ANOVA using the same factors showed the strongest evidence in support of a difference in apparent rotation speed for contingency only ($BF_{10} = 1.323 \times 10^{12}$), whereas for congruency, the evidence supported the null hypothesis ($BF_{10} = 0.206$) i.e. no difference in apparent visual rotation speed for Congruent/Incongruent trials.

Together these results indicate that the manual rotation speed of the cogs did not differ significantly between Live and Replay trials, whereas the apparent rotation speed of the virtual objects was faster for Live compared to Replay trials, regardless of congruency.

One scenario that could lead to this pattern of results is if manual rotation speeds increased over the course of the experiment. Since Replay trials draw object movements from early (practice) trials, this would lead to the observed discrepancy in apparent and manual rotation speed in Replay trials. A 2-way ANOVA with factors manual/apparent rotation speed and block number revealed that for the Replay condition there was a significant main effect of rotation type only, ($F(224, 1) = 11.400, p < 0.001, \eta^2 = 0.048, BF_{10} = 32.447$), but not for the block number ($F(224, 3) = 0.063, p = 0.979, \eta^2 = 0.001, BF_{10} = 0.022$) (Figure 3C). Overall, these results show that manual and apparent rotation speed did not increase

significantly across blocks, but support the conclusion that manual rotation speed was faster than apparent rotation speed in the Replay condition.

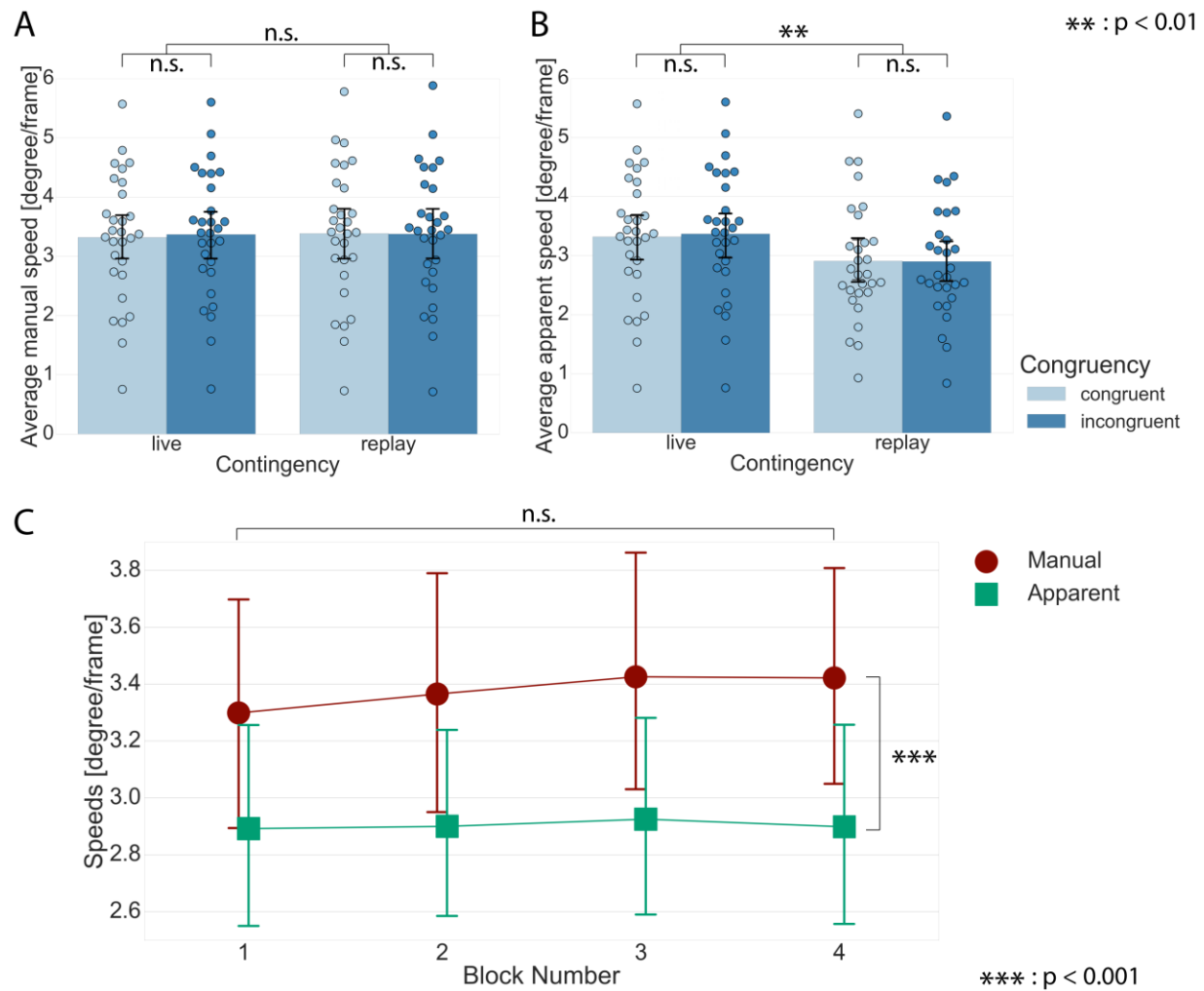


Figure 3. Apparent and manual rotation speeds in Experiment 1. **A.** Average manual rotation speed. There were no significant differences. Outliers have been removed (described in section 2.1.4) **B.** Average apparent visual object rotation speeds. A significant difference was found for contingency, but not congruency. Error bars indicate standard deviation. Dots in both panels show individual participant results. **C.** The time course of manual and apparent rotation speeds averaged across each block for the Replay condition. Error bars indicates standard deviation.

These results raise the concern that differences in breakthrough time, as observed for the contingency but not the congruency manipulation (Figure 2), could be attributed to differences in apparent rotation speeds. Indeed, previous research has found that breakthrough times during suppression paradigms can be influenced by the speed of a moving stimulus (Blake, Zimba, & Williams, 1985). If this were the case in Experiment 1, one might expect a correlation between breakthrough time and (either apparent or manual) rotation speed. To investigate this possibility, we first applied a Bayesian Pearson's correlation analysis at the group-level to look for evidence of a correlation between manual and apparent rotation speed and breakthrough time in the Live and Replay conditions. We found no correlation between breakthrough time and either manual (Live: $r = -0.065$, $p = 0.739$, $BF_{10} = 0.243$; Replay: $r = -0.136$, $p = 0.480$, $BF_{10} = 0.293$) or apparent rotation speeds (Replay: $r = -0.091$, $p = 0.640$, $BF_{10} = 0.256$) (see Supplemental Materials, Figure S1).

However, this group-level analysis is by design insensitive to any potential effect of rotation speed on breakthrough time for each trial. Therefore, for each participant we ran a separate within-subjects multiple linear regression (i.e. at the single-trial level) to model breakthrough time as a function of (i) contingency (Live/Replay), (ii) congruency (congruent/incongruent), (iii) interaction between contingency and congruency, (iv) manual rotation speed, (v) apparent rotation speed. This provided, for each subject, a coefficient estimate (beta) of how each predictor correlated with breakthrough time after

accounting for effects of the other predictors. We considered each of the five beta coefficients separately and tested whether each coefficient differed significantly from zero using both frequentist and Bayesian one-sample t -tests (see 2.2 and Supplemental Materials). A statistically significant result would indicate that the predictor significantly correlates with breakthrough time even after accounting for the effects of the other predictors. We found that the coefficients for both manual ($t(28) = -4.617, p < .001, BF_{10} = 323.640$) and apparent rotation speed ($t(28) = -4.133, p < .001, BF_{10} = 99.298$) differed significantly from zero showing, that both factors correlated significantly with breakthrough time. However, we found evidence supporting no difference from zero for the congruency ($t(28) = -0.783, p = 0.440, BF_{10} = 0.261$) and the interaction between contingency and congruency ($t(28) = 0.068, p = 0.946, BF_{10} = 0.198$). There was not sufficient evidence to support either a difference or no difference for the contingency (Live/Replay) of the object ($t(28) = -1.779, p = 0.086, BF_{10} = 0.793$) (see Supplemental Materials). Together these results suggest that in Experiment 1, at a single-trial level, we cannot exclude the possibility that differences in the manual or apparent rotation speeds influenced breakthrough time.

3.0 Experiment 2: Increasing the richness of sensorimotor coupling

Experiment 1 investigated whether manipulations of both the sensorimotor *congruency* and *contingency* affected breakthrough times for discrimination of rotation direction under bCFS, when sensorimotor interactions with the virtual 3D object were restricted to simple 2D rotational movements. We found an effect for contingency but not for congruency. In

this first experiment, we could not exclude the possibility that the difference in apparent rotation speed between live and replayed sensorimotor interactions (contingency manipulation) may have influenced breakthrough time. One limitation of the Experiment 1 was the constraints of the experimental setup. The use of 2D rotational movements meant that there was only a small difference between apparent and manual rotational movements in Replay trials. These strong sensorimotor constraints may not have been sufficient to fully decouple a participant's actions from their visual consequences during every Replay trial. This may explain why in Experiment 1 we found an effect of contingency when averaging across all trials (group-level), but do not at the single-trial level.

In Experiment 2, we developed a new setup, which utilized a motion-tracking device (Figure 4A) that allowed more naturalistic object-related sensorimotor interactions, with greater degrees of freedom. This arrangement allowed us to capture the spatial, rotational and non-stereotypical movements of each trial leading to a more complete decoupling of participant's sensorimotor interactions with an object during Replay trials. Due to the absence of an effect of congruency in Experiment 1, we focused solely on the contingency of sensorimotor interactions in Experiment 2. Finally, we chose a different perceptual task - object discrimination - due to the physical constraints of the new setup. Note that the previous motion discrimination task could not be used here because maintaining continuous contact using the motion-tracking stylus meant that it was not possible to rotate an object consistently in a single direction.

In Experiment 2, participants were asked to identify the category of an object presented using the same bCFS paradigm as in Experiment 1, while performing natural unrestricted rotational movements of the object using a stylus attached to a motion-tracking device (Figure 4A). We used the motion-tracking device to track the participant's interactions with the stylus and transferred those movements to the virtual object. As before, virtual objects were presented through the HMD to the non-dominant eye, while a dynamic Mondrian mask was presented to the dominant eye. Experiment 2 compared three aspects of sensorimotor coupling on breakthrough times. In the 'Live' condition, the object responded directly to the participant's rotational movements. In the 'Replay' condition, the object rotated according to the rotational movements of a randomly selected pre-recorded practice trial. To provide a baseline for breakthrough times we added a 'Static' condition, in which the 3D virtual object always maintained the same orientation (apparent visual angle) with respect to the participant, though its physical position could still change depending on stylus movement (i.e., translational movements were still mapped from stylus to object).

3.1. *Materials and Methods*

3.1.1 *Participants*

31 participants completed Experiment 2 (mean age = 24.7, SD = 7.76; 17 females, 3 left-handed, none had previously taken part in Experiment 1). Participants provided informed consent before taking part and received £5 or course credits as compensation for their time. The experiment was approved by the University of Sussex ethics committee.

3.1.2 Experiment Setup

Participants were seated approximately 50cm from a motion-tracking device (The Touch™ Haptic Device, 3D Systems, South Carolina, US) that was used to measure movements of the stylus. This device captures translational movements and rotations with 6 degrees-of-freedom (forward/backward, up/down, left/right), and is also capable of generating directional force. The virtual environment was developed in Unity with a Haptic plugin for Unity3D (<http://radar.gsa.ac.uk/3575/>). The same HMD as in Experiment 1 (Oculus Rift) was used to present the stimuli within a 3D virtual environment (Figure 4A). The size of the 3D virtual environment is described in terms of its apparent physical size (in cm) based on a mapping of the positions of the motion-tracking device to the Unity environment. The average frame rate within Unity for Experiment 2 was 51.61 frames per second ($SE = 1.19$). The latency of the hardware, measured as the time for a movement of the stylus attached to the motion tracker to trigger a visual change in the HMD, was approximately 19 milliseconds. The 3D virtual environment consisted of a virtual wooden textured box (28.3cm in width, 14.2cm in height, and 28.3cm in depth). A virtual camera was fixed at the centre of the box, placed 2.83cm horizontally back from the front edge of the box and 8.5cm vertically from the floor (Figure 4B left). The object (size 2.83cm in diameter) and the moving Mondrian mask (size 5.67cm in width and height) were positioned at the point of the motion-tracking stylus. The translational movements of the stylus were limited by a 'bounding box', positioned within the surrounding wooden box (bounding box dimensions: 17cm in width, 10cm in height, and 17cm in depth) (see Figure 4B right, the green line indicates the limits of the bounding box). Participants were allowed to freely move the

object within the 3D environment using the stylus, but were instructed to focus on making natural unrestricted rotational movements with their hand within the box rather than larger vertical or horizontal (translational) movements. This freedom of movement led to a variation in the distance between the virtual object and the camera of between 11.3cm to 17.0cm. To increase the sense of ‘realness’ of the virtual object, the motion-tracking device generated a constant downward force (1.22N) to simulate the weight of the virtual object.

Two distinct novel object families (3 in each family, 6 in total, see Figure 4C) were created using Blender (The Blender Foundation, Amsterdam, the Netherlands). The size and width of all 6 objects were roughly equivalent. A matt grayscale texture (saturation: 0.5) was applied to the virtual objects with natural shading from a directional light located directly above the object. Rotational movements of the object were updated at 52 frames per second, which was the refresh rate of our setup. The object was presented to the non-dominant eye 500ms after the mask onset and gradually increased in opacity from 0% to 100%, reaching 100% after 2000ms (Figure 4D, Right-top, see also Supplemental Video 2).

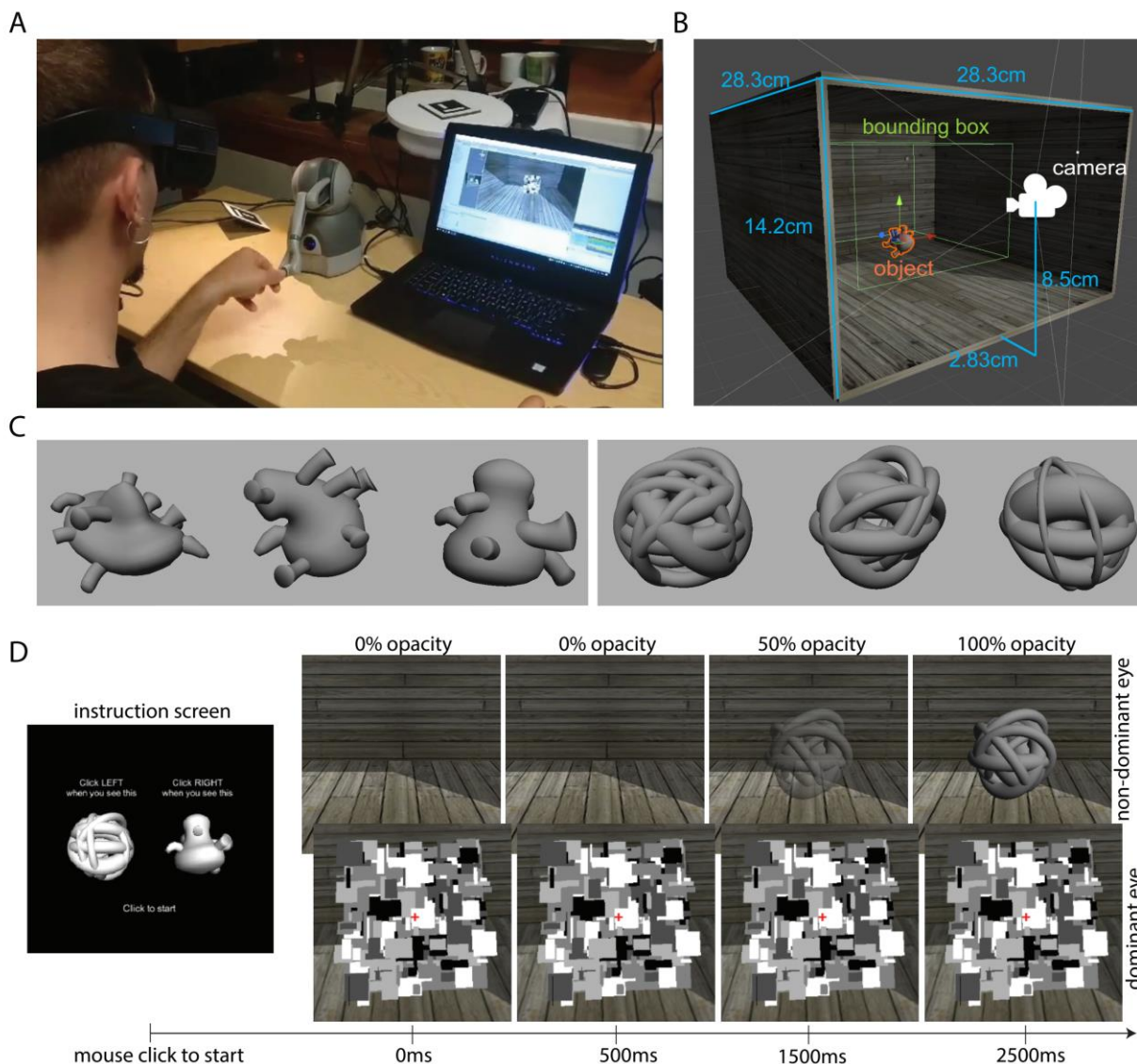


Figure 4. Experiment 2. **A.** Experimental setup. Participants viewed a virtual 3D object and dynamic Mondrian through a HMD. They manipulated a virtual object using a motion-tracking stylus with their left hand, and responded using a computer mouse, with their right hand, to identify the object as soon as it entered visual awareness. **B.** Overview of the virtual environment. Camera symbol indicates the participant's point of view. **C.** The six virtual objects used in this experiment, divided into two families). **D. Left:** Instruction screen which indicated how to respond (left or right mouse click) for each object. The association between

response option and object family was consistent throughout the experiment for each participant, but was counterbalanced across participants. **Right-top:** images presented to the non-dominant eye. The object appeared 500ms after trial onset and its opacity gradually increased, reaching 100% opacity at 2000ms. **Right-bottom:** The Mondrian mask presented to the dominant eye.

3.1.3 Procedure

For each participant, ocular dominance was determined using the Miles test (Miles, 1930). Participants then put on the HMD and completed a practice session designed to familiarize them with the task. All participants held a standard computer mouse in their right hand and controlled the stylus with their left hand (regardless of handedness). The practice session consisted of 20 trials of the Live condition. At the beginning of each trial, participants were shown an instruction screen with two virtual 3D objects, one randomly chosen from each family. The instruction screen indicated which mouse button (left or right) the participant should press for each (Figure 4D Left). Participants initiated the onset of the trial, when ready, by pressing any mouse button.

The Mondrian mask was then presented to the dominant eye in the virtual environment, which was followed by a virtual 3D object gradually appearing. Participants were required to identify the object, using the appropriate response option, as quickly as possible. During each trial, the position and orientation of the object was continuously updated based on the position of the stylus pen, with the Mondrian mask always centred on the object. As before,

participants were instructed to fixate on a red cross shown in the centre of the Mondrian mask and to reduce their blink rate during each trial. During the practice session, the dimensional rotational movements were recorded for later use in 'Replay' trials. The same training procedure of rotational speed was used as in Experiment 1 (i.e. using a 'speed indicator' bar).

The main experiment consisted of 4 blocks, each with 30 trials. Across the 4 blocks, there were 40 trials for each condition (Live, Replay, and Static), each of which used the same trial structure as in the practice session. Participants were encouraged to take a break at the end of each block by removing the HMD for a short period. Each block contained 10 trials of each condition, the order of which was randomised for each participant. If breakthrough did not occur by the end of the pre-recorded movements during Replay trials, we continued replaying the objects movements from the pre-recorded trial forwards and backwards until the object broke through suppression and the participant responded.

3.1.4 Analysis

Exclusion criteria of data were similar to Experiment 1. For Replay and Live trials, we calculated the average difference in apparent rotation speed between these conditions across all trials. Participants with an average difference in apparent rotation speed between Live and Replay conditions of more than 2 standard deviations (SDs) from the group average were excluded from all further analyses. For the remaining participants, trials where breakthrough times were >30 sec or were more than 2.5 SDs from the mean

breakthrough times across participants were also excluded. Finally, incorrect trials were removed from all further analyses, and the error rates were calculated for each condition (see section 3.2 for results of exclusion criteria). All further analyses and plots were used the above exclusion criteria.

A one-way repeated measures ANOVA with main factors Live/Replay/Static was used to assess the effects of the different types of contingency on breakthrough time. Additional Bayesian one-way repeated measures ANOVA were applied to the same data. As in Experiment 1 we compared the average manual and apparent rotation speeds across conditions. Average manual speeds of stylus movements were analysed using both standard and Bayesian one-way repeated measure ANOVA with main factors of Live/Replay/Static. The rotational speed was derived by measuring the angle between stylus location from one frame to the next (using the function `Vector3.Angle` in Unity), therefore capturing all 3-dimensional movements. We divided the sum of the angles by the number of frames per trial to provide the average rotational speeds in degrees per frame for each trial and participant. The average apparent speeds of the virtual object movements during the experiment were analysed using both standard and Bayesian paired samples *t*-test between Live/Replay conditions. The ANOVA results also included the Eta Squared effect size denoted by η^2 , while the *t*-test result includes Cohen's *d* to report the effect size. The Holm–Bonferroni method (Holm, 1979) was used to correct for multiple comparisons made using the ANOVA.

As with Experiment 1, at the group level, we conducted Bayesian Pearson's correlation analyses, while at the single-trial level we used multiple linear regression coefficients to investigate the influence of the apparent or manual rotation speeds of virtual objects on breakthrough time.

Finally, another potential factor that may have contributed to differences in breakthrough times between conditions is the potential variance in the rate of participant's change in movement direction during each trial, with the possibility of more frequent changes in movement direction leading to faster breakthrough times. To investigate this question, for Experiment 2, we analysed the complexity of the motion trajectories of the virtual objects during each trial using the Lempel-Ziv (LZ) complexity measure (Lempel & Ziv, 1976) (for details of analysis and results see Supplemental Material). LZ complexity has been shown to be a reliable index for tracking differences in motion regularities across conditions (Peng, Genewein, & Braun, 2014). We first compared the average LZ complexity across the conditions (Live, Static, Replay), then applied the same group-level and single-trial level analyses as described for both experiments, examining the correlation between the complexity of movement and breakthrough time. We refer to this normalised Lempel-Ziv complexity of the 2-dimensional angle movements as 'LZ complexity' in the following text.

3.2 Results

Two participants were excluded due to differences in apparent rotation speed between Live and Replay trials (> 2.0 SDs; $M = -0.31$ degree/frame, $SD = 0.43$ degree/frame). For the remaining 29 participants, the following trials were excluded from further analysis:

incorrect trials (90 out of 3480, 2.59%), trials with breakthrough times > 30 sec (6 out of 3390, 0.18%) and breakthrough outliers (>2.5SDs; 96 out of 3384 trials, 2.84%).

The remaining data, consisting of 3288 trials out of 3480, were submitted to a 1-way repeated measures ANOVA consisting of the main factors Live/Replay/Static. The results revealed a significant main effect ($F(56,2) = 4.125$, $p=0.021$, $\eta^2 = 0.128$) for breakthrough time, with Live ($M = 3.38$ s, $SE = 0.18$ s) showing shorter breakthrough times compared to Replay ($M = 3.58$ s, $SE = 0.21$ s) or Static coupling ($M = 3.67$ s, $SE = 0.21$ s) (Figure 5A).

Post-hoc t -tests, with Holm–Bonferroni correction, revealed a significant difference in breakthrough time only between Live and Replay conditions ($t(28) = -2.905$, $p_{\text{holm}} = 0.021$)

(Live/Static: $t(28) = -2.354$, $p_{\text{holm}} = 0.052$; Replay/Static: $t(28) = 0.732$, $p_{\text{holm}} = 0.470$). An

additional 1-way Bayesian repeated measures ANOVA provided evidence in support of a trend towards the alternative hypothesis in favour of a difference in breakthrough times between conditions ($BF_{10} = 2.253$). Post-hoc Bayesian t -tests revealed strong evidence in support of a differences in breakthrough times between Live and Replay trials

($BF_{10} = 6.090$) and weaker evidence for a difference between Live and Static trials

($BF_{10} = 2.067$), whereas it revealed evidence in support of no difference in breakthrough times between Replay and Static trials ($BF_{10} = 0.252$). In line with Experiment 1, these

analyses indicate that breakthrough into awareness of a virtual objects (family) identity was faster for interactions that were directly coupled to (i.e., contingent upon) participants' movements, compared to Replay or Static trials.

Similar to Experiment 1, there was a low error rate across participants 2.5% ($SE = 0.40$). A 1-way ANOVA showed no significant difference in the proportion of correct responses between Live/Replay/Static conditions ($F(56, 2) = 0.994, p = 0.376, \eta^2 = 0.034$) (Figure 5B). Additional Bayesian repeated measure ANOVA showed strong evidence for the null model, i.e. no difference in error rate between conditions ($BF_{10} = 0.229$).

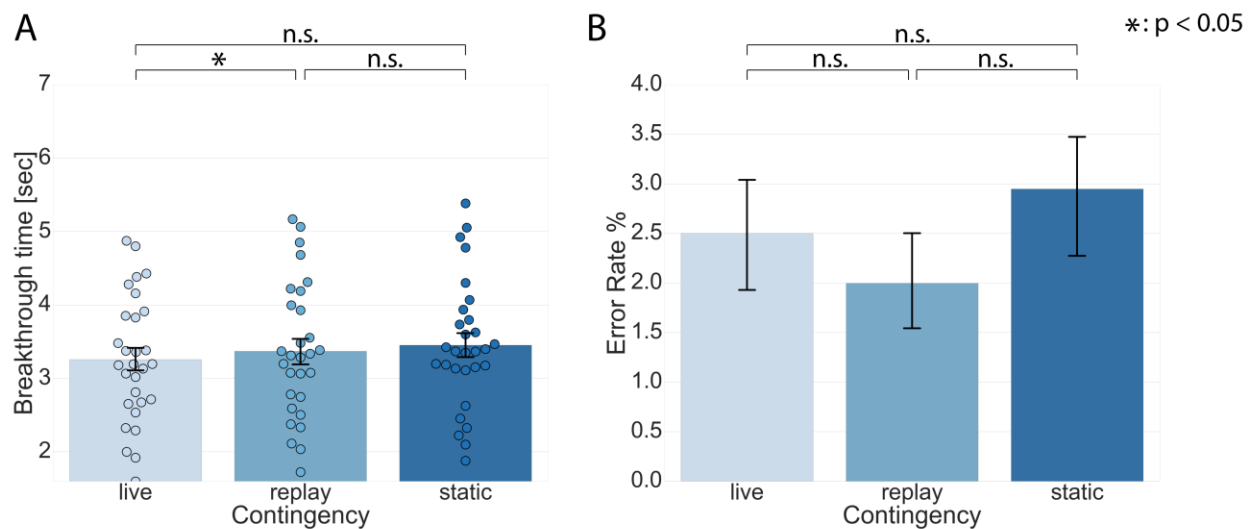


Figure 5. Experiment 2. **A.** Breakthrough time by sensorimotor coupling type (Live, Replay, Static). Significantly shorter breakthrough times were found for the Live compared to the Replay condition. Dots show individual participant results. **B.** Error rate by condition. No significant differences in error rate were found. Error bars indicate standard errors.

We next investigated the relationship between average manual and apparent rotation speeds of the virtual objects across conditions. Figure 6A shows the average speed of participant's manual movements of the stylus. A 1-way repeated measures ANOVA

revealed that there was no significant difference in manual rotation speed between Live/Replay/Static trials ($F(54,2) = 0.176, p = 0.839, \eta^2 = 0.006$) (Live trials: $M = 1.97$ degree/frame, $SE = 0.23$ degree/frame, Replay trials: $M = 1.96$ degree/frame, $SE = 0.22$ degree/frame, Static trial: $M = 1.96$ degree/frame, $SE = 0.22$ degree/frame). An additional 1-way Bayesian repeated measures ANOVA showed strong evidence for the null model, i.e. no difference in manual rotation speed between conditions ($BF_{10} = 8.362$). Figure 6B shows average apparent rotation speed of the virtual 3D objects in Experiment 2. As in Experiment 1, a 2-tailed t -test revealed a significant difference in apparent rotation speed between the Live and Replay conditions ($t(27) = 4.583, p < 0.01$, Cohen's $d = 0.866$), with the Live condition showing faster apparent rotational movements of the virtual 3D objects ($M = 1.97$ degree/frame, $SE = 0.23$ degree/frame) compared to Replay trials ($M = 1.65$ degree/frame, $SE = 0.19$ degree/frame). An additional 1-way Bayesian t -test supported this finding by showing strong evidence for a difference in apparent rotational speed of the virtual 3D objects between the Live and Replay conditions ($BF_{10} = 279.8$). Together, these results indicate that while participant's manual rotation speed of the stylus did not differ significantly between Live, Replay, or Static trials, the apparent rotation speed of an object was significantly faster during Live compared to the Replay condition.

As in Experiment 1, this pattern of results could arise if manual rotation speeds increased over the course of the experiment. Since Replay trials draw object movements from early (practice) trials, this would lead to the observed discrepancy in apparent and manual rotation speed in Replay trials. Again as in Experiment 1, we next examined the average manual and apparent rotations speeds for each experimental block for the Replay condition (Figure 6C). A 2-way ANOVA with factors rotation type (manual/apparent

speeds) and block number for Replay condition revealed a significant main effect for the rotation type ($F(224, 1) = 4.085$, $p < 0.044$, $\eta^2 = 0.018$, $BF_{10} = 3.886$), but not for block number ($F(224, 3) = 0.158$, $p = 0.924$, $\eta^2 = 0.002$, $BF_{10} = 0.025$). These results demonstrate that as in Experiment 1, the apparent rotation speed, taken from the practice session, was always slower than the manual rotation speed in the Replay condition.

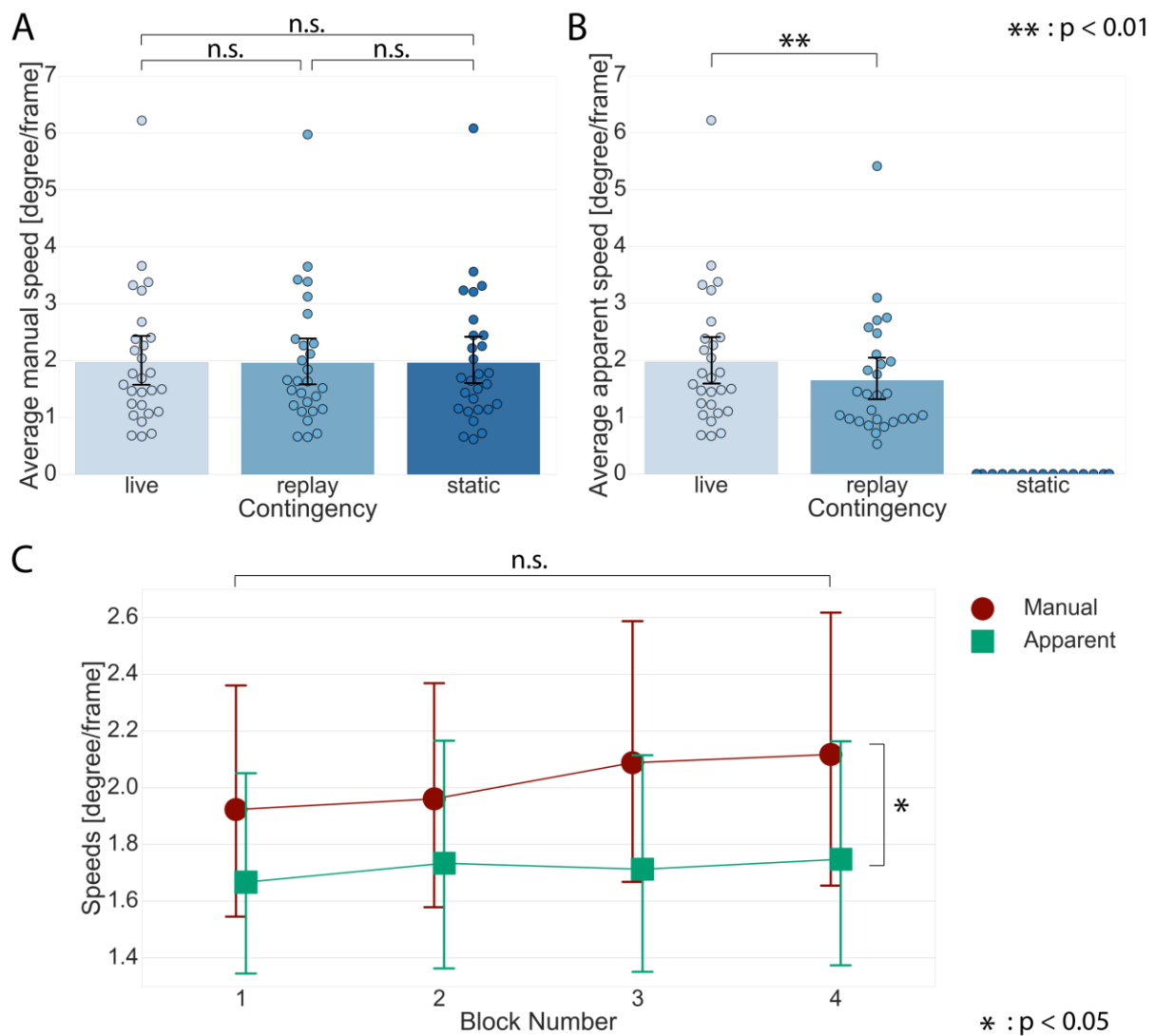


Figure 6. Rotation speeds in Experiment 2. **A.** Average manual rotation speed. There were

no significant differences. Outliers have been removed (described in section 3.1.4). **B.** Average apparent object rotation speeds. A significant difference was found for the Live compared to the Replay condition. Error bars indicate standard deviations. Dots in both panels show individual participant results. **C.** The time course of the manual and apparent rotation speeds for each block for Replay condition. Error bars indicates standard deviation.

Examining the correlation between breakthrough time and rotation speeds we found, similar to Experiment 1, at the group-level there was no correlation between manual rotation speed (Live: $r = 0.040$, $p = 0.841$, $BF_{10} = 0.239$; Replay: $r = 0.019$, $p = 0.923$, $BF_{10} = 0.236$; Static: $r = 0.166$, $p = 0.398$, $BF_{10} = 0.330$) or apparent rotation speed of the virtual objects (Replay: $r = -0.091$, $p = 0.647$, $BF_{10} = 0.259$) and breakthrough time (see supplemental Figure S2). We next analysed data at the single trial level. We modelled breakthrough time as a function of (i) contingency between Live, Static and Replay, (ii) manual rotation speed and (iii) apparent rotation speed using multiple linear regression. Crucially, in contrast to Experiment 1, we found that the coefficients for Live vs Static and Replay differed significantly from zero ($t(28) = -2.389$, $p = 0.024$, $BF_{10} = 2.205$), indicating that at the single-trial level the contingency condition significantly affected breakthrough time, even after accounting for effects of the other predictors (manual and apparent rotation speed). In contrast, we found that the coefficients for manual ($t(28) = -0.688$, $p = 0.497$, $BF_{10} = 0.245$) and apparent rotation speed ($t(28) = -1.359$, $p = 0.185$, $BF_{10} = 0.453$) did not differ significantly from zero (see Supplemental Materials) indicating that for this experiment they were not a likely factor that contributed to condition-specific differences in breakthrough time.

Together these results suggest that in Experiment 2 at both the group and single-trial level it was the contingency of the virtual object (with respect to action), and not any differences in the manual or apparent rotation speed of the object, that were responsible for differences in breakthrough time between Live and Replay trials.

Lastly, we examined the correlation between the LZ complexity of manual and apparent movements and breakthrough time (for details see Supplemental Material). Comparing the average LZ complexity across the conditions (Live, Static, Replay), we found there was no evidence in support of a difference in the LZ complexity of manual movements across the three conditions (Live trials: $M = 2.53$, $SE = 0.025$, Replay trials: $M = 2.52$, $SE = 0.026$, Static trial: $M = 2.52$, $SE = 0.025$) (statistics reported in Supplemental Material). Similarly, our analysis revealed no evidence in support of a difference in the LZ complexity of apparent movements between Live and Replay conditions (Live trials: $M = 2.53$, $SE = 0.025$, $M = 2.50$, $SE = 0.025$). Second, at the group-level, we found no evidence of a correlation between average LZ complexity of either manual or apparent movements and breakthrough time in any condition. Third, at the single-trial level, our Bayesian analyses were not sensitive to whether there was a correlation or not between the LZ complexity of manual and apparent movements and breakthrough time. Overall, these results provide no evidence that the LZ complexity of the participant's movements during Experiment 2 can account for the difference in breakthrough time between Live and Replay trials.

4.0 Discussion

Across two experiments, we examined how manipulating the sensorimotor contingencies of unfamiliar virtual 3D objects affected breakthrough to visual awareness during bCFS. We developed two novel experimental setups. The first combined VR and AR, and the second combined VR with motion-tracking. Both setups allowed participants to interact with realistic virtual objects within a highly immersive environment. In each experiment, we examined the influence of differing types of sensorimotor coupling on breakthrough to awareness of specific features of the virtual objects.

Experiment 1 investigated how *contingency* and *congruency* of sensorimotor coupling affected breakthrough times, with respect to the target property of object rotation. Participants were asked to detect the rotation direction of an object, while they used a (physical) cog to rotate the virtual object. At a group level, breakthrough times (for correct reports of rotation direction) were significantly shorter when the virtual object's rotational movements were contingent on the participant's on-going actions (Live condition) compared to when movements were replayed from a practice trial (Replay condition). Interestingly, the congruency of sensorimotor interactions with an object did not affect breakthrough times, where congruency represents whether the object rotated in the same (congruent) or opposite (incongruent) direction to the participant's movements. However, by examining the correlation between apparent and manual rotation speed and breakthrough times for each trial (single-trial level), we could not exclude the possibility that the differences in breakthrough time (for the contingency manipulation) might have

been affected by differences in the apparent rotation speed objects between the Live and Replay conditions.

Experiment 2 asked whether breakthrough times for object discrimination – rather than motion discrimination – would also be affected by manipulating the sensorimotor coupling of an object. This experiment combined VR and motion tracking to allow participants to experience more naturalistic object-related sensorimotor interactions. In line with Experiment 1, we found that at the group-level breakthrough times for object discrimination were shorter when the virtual object was directly coupled to participant's on-going actions ('Live'), compared to when the movements of the object were either replayed from a previous trial ('Replay') or were locked to the same visual angle ('Static'). Crucially, in contrast to Experiment 1, a single-trial analysis allowed us to establish that the contingency of sensorimotor actions, and not differences in manual or apparent rotation speed contributed to the differences in breakthrough times between Live and Replay trials. Congruency was not manipulated in this experiment. Supporting this conclusion, we also observed that for the Static condition breakthrough times were not significantly different from either the Live or Replay conditions (Figure 2A), with Bayesian analysis providing evidence in support of no difference between Replay and Static conditions. If differences in manual or apparent rotation speed were influencing breakthrough times in Experiment 2 then one would expect that in the Static condition, in which there was no apparent rotation of the object, there would be a pronounced difference in breakthrough time compared to the other conditions. A lack of such a difference suggests that in this experiment the apparent rotation speed of the object did not strongly influence breakthrough times.

Altogether, our results demonstrate that manipulating the veridical sensorimotor coupling of an object, using a setup which allows naturalistic object-related sensorimotor interactions, affects the time it takes for multiple object features (motion direction and object category) to enter visual awareness, as measured by breakthrough time under bCFS. While the contingency of the coupling affected breakthrough times in both experiments, the congruency of the coupling did not (tested in Experiment 1 only). These data provide support for embodied theories of perception which emphasise the dependence of visual experience on the dynamic causal coupling between actions and their sensory consequences (Noë, 2004; O'Regan & Noë, 2001; Seth, 2014).

Breakthrough times in CFS are known to be influenced by many factors, shaping any subsequent interpretation (for review see Stein et al., 2011). Factors such as attentional load (Bahrami, Lavie, & Rees, 2007), face orientation (Jiang et al., 2007), and the content of a scene (Mudrik, Faivre, & Koch, 2014) have all been shown to modulate breakthrough times. Of particular relevance to the present study, the speed of a moving stimulus is known to affect binocular suppression (Blake et al., 1985). This is why much of our analysis focused on the question of whether differences in object rotation speed, between conditions, could account for our findings. We conducted a number of analyses to investigate this possibility. We found in both experiments that the average apparent rotation speed of an object (the rotation speed of the object viewed by participants) were significantly different between Live and Replay conditions (Figures 3 and 6). The

condition-specific difference in apparent rotation speed was most likely due to the movements for Replay trials being taken from the practice session, when participant's actions were more tentative. Additionally, the absence of a speed meter in the experimental blocks led to difficulties in maintaining a constant manual rotation speed over the course of the experiment.

Similar to other studies that have investigated how sensorimotor contingencies can affect the formation of a visual percept which are processed outside of awareness (Maruya et al., 2007), a group-level analysis revealed no correlation between the average manual or apparent movement speed of an object and breakthrough times for both Live and Replay conditions in either experiment (see supplementary material). However, examining the correlation between the manual and apparent movement speed on breakthrough time at a single-trial level, we could not exclude the possibility, that in Experiment 1 differences in the apparent rotation speed influenced breakthrough time (section 2.2). We note that such a single-trial analysis was not performed by Maruya et al., (2007), highlighting the benefits of performing fine-grained analyses of the underlying factors affecting breakthrough times within suppression paradigms.

In contrast, in Experiment 2 a single-trial analysis revealed that it was the contingency of the sensorimotor interactions, and not differences in the apparent or manual rotation speeds, that best accounted for the differences in breakthrough times between conditions. Another potential factor that may have contributed to differences in breakthrough times

between conditions in Experiment 2 are the potential variance in the rate of participant's change in movement direction during each trial. However, further exploratory analyses provided no evidence that the LZ complexity of participant's movements affected breakthrough time during Live or Replay trials (for more details see Supplemental Material).

The purpose of the Replay condition was to decouple participant's sensorimotor interactions with an object. However, in Experiment 1, due to the simple 2D rotational sensorimotor interactions with the object during Replay trials there was only a minimal mismatch between participant's movements of the cogs and the apparent rotational movement of the object. One possible explanation for not finding an effect of contingency at the single-trial level in Experiment 1 could be that decoupling of sensorimotor interactions with the object did not occur for all trials in the Replay condition. To address this concern, we focused in Experiment 2 on creating an experimental setup that allowed more naturalistic unconstrained sensorimotor interactions with an object. The use of a motion-tracking device allowed us to capture translational and rotational movements with 6 degrees-of-freedom (forward/backward, up/down, left/right). This added directional freedom when manipulating an object meant that in Experiment 2, the mismatch between manual movements and apparent visual movements of an object in Replay trials was far greater than in Experiment 1. Compared to Experiment 1, the unconstrained sensorimotor interactions with an object delivered a more complete decoupling of participant's sensorimotor interactions during Replay trials, in line with the observed effect of contingency at the single-trial level in Experiment 2.

Previous research, using a variety of paradigms including bCFS, has shown that the congruency between visual information and signals from other sensory modalities can alter the time it takes for the visual stimulus to enter awareness (Lunghi, Binda, & Morrone, 2010; Lunghi, Morrone, & Alais, 2014; Salomon et al., 2015, 2013; van der Hoort, Reingardt, & Ehrsson, 2017). Note that these studies manipulated congruency rather than contingency, as the systematic manipulation of the contingency of cross modal signals is generally much more difficult than manipulation of congruency. For example, congruency can be manipulated in a purely passive design (where it applies to congruency between different modalities), whereas contingency requires an active design by definition. In our experiments, we found that the *contingency* of sensorimotor interactions associated with an object, but not the *congruency*, modulated breakthrough times. Our results are in line with the few studies that have compared the effects of manual (contingent) and automatic (replay) actions on perception. The study by Maruya et al., (2007), for example, found, in a binocular suppression paradigm, that visual stimuli that are contingent on the participant's voluntary actions showed longer ocular dominance durations and shorter suppression times, compared to stimuli that moved independently from a participant's actions (Maruya et al., 2007). However, Maruya et al., (2007) used very basic visual stimuli (dot stereogram) coupled with trained stereotypical movements, making conclusions about how naturalistic embodied interactions with realistic objects affects visual perception difficult, in addition they did not test the effects of congruency. We suggest that, for live sensorimotor interactions, the contingency between our actions and sensory signals is a more salient feature than congruency, and therefore key in facilitating access to visual awareness. This

notion is in line with (Salomon, Szpiro-Grinberg, & Lamy, 2011; Wen & Haggard, 2018) who suggest that visual events are perceived more accurately or draw more attention when they are the consequences of our actions .

Breakthrough time in bCFS has been interpreted by some authors as indicating unconscious processing associated with a specific stimulus feature (Salomon et al., 2013; Stein & Sterzer, 2014). Our findings are in line with these suggestions. The use of realistic virtual 3D objects under binocular suppression in this study allowed us to assess the effects of contingency on differing object features, finding an effect of breakthrough time during bCFS of contingency for both lower (movement) and higher (identity) level features of realistic objects. These findings support the interpretation that even high-level areas of visual cortex, associated with object processing can be recruited during suppression paradigms (Almeida, Mahon, Nakayama, & Caramazza, 2008; Jiang et al., 2007; Stein & Sterzer, 2011). Future investigations are warranted to examine how differing features of an object affect breakthrough times during suppression paradigms. For example, by comparing breakthrough time to visual awareness using a set of objects that specifically emphasise certain object features, for example their shape, while hiding other characteristics (e.g. complex-shape, wire-framed objects) it should be possible to systematically map how different object features affect breakthrough time in the bCFS paradigm.

Others have suggested that differences in breakthrough times in bCFS could be accounted for by priming or post-perceptual biases (Stein et al., 2011; Stein & Sterzer, 2014). The difficulties inherent in interpreting bCFS results are not unique to our study. All studies that employ visual suppression paradigms encounter difficulties dissociating between the time needed for a stimulus to enter visual awareness, and the time needed for behavioural responses to be elicited (see, for example, (Pinto, van Gaal, de Lange, Lamme, & Seth, 2015)). We attempted to reduce the influence of response-related factors by randomizing the order of trials across conditions, so participants could not prepare a specific response based on the anticipated sensorimotor coupling of a trial. We also used identical stimuli across differing sensorimotor coupling conditions, so that participants could not prepare a specific response based on object type. However, the extent to which post-perceptual biases contribute to (breakthrough) response times during suppression paradigms remains an open question, in this and other similar studies. Future investigations addressing this issue may potentially take advantage of so-called “no-report” bCFS paradigms, in which breakthrough times are assessed using objective physiological measures rather than by conventional subjective report (for example see (Tsuchiya, Wilke, Frässle, & Lamme, 2015)).

Experimental investigation of naturalistic sensorimotor interactions with realistic objects is a challenging domain. Compared to previous attempts (Maruya et al., 2007), our study – especially Experiment 2 - allowed the presentation of highly realistic virtual 3D objects, with which participants could freely interact in relatively unconstrained ways. While there have been many attempts to investigate the relationship between action and perception,

many of which using the CFS paradigm, they have mainly used simple visual stimuli presented on a computer display. Recently, there have been attempts to apply the bCFS paradigm to real-world objects (Korisky, Hirschhorn, & Mudrik, 2018; Korisky & Mudrik, 2018). While there are many advantages to using real-world objects in bCFS, our setup allows greater flexibility when manipulating the visual and structural properties of 3D objects. Importantly, our setup also permits naturalist interactions with an object, which can be programmed to display any imaginable form of sensorimotor coupling (e.g. non-geometric transformations). Finally, our setup extends the use of binocular suppression paradigms into more dynamic and realistic environments, allowing future research to further explore relationships between action, perception, and awareness.

5.0 Conclusion

In two experiments we developed novel combinations of Virtual Reality (VR), Augmented Reality (AR) and motion tracking technologies within an adapted breaking continuous flash suppression (bCFS) to explore how manipulations of sensorimotor dependencies affect visual awareness of realistic 3D virtual objects. Overall, our results show that the *contingency*, but not the *congruency*, of a person's actions and their visual consequences influences access to visual awareness, in line with theories of conscious perception that emphasises embodied sensorimotor interactions. Our setup also extends the use of binocular suppression paradigms into more dynamic and realistic sensorimotor environments.

Author Contributions

A.K.S and K.S. developed the study concept. A.K.S., K.S., R.A., and D.J.S. contributed to the study design. K.S. developed the experiment platform and, with R.A., performed testing and data collection. K.S., D.J.S, and A.K.S. performed the data analysis and interpretation. K.S. and D.J.S. drafted the manuscript, and A.K.S provided critical revisions. All authors approved the final version of the manuscript for submission.

Acknowledgments

Keisuke Suzuki, David J Schwartzman and Anil K. Seth are grateful to the Dr. Mortimer and Theresa Sackler Foundation, which supports the Sackler Centre for Consciousness Science. Rafael Augusto is grateful to Erasmus, the European Commission's for education, training, youth and sport. Anil Seth is also grateful to the Canadian Institute for Advanced Research Azrieli programme on Mind, Brain, and Consciousness.

References

- Almeida, J., Mahon, B. Z., Nakayama, K., & Caramazza, A. (2008). *Unconscious processing dissociates along categorical lines. PNAS September* (Vol. 30). Retrieved from <http://www.pnas.org/content/pnas/105/39/15214.full.pdf>
- Bahrami, B., Lavie, N., & Rees, G. (2007). Attentional Load Modulates Responses of Human Primary Visual Cortex to Invisible Stimuli. *Current Biology*, 17(6), 509–513.
- Bekkering, H., & Neggers, S. F. W. (2002). Visual search is modulated by action intentions.

- Psychological Science*, 13(4), 370–374.
- Blake, R., Zimba, L., & Williams, D. (1985). Visual motion, binocular correspondence and binocular rivalry. *Biological Cybernetics*, 52(6), 391–7.
- Brunel, L., Carvalho, P. F., & Goldstone, R. L. (2015). It does belong together: cross-modal correspondences influence cross-modal integration during perceptual learning. *Frontiers in Psychology*, 6, 358.
- Chan, D., Peterson, M. A., Barense, M. D., & Pratt, J. (2013). How action influences object perception. *Frontiers in Psychology*, 4, 462. <http://doi.org/10.3389/fpsyg.2013.00462>
- Clark, A. (2013). Whatever next? Predictive brains, situated agents, and the future of cognitive science. *The Behavioral and Brain Sciences*, 36(3), 181–204.
- Dieter, K. C., Hu, B., Knill, D. C., Blake, R., & Tadin, D. (2014). Kinesthesia Can Make an Invisible Hand Visible. *Psychological Science*, 25(1), 66–75.
- Fagioli, S., Hommel, B., & Schubotz, R. I. (2007). Intentional control of attention: action planning primes action-related stimulus dimensions. *Psychological Research*, 71(1), 22–29.
- Friston, K. (2010). The free-energy principle: a unified brain theory: Supplementary information S3. *Nature Reviews. Neuroscience*, 3(February), 3–4.
- Hannus, A., Cornelissen, F. W., Lindemann, O., & Bekkering, H. (2005). Selection-for-action in visual search. *Acta Psychologica*, 118(1–2), 171–191.
- Hohwy, J. (2013). *The Predictive Mind*. Oxford University Press.
- Holm, S. (1979). A Simple Sequentially Rejective Multiple Test Procedure. *Scandinavian Journal of Statistics*. *Scandinavian Journal of Statistics*, 6, 65–70.
- Jiang, Y., Costello, P., & He, S. (2007). Processing of Invisible Stimuli: Advantage of Upright

- Faces and Recognizable Words in Overcoming Interocular Suppression. *Psychological Science*, 18(4), 349–355.
- Korisky, U., Hirschhorn, R., & Mudrik, L. (2018). “Real-life” continuous flash suppression (CFS)-CFS with real-world objects using augmented reality goggles. *Behavior Research Methods*, 1–13. <http://doi.org/10.3758/s13428-018-1162-0>
- Korisky, U., & Mudrik, L. (2018). Get real: Suppressing the real world from awareness using augmented reality goggles. *Journal of Vision*, 18(10), 943. <http://doi.org/10.1167/18.10.943>
- Lindemann, O., & Bekkering, H. (2009). Object manipulation and motion perception: Evidence of an influence of action planning on visual processing. *Journal of Experimental Psychology: Human Perception and Performance*, 35(4), 1062–1071.
- Lunghi, C., Binda, P., & Morrone, M. C. (2010). Touch disambiguates rivalrous perception at early stages of visual analysis. *Current Biology : CB*, 20(4), R143-4.
- Lunghi, C., Morrone, M. C., & Alais, D. (2014). Auditory and Tactile Signals Combine to Influence Vision during Binocular Rivalry. *The Journal of Neuroscience*, 34(3), 784–792.
- Maruya, K., Yang, E., & Blake, R. (2007). Voluntary Action Influences Visual Competition. *Psychological Science*, 18(12), 1090–1098.
- Moors, P., Wagemans, J., & De-Wit, L. (2014). Moving Stimuli Are Less Effectively Masked Using Traditional Continuous Flash Suppression (CFS) Compared to a Moving Mondrian Mask (MMM): A Test Case for Feature-Selective Suppression and Retinotopic Adaptation. *PLoS ONE*, 9(5), e98298.
- Mudrik, L., Faivre, N., & Koch, C. (2014). Information integration without awareness. *Trends in Cognitive Sciences*, 18(9), 488–496.

- Noë, A. (2004). *Action in Perception*. *books.google.com*.
- O'Regan, J. K., & Noë, A. (2001). A sensorimotor account of vision and visual consciousness. *The Behavioral and Brain Sciences*, 24(5), 939-73; discussion 973-1031.
- Peng, Z., Genewein, T., & Braun, D. A. (2014). Assessing randomness and complexity in human motion trajectories through analysis of symbolic sequences. *Frontiers in Human Neuroscience*, 8, 168. <http://doi.org/10.3389/fnhum.2014.00168>
- Pinto, Y., van Gaal, S., de Lange, F. P., Lamme, V. A. F., & Seth, A. K. (2015). Expectations accelerate entry of visual stimuli into awareness. *Journal of Vision*, 15(8), 13.
- Salomon, R., Kaliuzhna, M., Herbelin, B., & Blanke, O. (2015). Balancing awareness: Vestibular signals modulate visual consciousness in the absence of awareness. *Consciousness and Cognition*, 36, 289–297.
- Salomon, R., Lim, M., Herbelin, B., Hesselmann, G., & Blanke, O. (2013). Posing for awareness: Proprioception modulates access to visual consciousness in a continuous flash suppression task. *Journal of Vision*, 13(7), 2–2.
- Salomon, R., Szpiro-Grinberg, S., & Lamy, D. (2011). Self-Motion Holds a Special Status in Visual Processing. *PLoS ONE*, 6(10), e24347. <http://doi.org/10.1371/journal.pone.0024347>
- Seth, A. K. (2014). A predictive processing theory of sensorimotor contingencies: Explaining the puzzle of perceptual presence and its absence in synesthesia. *Cognitive Neuroscience*, 1–49.
- Seth, A. K. (2015). Presence, objecthood, and the phenomenology of predictive perception. *Cognitive Neuroscience*, 6(2–3), 111–117.
- Stein, T., Hebart, M. N., & Sterzer, P. (2011). Breaking Continuous Flash Suppression: A New

- Measure of Unconscious Processing during Interocular Suppression? *Frontiers in Human Neuroscience*, 5, 167.
- Stein, T., & Sterzer, P. (2011). High-level face shape adaptation depends on visual awareness: Evidence from continuous flash suppression. *Journal of Vision*, 11(8), 5–5. <http://doi.org/10.1167/11.8.5>
- Stein, T., & Sterzer, P. (2014). Unconscious processing under interocular suppression: getting the right measure. *Frontiers in Psychology*, 5, 387.
- Tsuchiya, N., & Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nature Neuroscience*, 8(8), 1096–1101.
- Tsuchiya, N., Wilke, M., Frässle, S., & Lamme, V. A. F. (2015). No-Report Paradigms: Extracting the True Neural Correlates of Consciousness. *Trends in Cognitive Sciences*, 19(12), 757–70.
- van der Hoort, B., Reingardt, M., & Ehrsson, H. H. (2017). Body ownership promotes visual awareness. *ELife*, 6.
- Wen, W., & Haggard, P. (2018). Control Changes the Way We Look at the World. *Journal of Cognitive Neuroscience*, 30(4), 603–619. http://doi.org/10.1162/jocn_a_01226