The predictive brain in action

Involuntary actions reduce body prediction errors

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Abstract

The perception of our body in space is flexible and manipulable. The predictive brain hypothesis explains this malleability as a consequence of the interplay between incoming sensory information and our body expectations. However, given the interaction between perception and action, we might also expect that actions would arise due to prediction errors, especially in conflicting situations. Here we describe a computational model, based on the free-energy principle, that forecasts involuntary forces in sensorimotor conflicts. We experimentally confirm those predictions in humans by means of a virtual reality rubber-hand illusion. Participants generated reactive arm forces towards the virtual hand, regardless of its location with respect to the real arm, with little to no forces produced when the virtual hand overlaid their physical hand. The congruency of our model predictions and human observations shows that the brain-body is generating actions to reduce the prediction error between the expected arm location and the new visual arm. This observed unconscious mechanism is an empirical validation of the perception-action duality in body adaptation to uncertain situations and evidence of the active component of predictive processing.

Public abstract

Humans' capacity to perceive and control their body in space is central in awareness, adaptation and safe interaction. From low-level body perception to body-ownership, discovering how the brain represents the body and generates actions is of major importance for cognitive science and also for robotics and artificial intelligence. The present study shows that humans generate involuntary actions to correct the expected location of the body, which corresponds to reducing the prediction error. This means that the brain adapts to conflicting or uncertain information from the senses by unconsciously acting in the world.

Introduction

Humans' capacity to perceive and control their body in space is central in awareness, adaptation and safe interaction. The mind and the body[1,2] as a refined sensorimotor system that perceives and acts in an uncertain world[3]. Unveiling the brain mechanisms that integrate and deal with incomplete or conflicting information from the senses and actively compensate for external perturbations has puzzled researchers for decades[4–9]; especially the relation between the perceptual and the motor systems[10–13] in conflicting sensorimotor situations.

Despite the numerous experiments studying this association between perception and action, how perception affects the action (and vice versa) is still a controversial open question[14,15], essential for understanding brain-body representation and body adaptation[16,17]. If the sensory information is learnt by acting in the environment, action should be encoded within the perception process[11,18]: "The way we use sensory information determines the way we encode it"[16]. However, contradictory results were observed depending on the experiment, against or standing for the independence of the motor system[15]. Visual[3] and body illusions[19] have been useful paradigms to study this relation, as well as to investigate how the sensorimotor system integrates conflicting information, e.g., visual, tactile and proprioceptive cues. For example, using the Titchener circles illusion in a grasping task, perceptual judgements of the circle size were strongly affected but the grip aperture (action) was not[20]. By means of a rubber-hand illusion experiment, it was shown that ballistic pointing movements (action), using just proprioceptive feedback after stimulation, were also not affected by the perceptual sensorimotor conflict[16]. Why these experiments do not reflect the expected action-perception relation? One of the most accepted explanation is due to different brain representations of the body (e.g., body-schema vs body image[21]) and distinct visual pathways[13,22] that operate differently depending on the task.

Body perception in sensorimotor conflicts is less controversial. Since the introduction of the (passive) rubber-hand illusion[19] (RHI), many derived studies have focused on understanding body perception, body-ownership and self-consciousness in humans [23–26] and non-humans primates[27], by causing participants to embody artificial (rubber or virtual) body parts as their own. In the original experiment, the subject sees a plastic hand while his own hand lying next to it is covered. After visuotactile stimulation of the unseen hand, an essential effect appeared: when participants were asked to localize their hand in the space they reported a position biased to the artificial hand. They experienced a mislocalization (proprioceptive drift) on the estimated location of their unseen hand towards the artificial hand, suggesting a change of the body's "state" or body-schema. This effect was particularly effective when the visual and tactile stimulation was synchronous and its intensity depended on other characteristics, such as spatial constraints and appearance cues[28]. Recently, a drift on the localization of the artificial hand towards the real hand was also shown (visual drift), exemplifying the blending nature of perception in sensorimotor conflicts[29]. Finally, active paradigms, like the active finger illusion[30], further showed that active control of the body parts is one of the strongest cues for body-ownership and agency[31], illustrating how the action affects body perception.

Here we revisit the relation between perception and action in sensorimotor conflicts sustained by the predictive brain hypothesis[3,7,9,24,32] and show that the RHI is both a perceptual and an active illusion. We suggest that both perceptual and action effects in the

RHI can be explained as the brain's attempt to reduce the mismatch between the expected and the perceived body location. This means that involuntary actions would arise to reduce the prediction error, especially in conflicting situations. Our findings describe a relevant example where *perception reactively generates body actions*, supporting a multisensory on-line feedback system driven by prediction error and that the body-schema is more than the perceptual representation of the location of body parts in space[33].

We observed that when deploying an *active inference* model[34,35], based on the Free-Energy Principle[36] (FEP), in a humanoid robot, reactive forces appeared to correct the body model error towards the visual end-effector input. This effect has a strong parallelism with sensorimotor conflicts, thus, implying that our model would predict reactive forces towards the artificial arm in a RHI setting. Previous experiments also support this prediction. A human study reported small compensatory movements towards an artificial hand placed in the body midline in a RHI experiment[37]. Unfortunately, the experimental design was not able to disambiguate whether those observations were a result of body posture correction or due to a body midline effect. These findings were later attributed to the high weighting of the visual input[38], and it was further shown, using a computational model, how attention benefited visual cues in a conflicting situation biasing the action[39]. Besides, it was observed that reactive movements were induced in participants during the RHI experiment when the artificial hand was moved[40].

In this work we 1) provide a predictive brain-inspired computational model able to predict RHI perceptual and active drifts, as described in Figure 1A, 2) show robust evidence of action responses in human participants during the sensorimotor conflict, and 3) indicate a plausible explanation of these observed actions. For that purpose, first, we studied an *active inference* computational model adapted to the rubber-hand experiment. Secondly, in order to validate our model predictions, we systematically examined the body actions using a virtual reality version of the passive RHI[41], where no voluntary control tasks were involved (Figure 1B,C). To avoid body postural or midline biases we analysed the exerted forces in three location conditions of the virtual hand: left, centre and right with respect to the real arm position. We found that participants generated arm forces towards the virtual hand in all conditions. Finally, we compared the observed human forces with model predictions. The forces were congruent suggesting that the actions were generated to minimize the mismatch between the proprioceptive information and the virtual hand. The mechanism behind these observed forces may be essential for understanding body adaptation to uncertain situations and embodiment.

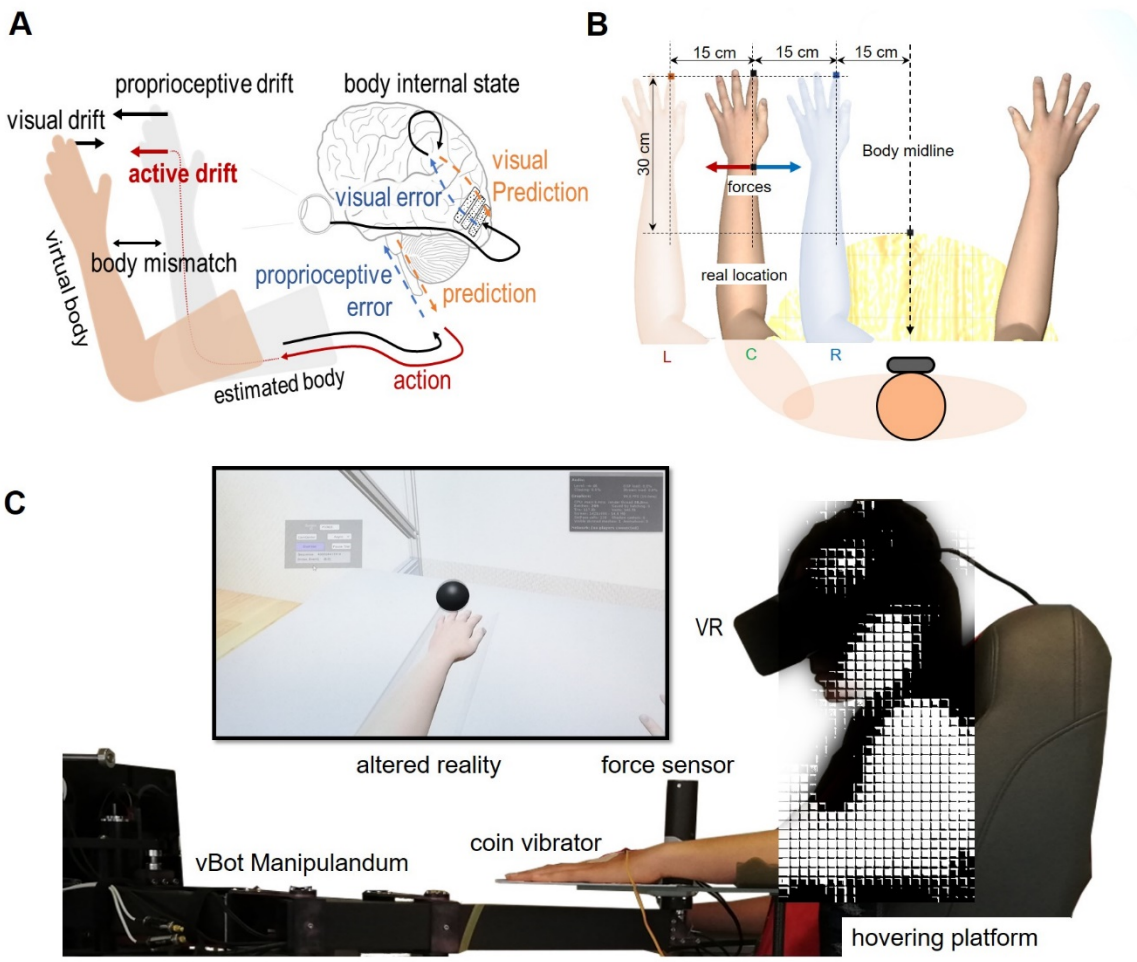

Figure 1: Predictive brain approach and experimental setup. (A) Schematic of the expected drifts (visual, proprioceptive and active) and its relation to prediction minimization. The proprioceptive drift is produced due to body estimation under visual error mismatch, the visual drift is a multisensory integration collateral effect and the active drift (forces towards the virtual hand) is a consequence of proprioception error minimization through the reflex arc pathway. (B) RHI conditions. At each trial the virtual hand was placed in one of the three different locations: Left (-15cm), Center (0cm) and Right (+15cm) with respect to the real hand location, i.e., the centre corresponds to the real hand position. The real hand was placed 30 cm away from the body midline. (C) The perceptual stimulation was performed by means of virtual reality immersion and a coin vibrator for the tactile stimulation. Lateral force measurements were recorded using a 6DOF force sensor on the robotic manipulandum vBot.

Results

Computational model predictions

We simulated 20 participants (10 synchronous and 10 asynchronous) following the RHI experimental design presented in Figure 1B. The simulated RHI had three different visual conditions, corresponding to three different locations of the virtual hand: left, right and centre (i.e., in the same location of their real hand). Perception and action were modelled as an inference problem using a FEP[36,42] based algorithm (see Methods section for details). As depicted in Figure 2E, during stimulation the real hand location was hidden (grey hand) and

hence the proprioceptive information was providing the current body pose (i.e., expected location). The virtual hand was treated a possible source of information and integrated into the body posture estimation as the visual cue weighted by causality. The model computed the force as a result of the prediction error generated in the multisensory integration process of the visual input and the estimated body joint angles.

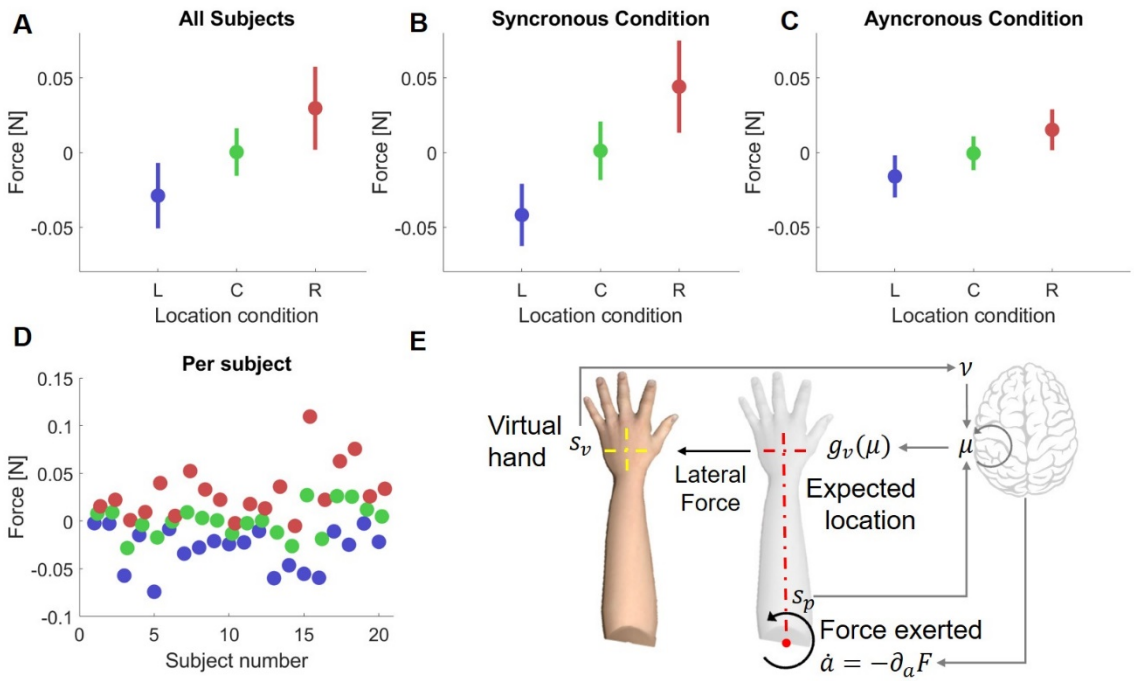

Figure 2: Computational model predicted forces and comparison against the human recorded average. (A) Average force of 20 simulated participants with the *active inference* model for Left, Center and Right conditions. (B) Average force comparison for the synchronous condition. (C) Average force comparison for the asynchronous condition. (D) Mean force predicted by the model during stimulation for each simulated subject. (E) Arm model description with one degree-of-freedom and the VR hand as the visual input. The torque direction corresponds to reducing the prediction error: expected hand location minus the VR location.

The results, summarized in Figure 4, predicted lateral forces in the direction of the artificial hand in all conditions. Figure 4A shows the mean force for all simulated participants split by the location of the virtual hand (Left in blue, Center in green and Right in red), indicating three differentiated patterns. Furthermore, the model in the asynchronous condition predicted attenuated forces (Figure 4B vs Figure 4C). Participants variability was modelled by assigning different proprioceptive weighting (i.e., the precision or inverse variance of the proprioceptive cue) and randomizing the length of the limb. Accordingly, Figure 4D shows the mean force predicted by the model for each location condition during stimulation for each simulated subject. The model predicts an action towards the artificial hand to correct the error of the predicted body location that we should observe in human participants.

Active RHI experiment with human participants

Fourteen participants were investigated using a passive virtual reality rubber hand illusion experiment described in Figure 1. Analogously to the computational model experiment,

participants were presented with three different visual conditions, corresponding to three different locations of the virtual hand (Figure 1B): left, right and centre (i.e., in the same location of their real hand). In order to analyze the forces exerted by the participant during visuotactile stimulation, we recorded the horizontal force applied at the manipulandum using a 6DOF force and torque sensor (Figure 1C).

Lateral forces analysis

Figure 2 shows the lateral force profile during the stimulation period of 40 seconds, averaged for all participants and trials. Although in both synchronous and asynchronous conditions had clear right vs left force patterns, the variability was higher in the asynchronous case producing noisier force profiles. The periodic bumps in the force signal are associated with the actuator vibration.

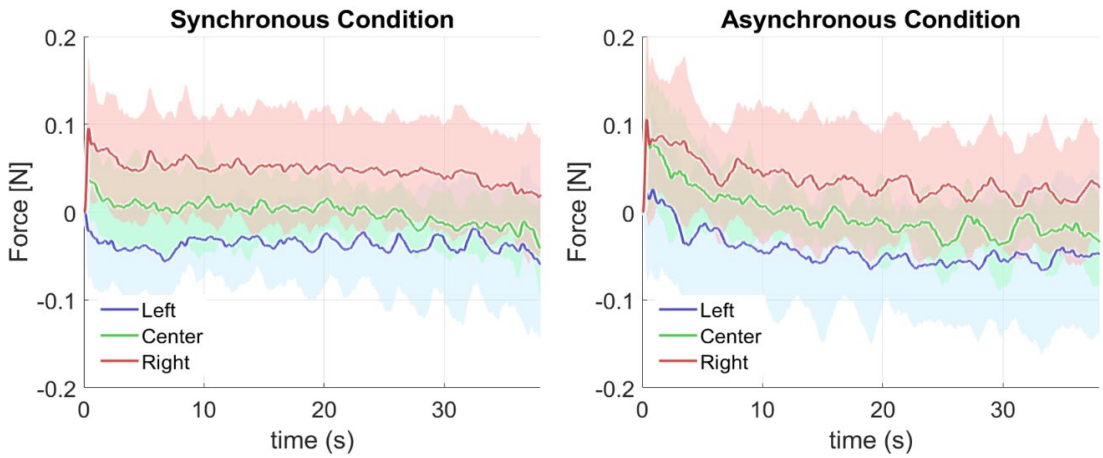

Figure 3: Average participant lateral force exerted during stimulation for the synchronous and asynchronous condition. Left (blue), Center (green) and Right (red) lines are the mean value across all trials and the shading region represents the standard deviation.

Figure 3 shows the registered average force (stimulation phase) and standard deviation for all trials and participants for the Left (blue), Center (green) and Right (red) condition. The marker indicates the mean force and the line express the standard deviation. Both synchronous and asynchronous conditions showed differentiated directional forces patterns towards the virtual hand. Figure 3D also shows the mean force for each subject indicating the variability of the forces gains and Figure 3E shows the forces histogram for all subject split by VR arm location condition. Furthermore, the appearance of forces in left and right directions falsifies the hypothesis of the body midline effect.

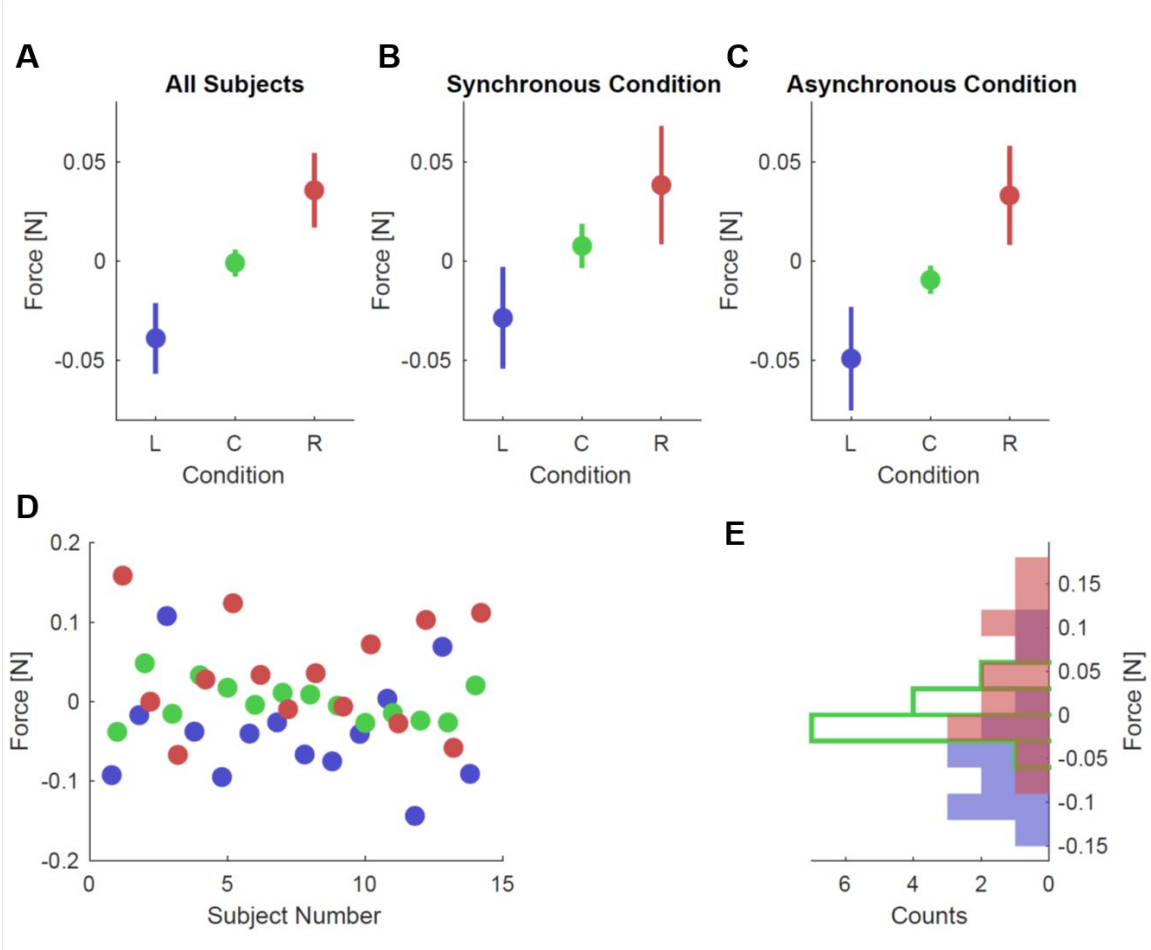

Figure 4 Mean forces applied during stimulation for the different virtual hand location conditions: Left (blue), Center (green), Right (red). The centre condition corresponds to the location of the real hand. (A) The average force applied by all the 14 subjects for the three different locations. Average force in the synchronous condition, where tactile (vibrator) and visual stimulation (ball hitting the hand) events were concurrent (less than 100 ms). (C) Average force in the asynchronous condition, where the tactile and visual event did not match. (D) Mean force registered during stimulation for each participant. (E) Mean force histogram for the three location conditions (all subjects).

The rubber-hand illusion is active

Our study shows involuntary actions towards the virtual hand during the stimulation phase, despite the inhibitory control and the passive nature of the experiment. We then tested the significance of this effect of the endpoint forces of the hand using a repeated measures ANOVA with main effects of visual hand location (3 levels) and trial block order, and between-subjects effects of conditions (synchronous or asynchronous). We found a significant main effect on the forces exerted depending on the location of the virtual hand using a repeated measures ANOVA test ($F_{2,24}$= 3.851; p=0.035), with no effect of trial block order ($F_{39,468}$=0.598; p=0.598) and no interaction effects (all p>0.398). Doing a simple contrast between the posture conditions we validated that the **right condition had a different effect than the left condition** (p=0.011), indicating different forces pattern: left direction forces in the Left condition and right forces in the Right condition. A significant between-subjects effect of condition (F1,12=5.241; p=0.041) indicated a difference in the offset between the two conditions. However, we did not find statistical differences in the

interaction between the synchronous/asynchronous condition and the visual location ($F_{2,24}$=0.045; p=0.956), indicating that both conditions produced the same effect.

Model predictions vs human observations

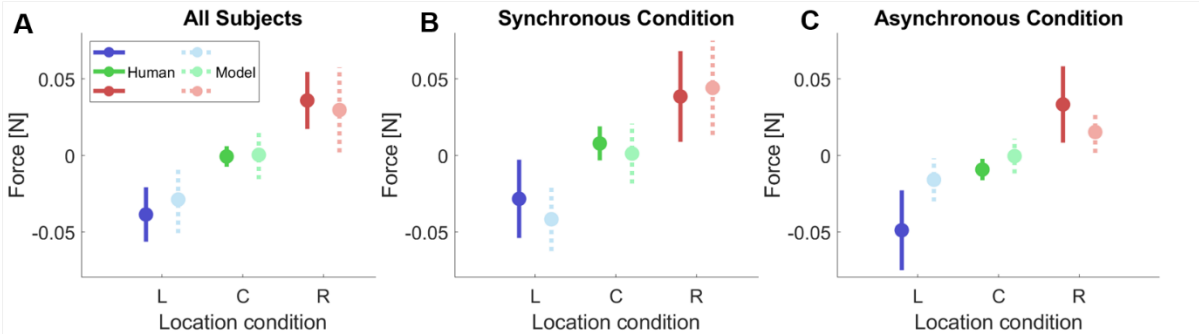

Figure 5: Comparison between the model predictions and the human experiment. (A) Average force comparison between the 14 human participants and 20 simulated ones with the active inference model for Left, Center and Right conditions. The continuous line corresponds to the human data and dashed line with a lighter colour to the model predictions. (B) Average force comparison for the synchronous condition. (C) Average force comparison for the asynchronous condition.

Figure 5 shows the comparison between the mean forces registered in the human experiment and the predicted by the model. The model was able to predict lateral forces exerted by the participants in the virtual rubber-hand illusion for the left, centre and right condition. The directions were congruent in all location conditions. Furthermore, a mismatch in the strength of the effect was found in the asynchronous condition. While the computational model predicted an attenuated response, in the human experiment similar gains were found in the synchronous and asynchronous condition. This result might be connected with the strong proprioceptive drifts found with this virtual setup in the asynchronous condition (see Appendix).

Discussion

Incorporating body illusions into body perception and action models

Several seminal computational models have been proposed in the literature for sensorimotor control[43]. However, these models were mainly designed for voluntary control tasks and have usually disregarded the effects observed during sensorimotor conflicts like body illusions. We cannot neglect the relevance of such alterations because they are the basis of sensorimotor integration, embodiment and body ownership[38].

In particular, sensorimotor computational models should be able to predict the three drifts involved in the RHI: proprioceptive[19], visual[29] and active. In the literature, proprioceptive drift patterns were replicated by using a Bayesian causal model[44] and by means of a predictive coding model[45]. Furthermore, congruency was also analysed using dynamical causal modelling[46]. Here, our proposed approach is able to address the three drifts. The

proprioceptive drift is produced due to the visual error mismatch, the visual drift is obtained by representing the virtual hand location as another causal variable that is affected by the multisensory fusion process, and finally, the active drift (lateral forces) is a consequence of proprioception error minimization through the reflex arc pathway.

The attenuated forces predicted by the model in the asynchronous condition did not adjust to human observations. The reason might be found in the level of immersion in the VR setting. We measured the proprioceptive drift and the body-ownership level under the same experimental setup (see Supplementary material). We observed that participants presented strong proprioceptive drifts also in the asynchronous condition, something coherent with other perceptual drifts registered under asynchronous stimulation[44].

The boundaries of an action-perception body-schema

Our results suggest that forces are generated to adjust our body posture with the observed reality. The action bias towards the virtual hand is comparable to those observed with perceptual localization[47]. Although this seems to contradict the ballistic pointing results[16], where no effect was found due to the sensorimotor conflict, in this experiment we included a strong visual cue. Therefore, the multisensory integration process remains, but the weighting has changed[38,39].

The forces registered indicate the coupling between action and perception, strengthening the stance of a body-schema representation that includes action codes (i.e., an “action-perception representation” driven by inference), probably mapped during learning when interacting with the body in the world. Similarly, as the reactive actions observed in mice for correcting wrong perceptual expectations[48] humans would exert reactive forces in any conflicting or uncertain situations. Furthermore, we might rethink about the boundaries between body-schema, body image and its relation with the action[49].

An action-perception body-schema, similar to the dynamic body-schema[50] or the peripersonal space[51,52], would be advantageous in terms of adaptation during interaction as world changes can be instantly taken into account while maintaining a coherent body pose estimation and reducing prior model errors. Our model, apart from indicating the potential mechanism underneath perceptual and action alterations observed in body illusions, also explains behaviours, such as follower effect in VR settings[53]. Deeper studies should be performed to understand the relation between this observed action-perception coupling and its impact in body-ownership and agency[54,55], and thus, into the development of the self. Furthermore, if this reactive process is compatible with optimal control models[4,56] we should observe action biases when participants perform a task. According to our model, this would indicate that involuntary or unconscious actions driven by inference and triggered by prediction errors would play an important role in body adaptation and interaction, in addition to voluntary control[57].

Active Inference empirical evidence

Although the FEP[7] has been widely proposed to account for several brain processes, such as perception and action[36], interoception[58] or self-recognition[59,60], it is has been difficult to

find behavioural validation for this theoretical construct. The FEP postulates that both perception and action minimize the surprise, formalized as the discrepancy between our belief and the real world. Thus, there are two ways of minimizing this discrepancy or prediction error: either we change our perception or we exert an action. In the case of sensorimotor conflicts, such as body illusions, we can change our belief of where our body is or we can act to reduce this discrepancy. Hence, during the RHI, the new visual input (virtual hand) is expected to be merged with proprioceptive information generating an error on the body location estimation[45]. When modelling the action inside the FEP (i.e., *active inference*) it predicts that actions will reduce the prediction error. Here, conversely to other related works, instead of fitting the model to human observations, we designed the experiment to validate the predictions that we were already observing in our model.

The lateral force directions found in human participants agreed with the model forecast. In particular, our FEP based model correctly predicted forces towards the virtual hand to reduce the error of the predicted body location altered by the new visual input. These forces were congruent to the ones observed in the behavioural experiment. Thus, a possible explanation is that the same process of inferring the body state generates actions that reduce the prediction error. As the model can account at the same time for the three observed drifts in the rubber-hand illusion (visual, proprioceptive and active), yields to a potential experimental evidence of the FEP.

However, it is critical to be very cautious regarding the model comparison. There are other possible computational approaches that could also fit, such as acknowledging those forces as a consequence of body representation learning while interacting with the world. For instance, cross-modal learning[61] that includes action and perception cues as inputs could also retrieve these forces by means of sensory reconstruction. Moreover, there are relevant differences between the simplified joint model and the real musculoskeletal human body. Although the perceptual and force directions were in accordance with our model predictions, the observed forces profiles, i.e., the gains, were adjusted by an action gain hyperparameter. Besides, visual and proprioceptive precision optimization turned out to be essential in order to obtain human participants force profile.

The hands that ‘act’ to ‘feel’

This systematic study reveals an effect in sensorimotor conflicts that may have important implications on how the body adapts to uncertain situations. Subjects' recorded forces (action) had the same direction than the proprioceptive drift (perception), i.e. towards the virtual hand. This evidence that the RHI is both a perceptual and an active illusion. Moreover, its congruence with the FEP predictions suggests that the body deals with the conflict by acting to reduce the prediction mismatch, or in other words, ‘act’ to permit the proper embodiment of the visual arm.

Methods

Figure 6: Experimental setup. Back-top view of the participant on the vBOT manipulandum with the VR system and the coin vibrator attached to the dorsum of the left hand.

Ethics

Informed consent was obtained, and the study was approved by the ethics committee of the Medical Faculty of the Technical University of Munich, and adhered to the Declaration of Helsinki. The study was performed in accordance with the ethical guidelines of the German Psychological Society (DGPs).

Devices

Subjects were seated with their shoulders restrained against the back of a chair by a shoulder harness and their hand and forearm were rested by a flat surface attached to the vBOT robotic manipulandum[62] with their forearm supported against gravity with an air sled (Fig. 1A). The robotic manipulandum generated environmental dynamics and measured the subjects' behaviour. Position and force data were sampled at 1KHz. Endpoint forces at the handle were measured using an ATI Nano 25 6-axis force-torque transducer (ATI Industrial Automation, NC, USA). The position of the vBOT handle was calculated from joint-position sensors (58SA; IED) on the motor axes. Visual feedback was provided using a virtual reality (VR) device (Oculus Rift V1, Facebook technology). When using the VR system, any visual information about their body location was prevented. The virtual environment was designed and programmed in C# using the Unity engine (Fig. 1B). Tactile feedback was provided with commercially available coin vibrators, controlled with an embedded chip and connected via USB to the VR engine. The vibration events are controlled by means of a visual animation of a bouncing ball.

Participants

Fourteen right-handed volunteers (7 male and 7 female) from 18 - 40 years old with normal or corrected-to-normal vision, who were able to use the VR participated in this study. All participants had no neurological or psychological disorders, virtual sickness, nor skin hyper sensibility[1] as indicated by self-report. We ensured that all participants were not wearing nail polish or had remarkable visual features on the left or right forearm and hand. Participants height was between 1.6 and 1.9 m to fit within the constraints of the experimental apparatus. Participants were economically compensated with eight euros per hour.

Experimental design and procedure

First, we randomly assigned 7 participants for the synchronous and 7 for the asynchronous condition. In total, we registered 1680 trials or samples. The generation of the conditions was computed randomly in blocks as described in *Figure 6*.

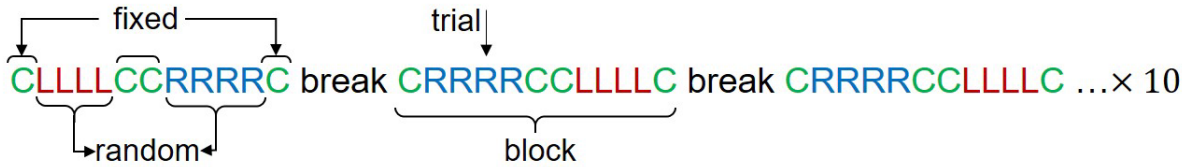

Figure 7: Conditions generation. Each participant did 10 blocks of 12 trials (4 for each VR location condition). Center trials positions were fixed while the right and the left set of four trials were randomly distributed between the centre trials.

The centre condition was always fixed in the beginning, the middle and the end of every trial. Four trials of the left or right condition were randomly selected between the centre conditions. In this way, the perceptual bias generated from stimulation in lateral locations was reduced during the centre condition.

Each trial corresponded to a 40-second of visuotactile stimulation where the force was recorded. In order to register the samples, we performed 10 blocks per participant separated by a short break. Each block was composed of 12 trials (4 trials for each virtual hand location condition, left, centre, right). In total, each participant performed 120 trials (40 per visual hand location condition).

Participants were seated on the experiment chair, in front of a table, following the instructions of the experimenter. Once the chair was adjusted to the needed height, the experimenter attached the vibrator to the middle point of the hand dorsum, as described in *Figure 1*. Participants then wore the Oculus Rift VR system. The left hand rested on the air sled and the right hand on the table (Figure 5).

The initial location of the left hand was fixed for all participants and was programmed in the Manipulandum. Each trial consisted of two phases and then a resting period:

[1] A pretest with the vibrator was performed on the participant hand who gave a written statement that the vibrator did not harm himself.

1) *Cross*: Participants were asked to face directly forward to look at a cross that appears in a random location around the middle of the scene to avoid the use of the head angle as a cue.
2) *Stimulation*: At the start of the trial a virtual arm appeared in the virtual scene with a ball on the top of the hand. Participants were asked to look at the index finger of the left hand. In the synchronous condition, every time the ball touches the virtual hand there is a tactile stimulus through the vibrator (a touch event every two seconds approximately). In the asynchronous stimulation, the vibration occurs with a random delay after the visual stimulation.
3) *Resting*: At the end of each trial, participants rested for 1 minute alternating removing the VR system and moving the arms without removing the VR.

We tested both synchronous and asynchronous visuotactile stimulation. At the synchronous condition, the ball contacted with the virtual hand and the vibration on the real hand events happened at the same time (less than 100 ms difference). On the other hand, the asynchronous condition vibration events were generated randomly between the visual hit and the highest height reached by the ball.

Data was analyzed offline using Matlab (R2019a) and statistical tests were performed using the repeated measures ANOVA in JASP 0.11.1.

Computational model

We model body perception as inferring the body posture, defined by the joint angles, by means of the sensation prediction errors (visual and proprioceptive) and the error in the predicted dynamics. To design the arm model we only consider one degree of freedom: the elbow that rotates over the vertical axis (Figure 4E). Thus, we define s_p as the measured/observed joint angle of the elbow and $\mu^{[0]} \in (-\pi/2, \pi/2)$ as the inferred elbow joint angle[2]. Visual information is given by the horizontal location of the centre of the hand s_v and the center of the virtual hand s_r. We further define that zero degrees measurement indicates when the arm is in perpendicular to the horizontal axis. Hence, left and right rotations are negative and positive respectively. Given the length of the arm L, the generative model that predicts the hand visual location depending on the state is as follows: μ by means of the sensation prediction errors (visual and proprioceptive) and the error in the predicted dynamics. To design the arm model we only consider one degree of freedom: the elbow that rotates over the vertical axis (Figure 4E). Thus, we define s_p as the measured joint angle of the elbow and $\mu \in (-\pi/2, \pi/2)$ as the inferred elbow joint angle. Visual information is given by the observed horizontal location of the centre of the virtual hand s_v and v is the perceived location of the virtual hand. We set the joint angle in zero degrees when the arm is in perpendicular to the horizontal axis. Hence, left and right rotations are negative and positive respectively.
Given the length of the arm L, we define the generative function that predicts the hand visual location $\hat{s}_v$ depending on the body state is:

[2] The notation reflects the order of the dynamics. $\mu^{[0]}$, $\mu^{[1]}$, $\mu^{[2]}$ represents the position, velocity and acceleration of the inferred brain variables[65,66].

$$\hat{s}_v = g_v(\mu^{[0]}) + z_v = L\cos(\mu^{[0]} - \pi/2)\,) + b + z_v \tag{1}$$

where b is a perceptual bias that depends on each participant and z_v is normally distributed noise. The rest of the observations can be predicted with a Gaussian with mean 0. Thus, the observed sensations $\boldsymbol{s}$ and the brain generative model $g(\mu, v)$ that predicts the sensations are:

$$\boldsymbol{s} = \begin{bmatrix} \mu^{[0]} \\ \mu^{[1]} \\ v \\ s_v \end{bmatrix} + Z \qquad\qquad g(\mu, v) = \begin{bmatrix} \mu^{[0]} \\ \mu^{[1]} \\ g_v(\mu^{[0]}) \\ v \end{bmatrix} + Z \tag{2}$$

Where Z is the noise associated with each variable.

The brain generative model $f(\mu, \rho)$ that drives the dynamics of the internal variables (state) does not expect any action as there is no task involved[3] and it is modelled as a mass-spring system. Note that this function is an approximation of the real model of the arm:

$$f(\mu, \rho) = \begin{bmatrix} \mu^{[1]} \\ -k\mu^{[0]}/\,m \\ 0 \end{bmatrix} + W \tag{3}$$

Where W is the associated noise of the process, m is the mass of the arm and k is the viscosity parameter.

We infer the elbow angle by optimizing the free-energy bound under the Laplace approximation[63]. Defining the error between the inferred brain variables and the dynamics generative model as $\boldsymbol{e}_\mu = \boldsymbol{\mu} - f(\mu, \rho)$, the differential equation that drives $\boldsymbol{\mu} = \left[\mu^{[0]}, \mu^{[1]}, \mu^{[2]}\right]^T$ is:

$$\dot{\boldsymbol{\mu}} = \begin{bmatrix} \mu^{[1]} \\ \mu^{[2]} \\ \mu^{[3]} \end{bmatrix} + \frac{\partial g}{\partial \boldsymbol{\mu}}^T \Sigma_s^{-1}\left(\boldsymbol{s} - g(\boldsymbol{\mu})\right) + \frac{\partial f}{\partial \boldsymbol{\mu}}^T \Sigma_\mu^{-1}\left(\begin{bmatrix} \mu^{[1]} \\ \mu^{[2]} \\ \mu^{[3]} \end{bmatrix} - f(\mu, \rho)\right) - \Sigma_\mu^{-1}\begin{bmatrix} e_\mu^{[1]} \\ e_\mu^{[2]} \\ e_\mu^{[3]} \end{bmatrix} \tag{4}$$

Regarding the action, it only depends on the sensory input, as during the RHI the participant only relies on the proprioceptive input. Thus, we define its differential equation as:

$$\dot{a} = -\frac{\partial F_s}{\partial a} = -K_a \frac{\partial s_p}{\partial a}\,\Sigma_s^{-1}(s_p - \mu^{[0]}) \tag{5}$$

Experiments have shown that during the RHI participants modify the precision of visual and proprioceptive cues[64]. Thus, we optimize their precision also to reduce the prediction error:

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[3] In the case of having a task we shall include a perceptual attractor in the sensory manifold and its transformation to the joint variables. For instance we can include the virtual arm as the goal by substituting in equation (3) the second row by $\left(T(\mu^{[0]})A(\mu^{[0]}, \rho) - k\mu^{[0]}\right)/m$, where is $A(\mu^{[0]}, \rho) = \beta\left(\rho - g_v(\mu^{[0]})\right)$ and the $T(\mu^{[0]}) = -L\sin(\mu^{[0]} - \pi/2)$

$$\Sigma_s^{-1} = -\frac{\partial F}{\partial\, \Sigma_s^{-1}} = -\frac{1}{2}\left(\boldsymbol{s} - g(\boldsymbol{\mu})\right)^2 + \Sigma_s \tag{6}$$

We set a minimum of $\exp(1)$ and $\exp(0.1)$ for visual and proprioception precision respectively.

Finally, we considered that the perception of the virtual hand location is another unobserved variable. Thus, the model also infers the visual horizontal location, allowing the blending of the real hand perception error with the virtual hand and therefore, producing a visual drift.

$$\dot{\nu} = \frac{\partial F}{\partial \nu} = \frac{\partial \mathrm{g}}{\partial \nu}\Sigma_s^{-1}\left(\boldsymbol{s} - g(\boldsymbol{\mu})\right) \tag{7}$$

To generate individual differences between participants we fixed all parameters and we randomly selected the initial proprioceptive variance $\sigma_{s_p}^2 \sim \mathcal{N}(1,0.5)$. This means that each participant has a different precision of the proprioceptive cue. We further included the bias in the predicted real hand location based on reported data of RHI human experimentation (in cm) $b \sim \mathcal{N}(0,4.2794)$. The length (in cm) of the forearm was drawn from a normal distribution $L \sim \mathcal{N}(44.7208,2.4807)$. Bias and the forearm lengths data were taken from participants real data[29]. During stimulation we also introduced artificial noise in $\mathrm{s_p}$ and $\mathrm{s_r}$ readings.

Finally, in order to generate the synchronous and the synchronous condition differences we modelled the parameter κ as the probability of touch and visual cues being generated by the same source[44]. For that purpose, we synthetically produced tactile and visual events in the ranges of 100 ms in the synchronous condition and 800 ms otherwise[34]. This parameter weights the error between the expected visual location of the arm and the virtual hand location input: $\kappa(\nu - g_\nu(\mu))$. A κ value of 1 means that the visual input is generated by our body. A κ value of 0 implies that the virtual hand comes from another source.

Code and data

For reproducibility of the results, we provide an instance of the developed model (in python, Google colab) with fixed parameters that can be executed in the following link. Statistical force data that support the findings as well as human raw data from the manipulandum is available from the corresponding author upon request.

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Appendix

Body-ownership and proprioceptive drift study

We performed an aside study to verify the level of body-ownership and proprioceptive drift with our experimental setup. Eight participants were tested under the same experimental setup as for the action paradigm. We measured the proprioceptive drift and the body-ownership score. The experiment had ten conditions (five synchronous and five asynchronous), where the virtual hand was placed in one of the three locations: left, centre, right. At the synchronous condition, the ball contact with the virtual hand and the vibration on the real hand events happen in less than 100 ms of difference. On the other hand, the asynchronous condition events are separated in time with more than 800 ms with random noise added of 100 ms.

Participants were seated on the experimental chair, in front of a table, following the instructions of the experimenter. Once the chair was adjusted to the needed height, the experimenter attached the vibrator to the middle point of the hand dorsum. Participants then wore the VR system. The left hand rested on the air sled and the right hand rested on the table. The initial location of the manipulandum was fixed and programmed for all participants. Each condition trial consisted of four phases: 1) *Pre-localization*: Only a table was displayed in the VR and a vertical ruler (depending on the condition) appeared. The participants had to indicate where they currently perceive the location of the index finger of their left hand. This process was repeated 8 times. Between each measurement, participants were asked to face directly forward to look at a cross that appears in a random location around the middle of the scene to avoid the use of the head angle as a cue; 2) *Stimulation*: the trial started and a virtual arm appears in the scene with a ball on the top of the hand that bounces; 3) *Post-localization*: Participants were asked to indicate where they perceived the index finger of the hand in the same horizontal or vertical ruler as stage 1; Finally, 4) *Resting*: at the end of each trial, participants removed the VR system and rested for 1 minute while filling the illusion questionnaire.

Proprioceptive drift and body-ownership

As expected, proprioceptive drifts were found in the left and right conditions (Figure 8*A*). Perceptual drifts effects were also found in the asynchronous condition indicating that random vibrations were also integrated although to a lesser degree. The virtual immersion made that even in the asynchronous condition participants experienced some degree of partial body-ownership. We also evaluated their level of body-ownership with the virtual hand. Figure 8*B* shows the questionnaire results using a seven-point Likert scale (3 indicating strong agreement and –3 indicating strong disagreement). Then synchronous condition yielded to embodiment effects and the asynchronous condition also showed partial embodiment due to the VR immersion and the causality of random vibration events (as shown in the positive values of Q1 and Q3).

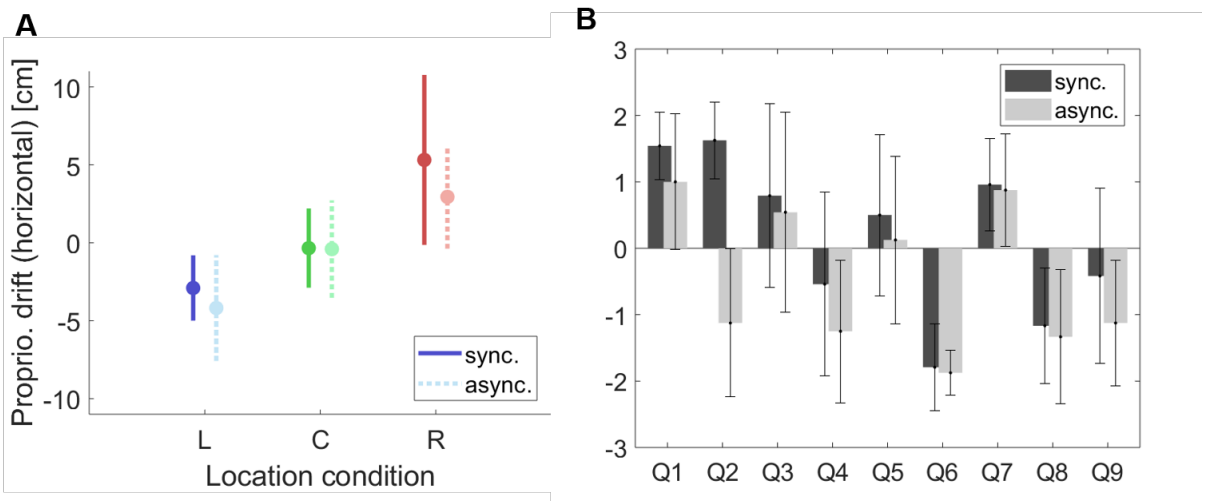

Figure 8: (A) Proprioceptive drift for synchronous (continuous line) and asynchronous (dashed line) for the three VR arm location conditions (Left, Center, and Right). (B) Body-ownership scoring results from a questionnaire answered by the participants using a 7-point Likert scale (3 indicating strong agreement and -3 indicating strong disagreement).

Questionnaire

The illusion questionnaire was developed by adapting the one presented in Nina et al.[45] to virtual environments with previously developed questionnaires for virtual reality RHI[31,41]. It is compounded by nine questions, where Q1-Q3 describe the RHI effect[19] and Q4-Q9 are control questions.

1. It seemed as if I was feeling the vibration in the location of the virtual arm.
2. Sometimes I had the sensation that the vibration I felt in my hand was caused by the contact of the ball with the virtual hand.
3. There were moments in which I felt that the virtual hand was my own hand
4. There were moments where the touch I was feeling came from somewhere between my own hand and the virtual hand.
5. There were moments in which I felt as if my real hand was becoming virtual
6. It seemed as if I might have more than one left hand
7. The virtual hand started to look like my hand, in terms of shape, skin tone, freckles or some other visual aspects.
8. I felt as if the virtual hand was drifting towards the real hand.
9. I felt as if my real hand was drifting towards the virtual hand.