One Self, Too Many Tasks: Bimanual Interference from a Predictive Coding Framework

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Abstract:

In this work we use the predictive coding framework to examine bimanual interference in human hand movements. Based on previous experiments, we hypothesize that bimanual interference can be understood from a similar framework as binocular rivalry, as a bi-stable system created as a Bayesian optimal solution dealing with “un-ecological” conditions under strong hyper priors learnt by the brain in “ecological” conditions. Specifically, we postulate that the layer of the brain in which a single *minimal-self* is created to predict the correlation of information from the different modalities, includes a hyper prior that only one task goal is possible at any given time. While most tasks require many effectors to work together as one coordinated unit and not interfere with each other, like riding a bike, eating with fork and knife or driving a stick shift car, under usual “ecological” conditions these actions emerge as a solution to a single task goal and individual motion paths are undefined under the task goal.

We test this hypothesis by manipulating top down task goal and bottom up visual feedback of subjects’ own hands in an immersive virtual reality environment. We instructed subjects to either follow an avatar’s motion or create a self-motion and manipulated the visual feedback to influence the predictions created by the *minimal-self*.

Our main findings are that providing false visual feedback that is in total opposition to the *minimal-self* predictions lowers interference for the follow task and increased interference for the self-task. We further discovered that providing a first person view, showing the subject performing bimanual independent movements, increased the interference of the hands despite subjects’ belief that the task is easier. We explain these results using the predictive coding framework and discuss the implications regarding possible rehabilitation programs and notions regarding the relative weakness of the proprioceptive system in comparison to the visual system.

1. Introduction to Bimanual Movement

For many years, it was thought that bimanual independent movements, such as to draw two different shapes with the two hands at the same time (Franz, Zelaznik, & McCabe, 1991), to wave the two arms at different frequencies (Turvey, 1990), and to generate polyrhythms with the two hands (Klapp, Nelson, & Jagacinski, 1998) were impossible for healthy individuals without long periods of training. The symmetric coupling constraining independent hand movements was considered to be an inherent low level property of the motor system, such as a tendency for the simultaneous activation of homologous muscles (Kelso, 1984).

However, more recent research has shown that bimanual interference between the hands can be modulated by top down cognitive factors. For example, Kunde at al. (2005) performed an experiment in which participants placed two objects at the same time in either parallel or opposite orientations, requiring them to move their hands symmetrically or anti-symmetrically. They found that substantial interference between the hands, as measured by slower reaction time of antisymmetric movements, happened only if the movements themselves were the goal of the task and not if the movements emerged as the solution of attaining an extrinsic, higher order, single goal. The extrinsic goal was imposed by using blocks that had a black stripe on them and showing a target image in which the stripes had different orientations. Subjects were instructed to move the blocks so they resemble the target image. This was contrasted with a condition without the marks and target images, with the instruction to perform a specific movement without any goal beyond that.

Similarly, Mechsner at al. (2001) showed that bimanual independent hand movements were possible if an extrinsic single goal was imposed. In this experiment, subjects were asked to rotate two flags in symmetry. Unknown to the subjects, a complex hidden gear system was put in place so the hands had to move in a 4:3 frequency difference for the flags to rotate together. Likewise, Klaap et al. (1998) have shown that subjects could perform a 3:2 bimanual rhythmic tapping pattern, thought to be impossible, if the task goal was to say the mantra “not- dif-fi-cult” while tapping the index finger of one hand on “not”, “dif”, “cult”, and tapping the other hand while saying “not”, “fi”. In this case, the task was not defined anymore by a low level instruction regarding how to move the hands, but by coupling the movement to a single high-level goal of speaking.

Furthermore, the type of task cueing has been shown to influence bi-manual interference. Diedrichsen, Hazeltine, Kennerley, & Ivry, (2001) asked subjects to perform, simultaneously, a short movement with one hand and a long movement with the other hand. In the symbolic conditions, circles at all possible target locations were presented, and the letters “S” (“short”) and “L” (“long”) indicated the required movements. In the direct conditions, circles indicated only the current target locations. Only in the condition with symbolic cues, which required the high-level task goal to take into account the length of both movements, showed interference as measured by longer reaction times.

Finally, Rosenbaum, Dawson, & Challis (2006) found that haptic tracking, a task in which subjects have to follow a slight sensation, easily enables bimanual independent movements (Rosenbaum et al., 2006). In this task, subjects were blind folded and created a circular movement with one hand and a square with the other, by following a very light haptic sensation. Here too, high level cognitive processes were not concerned with the exact movement plans, as the higher order single goal of the task was to *follow* a slight external haptic cue. Subjects performing the haptic tracking task were aware that they were making circles and squares but surprised that they were doing so at the same time.

In all the above cases, whether the bimanual movement was tapping at different rhythms, circling the hands in different frequencies or creating different motion paths, the hands did not interfere with each other, and independent bimanual movements were possible, as long as there was a single task goal that did not include the individual hands’ motor plans.

In the next section, I will argue that the predictive coding framework, which proposes that the brain creates a hierarchical model dealing with task goal predictions and motor predictions at different levels, provides a natural framework to interpret these findings. I will then introduce the experimental design to test the hypothesis that is based on this predictive coding framework.

2. Introduction to Predictive Coding.

The predictive coding framework postulates that the brain is a prediction machine that constantly tries to predict future sensory, motor and cognitive states. In doing so, it minimizes entropy or surprise, which is considered to be an evolutionary necessity (Friston, 2006). In this framework the minimization of entropy is accomplished by the brain modelling the environmental causes of its sensory input. Uncertainty about the hypotheses that generate the causes will generate a distribution over different predictions about the incoming sensory information based on the brain's prior knowledge. The brain can now compare the different predictions stemming from different hypothetical causes with the actual incoming information. By performing a Bayesian calculation, combining the probability of each hypothesis before the incoming information (i.e., the prior probability) with how well the hypothesis explains the incoming data (i.e., the likelihood), the brain can select the best hypothesis. This best hypothesis eventually determines the perception of the observer and/or actor.

Furthermore, it is thought that the brain generates these perceptual inferences using a cascading hierarchy of generative models (Bastos et al., 2012). For any pair of levels, the higher-level will have hypotheses predicting the bottom-up signals from the lower-level. If the predictions are good, the bottom-up signals will be 'explained away' and will not propagate to higher levels. Only bottom-up signals that are not well predicted by the higher levels, will propagate further up the hierarchy and are called "prediction error".

The predictive coding framework provides a parsimonious account of perception, but it can also describe actions by considering them as an inversion of the perception model. In effect, higher brain areas produce perceptual predictions which create prediction errors in lower areas that must be minimized. The minimization of these prediction errors results in movements that generate the predicted sensory input (Friston, 2009). The predictive coding framework has strong parallels with Vallacher and Wegner's 'action identification theory' (Vallacher & Wegner, 1987) in which the "Relationship between cognitive representations and overt behavior is not unidirectional, but cyclical. Through the intent connection, cognitive representations generate action, and through the reflective connection, new representations of what one is doing can emerge to set the stage for a revised intent connection." (Vallacher & Wegner, 1987, p. 4). 'Intent' can be translated to 'top down prediction' and 'reflective connection' would be 'bottom up prediction error' allowing for updating of a prediction in a cyclical manner. An integral part of both these theories is the hierarchical organization of these predictions (intents) and prediction errors (reflective connection). "Lower level identities in this hierarchy convey the details or specifics of the action and so indicate how the action is done. Higher level identities convey a more general understanding of the action, indicating why the action is done or what its effects and implications are. Relative to low-level identities, higher level identities tend to be less movement defined and more abstract and to provide a more comprehensive understanding of actions" (Vallacher & Wegner, 1987, p, 4)). In other words, higher layers in the brain hierarchy predict abstract goals and outcomes of movements and lower areas predict the actual motion pathways.

Furthermore, the predictive coding framework further postulates that in order for movement to occur, there has to be a modulation of the proprioceptive information representing the current location of the body (Friston, Daunizeau, Kilner, & Kiebel, 2010). In the discussion part we shall delve into the implication of this postulate with regard to experimental results of our study.

2.1 Minimal-self model and virtual reality

In predictive coding, some of the higher level layers are thought to predict whether a movement is self-generated or stemming from an external source (Ishida, Suzuki, & Grandi, 2015; Seth, 2014). This requires the notion of a so-called *minimal-self*, existing even in primitive life, allowing for differentiation between the organism and the environment (Apps & Tsakiris, 2013; Limanowski & Blankenburg, 2013). This *minimal-self* is supposed to arise from the brain's top down, multi-model, probabilistic representations of sensory input that explains away much of the separate sensory information, binding together these information streams based on prior probabilities and thus minimizing prediction error.

This *minimal-self* has been shown to be flexible and prone to mistakes by examining illusions such as the Rubber Hand Illusion (Botvinick & Cohen, 1998). In these types of illusions the most probable explanation of two (or more) data streams occurring at the same time result in the wrong integration of sensory data and thus a false percept. For instance, the visual stream of a rubber hand being touched and the proprioceptive stream carrying the sensation of touch from sensors in the hand being stimulated at the same time results in a top-down explanation that the rubber hand is part of the body and the *minimal-self*.

Immersive virtual reality headsets, as used in the current study, allow for manipulation of the *minimal-self* by controlling the relationship between the visual information and the proprioceptive information. An experimenter can create an experience that either fits the visual and proprioceptive predictions created by the *minimal-self* model, or contradict them. Virtual reality headsets have recently been used to manipulate the *minimal-self* to investigate phenomena such as the rubber hand illusion by creating full body illusions (Slater, Spanlang, Sanchez-Vives, & Blanke, 2010), treat body image disorders like anorexia (Keizer, van Elburg, Helms, & Dijkerman, 2016), investigate mirror box therapy for amputees (Wittkopf & Johnson, 2016) and help heal spinal cord injuries (Donati et al., 2016).

2.2 Bistability

In this section I will argue that bimanual interference can be understood in terms a bi-stable system that emerges from the notion of a *minimal-self* and thus from the predictive coding framework.

Systems which display two stable steady states with a third unstable state are usually termed bi-stable systems. In neuroscience, the most investigated bi-stable percept is binocular rivalry. Binocular rivalry occurs when one stimulus is shown to one eye and another to the other eye. Two different objects seem to occupy the same spatiotemporal position, yet perception keeps alternating between the two different objects. Thus, the two stable states in the system occur when perceiving the individual objects, but only in the unstable state both objects are perceived simultaneously. Presenting each eye with a different stimulus is an ‘‘un-ecological” condition that is very different from the usual information reaching the eyes.

Hohwy et al. (2008) discuss binocular rivalry from the predictive coding perspective. They describe the phenomenon as a combination of two problems: 1. The selection problem, and 2. The alternation problem. The first asks the question why the perceptual system needs to select a single stimulus and the second asks why perception switches between percepts. They argue that the selection problem exists because the brain has learnt that there can only be a single underlying cause of sensory input at the same place and time. This is strong prior constraint (a ‘‘hyper prior”) that reflects the way we usually sample the visual world. They explain the switching between percepts stems from one hypothesis “winning” and only “explaining away” bottom up information from one of the two possible visual percepts, causing a prediction error for the other stimulus that builds up until perception again becomes unstable and the percept switches.

Bimanual dependence can be seen in a similar way. A task that involves the creation of a self-directed motion path can also be viewed as an “un-ecological”. Instead, in most tasks the motion path is enslaved to a higher order goal without the path being a goal of itself. In many of the tasks described in the previous sections, the bimanual movement was the result of two such tasks of self-directed motion. Similar to binocular rivalry, the brain’s optimal solution to this “un-ecological” condition might be creating a bi-stable system. In this case we postulate that the hyper prior constraint regards the *minimal-self*. Specifically, the *minimal-self* which is created as a hypothesis predicting information streams from different sensory modalities is constricted by a hyper prior that the body is engaged in only one task at a given time. This might be because executing two tasks will usually result in conflict of resources in a single body. While bimanual hand movements themselves probably do not have a conflict of resources, the feedback system in which the eyes (and head) move to collect accurate distal information about the hands’ locations results in a conflict of resources if there are separate tasks for the hands. Visual feedback is especially important for non-experts as seen by tracking the eye movements in juggling experiments (Huys & Beek, 2002). Another example showing that visual information is an important component when creating motion paths even with only one hand comes from (Müsseler & Sutter, 2009, Knoblich & Kircher, 2004) who showed that proprioceptive information was insufficient to recognise one’s own movements when drawing ellipses.

Just as in binocular rivalry, focusing on the task goal of a single hand, such as drawing a circle with your left hand, will increase prediction error for the other task goal, such as drawing a square with the other hand. This results in a switching between actions, which will bring about shapes that switch between circle and square.

Based on the ideas outlined above we wanted to check if interference between the hands could be reduced by manipulating either the task goal or the visual feedback which would affect the *minimal-self* (see figure 1). We postulated that framing the movements of the hands in terms of a single task, in which the bimanual motions emerge as a solution to a single problem and the task goal does not refer to the two separate motion paths, would lower interference stemming from the switching mechanism. For this manipulation we instructed subjects to simply follow an avatar's movements in virtual reality, while the avatar drew a circle with one hand and a square with the other (follow condition, see figure 4a). We further postulated that interference between the hand motions could be further reduced by providing bottom up information that does not fit the predictions of the *minimal-self* by crossing the visual feedback coming from the hands (*crossed follow condition*, see figure 4c). In addition, we hypothesized that the opposite would happen in the *self condition*, where instructions involved drawing 2 explicit motion paths of circle and square. In this case interference would grow when providing the crossed visual feedback (*crossed self condition*, see figure 4d). Finally, we tried weakening the prior that a *minimal-self* can't perform two tasks at the same time by providing bottom up information of a first person view of an avatar that is able to perform bimanual independent hand movements (*within avatar condition*, see figure 4e).

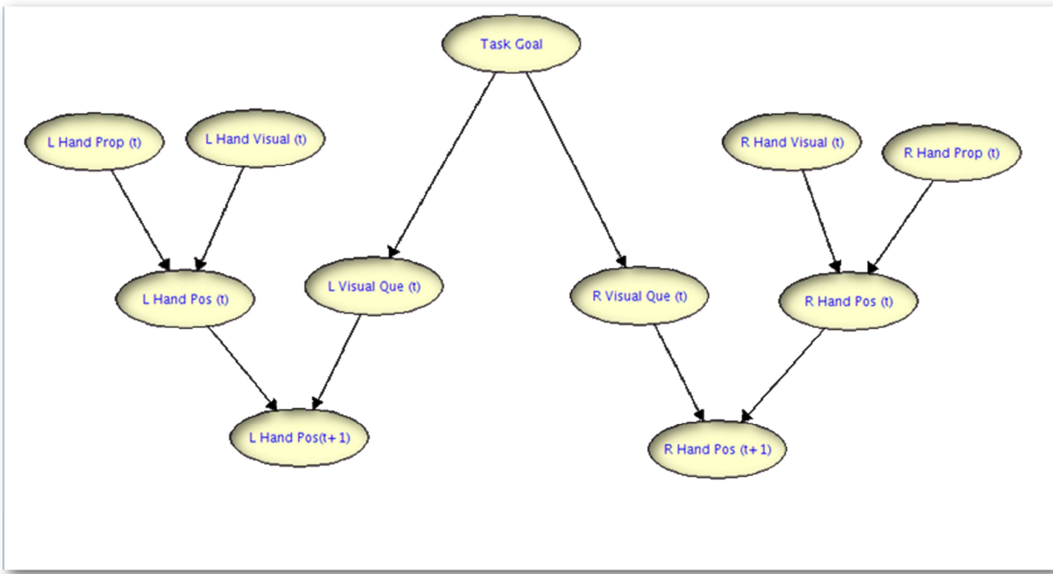

Figure 1. The figure shows a graphical model of the dependencies of the variables in the experiment. In the experiment we manipulated either the high level task goal which has a hyper prior of allowing only one task or the visual feedback of subjects hands which effects the *minimal-self*.

Materials and Methods

3.1 Participants

Fourteen subjects were recruited for this experiment, aged 18-31 with a mean age of 20. All were right handed, had normal or corrected to normal vision and were free of any known sensory or motor disorders. All participants gave their written informed consent in accordance with the institutional guidelines of the ethics committee of the Social Sciences Faculty of the Radboud University Nijmegen. One subject was excluded from the analysis due to moving his/her hands in an anti-phase manner, the opposite of what was described in the instructions.

3.2 Setup

Subjects were put into an immersive 3d environment using the oculus rift™ sdk2 headset. Their hand motions were tracked using an Optotrak™ motion capture system. Six infra-red markers were placed on each hand with two sets of cameras positioned at each side of the room recording the locations of the markers. An additional IR-marker was placed on the oculus headset to provide a more accurate estimate of the head position and orientation in space, which allowed us a more accurate projection of the avatar in the virtual world. The Vizard™ software package was used to design the experiment and to create a real time avatar of the subject based on the motion capture data using inverse kinematic algorithms that come with the package. Vizard also recorded the movement of the hands for later offline analyses. The hands' positions were recorded at 50hz.

3.3 Paradigm

Before the experiment began, subjects were seated in a chair and first given a few minutes to acclimatize to the virtual world by looking around and moving their hands. Only after subjects confirmed they had clear vision and that their hands in the virtual world 'felt' like their own hands did the experiment begin. The experiment consisted of 20 trials, each requiring a 30 seconds smooth motion of both hands.

The square and circle motions subjects were supposed to make in all conditions were 30 cm in diameter for the circle and 30 cm for each side of the square. The center of each shape was positioned at a distance of 22.5 centimetres from the subject's mid-sagittal plane and at a height of 85 centimetres from the floor (see Figure 2). Subjects were instructed to position the chair such that their hands could easily touch the shapes. The shapes' right or left location were counter balanced and randomized across trials.

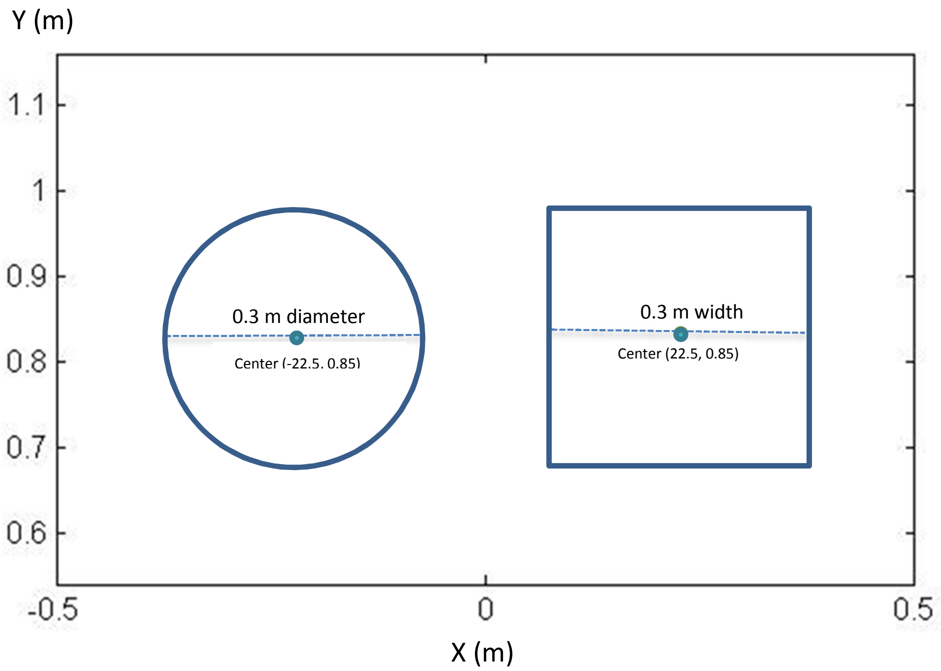

Figure 2. An example of the square and circle that the subjects had to trace in the *self conditions*. In the *follow conditions* the same circle and square were used, but only the current required position was shown to the subject.

The experiment consisted of three separate blocks. The first two blocks contrasted two conditions, *follow* and *self*. In the *follow condition*, subjects were asked to simply follow Lana's hand movements as accurately as possible. Lana is a 3d avatar created with Qualisys QTM ™ and Motionbuilder™. To make Lana's motions as human like as possible, motion capture from a real human model that drew either a circle or square with only one hand at a time was used. The two motions were later merged to allow Lana to draw a circle with one hand and a square with the other hand at the same time. Lana's motions consisted of 20 seconds of tracing the square and circle motions, split into 4 epochs of 5 seconds. In between these epochs, Lana performed semi random motions for 2 to 3 seconds (see Figure 3). The avatar drew each shape in 2.4 sec with a frame rate of 30 fps.

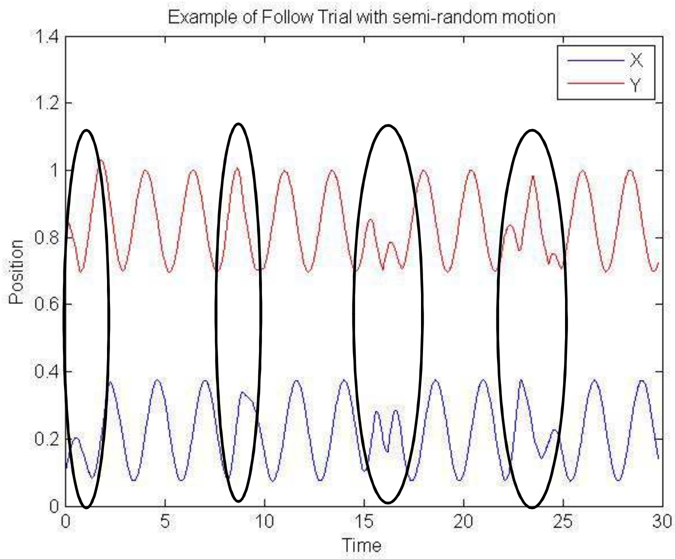

Figure 3 Lana's movements on x and y-axis, ellipses indicate approximate timing of semi random motions

The randomness was inserted to make sure that subjects were really tracking the motions instead of inferring that they had to make a circle with one hand and a square with the other. In other words, we tried to avoid the build-up of higher cognitive level motor predictions and really enforce very attentive following.

In the *self condition*, subjects were presented with only a square and a circle and asked to trace the shapes as accurately as possible with both hands at the same time (Figure 2). In both these conditions the positions of the square and circle were counterbalanced between the left and the right hand. Furthermore, in both these conditions the movement required the subject to move both hands independently in an in-phase manner (i.e. the left hand moved counter-clockwise and the right hand clockwise). Subjects conducted a total of 8 randomized trials in this phase, 4 in the *follow condition* and 4 in the *self condition*.

In the second block of the experiment the conditions were the same but subjects received false visual feedback, their hands were now crossed in the virtual world (Figure 4c and 4d). Due to this false feedback, if the right hand was actually drawing a circle, subjects saw their left hand drawing it. Again, subjects conducted a total of 8 randomized trials in this phase, 4 in the *follow condition* and 4 in the *self condition*.

For the third block, subjects were told to complete 4 more trials of the *self condition* (counter balanced for left and right circle and square) but this time the visual feedback they got was a first person's view of Lana's movements, as if their own hands where drawing the circle and square correctly. Instead of seeing Lana from a third person view, like they did in the *follow condition*, they now saw Lana's hands as if they were their own. This condition was called *within avatar* (Figure 4e).

See figure 4 for detailed images of the paradigm.

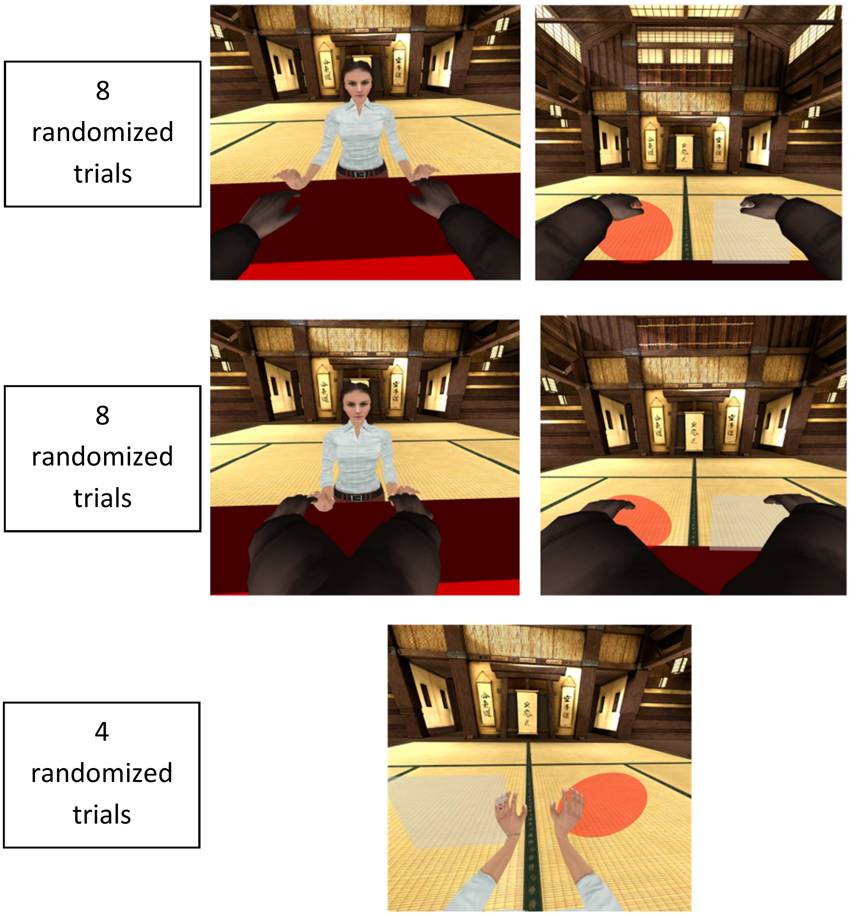

Figure 4: Experimental design. The 3 experiment blocks, the conditions within each block and the order of appearance in the experiment. Top: *follow* (4a), *self* (4b). Middle: *crossed follow* (4c), *crossed self* (4d). Bottom: *within avatar* (4e). All conditions were counter balanced between the left and right shapes and the order of appearance of the conditions within each block was randomized.

3. Data analysis

The recording of the subjects' hand positions were imported into Matlab. A 4th order two-way low pass Butterworth -filter at 10Hz was applied to the data. Missing points, where the Optotrak™ motion capture system didn't record the movement, where found and removed by looking at points in which there was absolutely no change from one recording to the next. Subsequently the velocities were computed.

Points in which one or both of the hands slowed down below the threshold of 6 cm/s where also excluded from the analyses, as the task directive was to move both hands smoothly and continuously.

In order to test the hypothesis regarding task switching between drawing a circle and a square for the baseline *self condition* we calculated the center of each trial by averaging the points and segmented the continuous data into quarters around the center. By measuring the standard variation of the distance of points to the center for each quarter, we were able to differentiate the circular form the square quarters with the circular quarters having a much lower standard deviation. A square, as well as other shapes, results in a much higher standard deviation and thus our analysis only shows switching in and out of circler movement. Since creating totally exact circles is very difficult we needed to take into account the variations in the hand movements that slightly squashed or stretched the circles. To do that the center point for each quarter was recalibrated by calculating the point on the y-axis that had an equal distance to the first and last point of each quarter. We then calculated the standard deviation of the distance from this new point. Clean sample data taken from our recorded avatar run through this analysis showed circles trials with an average standard deviation of 0.0004 (min 0.00017, max 0.00077 and square trials with an average standard deviation of 0.022 (min 0.0205, max 0.023). Based on these number we classified quarters with a standard deviation smaller than 0.005 as circles. Finally after the quarters were categorised for each trial for both the left and right hand, a correlation coefficient of the categorisation of the hands' circular motion was run.

In order to further quantify bimanual dependence or interference between the hands, we calculated the correlation between the velocity vectors of both hands, for each axis separately. The correlation calculation did not include the missing points or the slow points.

Note that in the "follow" condition, only the parts corresponding to Lana, the avatar, performing circle and square motions were included in the analysis and the random parts were ignored (see figure 3).

Two ANOVA analyses were run in Matlab taking the subject as a random factor. One analysis contrasted the follow and *self condition*s as one factor and the crossed and *uncrossed conditions* as another factor. The second analysis contrasted, *follow*, *self* and *within avatar conditions*.

5. Results

5.1 Switching mechanism

One of the central hypotheses for our research was that bimanual movements can be explained similarly to binocular rivalry, as a bi-stable state created as a solution for un-ecological conditions. As such we expected to see switching between circular and non-circular motion. Figure 5 shows four exemplar traces in which switches between circular and non-circular motion took place. Our analysis showed that all trials in the baseline *self condition* had switches in and out of highly circular motion.

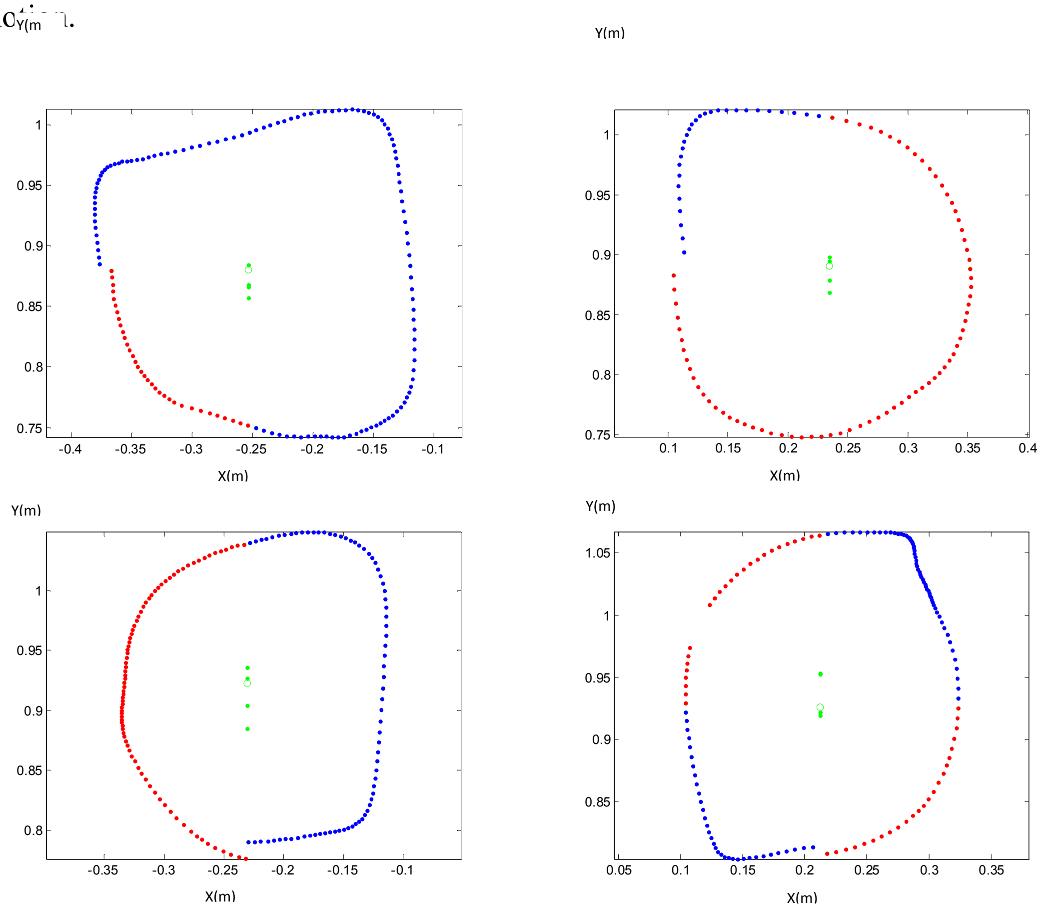

Figure 5: Exemplar of the task switching behaviour between quarters. Motion categorized as circular in red and non-circular in blue. Large green circle represents the center of the shape as averaged throughout the trial. Green dots represent the equal distance of the beginning and end point of each quarter from the y-axis and the point from with the average distance and standard deviation of the quarter was calculated.

On average subjects switched in and out of circular movement 13.9 (SD 4.1) times per trial per hand. This is indicative of a bi-stable state.

Furthermore, the average correlation coefficient between the left and right hand circular categorised movements was 0.18 (SD 0.09). Note that 6 out of the 52 trials had to be removed from the above analyses as the number of quarters was not equal between the hands, meaning one hand performed more rotations around the center than the other.

5.2 Self vs Follow

Figure 6 depicts exemplar hand trajectories from the *self condition* and shows large variations between subjects in this condition. For 3 subjects the task was so hard that they could not follow the instructions: Two subjects kept slowing down to a near stop of both hands or moving just one hand at a time. A third subject was not able to move both hands around the outline of the shapes and moved one hand randomly throughout the shape while the other performed the task. For our correlation calculation to be valid, both hands need to be moving together. As a result, these subjects were getting low correlation, especially for the *self condition* (see subjects 8, 10 and 13 in appendix table). However, the low correlation in these participants is not an indication of independent movements of the hands, but actually an indication that they were not able to move both hands without interference (see figure 6a).

Two other subjects were remarkable good in the *self condition.* The correlation between their hands was very low compared to others and they were able to draw a square and a circle that are easily distinguishable while moving both their hands continuously (see figure 6b).

This variance between subjects in the *self condition* also clearly shows from the group statistics on the correlation coefficients for the *self condition* (figure 8, 2nd and 4th bar) and the number of slow points in which one of the hands moved at less than 6 cm/s (see figure 9).

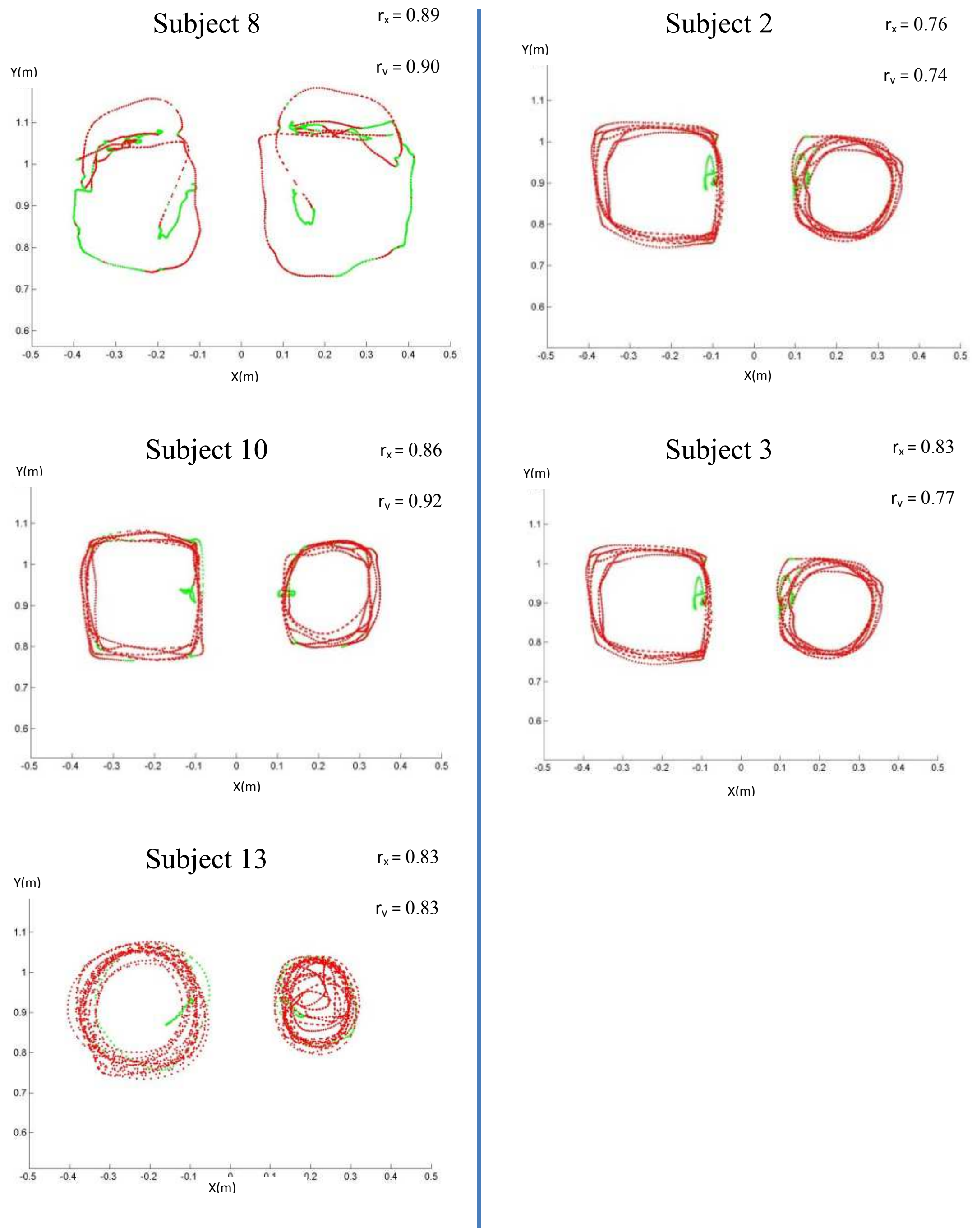

Figure 6: Exemplar trajectories in the *self condition*, showing the large variance between subjects. Green points show movement with at least one hand slowing to below 6 cm/sec, r is the correlation coefficient between the hands. Left column (6a) shows examples of subjects who could not follow the instructions. Right column (6b) shows subjects who were very good at the task.

The 8 subjects remaining performed the self-task as expected, creating shapes that were a mixture of a square and circle (see figure 7 for two exemplar subjects), resulting in high correlation measures between their hands.

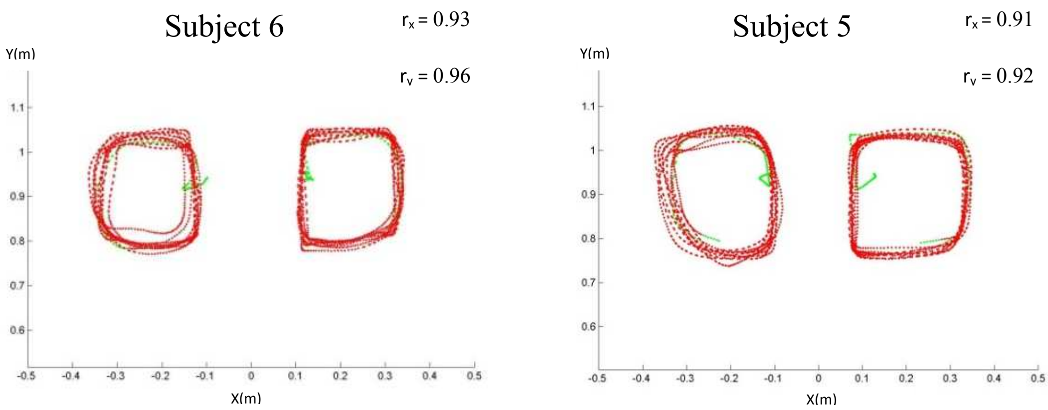

Figure 7: Two examples from the 8 subjects performing *self condition* as expected drawing a shape that is a mixture of a square and circle with high correlation between their hands.

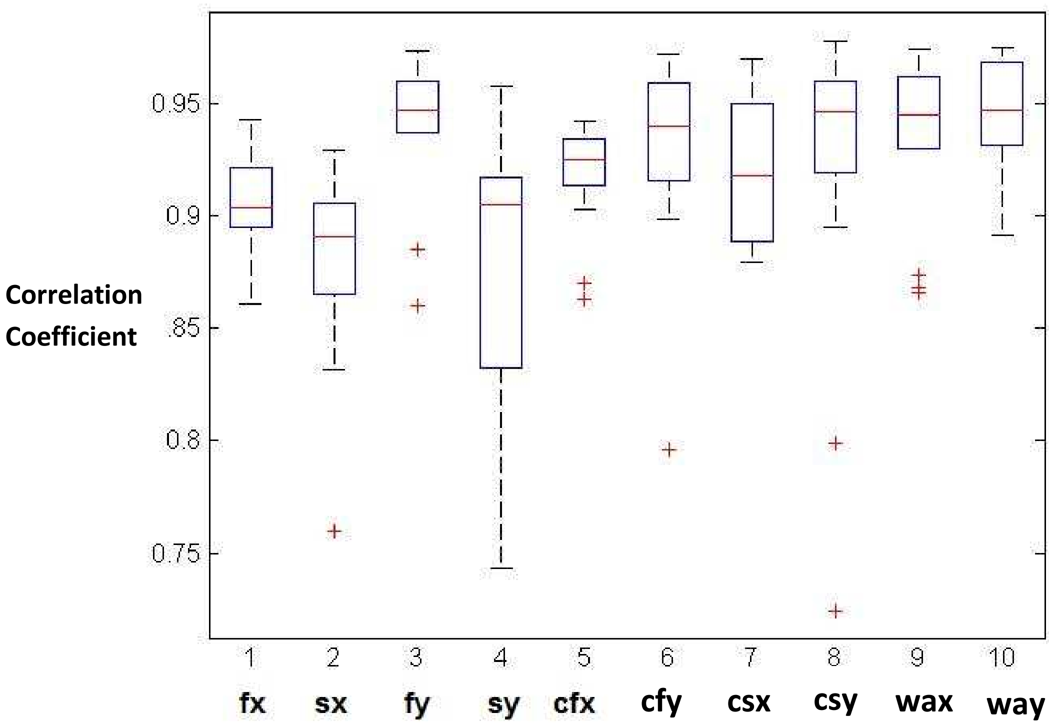

Figure 8. Correlation coefficient based on left and right hand velocity (separate for each axis) for all experimental conditions. From left to right, follow x (fx), self x (sx), follow y (fy), self y (sy), crossed follow x (cfx), crossed follow y (cfy), crossed self x (csx), crossed self y (csy), with in avatar x (wax), within avatar (way).

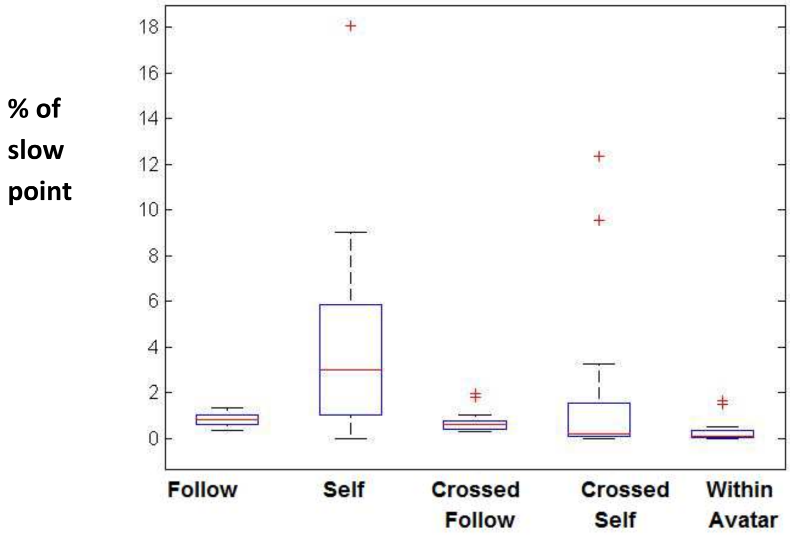

Figure 9. Fluency of movement. Subjects were instructed to move their hand simultaneously and continuously. However, sometimes they would stop moving one of their hands. Here we show the percent of data points in which at least one of the hands moved too slowly (below 6m/s). It is clear that in the *self condition* subjects more often stopped moving, indicating the difficulty of the task.

A repeated measures ANOVA was conducted on the data from all 13 subject to compare the effects of top down influences of execution of instruction (*follow* and *self)* and bottom up visual feedback of hand crossing (*crossed* and *uncrossed*) on the correlation between the hands. The analyses revealed no main effects of hand crossing or execution instruction, but there was a trend for an interaction between follow/self and crossed/uncrossed ($F(1,12)=2.27$, $p=0.09$). This trend fits our hypothesis that providing bottom up visual feedback of crossed hands, that does not fit predictions from the *minimal-self* will affect the different task in an opposite direction, lowering interference in the *follow* condition and increasing interference in the *self condition*. We shall examine this in depth in the discussion section.

5.3 Within-avatar

A repeated measures ANOVA was conducted to compare the effect of the *follow*, *self*, vs. *within avatar* condition on hand interference. The analyses found a significant effect ($F(1,24)=15.13$, $p=0.002$). There was also a significant effect of the direction of movement on the x or y-axis ($F(2,24)=9.84$, $p=0.0008$). Paired samples t-tests were used to make post-hoc comparisons between the conditions of *within avatar* vs self and *within avatar* vs *follow* for the x and y-axis correlations separately. The test concluded that there was a significant difference between the interference in the *within avatar* and *self condition* on the x and y-axis ($t(24)= -3.2572$, $p=0.0033$ and

$t(24)= 3.3836$, $p= 0.0025$). Between the follow and *within avatar condition* there was only a significant difference on the (x-axis $t(24)= -2.1895$, $p= 0.0385$). See the appendix for a table of all coherence results.

6. Discussion

This paper takes a novel approach regarding bimanual interference. Using ideas from the predictive coding framework we postulated interference is caused due to bi-stable switching at the task level as an optimal way to deal with an "un-ecological" condition of two specific motion tasks. Our results show that subjects did move in and out of periods of highly circular movement, which is in accordance with our hypothesis. The low correlation between the left and right circular phases might indicate some phase shift between the hands is taking place. Slight differences between the initial locations of the right and left hand compared to the center and the speed differences which forced us to remove some trials might also be playing an important role and further research is needed. Specifically it would be interesting to track the motion of the eyes to see if that is a factor that effects the task switching.

While the high variance between subjects in the baseline 'self' condition is likely to be one of the main causes for our mixed results it is an interesting finding in itself as none of the previous research known to us and reviewed in the introduction, mentions this effect. This task has been considered a difficult task but we have seen that for some it isn't and for others it is so difficult that they aren't even able to move both hands together under these conditions. This observation fits with findings from other domains in motor control of hand movement, where large differences of behavior between subjects have been shown. For instance, Fourneret & Jeannerod (1998) had subjects trace a straight line by moving a stylus on a tablet with some trials being perturbed and showing a 10 degree angular difference between the actual hand movement and the movement on the screen. One group of subjects misperceived the direction of their hand movement in the direction opposite to the perturbation while the other gave responses in the correct direction.

As discussed previously, bimanual (in-)dependence can be seen as a bi-stable system, similar to binocular rivalry. Subjects who succeeded in the *self condition*s and were able to trace the shape of circle and square at the same time are akin to subjects who perceive mixed states in binocular rivalry conditions. Interestingly, autistic individuals are known to perceive longer mixed states in binocular rivalry

(Robertson, Kravitz, Freyberg, Baron-Cohen, & Baker, 2013). Speculating about the difference in autistics' *minimal-self* goes beyond the scope of this work, but this might indicate that differences in predictive mechanisms that create the *minimal-self* might be at the core of this variance. Subjects with a weak *minimal-self*, perhaps due to a mismatch between the different sensory modalities or due to an overly precise single sensory module, might also be better able to maintain two motions based task goals that do not interfere with each other. Otherwise expertise at other tasks that might require low interference between the hands, such as playing a certain instrument, might have played a factor. Further experimentation controlling these factors is needed. The subjects in our experiment that were not able to move both hands simultaneously might have tried to accomplish the task by totally ignoring one of the two task goals, thereby collapsing the system into one stable state.

In the *self condition*s, the number of slow points, i.e. the number of stops, was higher than in the *follow* or *within avatar condition*s, which might indicate that the *self condition* is harder for most subjects. This is another indication that at the higher level there might indeed be a prior for only one task, causing a switching mechanism and one of the two tasks being shut down each time.

Our hypothesis was that participants would be better in producing a circle and square in the follow compared to the *self condition*, i.e. there would be less interference. This hypothesis was not confirmed, at least at the level of inter-manual correlation. Besides the variance in the baseline task this might also be due to Lana, the avatar's, movements still being too predictable and subjects quickly realizing she was making a circle with one hand and a square with the other, creating once more two separate task goals at a higher level of the hierarchy.

The trend towards interaction between crossed/uncrossed and self/follow is inline with our hypothesis that interference between hands is caused by a switching mechanism at the level of the *minimal-self*, by a Bayes optimal solution to an 'un-ecological' condition of having two high level task goals that deal with direct motion paths. The *follow condition* is supposed to depend on low level mirroring mechanisms that are already apparent from birth (Gallagher, 2005). In contrast, the *self condition* task requires the creation of a *minimal-self* to generate the goal directed motions of the hands. We postulated that this *minimal-self* would not only results in bi-stable percepts, like in binocular rivalry, but also bi-stable actions based on a hyper prior allowing only a single task at a given time.

Providing false visual information of crossed hands results in violations of the predictions stemming from this *minimal-self*, which would increase the prediction error in the brain and as a result the brain would attempt to minimize this added error. The brain is thought to be able to decrease prediction error in a number of different ways (Friston, 2010; Friston et al., 2012, Kwisthout, 2015): It could update the predictions, it could update the causal model that generated the predictions or it may lower prediction error by intervening in the world. The latter either by actively intervening, known as active inference (Brown, Friston, & Bestmann, 2011) or by passively gathering additional observations and sampling information in a different way. We suggest that the brain would use different strategies to minimize prediction error in the *self* and *follow condition.*

In the *follow condition* subjects might reduce the precision of the conflicting visual predictions and increase the precision of the proprioceptive information allowing each hand to gain independence and perform more precise movements. This strategy might be influenced by the subjects knowing they are in a virtual reality environment and their eyes are not to be trusted.

In the self-task the higher layer of a *minimal-self* must be involved in order to maintain goal oriented movement paths. As we shall see in our conclusions, maintaining this high level task goal might be in direct conflict with increasing the weight for proprioceptive compared to visual information in evaluating task performance. This would force the brain to minimize prediction error in a different way. We suggest that under these conditions the brain might attempt to update its top down predictions by providing stronger, i.e. less detailed predictions, that would explain away the noisy bottom up data. In this case the hyper prior allowing only one task would be strengthened causing interference between the hands to increase as a result of the switching mechanism explained above.

For the *within avatar condition* we observed more interference between the hands (i.e. higher correlation values) than in the other conditions. This is opposite our postulated hypothesis that a first person view of the hands performing independent movements might weaken the hyper prior preventing two task goals and change the brain's predictions to allow for independent movement. Just like in the *crossed condition*, subjects received false visual information that did not fit their proprioceptive inputs. This would increase their prediction error. However, unlike the *crossed condition* the feedback was not the total opposite of the predictions arising from the *minimal-self*, it was just a discrepancy between visual and proprioceptive information. In this condition it seems that for most subjects the optimal strategy for reducing prediction error was decreasing the contribution of the proprioception modality in their own state estimate based on vision and proprioception. In this way high level task goal predictions could still be fulfilled and lower levels of the separate motor prediction were not receiving the prediction error and so interference between the hands grew.

Taken together, our finding have important implications on creating rehabilitation programs using virtual reality. Programs in which the motion emerges as a solution to an external task are likely to fit the hierarchical computations in the brain more than programs focusing on tasks that involve the creation of explicit motion paths. Furthermore, this research sheds light on the possible reasons for mirror box therapy being effective for chronic pain treatment (Wittkopf & Johnson, 2016). Our subjects believed they were doing better in the first person view of an avatar performing the movements and this seems to have reduced their proprioceptive sensations in order to minimize prediction error. The same might happen with pain sensations. Patient's seeing a different body than what they are used to, might reduce prediction error by decreasing the sampling from their nociceptors.

However, if we want to actually induce correct movements in patients, for example after a stroke, showing them they are performing the movements is not enough. We must find ways to increase their proprioceptive sense in which case providing them with visual feedback that is in direct opposition to the predictions created by the *minimal-self*, for instance their hands being crossed while being in a low level task of *following* might provide an innovative new approach. It is important to note that this research was done on a small sample of healthy subjects so further research focusing on various patient groups is needed to confirm these hypotheses.

7. Summary and Conclusions

Our results show that in order to generate bimanual movements, the brain uses different tactics to minimize prediction error based on different task goals and based on how much the bottom up information fits with the predictions coming from the "*minimal-self*". Our results fit in with previous findings of visual information dominating over proprioceptive information (Müsseler & Sutter, 2009, Knoblich & Kircher, 2004). Müsseler & Sutter claim the relative weakness of the proprioceptive modality compared to the visual modality is likely to be connected with the evolutionary necessity of using tools, as the use of tools requires a focus on the end result and not on the propreceptive percept. Howerver this experiment might offer another suggestion. In order for an organism to perform any high level, goal oriented, movement that requires coordination of many body parts creating different motion paths, the higher level task goal must be able to impose it's predictions regarding the task outcome on lower areas. According to active inference theory (Friston, Daunizeau, Kilner, & Kiebel, 2010) this would require a reduction of the weighting of proprioceptive information in order for the prediction to 'pull' the various body parts to their intended location. On the other hand, a larger reliance on proprioceptive information might allow for more independent movement of body parts, as seen in the "crossed-follow" condition, but would at the same time interfere with top down predictions, stemming from higher levels in the hierarchy, as seen in the "crossed-self" condition. This indicates a type of reverse relationship between precision of the proprioceptive modality and goal oriented movements. This might shed some interesting light on research regarding athlete peak performance known as *flow states*. These states are characterized as the athlete being freed from self-consciousness (Jackson & Marsh, 1996) which might be interpreted as states in which higher layer abstract goals are being inhibited allowing a hyper accuracy of the proprioception modality leading to better performance of certain motoric tasks.

This hypothesis can also explain why in Rosenbaum et al's. (2006) experiment, blindfolded subjects could easily track bimanual haptic signals, necessitating independent hand movements that do not interfere with eachother. Higher levels of the predicitive hierachy were not informed about these movements because subjects were not making predictions about more abstract goals as the task goal was framed as *following* requiring a precise read-out of the haptic and proprioceptive modality, even further encouraged by closing the eyes, thereby reducing interference and allowing for separation of the motion paths at the lower levels of the hierarchy. Our results and their interpretation do not only shed light on bimanual movement, but also on the general relationship between task goals, the notion of a *minimal-self* and sensory information traveling up in the motor hierarchy. This might aid in designing theraputic interventions using virtual reality for a variety of disorders.

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Appendix

subject	fx	sx	fy	sy	cfx	csx	cfy	csy	wax	way
1	-0.86	-0.90	0.86	0.92	-0.86	-0.92	0.89	0.95	-0.87	0.92
2	-0.89	-0.76	0.94	0.74	-0.94	-0.97	0.88	0.95	-0.96	0.97
3	-0.89	-0.83	0.94	0.78	-0.87	-0.80	0.88	0.72	-0.87	0.89
4	-0.93	-0.88	0.96	0.90	-0.90	-0.90	0.97	0.93	-0.94	0.96
5	-0.91	-0.91	0.95	0.92	-0.93	-0.92	0.95	0.90	-0.95	0.94
6	-0.90	-0.93	0.95	0.96	-0.93	-0.95	0.93	0.95	-0.97	0.95
7	-0.94	-0.90	0.97	0.89	-0.93	-0.95	0.89	0.93	-0.94	0.95
8	-0.89	-0.89	0.89	0.91	-0.91	-0.92	0.91	0.95	-0.87	0.89
9	-0.90	-0.89	0.94	0.82	-0.93	-0.91	0.90	0.80	-0.95	0.93
10	-0.92	-0.86	0.97	0.92	-0.93	-0.95	0.92	0.97	-0.93	0.93
11	-0.91	-0.92	0.96	0.91	-0.92	-0.96	0.95	0.97	-0.96	0.97
12	-0.90	-0.92	0.96	0.91	-0.94	-0.97	0.93	0.98	-0.97	0.97
13	-0.94	-0.83	0.94	0.83	-0.92	-0.96	0.95	0.96	-0.97	0.97

Table 1. Correlation coefficient based on left and right hand velocity (separate for each axis) for all experimental conditions per subject. From left to right, follow x (fx), self x (sx), follow y (fy), self y (sy), crossed follow x (cfx), crossed follow y (cfy), crossed self x (csx), crossed self y (csy), with in avatar x (wax), within avatar (way).