Can the Left Hand Benefit from being Right?

The Influence of Body Side on Action Estimates

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Declaration

I declare that this thesis is my own work under the supervision of Dr Sally Linkenauger, Professor Trevor Crawford and Dr Helen Nuttall and that it has not been submitted in substantially the same form for the award of a higher degree elsewhere.

Signature: **Date:** 14.08.2023

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Thesis Abstract

Right-handed individuals (RHIs) possess various perceptual, visual, and somatosensory biases that facilitate more precise and efficient control of the right hand. For example, RHIs have asymmetries in the cortical representation of both hands, with the right hand representation in left motor cortex being significantly larger than the left hand representation in right motor cortex. These biases have consequences on RHIs' perceptions of their bodies, with them estimating their right hand and arm to be visually larger than their left. Subsequently, they estimate that they can reach further distances or grasp larger objects using their right hand than their left, despite no significant differences in the real morphology of the hands. One key question is whether such visual biases RHIs experience sufficiently explain these asymmetries in action perception between the left and right hand.

This thesis aims to explore both the visual and non-visual (somatosensory) factors that underlie both the strong right-hand preference and impression of greater capabilities using the right hand in RHIs. To do this, virtual reality (VR) and motion capture technology were used in a series of 9 experiments to isolate visual feedback associated with moving the right hand from the somatosensory feedback that would ordinarily be experienced. Three of these 9 experiments explored the impact of visual feedback specifying handedness on perceptions of reaching and grasping abilities, four explored the ability for people to embody virtual limbs that are visually presented incongruently to somatosensory feedback, and two explored whether the left-hemisphere processing advantage for visually guided actions could be exploited in the context of visual illusions.

Overall, the key findings of this thesis were that: 1) visual feedback specifying hand use did not have a significant impact on action estimates; 2) action estimates were based on the physical hand that was being used, and the right hand was estimated as more capable even when viewed as the left; 3) differences in action estimates between the left and right hands is

contingent on the complexity of the action being performed. Thus, the findings suggest that RHIs' perceptions of greater action capabilities with their right hand are primarily rooted in cortical asymmetries that lead to an enlarged sensorimotor representation of the right hand. Moreover, more efficient sensory feedback aside from vision better accounts for differences in action perception than visual feedback specifying the hand being moved during visually guided actions. The findings of this thesis have broader implications for understanding the factors that underlie biases in action perception in RHIs.

Chapter 1

Literature Review

1.1 Development of Handedness and Hand Preference

The hand is arguably one of the most important tools our bodies possess for interacting with the environment. Used in many human skills, the hand is central to creating gestures when socialising, using tools, writing, and making music. Most humans develop a preference for a specific hand over the lifespan, with 90% of the population ultimately developing a preference for their right hand (Hardyck & Petrinovich, 1977). Unimanual hand preference emerges early in development, with infants as young as 7 months demonstrating a preference for one hand when reaching (Ramsay, 1980) and infants with no preference shifting to left or right lateralised hand use as toddlers (Nelson et al., 2013). When completing bimanual tasks in which each hand has distinct roles, children at around 18 months of age demonstrate a preference for one hand to complete the role of carefully manipulating an object and one to act as a stabiliser (Ramsay & Weber, 1986; Fagard & Lockman, 2005). By the age of 3, the direction of handedness seems to be fixed, though the degree of handedness continues to increase throughout childhood (McManus et al., 1988; Gooderham & Bryden, 2013). In adolescence, individuals tend to have an overreliance on the preferred hand, with children between 10-12 years old demonstrating a consistent hand preference when performing tasks, regardless of the task or the location of an object they may be interacting with (Nelson et al., 2013).

In the case of right-handedness, this tendency to rely on the preferred hand continues, though to a slightly lesser extent, into adulthood. For example, Gonzalez et al. (2007) found that in natural grasping tasks involving picking up Legos right-handed individuals (RHIs) used their right hand 82.2% of the time. This finding included reaching ipsilaterally, to the body midline, and contralaterally. More evidence demonstrates the tendency for RHIs to prefer their right hand, even for tasks in contralateral space, for tasks that require a high level of dexterity. Calvert (1998) had RHIs point to the location of a letter or pick up a marble to place it within a small receptacle. Within ipsilateral space, RHIs overwhelmingly preferred their right hand to complete tasks. However, the skill demand needed to complete the task influenced which hand RHIs chose for tasks in contralateral space. That is, the right hand was used more often for the difficult reach and place task than it was for the simpler reach to point task.

Similar findings were found in Gabbard et al. (2003), in which blindfolded participants were required to grasp a small cube at one position and release it to the opposite side of space. In this task, 96% of RHIs used their right hand to reach for the cube in the right side of space to move it to the left side of space, while 60% used their right hand to reach to the left side of space to move the cube to the right. Compared to a similar but simpler version of the task in Gabbard et al. (1997) in which people were required to move a small box from one side of space to the midline, the percentage of RHIs opting to use their right hand to reach to contralateral space increased by 30%. Thus, the difficulty of the task influences the frequency at which the preferred hand is used to reach into contralateral space.

Furthermore, research by Bryden et al. (2003) examined the effect of skill demands on preferential reaching. RHIs were asked to either pick up or pantomiming picking up the use of various tools such as a pencil, toothbrush, hammer, paintbrush, and spoon. Preferred hand use was greater when the goal was to use the object versus merely picking it up. The preferred hand was also more likely to reach contralaterally than the non-preferred hand, even though using the non-preferred hand to reach into left space would be more biomechanically efficient (Bryden et al., 2003). Mamolo et al. (2004) extended this research by adding in an additional task, which was to actually use the tool with its associated object. In support of prior research, they found that preferred hand use was greater for the more complex use task and, additionally, participants were more likely to reach into left hemispace using their right hand when the task was more demanding. Overall, despite the biomechanical inefficiency associated with the strategy of reaching into left hemispace using the right hand due to needing to reach across the body, RHIs have repeatedly demonstrated a strong preference in using their right hand for a variety of tasks (Bryden et al., 2003; Gabbard et al., 2003; Mamolo et al., 2006; Gonzalez et al., 2007).

One may assume that left-handed individuals (LHIs) would demonstrate a similar degree of preference for their left hand as RHIs show for their right hand. However, various studies exploring preferred hand use for tasks such as reach-to-grasp find that LHIs are far more willing to use their non-dominant hand than RHIs. In Gabbard et al. (1997), LHIs were more likely to use their right hand when reaching to the right side of space compared to RHIs using their left hand to reach to the left side of space. Steenhuis (1999) examined differences in preferred hand use and proficiency in both RHIs and LHIs in a variety of tasks. They found that LHIs used their non-preferred hand to pick up and manipulate tools more so than RHIs, with LHIs showing more proficiency in using their non-preferred hand than did RHIs. In the natural grasping task described earlier, Gonzalez et al. (2007) found that LHIs used their left hand to pick up Lego Pieces just 44.4% of the time. Additionally, LHIs were 20 times more likely to reach across into left hemispace using their non-dominant hand to pick up these Lego pieces.

Moreover, Mamolo et al. (2006) explored which hand both RHIs and LHIs used to either pick up, pantomime, or use various tools such as paintbrush and hammer. These tools were placed at various positions across the body, spanning both left and right hemispace. Mamolo et al. (2006) found that LHIs made significantly fewer preferred hand reaches than did RHIs across all reaching directions. Exploring the hand use at contralateral positions to the preferred hand presents even more striking differences in the frequency of preferred hand reaches. When participants were required to use the tools in near-contralateral space, LHIs opted to use their preferred hand just 40% of the time in comparison to 70% of the time for RHIs. At far-contralateral space, when participants were simply required to pick up the tool, LHIs used their preferred hand less than 1% of the time compared to 35% of the time in RHIs. For pantomiming, RHIs used their right hand 30% more often than LHIs used their left hand. However, frequency of preferred hand reaches did not differ between RHIs and LHIs when they were required to use the tool. Mamolo et al. (2006) demonstrate that, though RHIs and LHIs behave similarly in opting to use their preferred hand most often for highly skilled tasks, LHIs are far less reliant on using their preferred hand than RHIs when completing simpler tasks and reaching into contralateral space.

Overall, RHIs show an overreliance on using their preferred hand in comparison to LHIs. Even for low-demand tasks, such as simply picking up an object, RHIs are far less willing than LHIs to use their non-dominant hand even if such a strategy would be more biomechanically efficient (Bryden et al., 2003; Mamolo et al., 2004; Mamolo et al., 2006). A key question is why RHIs demonstrate such a keen preference for their right hand when LHIs do not mirror this degree of preference for their left hand. To further understand this phenomenon, I will review research that covers key areas of handedness in RHIs, such as cortical asymmetries, asymmetries in attention, and asymmetries in sensory and visuomotor processing.

1.2 Cortical Asymmetries in RHIs

Various neuroimaging studies demonstrate hemispheric asymmetries in the cortical representation of the right hand in RHIs (Linkenauger et al., 2009). For example, the left hemisphere central sulcus – thought to be a marker for the size of the hand sensorimotor representation – is deeper than the equivalent area in their right hemisphere (Amunts et al., 1996). Degree of handedness mediated this asymmetry, with male consistent right-handers showing a significantly deeper left central sulcus than mixed handers. Additionally, there is evidence of increased area for intracortical connections in the left motor cortex (Amunts et al, 1996). These findings are further supported by Volkmann et al. (1998) who found an enlarged hand representation in left motor cortex in RHIs, with the degree of cortical asymmetry being correlated with asymmetry in hand performance. Moreover, there is a close relationship between hand preference and cortical somatosensory representation of the right hand in RHIs (Sörös et al., 1999). However, since some previous research failed to find a gross anatomical lateral asymmetry of the primary motor system in RHIs (White et al., 1997), this larger cortical representation in the left hemisphere in RHIs and the resultant right-hand preference may be due to functional rather than gross morphological differences between the hemispheres (Sörös et al., 1999).

As well as some evidence for structural and functional asymmetries, evidence for greater neural activation and greater cortical excitability in the left hemisphere provides further insight into the asymmetries in hand preference and performance in RHIs. During a simple motor task, neural activation as shown through electroencephalography (EEG) was greater in the left somatosensory cortex than in the right somatosensory cortex (Buchner et al., 1995; Jung et al., 2003). Moreover, the amplitude and asymmetry in neural activation likely indicated an anatomical asymmetry of the somatosensory cortex (Buchner et al., 1995). Transcranial magnetic stimulation (TMS) studies offer evidence of greater cortical excitability of the left motor cortex. Macdonell et al. (1991) found that the minimum stimulus intensity to the left hemisphere to elicit action potentials of the abductor digiti minimi (ADM) in the right hand was significantly lower than the intensity needed to evoke action potentials for the left hand.

Further support comes from Triggs et al. (1994), who compared the thresholds for electromyographic activation of two muscles in both arms of RHIs. They found that the threshold for activating muscles in the right arm was lower than for the same muscles in the left arm. This asymmetry in activation threshold was significantly influenced by the consistency of hand use, meaning that greater asymmetry was present in consistent right-handers than non-consistent right handers. Extending this research, Triggs et al. (1997) correlated right and left-hand differences in muscle evoked potential (MEP) TMS thresholds with their performances in three tasks. These tasks assessed the speed, dexterity, and strength of each hand. Triggs et al found that a lower TMS threshold for the dominant hand was strongly associated with stronger performance in these manual tasks, more so with dexterity and speed than strength. Thus, in RHIs these asymmetries in MEP thresholds represent a functional asymmetry in the control of independent finger movements of the dominant hand, necessary for fine motor control (Triggs et al., 1997). Additionally, Dassonville et al. (1997) found greater functional activation of the left hemisphere in RHIs when moving their dominant hand. A correlation between degree of handedness and the degree of functional lateralisation was found, with lower degree of activation of the ipsilateral hemisphere when moving the dominant hand for strong RHIs (Dassonville et al., 1997).

Interestingly, functional asymmetries in the left hemisphere of RHIs is not limited to voluntary movements of the dominant hand, as shown through studies that explore ipsilateral finger movements (Civardi et al., 2000). Kim et al (1993) found that, while the right motor cortex was activated mostly during left hand finger movements in RHIs, the left motor cortex was also substantially activated during movement of the left hand. Moreover, Kawashima et al. (1993) found that in RHIs movement of both the dominant and non-dominant hand increased regional cerebral blood flow (rCBF) significantly in the contralateral motor area (MA) and premotor area (PMA), as well as small increases in the supplementary motor area.

Importantly, movement of the non-dominant hand also elicited significant increases in rCBF in the MA and PMA of the left hemisphere, corroborating the findings of Kim et al. Moreover, evidence from repetitive TMS studies has found that disturbing normal processing in the left motor cortex leads to timing errors in completing a complex piano sequence using the left hand (Chen et al., 1997). Therefore, the left motor cortex seems to be vital for the processing of complex motor programs in RHIs, even when using the non-dominant hand (Chen et al., 1997; Civardi et al., 2000).

Various studies provide evidence for functional asymmetries in the left and right hemispheres of consistent RHIs (Amunts et al., 1996; Buchner et al., 1995; Dassonville et al., 1997; Sörös et al., 1999; Volkmann et al., 1998) though evidence of gross morphological differences between the two hemispheres is less consistent (White et al., 1997). However, evidence for functional and morphological asymmetries in LHIs is largely inconsistent. While some researchers have found that LHIs demonstrate an opposite pattern of lateralisation to RHIs (Triggs et al., 1994; Triggs et al., 1997), others have found that LHIs often do not mirror the same degree of asymmetries that RHIs possess (Civardi et al., 2000; Kim et al., 1993). For example, Amunts et al. (1996) found that LHIs did not demonstrate the same degree of asymmetry in the depth of their right central sulcus, nor did they show the same association between hand preference and the cortical somatosensory representation of the left hand (Sörös et al., 1999). Thus, LHIs are far less lateralised than RHIs, possibly accounting for their willingness to use their non-dominant hand more often than RHIs.

Overall, RHIs demonstrate various asymmetries in the sensorimotor representation of their right hand (Amunts et al., 1996; Volkmann et al., 1998), greater cortical excitability of the left hemisphere (Macdonell et al., 1991; Triggs et al., 1994; Triggs et al., 1997), and greater neuronal activation in the left hemisphere when moving their dominant hand (Buchner et al., 1995; Dassonville et al., 1997; Jung et al., 2003). RHIs also demonstrate a left hemisphere dominance for motor control that carries over to the left hand, as the left hemisphere shows substantial activation during ipsilateral hand movements (Kawashima et al., 1993; Kim et al., 1993) and is vital for processing complex motor tasks (Chen et al., 1997). These asymmetries provide insight into why RHIs prefer their right hand so strongly and may also contribute to various perceptual biases that RHIs possess towards their right hand. These perceptual biases will be discussed more thoroughly, after addressing asymmetries in attention and sensory processing towards the right side of the body.

1.3 Asymmetries in Attention

Another contributing factor to RHIs preference for their right hand may lie in the distribution of attentional resources (Grouios, 2006). Various researchers suggest that during goal directed movements ,such as manual aiming, attention is biased towards the right hand, resulting in preferential visual monitoring of the right hand (Grouios, 2006; Helsen et al., 1998). For example, Honda (1982) measured differences in eye movements during bimanual aiming tasks. They found that participants monitored the right hand more than the left, leading to better performance with the right hand. Generally, there were substantially greater saccades to the right side of space, indicating a rightward bias in attention. In addition, Honda (1984) found that, during both saccades and pursuit eye movements to track a moving target, the influence of the eye movement was more prominent on the preferred right hand. Thus, asymmetries in skilled movements between the left and right hands in RHIs may be due to greater efficiency of visual monitoring towards the right hand.

Moreover, various studies exploring attentional asymmetries during bimanual tasks provides further support for the hypothesis attentional biases may underlie preference for using the right hand. Peters (1981) explored manual asymmetries in a task in which both RHIs and LHIs had to tap one hand to the beat of a metronome whilst the other tapped at its maximum rate. RHIs performed well when the right hand was assigned the more difficult rapid tapping task while the left hand tapped to the beat of the metronome. However, when RHIs were required to use their left hand for the rapid tapping task, both hand performances reduced significantly. Therefore, the poor performance in both tasks when the left hand is assigned the more difficult task can be inferred to be because of an attentional bias towards the right hand (Buckingham & Carey, 2015). Since attention must be diverted from the right hand to the left when the left takes on the more difficult task, the normal right-hand advantage is lost.

Further evidence for this attentional bias hypothesis comes from Buckingham and Carey (2009), who explored rightward biases during bimanual reaching in two experiments. In the first experiment, RHIs had to complete a unimanual reach using either the left or the right hand after completing a bimanual reach. The downtime between completing the bimanual reach and unimanual reach was referred to as the refractory period. Buckingham and Carey found a shorter right hand refractory period in this task, suggesting that attention was biased towards the right hand, priming it to move. In the second experiment the instructions were altered to encourage different attentional strategies, such as to attend to the right hand more than their left during the task. They found a trend towards a right-hand advantage when attention was directed to either both hands or the right hand. Moreover, directing attention to the left hand created a longer refractory period for the right hand compared to the left. This change to the pattern of the refractory period in the hands is more likely due to reducing the performance of the right hand, rather than enhancing the performance of the left (Buckingham & Carey, 2009). Thus, these two experiments support the idea that a right-hand preference in RHIs could be due to attentional biases that favour attention towards the right hand.

To extend on the finding that RHIs have attention biased towards their right hand in bimanual tasks, Buckingham et al. (2011) had both LHIs and RHIs perform another reaching task in which the preselected limb may need to be inhibited. Participants first completed a bimanual reach to a pair of targets and then had to reach to another target that appeared soon after using the closest hand to the target. A tactile cue was delivered to one of the hands when the initial pair of targets appeared, which would correctly cue participants to which limb would need to be used for the upcoming manual reach 80% of the time. On the 20% of trials in which the incorrect limb was cued, participants needed to resist making the pre-selected reach with the cued hand. Buckingham et al. found that RHIs had a higher refractory period using their left hand than their right and made more errors with their right hand. A greater refractory period for the left hand is interpreted as RHIs having more difficulty inhibiting their dominant hand, suggesting that RHIs direct more attention rightwards and prime their right hand to move. In contrast, LHIs showed no reliable difference between the hands in terms of the refractory period or error rates. Thus, the asymmetry in attention found in RHIs is likely to be linked to cerebral lateralisation of handedness (Buckingham et al., 2011).

Overall, a multitude of evidence supports the notion that RHIs experience rightward attentional biases that facilitate a preference for the right hand, priming it to move (Buckingham et al., 2011; Buckingham & Carey, 2009; Buckingham & Carey, 2015). Leftward biases in attention are not generally found in LHIs, suggesting that asymmetries in cerebral lateralisation of handedness found in RHIs is linked to the uneven distribution of attention between the hands. Notably, when attention is directed away from the right hand during difficult tasks the right-hand performance becomes markedly worse (Peters, 1981). Therefore, greater right-hand performance in RHIs is likely due to greater visual monitoring of the right hand (Honda, 1982, 1984). This attentional bias favouring visual monitoring of the right hand is not the only way in which the right hand benefits from more efficient visual processing. Indeed, another key hypothesis for greater skill using the right hand in visually guided tasks is that sensorimotor feedback – especially from vision – is processed more efficiently. This theory and its supporting evidence will be discussed more thoroughly within the next section.

1.4 Asymmetries in Sensorimotor Processing

One key theory is that differences in skill between two hands - and therefore a preference for one hand – can be accounted for by differences in the efficiency of sensorimotor processing (Flowers, 1975). Flowers (1975) explored both monitored and ballistic movements and found that, in participants who were strongly lateralised to either the right or left hand, a reliable difference in performance between the preferred and non-preferred hand exists in a visually guided aiming task. However, in the ballistic task in which movements are generated without much monitoring, there was not much difference between the two hands. Therefore, Flowers suggests that the key difference between the preferred and non-preferred hand concerns a sensorimotor feedback loop in which sensory feedback – particularly visual - is transmitted back to the motor system to correct online movement. Notably, the lower performance of the non-preferred hand in visually guided tasks is not necessarily due to real, inherent differences in dexterity. Rather, it takes longer for sensory feedback to be processed and thus any needed corrections also take longer, creating the impression that the non-preferred hand is less capable.

More evidence supports this theory of more efficient sensory processing of the preferred hand, focusing mainly on RHIs. Many studies have established that RHIs demonstrate manual asymmetries in visual-guided reaching actions, performing pointing and aiming movements with greater accuracy and more quickly when using their right hand. For example, Roy et al. (1994) had RHIs point at two targets with each hand either with or without vision available. They found that pointing errors and movement time were lower using the right hand. This right hand advantage was present with or without vision, indicating that the right hand system is more efficient at processing sensory feedback regardless of its modality. These manual asymmetries in pointing movements are more pronounced if the task is more demanding. If the task requires a greater level of precision to complete, asymmetries in performance between the left and the right hand become more prominent. For example, van Doorn (2008) had RHIs complete a task in which they needed to hold a stylus in their thumb and index finger and place it on a 2cm diameter circle. Different conditions focused on different aspects of the movement; one condition required participants to hit the targets quickly without the need for precision, while the other required them to hit the target directly in the centre. They found that the time to complete the movement was significantly longer for the left hand in all cases, but this was more prominent during the high-precision task. Therefore, the right hand performed better due to its ability to process the sensory feedback more quickly in the high precision task.

1.5 Asymmetries in Processing Visual Feedback

Further research has focused specifically on the role of visual feedback on manual asymmetries in RHIs, extending initial findings from Flowers (1975). Flindall et al. (2013) explored the reach kinematics of an ecologically valid reach-to-grasp action whilst varying both the difficulty and degree of visual feedback experienced during the task. In this task, participants had to reach, grasp, and sip from a glass of water that was either nearly empty or nearly full. Flindall et al. found asymmetries in movement time, peak velocity, and maximum grip aperture (MGA) variability. Namely, right-handed actions were completed more quickly and produced more consistent MGAs than left-handed actions. Importantly, these right hand advantages became insignificant when full or recent vision was removed during the task. Therefore, the right hand/left hemisphere system may be specialised for visual control of action with more efficient processing of visual feedback specifically (Flindall et al., 2013).

Additional evidence comes from studies exploring visually guided grasping actions towards objects embedded within visual illusions. Gonzalez et al. (2006) had both LHIs and RHIs perform reach-to-grasp movements towards objects embedded within the Ponzo and Ebbinghaus illusions. They found that grasps using the left hand of both RHIs and LHIs were significantly impacted by the illusion. That is, MGA for the perceptually larger object was larger than MGA for the perceptually smaller object. The right hand, however, was resistant to these visual illusions. Thus, Gonzalez et al. provide evidence that the right hand and left hemisphere have an advantage in visuomotor control. That is, the left hemisphere processes visual information relevant to reach-to-grasp actions more efficiently and more precisely than the right hemisphere, allowing the right hand to complete grasps that are scaled to the actual metrics of the target object rather than being influenced by perceptual illusions. However, since Roy et al. (1994) found that the right hand was better in a pointing and aiming task with their right hand without vision, it raises the question of whether the left hemisphere is indeed better at processing visual feedback specifically. It is possible that for tasks requiring more dexterity, such as grasping, visual feedback plays a more important role in determining the success of the action. Thus, any left hemisphere advantage in processing visual feedback would be evident in more dextrous tasks.

1.6 Asymmetries in Visual Perception of the Hands and Arms

As well as asymmetries in processing of visual feedback during visually guided tasks, RHIs also show asymmetries in the visual perception of their right and left arms. Linkenauger et al. (2009) asked both LHIs and RHIs to estimate the length of each of their hands and arms. They did this by extending one arm out and instructing a researcher to adjust the length of a tape measure, oriented perpendicularly to the extended arm until it matched the perceived length of the participant’s arm. Participants were not able to see the numbers on the tape measure and so could not use them to direct their responses. Linkenauger et al. found that RHIs underestimated the length of their left arm more than their right, while LHIs accurately estimated the length of both of their arms. Linkenauger et al. conducted a similar procedure to assess perceptions of hand length and width and found the same pattern of estimates as was found in estimates of arm length. Unlike RHIs, LHIs did not demonstrate the opposite asymmetries in perception of arm length and hand size. Thus, Linkenauger et al. argue that the perceptual distortions in RHIs are a direct consequence of the functional and structural cortical asymmetries they possess.

If RHIs show asymmetries in the visual perception of their arms, it may follow that they also demonstrate asymmetries in their perceptions of their action capabilities with each arm. These asymmetries in affordance perception will be discussed further, within the context of affordances more generally.

1.7 Affordance Perception in RHIs

Affordances simply refer to aspects of the environment that offer an animal opportunity for action, whether this be for good or ill (Gibson, 1979). These aspects of the environment can refer to concrete parts of the world that cannot easily be manipulated, such as the solid ground we walk on that affords locomotion. We may also consider detached objects such as tools that can afford grasping, amongst many other affordances that different tools offer. All environmental features have properties - such as colour, texture, size, shape, rigidity - that determine whether an animal can successfully interact with them. Importantly, it is not necessary to perceive all the properties of an environmental feature to understand whether it affords us certain behaviours. Rather, an affordance is an invariant combination of variables that makes the perception of the world around us more economical (Gibson, 1979).

When we perceive our affordances, we not only consider properties of the target's environmental features. Rather, we must also consider the dynamic relationship between our own body and the environment. For example, if we need to traverse across a surface, we must consider both the rigidity of the surface and our own weight. Thus, we perceive our spatial layout with regards to relevant aspects of our body for an action we want to perform (Profitt & Linkenauger, 2013; Profitt et al., 2022). A key aspect of our body to consider is our morphology, which defines our action boundaries. That is, an action boundary refers to the maximum extent to which an action can be performed (Fajen, 2005). When perceiving whether an object is graspable, for example, we consider the size of the object relative to the maximum span of our hands. When reaching we consider the distance between ourselves and the target object, the length of our arm, and the posture we will assume when reaching (Wagman et al., 2018). Although we are generally very accurate at perceiving our action boundaries since we gain a lot of lifetime experience in interacting with our environment (Carello et al., 1989; Fajen et al., 2009) there may be biases in how we perceive our morphology that in turn impact how we perceive our action boundaries.

As stated earlier, Linkenauger et al. (2009) found that RHIs estimate their right hand and arm to be larger and longer than their left. Coelho et al. (2016) expanded on this finding, finding that right-handed participants overestimated the width of their right hand more than their left. Subsequently, estimates of maximum reaching ability and grasping ability reflect these perceptual biases. That is, RHIs estimated their maximum reaching distance to be significantly further using their right arm than their left, and they also overestimated their maximum grasping ability more with their right hand than their left. In contrast, LHIs did not demonstrate any differences between the left and right arms when estimating their maximum reaching capabilities. Thus, Linkenuager et al. assert that the perceptual biases favouring the right hand in RHIs have a direct influence on their perceptions of their action capabilities, with these biases being adaptive as they encourage continued use of the right hand. As LHIs do not demonstrate similar perceptual biases towards their left arm, their perceptions of reach between both hands remain relatively even. Differences between RHIs and LHIs in their patterns of reaching estimates support the assertion that perceptual biases originating from cortical asymmetries impact RHIs' perceptions of their action capabilities.

1.8 Recalibration of Affordances based on Visual Feedback

If inherent differences in the visual perception of each hand affects RHIs estimates of their reach and grasp, it is possible that artificially changing visual feedback when moving the hands can alter people's perceptions of their action capabilities. While altering the morphology of the hands is near impossible to do safely in real life, the development of virtual reality (VR) technologies has allowed researchers to explore how our bodies scale our affordance perception. Using VR and motion tracking, researchers can create realistic self-representing virtual avatars that are animated with the own participant's movements (Kilteni et al, 2012; Linkenauger et al., 2015; Lin et al., 2020; Slater & Sanchez-Vives., 2014).

Various studies demonstrate that participants can feel a sense of ownership over virtual bodies, even with extreme changes, provided they are given sufficient perceptual-motor experience. For example, Kilteni, Normand, et al. (2012) found that participants could embody a virtual arm that was three times the length of their real arm when there was visuo-motor congruence between the real and virtual arm. Furthermore, Normand et al. (2011) found that giving participants synchronous multisensory stimulation when placed into a virtual avatar with a larger stomach can produce changes in their body representation. Thus, people can readily embody different morphological properties of virtual avatars and temporarily update the perceptions of their own bodies.

While these studies demonstrate that people can embody virtual avatars, further research has shown that people can calibrate to visually specified changes in body representation and consider them in their estimates of their action capabilities. One such study is by Lin et al. (2020) who explored the impact of perceptual-motor variability on people's action boundaries for horizontal reach. In one experiment, participants performed a simple calibration task in VR in which they reached and pointed to a target placed on a virtual table. Participants were either given a long virtual arm (50% longer than the standard virtual arm), a short virtual arm (50% shorter than the standard virtual arm), or a virtual arm that changed size randomly between calibration trials. After this short calibration phase, participants estimated their action boundary for reach by adjusting the distance of a small blue dot on the virtual table until they felt it was just within their reach. Lin et al. found that when participants were given the long virtual arm their estimates of maximum reach were significantly further than when they were given the short virtual arm, while estimates of reach with the virtual arm that changed size randomly were between those two conditions. Therefore, when it comes to reaching, people are very capable of updating their perceptions of their action boundaries in line with visual feedback specifying their arm length.

Similar results have been found with grasping (Readman et al., 2021). In one experiment, participants performed a simple calibration task in which they placed their dominant hand's thumb on one small circle and placed their little finger on the other small circle in a pair of circles placed parallel to each other. Participants were either given a large virtual hand (50% larger than the standard virtual hand), a normal virtual hand (the standard virtual hand size), a small virtual hand (50% smaller than the standard virtual hand), or a virtual hand that changed size randomly (variable hand) between calibration trials. This calibration continued for 30 trials in which the distance of each circle from each other within the pair varied for each trial. After gaining the necessary synchronous visual motor experience to understand the action boundary for grasp associated with each virtual hand, participants then completed an estimation task. In this task, participants envisioned using a power grasp and adjusted the size of a white virtual block until they felt it was the maximum size they could grasp. Like Lin et al. (2020), Readman et al. found that estimates of grasp for the large virtual hand were significantly larger than for both the normal virtual hand and the small virtual hand. Estimates using the variable hand were larger than for the small hand and smaller than for the large virtual hand but did not differ significantly from the normal hand. Thus, Readman et al. demonstrate that individuals can readily calibrate to different sizes of virtual hands and consider changes to their morphology when estimating their action boundaries for grasping.

Overall, various studies demonstrate the efficacy of VR as a tool for exploring the role of one's morphology on their perceptions of their action capabilities. More specifically, they outline how people can readily embody virtual hands and consider visually specified changes to their body in their estimates of their action boundaries. If people adjust their perceptions of their action boundaries based on changes to a virtual hand's size, it raises the question of whether the inherent perceptual biases RHIs experience can also be manipulated using a similar methodology. That is, if the perceptually larger right hand is presented during movement of the left hand, will RHIs update their perceptions of their action boundaries in line with the perception that the right hand is larger?

1.9 Conclusion and Thesis Objectives

In summary, RHIs possess various biases that facilitate more skilled use and a greater preference for the right hand. Many of these biases have a cortical component, with evidence of greater representation of the right hand in left motor cortex than the left hand in right motor cortex. This greater right hand representation may have direct perceptual consequences in that RHIs visually perceive their right hand and arm to be physically larger than their left. Additionally, the left hemisphere may be more efficient at processing sensory – specifically visual – feedback from movement of the right hand, allowing for better correction when completing complex tasks. Overall, both visual and non-visual factors seem to underlie the strong right-hand preference in RHIs.

The primary aim of this thesis is to explore the degree to which visual feedback specifying hand use may alter RHIs' perceptions of their action capabilities. In doing so, I can investigate whether visual biases favouring the right hand play a significant role in the right-hand preference consistently demonstrated by RHIs. To do this, I will use VR to isolate the visual feedback associated with moving one hand from other types of sensory experience one would experience. That is, moving the left hand would provide the visual feedback normally reserved for moving the right hand, while retaining proprioceptive feedback from the left hand.

Chapter 2 will report three VR affordance experiments in which RHIs' perceptions of their maximum grasping and reaching ability are assessed. This experiment will differentiate between the impact of the real hand versus the visually specified hand on estimates of maximum grasp and reach, providing insight into whether the visual biases described in this review contribute significantly to RHIs' perceptions that their right hand is more capable than their left.

Chapter 3 will report four VR experiments that explore whether people are capable of calibrating to virtual hands when they are mirrored. These studies will provide further insight into the results of the previous affordance studies by determining whether people can calibrate to visually specified changes to hand size if the location of the virtual hand is not congruent to the physical hand being moved.

Chapter 4 will report a VR experiment that explores whether the right hand advantage in interacting with objects embedded within visual illusions can be utilised by the left hand.

More specifically, this experiment seeks to find out if the left hand can use the more efficient visual processing normally associated with the right side of the body when performing precision grasps towards objects embedded in the Ebbinghaus illusion. Chapter 4 will also report a follow-up study in which differences in interacting with visual illusions between VR and the real world are explored.

Finally, chapter 5 will provide an overview of the key findings of the empirical studies reported throughout the thesis. Implications of these findings on previous research into RHI perceptual biases will be discussed, as well as directions for future research.

Chapter 2

The Influence of Body Side on Estimates of Grasp and Reach

Previous research exploring the perceptions of action capabilities in RHIs has found that RHIs estimate that they can grasp significantly larger objects and reach significantly further distances using their right hand and arm than their left. This pattern of action estimates in RHIs may be a consequence of the perceptual distortion that the right hand and arm are visually larger than the left. The aim of the following three studies was to see whether visual feedback specifying handedness could impact RHIs' perceptions of their grasping and reaching capabilities. That is, if movement of the left hand is presented as the visually larger right hand, will RHIs estimate their action capabilities with this mirrored left hand to be greater than when the left hand is presented normally? Alternatively, if these biases are not enhanced by visual feedback, we would expect that estimates using the left arm would be lower than the right regardless of the visual presentation of the hands.

Can the Left Hand Benefit from Being Right? The Influence of Body Side on Perceived Grasping Ability

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Study materials and data used in analysis are publicly available on the Open Science Framework: https://osf.io/nsg8r/. Study analysis code is not available.

Abstract

Right-handed individuals (RHIs) demonstrate perceptual biases towards their right hand, estimating it to be larger and longer than their left. In addition, RHIs estimate that they can grasp larger objects with their right hand than their left. This study investigated whether visual information specifying handedness enhances biases in RHIs' perceptions of their action capabilities. Twenty-two participants were placed in an immersive virtual environment in which self-animated, virtual hands were either presented congruently to their physical hand or mirrored. Following a calibration task, participants estimated their maximum grasp size by adjusting the size of a virtual block until it reached the largest size they thought they could grasp. The results showed that, consistent with research outside of virtual reality, RHIs gave larger estimates of maximum grasp when using their right physical hand than their left. However, this difference remained regardless of how the hand was virtually presented. This finding suggests that proprioceptive feedback may be more important than visual feedback when estimating maximum grasp. In addition, visual feedback on handedness does not appear to enhance biases in perceptions of maximum grasp with the right hand. Considerations for further research into the embodiment of mirrored virtual limbs are discussed.

Keywords: right-handed individuals, grasp ability, virtual reality, mirror visual feedback

Public Significance Statement – Results of this study revealed that right-handed people estimate that they have significantly larger maximum grasp ability with their right hand than their left. This perception remains stable, regardless of visual feedback specifying which hand is being used. This study provides insight into the perceptual biases that right-handed people experience towards their right hand.

Can the Left Hand Benefit from Being Right? The Influence of Body Side on Perceived Grasping Ability

Right-handed individuals (RHIs) demonstrate a consistent preference for their right hand in most unimanual tasks, even in instances where using their left hand would be more biomechanically efficient (Bryden et al., 2003). For example, RHIs will opt to use their right hand more often than their left even when reaching into the left side of space (Gonzalez et al., 2007). Moreover, RHIs show a strong right hand preference for picking up various objects such as geometric 3D shapes (Gabbard et al., 2003), tools (Mamolo et al., 2004; Mamolo et al., 2006) and blocks (Gonzalez et al., 2007; Stone et al., 2013; Netelenbos & Gonzalez, 2015). Various factors may underlie this strong right hand preference in RHIs, including differences in cortical representation of the right hand, subsequent perceptual biases that favour the right side of the body, and processing of sensory feedback from moving the right arm.

Various studies provide evidence that RHIs have asymmetries in the cortical representation of their left and right hands. For example, Jung et al. (2003) reported enlarged hand representation in the left somatosensory cortex compared to right somatosensory cortex in RHIs. Furthermore, RHIs demonstrate greater cortical representation of the right hand in the left motor cortex compared to the left hand in right motor cortex (Amunts et al., 1996; Volkmann et al., 1998), and the threshold for muscle activation in the right arm is lower than that for the left, indicating greater excitability of the left motor cortex (Triggs et al., 1999). Left-handed individuals (LHIs), however, do not exhibit similar asymmetries in the representation of their left hand (Amunts et al., 1996; Sörös et al., 1999).

These cortical asymmetries correlate to RHIs' perceptions of the size of their left and right hands (Linkenauger et al., 2009). Linkenauger et al. asked both RHIs and LHIs to estimate the size and length of their hands and arms by visually matching them to the length of a tape measure. RHIs underestimated the length and size of their left arm and hand whilst the right was perceived accurately. LHIs estimated both of their arms and hands to be the same size and length, suggesting that the perception that the right hand is larger in RHIs is rooted in the enlarged sensorimotor representation of the right hand (Coelho et al., 2016; Linkenauger et al., 2009). If RHIs perceive their right hand as being visually larger, it may follow that RHIs also estimate their capabilities with their right hand to be greater than their left for actions where hand size is relevant.

How we perceive our opportunities for action (also known as ‘affordances’, Gibson, 1979) depends on how our morphology limits the extent to which an action can be performed, with the maximum extent known as an ‘action boundary’ (Fajen, 2005). While our actual morphology is important, what may also be important is our perception of our morphology. Indeed, Linkenauger et al. (2009) explored RHIs’ estimates of their action boundaries with each hand for reaching and grasping. They found that RHIs overestimated the maximum extent of reach and the maximum size of an object they could grasp more with their right hand than their left. As with perceptions of hand size, LHIs did not demonstrate any asymmetry in the perception of maximum reach with either arm. Linkenauger et al. argue that the exaggerated perception of the right hand in RHIs is adaptive in that it encourages greater use of the right hand than the left. Therefore, the strong right hand preference RHIs exhibit may be attributed to the perception that the right hand is visually larger than the left and thus has greater capabilities.

Another factor that promotes greater use of the right hand in RHIs may lie in better processing of somatosensory feedback from moving the right hand (Flowers, 1975). Flowers suggests that differences in skill between the preferred hand and non-preferred hand is primarily due to a more efficient sensorimotor feedback loop in which sensory feedback is transmitted back to the motor system to correct movement. This theory has been extended to focus specifically on processing of visual feedback from movement. That is, the left hemisphere may be better able to process visual feedback obtained from visually guided actions performed with the right hand (Flindall et al., 2013, 2015). However, it is important to note that the sensory feedback referred to by Flowers (1975) is not just limited to vision, but instead refers to sensory feedback from any source such as proprioception (Carson et al., 1990). Some evidence suggests that the right hand advantage in actions, such as reach-to-point, persists even without vision (Roy et al., 1994). Therefore, it is questionable whether visual feedback plays a role in the asymmetry in performance between the left and right hands in RHIs.

A key question here, then, is whether the biases in perception of RHIs' action capabilities are enhanced by visual factors. Linkenauger et al. (2009) find that the perception that the right hand and arm is larger in RHIs coincides with greater estimations of reach and grasp. This perception of having greater action capabilities may be reinforced by more efficient visuomotor feedback during visually guided actions that allows the right hand to perform more skilled movements. However, biases in the perception of hand size arguably originate from cortical asymmetries in hand representation. Similarly, the right hand's greater skill in various actions may also be rooted in hemispheric asymmetries in which sensory feedback aside from vision from the right arm is processed more efficiently. It is possible, therefore, that the relationship between the perception of larger right hand size and greater action capabilities is not that larger right hand size leads to estimates of greater capability. Rather, greater capabilities with the right hand lead to the perception that the right hand is larger in RHIs. If this is the case, visual feedback on the hand being used would not sufficiently explain differences in estimates of RHIs' action boundaries between the left and the right hands. Thus, the main question is whether visual feedback on handedness alone is sufficient to alter one's perceptions of their action capabilities.

Previous researching exploring perceptions of maximum grasp has found that manipulating the visual feedback associated with moving the hands can change people's perceptions of their abilities. For example, magnifying the real hand to increase its visual size can lead to the perception that larger objects can be grasped (Linkenauger et al., 2011). In addition, Readman et al. (2021) found that calibrating people to a large virtual hand led to larger estimates of maximum grasp than when they were calibrated to a small virtual hand. Thus, manipulating the visual sizes of the hands using VR can elicit changes in action perception. One key question is whether manipulating visual feedback specifying the hand being used can exploit pre-existing biases in hand size, rather than actively changing hand size in a dramatic manner.

To explore whether visual feedback of handedness enhances right handed biases in action perception, we used virtual reality (VR) to isolate visual feedback from other types of sensory feedback that would normally be experienced when moving the hand. We placed RHIs in a virtual environment (VE) with hand tracking sensors and mirrored the hands, so that when the participant's left hand moved an animation of the right hand would be shown in the virtual environment. We then took participants' estimates of their maximum grip size by adjusting the length of a virtual white block until it reached the perceived maximum size that they could grasp. There were two key hypotheses for this study. First, participants will give significantly larger estimates of grip when estimating with their right hand than their left, in line with previous research done outside of VR. Second, when the hand is animated as the right in the virtual environment, if visual feedback of handedness is sufficient to elicit right-hand biases, estimates of maximum grip will be larger than when the hand is animated as the left in the virtual environment.

Methods

Transparency and Openness

The study design, hypotheses and analysis plan were not preregistered. We report how we determined our sample size, all data exclusions (if any), all manipulations and all measures in the study. Data were analysed using SPSS version 28.0. Analysis code is not available as SPSS does not have the functionality to export syntax. Data and study materials are publicly available on the Open Science Framework: https://osf.io/nsg8r/.

Participants

We recruited 22 right-handed (16 female, 4 male, 2 prefer not to say) and 3 mixed-handed (2 female, 1 male) individuals from Lancaster University (age range: 18-21 years, *M* = 18.84, *SD* = 1.4). This sample size was chosen because Linkenauger et al. (2009) used a sample of 15 right-handed participants in a similar grasping estimate study and found a strong effect of hand (η_p^2 = .25). However, due to technical issues with the head-mounted display, three participants could not complete the full study.

Therefore, the final sample was 19 right-handed (14 female, 3 male, 2 prefer not to say) and 3 mixed-handed (2 female, 1 male, with laterality scores ranging from +20 to +58.35) individuals from Lancaster University (age range: 18-21 years, *M* = 18.68, *SD* = .95). Sensitivity power analysis using MorePower 6.0.4 (Campbell & Thompson, 2012) with the final sample of 22 was conducted, which shows that a repeated measures ANOVA with three factors would be sensitive enough to detect an effect size of $\eta_p^2 = .29$ ($\alpha = .05$, power = .8).

Handedness was assessed using the 10-item Edinburgh Handedness Inventory (Oldfield, 1971), with scores > +60 being assigned as right-handed, scores between +59 to -59 being assigned as mixed-handed, and scores < -60 being assigned as left-handed. The mixed-handed individuals were recruited as they all stated a strong right-hand preference for writing, with writing being a key predictor of handedness (Bryden, 1977; Rigal, 1992). Participants were recruited from Lancaster University SONA system and were awarded 2 credits as part of their undergraduate psychology course. All participants first gave written informed consent before participating. Data was collected February 2022.

Materials

For descriptions of specific objects in the virtual environment, it is difficult to give exact real-world dimensions as Unity Version 2021.1.24f1 (Unity Technologies, San Fransisco, California, United States) uses unique scaling. However, it is a standard assumption in Unity that 1 unit in Unity is equal to 1 real-world metre (Unity Technologies, 2018).

Virtual Environment

Participants wore an Oculus CV1 virtual reality (VR) headset which placed participants in a virtual environment (VE) that consisted of a wooden table (70cm height, 3m length) in a plain room with three grey walls and a light wooden floor. During the calibration phase, a pair of small red circles called 'calibration dots' (2cm in diameter, 2cm in depth) were placed on top of the virtual table to the left, right or centre of the participant. In the estimation phase, a white block (6cm, 8cm, 10cm, 12cm, 14cm or 16cm in length, 5cm in length and 5cm in depth) was placed 20cm away from the participant on the virtual table. Eye height was standardised for all participants at 46cm from the virtual table, with participants placed 8cm away from the virtual table. A LEAP motion sensor was attached to the front of the headset that tracked participants' hand movements in real time. Hand movements were animated using Leap Motion 'capsule hand' models (Leap Motion, Inc., San Francisco, California, United States). These hand models are white with small, coloured spheres indicating the position of different joints in the hand and wrist (see Figure 1). The capsule hands were used because more realistic hand models we had tested became distorted when we attempted to mirror them. Therefore, these simplistic hands were the best option to ensure participants could accurately move the virtual hand.

Design

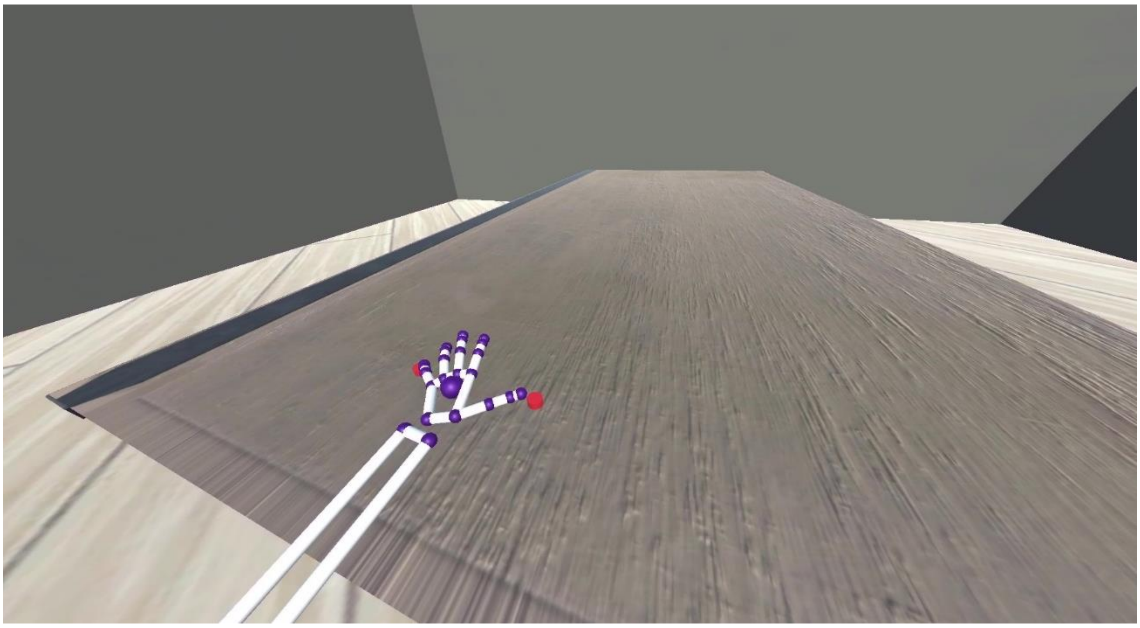
This was a 2 x 2 x 6 within-subjects design. There were three factors: first was the physical hand used during the calibration (right vs left); second was the virtual hand presented during the calibration (right versus left); third was the starting size of the white block during the estimation trials. We varied starting size to control for hysteresis (6cm, 8cm, 10cm, 12cm, 14cm or 16cm). Hysteresis is a phenomenon in which what is perceived depends on recent sensory experiences and can therefore affect future judgements (You et al., 2011). By varying starting size, we ensure that participants are completing the task properly and not simply repeating the same estimates over and over again, as we would expect that larger block sizes would elicit larger estimations of grasp based on hysteresis. The dependent measure was the maximum estimated grip, as measured by the final length of the white block after adjustment.

Procedure

This study received ethical approval from the Faculty of Science and Technology ethics committee at Lancaster University. Participants sat at a table with their chair pushed back against the wall so that they would not accidentally hit the table during the calibration. Before being placed in the virtual environment for each condition, participants were told which physical hand to use and whether the visual feedback would be normal or mirrored. After being placed in the virtual environment, participants first completed a calibration phase consisting of 60 trials. During the calibration, participants were instructed to stretch their hand out so that their thumb and little finger were each touching one of two red calibration dots positioned on the table (see Figure 1) and to follow the calibration dots as they changed position. The positions of the calibration dots were presented in a randomised order (see Appendix for exact positions of the calibration dots). When the right virtual hand was used, the calibration dots were situated from the right to the centre of the participant. When the left virtual hand was used, the calibration dots were situated from the centre to the left of the participant. This was so that participants did not need to reach across their body and strain to reach the calibration dots. The calibration lasted between 5-7 minutes, with the mirrored calibration trials often taking longer than the non-mirrored trials due to the visuomotor adjustment needed to control the virtual hand.

Figure 1

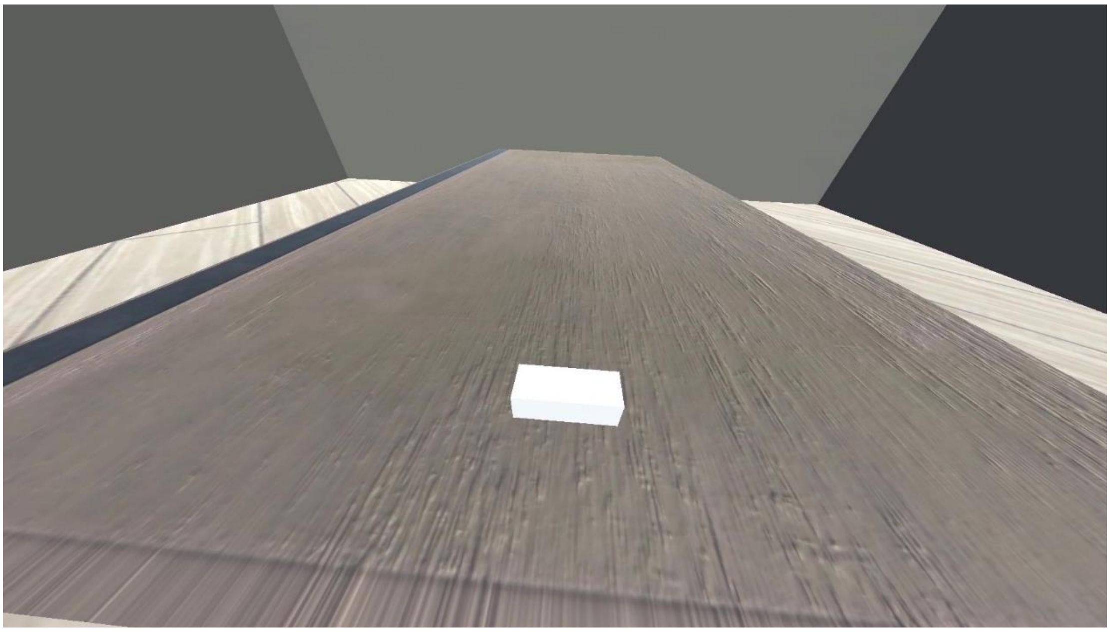
One of the Calibration Trials, as Shown when Using the Left Virtual Hand



After the calibration, participants were instructed to keep their hand in their lap so that they no longer received visual feedback from the virtual hand during the estimation phase. Then, the white block appeared on the table in front of the participant (see Figure 2). The researcher increased or decreased the white block's length by 1mm – using the left and right arrow keys on the computer – until the participant verbally stated that the length of the white block was at the maximum width that they could grip from the top using the thumb and index finger of the actual hand they had been moving throughout the calibration phase. Participants could also state that the block was fine as-is. The final size of the white block after adjustment was saved after each trial. The estimation phase lasted 12 trials, with 2 trials per starting length presented in a randomised order. This procedure was repeated four times, once for each condition. Overall, the study (with all four conditions) took around 30 minutes to complete.

Figure 2

One of the White Blocks used in the Estimation Trials



Results

We conducted repeated-measure analyses of variance (ANOVAs) on the final sample of 22 to test our key hypotheses. For all one degree-of-freedom tests, we report both p values and Bayes factors. Bayes factors are a continuous measure of relative evidence, calculated as the ratio of the probability of the data under one hypothesis (e.g., the experimental hypothesis

[H1]) to the probability of the data under another hypothesis (e.g., the null hypothesis [H0]). We used the Dienes and McLatchie (2018) R script calculator to calculate Bayes factors, and we provide robustness regions (RR) to indicate the range of effect sizes that support our conclusions.

We interpret Bayes factors greater than 3 and 10 as moderate and strong evidence, respectively, in support of the experimental hypothesis, and Bayes factors less than .33 and .10 as moderate and strong evidence, respectively, in support of the null hypothesis. Bayes factors between .33 and 3 are considered to provide weak or inconclusive evidence. Please note that these thresholds are provided to aid interpretation and transparency in decision-making, but the Bayes factor itself is a continuous measure. For further discussion and comparison of Bayes factors and p values, see Lakens et al. (2018).

A within-subjects ANOVA was conducted with actual hand (right vs left), virtual hand presented (right versus left) and white block starting length (6cm, 8cm, 10cm, 12cm, 14cm or 16cm) as the independent variables and *maximum* grip estimate (as measured by the length of the block after adjustment) as the dependent variable. There was a main effect of actual hand used, $F(1, 21) = 13.02$, $p = .002$, $\eta_p^2 = .38$, $B_{H(0,2.64)} = 54.05$, *RR[0.04,47.30[1]],* with participants giving significantly larger estimates of maximum grasp with their right hand ($M = 10.95$cm, $SD = 1.7$cm) than their left hand ($M = 10.56$cm, $SD = 1.63$cm; see Figure 3) and Bayes factors providing strong support for H1. There was also a main effect of starting length, $F(2.127, 44.67) = 37.61$, $p <.001$, $\eta_p^2 = .64$, with mean estimates of grasp increasing as starting length increased (see Figure 4). However, there was no main effect of virtual hand

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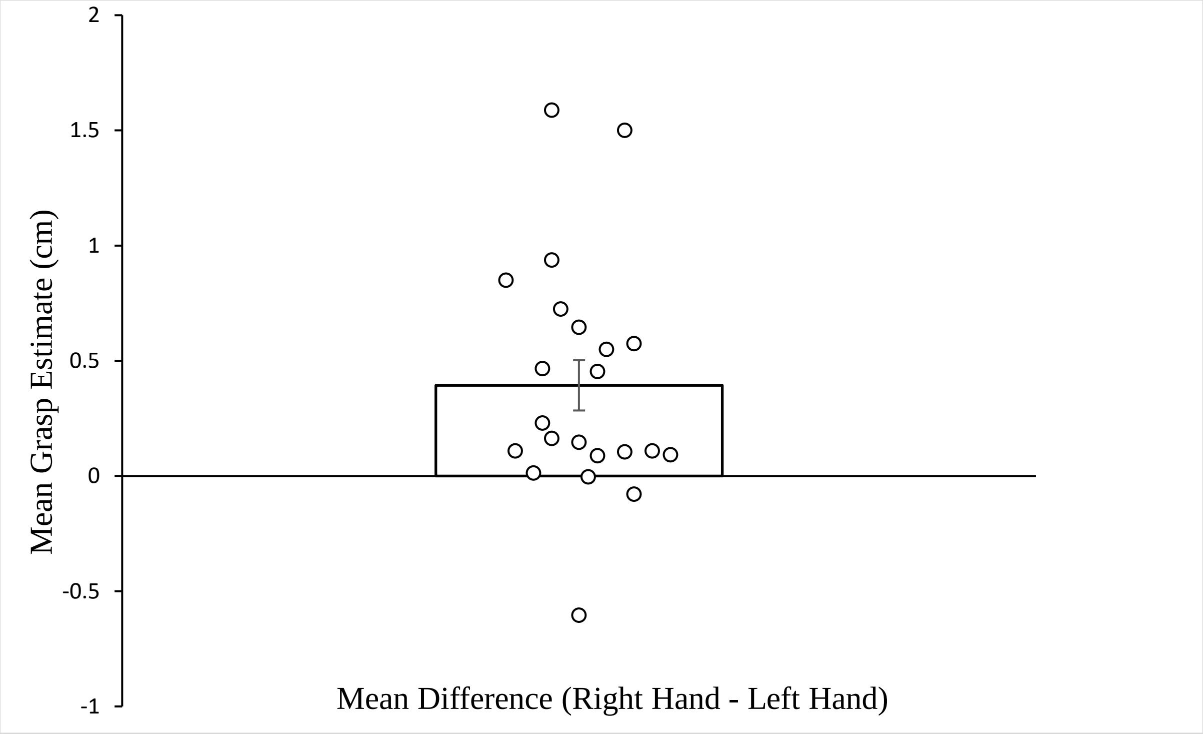
[1] H1 was specified assuming that a difference of 50% in perceived grasp would constitute an upper limit in terms of an approximate effect size. As the left hand was estimated by participants to be 10.56cm, this leads to an upper limit expected effect size of 5.28. Following Dienes (2011) we assumed a half normal prior distribution with a SD of 5.28 / 2 = 2.64.

[2] H1 was specified using the obtained mean difference from the actual hand data, 10.95 - 10.56 = 0.39, to provide an approximate scale of effect for the main effect of hand and for the interaction between the real hand and virtual hand. Following Dienes (2011) we assumed a normal prior with mode = 0.39 and SD = 0.195).

presented *F*(1, 21) = .001, *p* = .98, η_p^2 = .00005, $B_{N(0,0.39)}$ = 0.19, *RR[0.28,∞]* with no significant differences in estimates of maximum grasp between the virtual right hand (*M* =10.76cm, *SD* = 1.7cm) and the virtual left hand (*M* = 10.76cm, *SD* = 1.66cm), with the Bayes factor indicating moderate evidence for H0. There were no significant interactions between the real hand and virtual hand (*F*(1, 21) = 0.48, *p* = .49, η_p^2 = .02), $B_{N(0,0.39)}$ = 1.20, *RR[0,1.61²]*, the real hand and block starting length (*F*(5, 105) = 0.54, *p* = .75, η_p^2 = .03), the virtual hand and block starting length (*F*(3.083, 64.73) = 1.16, *p* = .52, η_p^2 = .05) nor real hand, virtual hand and block starting length (*F*(5, 105) = .81, *p* = .55, η_p^2 = .04).

Figure 3

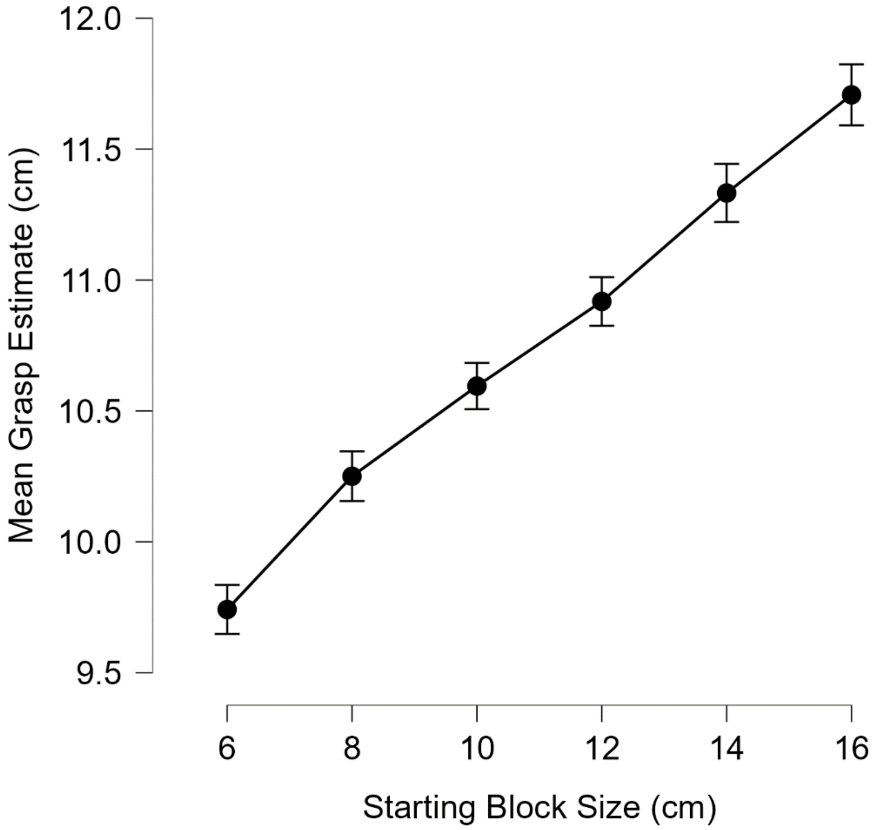
Mean Difference in Grasping Estimates between the Left and Right Hand



Note. Error bar represents standard error. Circles represent the mean difference in grasping estimates for each participant.

Figure 4

Mean Grasp Estimates as a Function of Block Starting Size



Note. Error bars represent standard error.

Discussion

Here, we investigated perceptions of grasping ability in a virtual environment, exploring how manipulating visual feedback specifying hand use would impact these perceptions. Firstly, we predicted that participants would give larger estimates of maximum grasp when using their right hand than their left. Secondly, we predicted that, if visual feedback on handedness significantly influences RHIs' perceptions of their action capabilities, estimates of maximum grip will be larger when the hand is animated as the right in the virtual environment.

Our results support the first hypothesis, as mean estimates of maximum grip size were significantly larger in the right hand conditions than in the left hand conditions and Bayes factors provide very strong support for H1. This finding replicates similar research conducted outside of VR (Linkenauger et al., 2009). However, we found no evidence that the visual presentation of the hand impacts maximum grip estimates, as we found was no evidence for a significant difference between estimates made after right virtual hand presentation or left virtual hand presentation, and with Bayes factors providing moderate evidence for H0. Finally, we found that as the size of the white block increased, mean maximum estimates of grip size did indeed increase, which is indicative of hysteresis. That is, participants' judgements of maximum grip were impacted by the initial presentation of block size.

Previous research demonstrates that the perceived action boundary for grasping can be manipulated through adjusting visual information on hand size (Linkenauger et al., 2011; Readman et al., 2021). Thus, it is possible for people adjust their perceptions of their action boundaries after visually manipulating the relevant body part for the action. However, manipulating the visually specified hand during the calibration did not lead to any adjustment of perceptions of maximum grasp ability in this study. Since participants estimated that they could grasp significantly larger objects using their right hand in a similar manner to real-world studies (see Linkenauger et al., 2009), this suggests that participants may have primarily used proprioceptive feedback specifying the hand being used during the calibration when estimating their maximum grasp ability, rather than offline visual models of the hands.

One reason for this could be that estimating one's action capabilities may involve the use of internal motor simulation (Witt & Profitt, 2008). Motor simulation theory (MST) suggests that all action involves a covert stage before motor execution (ME) (Jeannerod, 2001). This covert stage shares the same mechanisms as actual action, with neural activation in motor imagery (MI) overlapping with that seen in an executed action (O'Shea & Moran, 2017). A wide range of neurophysiological evidence supports this view, with MI and ME sharing brain regions such as pre-motor cortex, primary motor cortex and supplementary motor area, although neural activation is generally weaker during MI (see O'Shea & Moran, 2017 for a review). As discussed in the introduction, cortical asymmetries between the left and right hemispheres contribute to the perceptual biases towards the right side of the body in RHIs (Amunts et al., 1996; Volkmann et al., 1998). Thus, if participants were simulating the action when estimating their maximum grasp ability using their right hand, it is likely that they were employing some of the brain regions that underlie the right hand perceptual bias in RHIs. Similarly, when estimating using their left hand, the lower degree of cortical representation in these motor areas would also play a role in their estimates. Therefore, the mirrored visual feedback experienced during the calibration would not alter estimations of maximum grip because during the estimation task there is a reliance on cortical structures involved in motor imagery rather than visual feedback.

An alternative explanation as to why visually manipulating the seen hand during the calibration did not significantly impact estimates of maximum grasp is that the effect of real hand found in previous research (Linkenauger et al., 2009) cannot be accounted for by the visual perception of the hands. That is, RHIs perceiving their right hand as larger does not in turn lead to estimates of greater grasping ability. Rather, a perception of greater capabilities with the right hand drives the visual bias that the right hand is larger. Since the left hand does not possess the same level of skill and dexterity as the right in RHIs, this discrepancy in skill would lead to lower estimates of one's action capabilities regardless of whether it took on the visual appearance of the 'larger' right hand. Moreover, since the visual perception that the right hand is larger may also be a consequence of enlarged sensorimotor representation in the left hemisphere (Amunts et al., 1996; Volkmann et al., 1998), it is possible that participants did not retain the visual perception that the right hand was larger when the left hand was controlling it. Thus, for the right hand to be perceived as visually larger it must be paired with both the greater skill and enlarged somatosensory representation of the physical right hand.

Whether participants embodied the mirrored virtual hands well enough to consider them in their estimates is an important question. Research exploring illusions of body ownership over virtual limbs highlights the importance of congruent cross-modal multisensory stimulation between the real and virtual body (Kokkinara & Slater, 2014; Sanchez-Vives et al., 2010; Slater et al., 2008). The visuo-proprioceptive mismatch during the mirrored calibration could disrupt embodiment of the virtual limb, preventing offline models of hand representation from changing in response to the altered visual feedback experienced during the calibration. However, recent research has found that embodiment of mirrored virtual hands can be achieved in healthy users, with participants having both a sense of agency and ownership over the mirrored virtual hands (Heinrich et al., 2020). While more realistic avatars can create a stronger sense of embodiment (Ogawa et al., 2019), Heinrich et al. found that the use of the unrealistic capsule hands (the same models used in our study) did not prevent a sense of embodiment from being achieved. Therefore, it is highly likely that participants embodied the virtual limbs in this study.

Overall, this study provides insight into the nature of the perceptual biases that RHIs experience towards the right side of the body. Estimates of maximum grasp ability were dependent on the actual hand being used and not the visual information specifying the hand being used. This suggests that underlying cortical and sensory representations of the right hand are what primarily underlie the perceptual biases towards the right side of the body, and that visual information about the lateralisation of the hand may not enhance this bias. Additionally, proprioceptive information on the hand being used appears to be the most important when estimating maximum grasp. However, it is possible that the effect of virtual hand size was too small to be detected by our current sample, as the sensitivity analysis suggested that we would have good power to detect a large effect size. Though the lack of significant effect of virtual hand is not believed to be down to a lack of embodiment, more research should be conducted to explore the embodiment of mirrored virtual limbs.

Constraints on Generality

As all participants in this study were healthy undergraduate university students aged between 18-21 years, it is possible that the findings would not generalise to differently aged populations, such as older adults. This is because old age is associated with reduced mobility of the hand (Holt et al., 2013), hence reduced mobility could impact estimates of maximum grasp. Additionally, all were right-handed (or mixed-handed with right-hand writing preference) and so left-handed individuals may respond differently to the manipulations in this study, since they do not experience the same perceptual biases towards the left side of their body (Linkenauger et al., 2009). The experimental stimuli are all presented in a virtual environment; however, manipulating sensory feedback in the way we have done in this study is not easily achieved in the real-world. Overall, the results of this study would best generalise to young, healthy, right-handed adults who complete the procedure within an immersive virtual environment.

Data Accessibility Statement

The program used in this study and data used in analysis are publicly available on the Open Science Framework: https://osf.io/nsg8r/. Study analysis code is not available.

References

Amunts, K., Schlaug, G., Schleicher, A., Steinmetz, H., Dabringhaus, A., Roland, P., & Zilles, K. (1996). Asymmetry in the Human Motor Cortex and Handedness. *Neuroimage*, *4*(3), 216-222. https://doi.org/10.1006/nimg.1996.0073

Bryden, M. P. (1977). Measuring handedness with questionnaires. *Neuropsychologia*, *15*(4-5), 617–624. https://doi.org/10.1016/0028-3932(77)90067-7

Campbell, J. I., & Thompson, V. A. (2012). MorePower 6.0 for anova with relational confidence intervals and bayesian analysis. *Behavior Research Methods*, *44*(4), 1255–1265. https://doi.org/10.3758/s13428-012-0186-0

Carson, R. G., Chua, R., Elliott, D., & Goodman, D. (1990). The contribution of vision to asymmetries in manual aiming. *Neuropsychologia*, *28*(11), 1215–1220. https://doi.org/10.1016/0028-3932(90)90056-t

Coelho, L., Zaninelli, G., & Gonzalez, C. (2016). A kinematic examination of hand perception. *Psychological Research*, *81*(6), 1224-1231. https://doi.org/10.1007/s00426-016-0815-9

Dienes, Z. (2011). Bayesian versus Orthodox statistics: Which side are you on? Perspectives on Psychological Science, 6(3), 274–290. https://doi.org/10.1177/1745691611406920

Dienes, Z., & Mclatchie, N. (2018). Four reasons to prefer bayesian analyses over significance testing. Psychonomic Bulletin & Review, 25(1), 207–218. https://doi.org/10.3758/s13423-017-1266-z

Fajen, B. (2005). Perceiving Possibilities for Action: On the Necessity of Calibration and Perceptual Learning for the Visual Guidance of Action. *Perception*, *34*(6), 717-740. https://doi.org/10.1068/p5405

Flindall, J. W., Doan, J. B., & Gonzalez, C. L. (2013). Manual asymmetries in the kinematics of a reach-to-grasp action. *Laterality: Asymmetries of Body, Brain and Cognition*, *19*(4), 489–507. https://doi.org/10.1080/1357650x.2013.862540

Flindall, J., Stone, K., & Gonzalez, C. (2015). Evidence for right-hand feeding biases in a left-handed population. *Laterality: Asymmetries of Body, Brain and Cognition*, *20*(3), 287-305. https://doi.org/10.1080/1357650x.2014.961472

Flowers, K. (1975). Handedness and controlled movement. *British Journal of Psychology*, *66*(1), 39–52. https://doi.org/10.1111/j.2044-8295.1975.tb01438.x

Gabbard, C., Tapia, M., & Helbig, C. (2003). Task complexity and limb selection in reaching. *International Journal of Neuroscience*, *113*(2), 143-152. https://doi.org/10.1080/00207450390161994

Gibson, J. J. (1979). The ecological approach to visual perception. Boston,MA: Houghton Mifflin

Gonzalez, C., Whitwell, R., Morrissey, B., Ganel, T., & Goodale, M. (2007). Left handedness does not extend to visually guided precision grasping. *Experimental Brain Research*, *182*(2), 275-279. https://doi.org/10.1007/s00221-007-1090-1

Heinrich, C., Cook, M., Langlotz, T., & Regenbrecht, H. (2020). My hands? importance of personalised virtual hands in a neurorehabilitation scenario. Virtual Reality, 25(2), 313–330. https://doi.org/10.1007/s10055-020-00456-4

Holt, R. J., Lefevre, A. S., Flatters, I. J., Culmer, P., Wilkie, R. M., Henson, B. W., Bingham, G. P., & Mon-Williams, M. (2013). Grasping the changes seen in older adults when reaching for objects of varied texture. *PLoS ONE, 8*(7). https://doi.org/10.1371/journal.pone.0069040

Jeannerod, M. (2001). Neural Simulation of Action: A Unifying Mechanism for Motor Cognition. *Neuroimage*, *14*(1), S103-S109. https://doi.org/10.1006/nimg.2001.0832

Jung, P., Baumgärtner, U., Bauermann, T., Magerl, W., Gawehn, J., Stoeter, P., & Treede, R. (2003). Asymmetry in the human primary somatosensory cortex and handedness. *Neuroimage*, *19*(3), 913-923. https://doi.org/10.1016/s1053-8119(03)00164-2

Kim S.G., Ashe J., Hendrich K., Ellerman J.M., Merkle H., Ugurbil K., et al. (1993). Functional magnetic resonance imaging of motor cortex: Hemispheric asymmetry and handedness. *Science, 261*, 615–617

Kokkinara, E., & Slater, M. (2014). Measuring the Effects through Time of the Influence of Visuomotor and Visuotactile Synchronous Stimulation on a Virtual Body Ownership Illusion. *Perception*, *43*(1), 43-58. https://doi.org/10.1068/p7545

Lakens, D., McLatchie, N., Isager, P. M., Scheel, A. M., & Dienes, Z. (2018). Improving inferences about null effects with Bayes factors and equivalence tests. *The Journals of Gerontology: Series B, 75*(1), 45–57. https://doi.org/10.1093/geronb/gby065

Linkenauger, S., Witt, J., Bakdash, J., Stefanucci, J., & Proffitt, D. (2009). Asymmetrical Body Perception. *Psychological Science*, *20*(11), 1373-1380. https://doi.org/10.1111/j.1467-9280.2009.02447.x

Linkenauger, S. A., Witt, J. K., & Proffitt, D. R. (2011). Taking a hands-on approach: Apparent grasping ability scales the perception of object size. *Journal of Experimental Psychology: Human Perception and Performance*, *37*(5), 1432–1441. https://doi.org/10.1037/a0024248

Mamolo, C., Roy, E., Bryden, P., & Rohr, L. (2004). The effects of skill demands and object position on the distribution of preferred hand reaches. *Brain and Cognition*, *55*(2), 349-351. https://doi.org/10.1016/j.bandc.2004.02.041

Mamolo, C., Roy, E., Rohr, L., & Bryden, P. (2006). Reaching patterns across working space: The effects of handedness, task demands, and comfort levels. *Laterality: Asymmetries of Body, Brain and Cognition*, *11*(5), 465-492. https://doi.org/10.1080/13576500600775692

Netelenbos, N., & Gonzalez, C. (2015). Is that graspable? Let your right hand be the judge. *Brain and Cognition*, *93*, 18-25. https://doi.org/10.1016/j.bandc.2014.11.003

Ogawa, N., Narumi, T., & Hirose, M. (2019). Virtual hand realism affects object size perception in body-based scaling. *2019 IEEE Conference on Virtual Reality and 3D User Interfaces (VR)*. https://doi.org/10.1109/vr.2019.8798040

O'Shea, H., & Moran, A. (2017). Does Motor Simulation Theory Explain the Cognitive Mechanisms Underlying Motor Imagery? A Critical Review. *Frontiers in Human Neuroscience*, *11*. https://doi.org/10.3389/fnhum.2017.00072

Readman, M., Cooper, D., & Linkenauger, S. (2021). It's in your hands: How variable perception affects grasping estimates in virtual reality. *Psychonomic Bulletin & Review*, *28*(4), 1202-1210. https://doi.org/10.3758/s13423-021-01916-x

Rigal, R. A. (1992). Which handedness: Preference or performance? *Perceptual and Motor Skills*, *75*(3), 851–866. https://doi.org/10.2466/pms.1992.75.3.851

Roy, E. A., Kalbfleisch, L., & Elliott, D. (1994). Kinematic analyses of manual asymmetries in visual aiming movements. *Brain and Cognition*, *24*(2), 289–295. https://doi.org/10.1006/brcg.1994.1017

Sanchez-Vives, M., Spanlang, B., Frisoli, A., Bergamasco, M., & Slater, M. (2010). Virtual Hand Illusion Induced by Visuomotor Correlations. *Plos ONE*, *5*(4), e10381. https://doi.org/10.1371/journal.pone.0010381

Slater, M., Perez-Marcos, D., Ehrsson, H., & Sanchez-Vives, M. (2008). Towards a digital body: The virtual arm illusion. *Frontiers In Human Neuroscience*, *2*. https://doi.org/10.3389/neuro.09.006.2008

Sörös P., Knecht S., Imai T., Gürtler S., Lütkenhöner B., Ringelstein E., et al. (1999). Cortical asymmetries of the human somatosensory hand representation in right- and left-handers. *Neuroscience Letters, 271*, 89–92.

Stone, K., Bryant, D., & Gonzalez, C. (2013). Hand use for grasping in a bimanual task: evidence for different roles? *Experimental Brain Research*, *224*(3), 455-467. https://doi.org/10.1007/s00221-012-3325-z

Triggs, W., Subramanium, B., & Rossi, F. (1999). Hand preference and transcranial magnetic stimulation asymmetry of cortical motor representation. *Brain Research*, *835*(2), 324-329. https://doi.org/10.1016/s0006-8993(99)01629-7

Technologies, U. (2018, April 19). Preparing assets for Unity. Unity. Retrieved January 26, 2023, from https://docs.unity3d.com/2019.3/Documentation/Manual/BestPracticeMakingBelievableVisuals1.html

Witt, J., & Proffitt, D. (2008). Action-specific influences on distance perception: A role for motor simulation. *Journal Of Experimental Psychology: Human Perception and Performance*, *34*(6), 1479-1492. https://doi.org/10.1037/a0010781

Volkmann, J., Schnitzler, A., Witte, O., & Freund, H. (1998). Handedness and Asymmetry of Hand Representation in Human Motor Cortex. *Journal of Neurophysiology*, *79*(4), 2149-2154. https://doi.org/10.1152/jn.1998.79.4.2149

You, H., Meng, Y., Huan, D., & Wang, D.-H. (2011). The neural dynamics for hysteresis in visual perception. Neurocomputing, 74(17), 3502–3508. https://doi.org/10.1016/j.neucom.2011.06.004

Appendix: Coordinates of Calibration Circles

Calibration circle 1 (x-axis)	Calibration circle 2 (x-axis)	Both calibration circles (z-axis)
.05	.22	.1
.05	.1	.1
.05	.12	.2
.05	.1	.2
.0625	.175	.1
.0625	.175	.2
.075	.25	.1
.075	.15	.2
.0875	.225	.1
.0875	.125	.2
.1	.28	.1
.1	.2	.2
.1	.28	.2
.125	.275	.1
.125	.275	.2
.15	.25	.1
.15	.25	.2
.175	.225	.1
.175	.225	.2
.2	.38	.1
.2	.3	.1
.2	.3	.1
.2	.3	.2
.2	.38	.2
.225	.375	.1
.225	.375	.2
.25	.35	.1
.25	.35	.2
.275	.325	.1
.275	.325	.2

Note. The y-axis was kept constant at .47 across all trials. For calibration trials to the left side of space, simply make the x-axis values negative.

Can the Left Hand Benefit from Being Right? The Influence of Body Side on Perceived Reaching Ability

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Data used in analysis and study materials are publicly available on the Open Science Framework: https://osf.io/ut2gh/. Study analysis code is not available.

Abstract

Right-handed individuals (RHIs) demonstrate various perceptual and visual biases to the right side of their body and space that facilitate movement of their right hand. As a result, they estimate greater capabilities using their right hand than their left – namely, that they can reach further distances using their right arm than their left. We conducted two studies investigating whether manipulating visual feedback in virtual reality to present the left hand movements as the movements from the right hand– to exploit these right-side visual biases – can influence estimates of reachability in RHIs. Participants were placed in an immersive virtual environment in which virtual hands were presented congruently to their actual hand or mirrored. After completing a calibration task, participants estimated the maximum extent of their reach using the arm they had used to calibrate without actually reaching. They either anticipated simply reaching their arm out to touch an estimation target or anticipated reaching to grasp a small block. We found that perceptions of maximum reach can vary between the real left and right hands depending on the difficulty of the task. The effect of visual feedback depended on the task being performed, with estimates in the mirrored conditions of the simple reaching task being lower than estimates in the non-mirrored conditions. Overall, the results indicate that proprioceptive feedback during the calibration phase may be more important than visual feedback when estimating maximum reach. Additionally, visual feedback may not enhance existing biases that RHIs demonstrate towards their right hand.

Keywords: right-handed individuals, reaching ability, virtual reality, mirror visual feedback

Public Significance Statement – Results of this study revealed that right-handed individuals (RHIs) estimate that they have significantly further maximum reaching ability with their right hand than their left, but only when the reaching action is paired with a more complex grasp. This study provides insight into previous research into the perceptual biases that RHIs exhibit towards their right hand. Namely, the results suggest that RHIs' perceptions of greater reaching ability are not a consequence of the visual perception that the right arm is longer. Rather, greater abilities using the right hand contribute to the bias that the right arm is longer.

Can the Left Hand Benefit from Being Right? The Influence of Body Side on Perceived Reaching Ability

Understanding the relationship between our bodies and properties of the environment is vital for accurately perceiving our opportunities for action, also known as 'affordances' (Gibson, 1979). A key aspect of our body to consider when interacting with the environment is our morphology, which provides limits on the maximum extent over which an action can be performed (also known as an 'action boundary' Fajen, 2005). For example, the act of reaching an object is contingent upon the distance between the actor and the object, the length of the actor's arm, and the posture used when reaching (Wagman et al., 2018). However, our action boundaries are not static as we can find ways to temporarily alter our morphology to complete tasks beyond what our bodies are usually capable. For example, we can use tools to increase our reaching length (Witt et al., 2005), or vary the length of virtual arms in a virtual environment (Lin & Linkenauger, 2021; Lin et al., 2020). Therefore, our perceptions of our affordances must be extremely dynamic, changing from moment-to-moment to reflect alterations in our bodies and the environment (Wagman, 2012).

Although many of these changes to our action capabilities occur in the short term, more long-term factors also influence our perceptions of how we can interact with the environment. A key example is handedness, which influences our body perception even when no artificial change has been made. Specifically, right- handed individuals (RHIs) estimate their right and arm to be significantly longer than their left even though the right and left arms are typically the same length (Linkenauger et al., 2009; Linkenauger, Witt, Bakdash, et al., 2009). As such, the perception of a longer right arm translates into RHIs estimating that they can reach farther distances with their right arm than their left when their actual reaching capabilities in right and left arm are the same (Linkenauger, Witt, Bakdash, et al., 2009). However, left-handed individuals (LHIs) do not show such perceptual asymmetries that favour their left hand, and hence, do not estimate that they can reach significantly further with their left hand than their right. Thus, the results imply that the perception of our bodies has a direct impact on the perception of our action capabilities.

Different factors underlie the asymmetric perception of the right and left hands in RHIs. Since, in most cases, the left and right arms (and hands) are typically the same length and size, these perceptual biases and strong right-hand preference likely originate from asymmetries in brain morphology (Ocklenburg et al., 2015). As sensorimotor representations of different body parts define the perception of our bodies (Coelho et al., 2016), cortical representations of each hand likely explain the difference in perception between the right and left hands. A multitude of evidence supports this view. For example, RHIs have enlarged hand representation in the left somatosensory cortex compared to the right somatosensory cortex (Kim et al, 1993; Jung et al., 2003), as well as greater cortical representation of the right hand in the left motor cortex than the left hand in right motor cortex (Amunts et al., 1996; Volkmann et al., 1998; Sörös et al., 1999). Additionally, the left motor cortex may be more excitable than the right, as the threshold for muscle activation is lower for the right arm than the left (Triggs et al., 1994; Triggs et al., 1997; Triggs et al., 1999).

In conjunction with these cortical asymmetries, RHIs demonstrate an overwhelming right-hand preference, especially when reaching. Various free-reaching tasks demonstrate that RHIs will primarily opt to use their right hand, even when reaching into contralateral space where using the left hand would be more biomechanically efficient (Gonzalez et al., 2007; Mamolo et al., 2006). This effect has been shown to be heightened by task demand with RHIs opting to using their right hand to reach contralaterally more often in more difficult reaching tasks (Gabbard et al., 2003; Mamolo et al., 2004), such as when reaching to grab and pantomime the use of a tool instead of merely picking it up (Bryden et al., 2003; Mamolo et al., 2006).

Finally, evidence suggests that a left hemisphere advantage exists for processing visually guided actions, more generally (Flindall et al., 2015; Flowers, 1975). Specifically, in a task where RHIs were required to reach and pick up a glass of water, people completed the action faster and more accurately using their right hand than their left. This advantage did not persist when participants did not have either current or recent visual information to guide them, supporting the notion that more efficient processing of visuomotor feedback from the right hand contributes to its relatively stronger performance in visually guided tasks (Flindall et al., 2013). Additionally, this finding suggests that online visual feedback from the right hand is processed more precisely than information from the left apart from the mere dexterity differences between the two hands. Hence, the left hemisphere role in visuomotor processing can explain why RHIs show such a strong right-hand preference in many reaching tasks.

Overall, RHIs possess various perceptual and visual biases that likely underlie their right-hand preference for most unilateral tasks, including reaching. One question that has not been explored is whether RHIs can utilise these perceptual and visual advantages when using the left hand if visual feedback is altered so that the left hand appears as the right hand. One reason for this possibility is that evidence has shown better processing of visual spatial information in the left cortical hemisphere which contributes to advantages in spatial perception in the right visual field (Flowers, 1975; Carson et al., 1990). More specifically, a left-hemisphere visual processing advantage would allow movement of the right hand to be processed more effectively to correct online movement (Flindall et al., 2013; Roy et al., 1986; Roy et al., 1989). If visual feedback does indeed contribute significantly to the right-hand advantage in RHIs, we may expect that allowing the left hand to utilise the same degree of visual feedback could alter RHIs perceptions of what their left arm could do. That is, RHIs would estimate their abilities using their left hand to be greater when it is presented as the right hand than when it is presented normally as the left. However, if other types of sensory feedback aside from vision are more important in the right-hand bias in RHIs, manipulating visual feedback may not be sufficient to significantly alter RHIs perceptions of their action capabilities.

To explore this question, we placed RHIs in a virtual environment (VE) and used hand-tracking to animate their virtual hand movements in this VE in real-time. We mirrored the visual feedback associated with moving each hand – that is, movement of the real left hand would be tracked and animated as movement of the virtual right hand. Using an immersive virtual environment allows participants to move their real hands freely from a first-person perspective without them being seen (with only the virtual hand being visible), ensuring that visual feedback from each hand is well controlled. Indeed, various affordance studies have demonstrated how using an immersive virtual environment to alter visual information about the arms and hands can lead to changes in estimations of action capabilities (Lin et al., 2020; Lin & Linkenauger, 2021). After calibrating to this mirrored feedback, we took participants' estimates of their maximum reachability with each arm. We conducted two different studies to explore slightly different actions involving reach.

Study 1

In this study, we explored the impact of mirroring the arms on perceptions of maximum reachability without the end goal of grasping. We had two main hypotheses for this study. Firstly, participants will estimate that they can reach significantly further with their right arm than their left, as was found in previous studies outside of VR (Linkenauger et al., 2009). Secondly, if visual feedback contributes significantly to the right-hand bias in RHIs, estimates of maximum reach will be significantly higher when the real hand is animated as the virtual right than the left in the VE.

Methods

Transparency and Openness

The study design, hypotheses and analysis plan were not preregistered. We report how we determined our sample size, all data exclusions (if any), all manipulations and all measures in the study. Data were analysed using JASP version 0.16.4.0. Analysis code is not available as JASP does not have the functionality to export syntax. Data and study materials are publicly available on the Open Science Framework: https://osf.io/ut2gh/.

Participants

A priori power analysis using MorePower 6.0 (Campbell & Thompson, 2012) was conducted with the real hand x virtual hand interaction being the key area of interest, with an effect size of $\eta_p{}^2 = .59$, an alpha of 0.05 and desired power of 0.8. The effect size is based off the effect size of the main effect of arm found in RHIs in the reaching study in Linkenauger et al. (2009), on which this study is partly based. The results revealed a minimum sample size of eight is needed to achieve a power of 0.8. Therefore, we recruited 20 right-handed (13 female, 7 male) and 2 mixed-handed (2 female) individuals from Lancaster University (age range: 20-34 years, *M* = 23.27, *SD* = 3.65). Handedness was assessed using the 10-item Edinburgh Handedness Inventory (Oldfield, 1971), with scores > +60 being assigned as right-handed, scores between +59 to -59 being assigned as mixed-handed, and scores < -60 being assigned as left-handed. The mixed-handed individuals were recruited as they all stated a strong right-hand preference for writing, with writing being a key predictor of handedness (Bryden, 1977). Participants were recruited via Lancaster University SONA system, or by posters placed around the university campus, and were paid £8.50 for their time. Data was collected in July 2022.

Materials

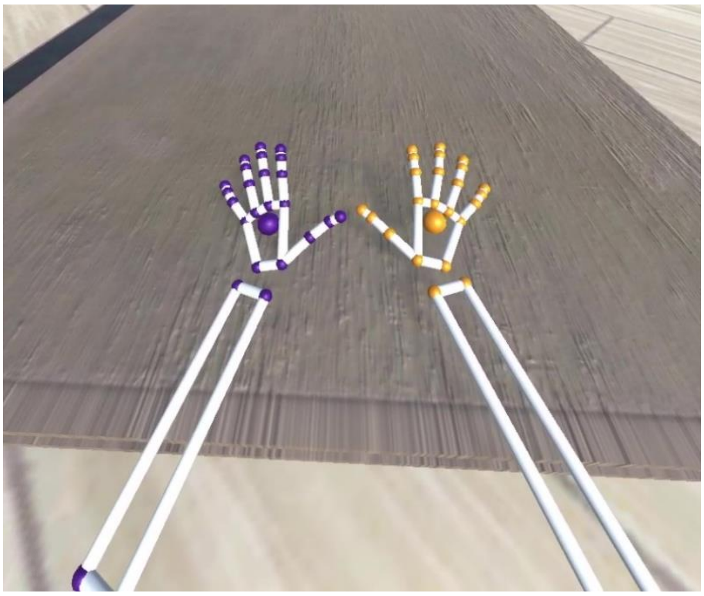
For descriptions of specific objects in the virtual environment, Unity Version 2021.1.24f1 (Unity Technologies, San Fransisco, California, United States) uses unique scaling. However, it is a standard assumption in Unity that 1 unit in Unity is equal to 1 real-world metre (Unity Technologies, 2018).

Virtual Environment

Participants wore an Oculus CV1 virtual reality (VR) headset which placed participants in a virtual environment (VE) that consisted of a wooden table (70cm height, 3m length) in a plain room with three grey walls and a light wooden floor. During the calibration phase, a single red circle called a ‘calibration dot’ (2cm in diameter, 2cm in depth) was placed on top of the virtual table to the left, right or centre of the participant. In the estimation phase, a small red circle known as the ‘estimation target’ (2cm in diameter, 2cm in depth) was placed on the virtual table 27.4cm away centrally from the participant on ‘near’ trials or centrally 90cm away or 100.6cm away to the left or right of the participant on ‘far’ trials. Eye height was standardised for all participants at 68cm from the virtual table, with participants placed 8cm away from the virtual table. A LEAP motion sensor was attached to the front of the headset that tracked participants’ hand movements in real time. Hand movements were animated using Leap Motion ‘capsule hand’ models (Leap Motion, Inc., San Francisco, California, United States). The capsule hand models are primarily white with coloured spheres indicating the positions of the different hand joints (see Figure 1). These models were used in lieu of more realistic models because realistic models become distorted and non-functional when mirrored. Therefore, these simplistic hand models ensured that participants could accurately move and perceive the virtual hand.

Figure 1

The Left and Right Leap Motion 'Capsule Hand' Models



Design

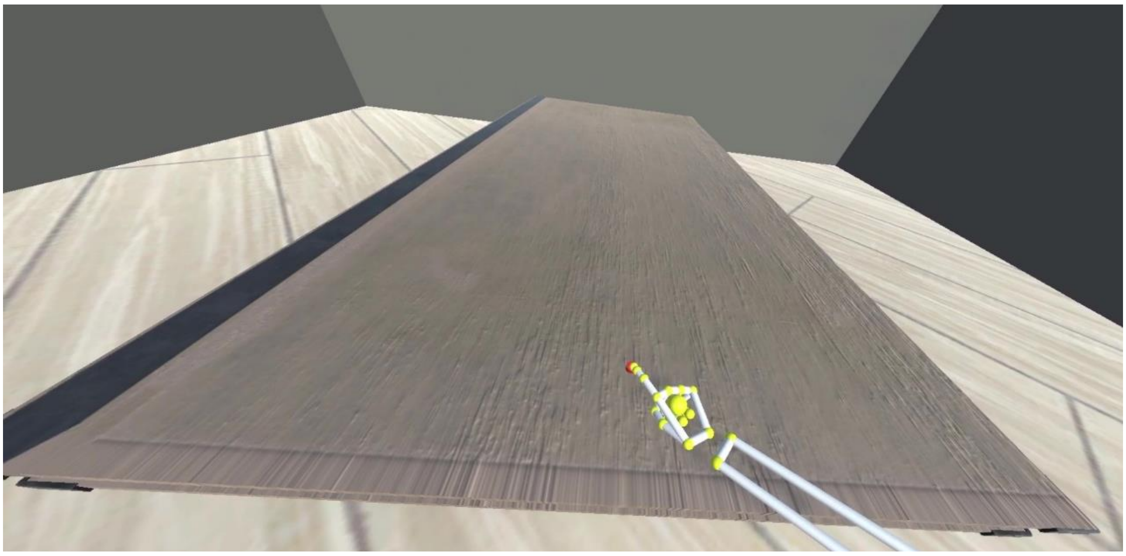
This was a 2 x 2 x 2 x 3 within-subjects design. There were four factors: first was the physical hand used during the calibration (right vs left); second was the virtual hand presented during the calibration (right vs left); third was the starting position of the estimation target used to control for hysteresis (near vs far); fourth was direction of reaching estimate (centre vs left vs right). We varied the starting position of the estimation target to control for hysteresis, a phenomenon in which our visual matching estimates of distance change based whether the starting distance is short versus long (You et al., 2011). The dependent measure was the maximum estimated reaching distance, as measured by the final position of the estimation target.

Procedure

Participants gave full informed consent before participation. Participants sat at a table with their chair pushed back against the wall so that they would not accidentally hit the table during the calibration. Before being placed in the virtual environment for each condition, participants were told which physical hand to use and whether the visual feedback would be normal or mirrored. After being placed in the virtual environment, participants first completed a calibration phase consisting of 60 trials. During the calibration, participants were instructed to use their index finger to reach and point to the calibration dot as it appeared (see Figure 2) and to follow the calibration dot as it changed position. The position of the calibration dot was presented in a randomised order (see Appendix for exact positions of the calibration dots). When the right virtual hand was used, the calibration dots were situated from the right to the centre of the participant. When the left virtual hand was used, the calibration dots were situated from the centre to the left of the participant. This was so that participants did not need to reach across their body and strain to reach the calibration dots. The calibration lasted between 5-7 minutes with the mirrored calibration trials often taking longer than the non-mirrored trials due to the visuomotor adjustment needed to control the virtual hand.

Figure 2

One of the Calibration Trials, as Shown when Using the Right Virtual Hand



After the calibration, participants were instructed to keep their hand in their lap so that they no longer received visual feedback from the virtual hand during the estimation phase. Participants were asked to estimate their maximum reaching distance by anticipating that they were simply reaching their arm out without bending or leaning forward at the hip. Then, one of the estimation dots appeared either close (on ‘near’ trials) or far away (on ‘far’ trials) from the participant on the virtual table. Participants were instructed to tell the researcher to increase or decrease the distance of the estimation target away from them until they felt that the estimation target was at the maximum distance that they could reach using the physical hand they had just used to calibrate. The researcher used the left and right arrow keys on the computer to decrease and increase the distance of the estimation target by approximately 2cm per key press. The final position of the estimation target on the virtual table was saved after each trial. The estimation phase lasted 12 trials, with 2 trials per estimation target start position presented in a randomised order. That is, participants made 4 estimates on each of the left, centre, and right axes. On each axis they made 2 estimates when the target began close and 2 estimates when the target began far away. This procedure was repeated four times, once for each condition. Overall, the study took around 30 minutes to complete. All study materials are available on the open science framework: https://osf.io/ut2gh/.

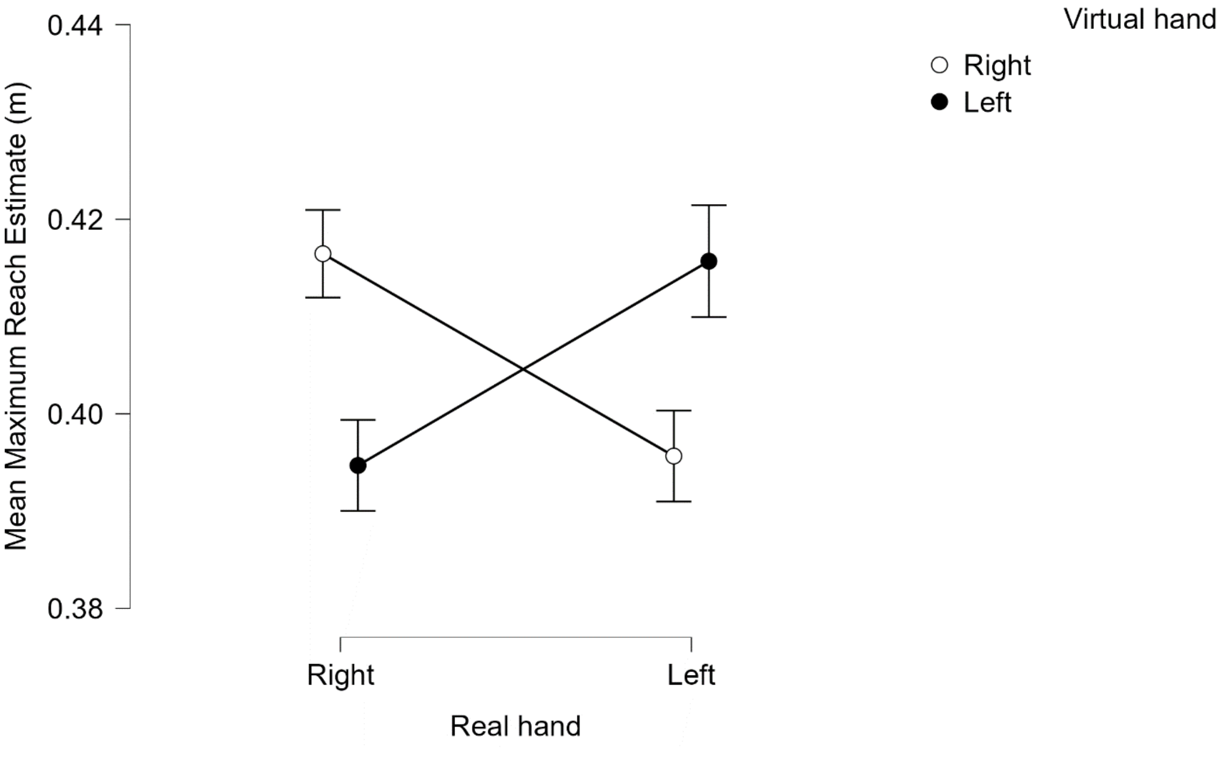
Results

A within-subjects ANOVA was conducted with actual hand (right vs left), virtual hand presented (right vs left), hysteresis (near vs far), and direction of reach (centre, left, right) as the independent variables and maximum reach estimate (as measured by the final position of the estimation target at the end of each trial) as the dependent variable. The key areas of interest are the main effect of real hand, main effect of virtual hand, and a real hand x virtual hand interaction.

There was no main effect of actual hand used, *F*(1, 21) = 0.0002, *p* = .99, η_p^2 = .000008, with no significant differences between the right (*M* = 40.6cm, *SD* = 10.9cm) and left (*M* = 40.6cm, *SD* = 11.2cm) hands. Additionally, there was no effect of virtual hand presented *F*(1, 21) = 0.01, *p* = .99, η_p^2 = .00005, with no significant differences between the virtual right (*M* = 40.6cm, *SD* = 11.2cm) and virtual left (*M* = 40.5cm, *SD* = 10.9cm) hands. However, there was a significant crossover interaction between real hand and virtual hand, *F*(1, 21) = 5.1, *p* = .04, η_p^2 = .2 (see Figure 3). Analysis of simple main effects showed that, when using the real right hand, estimates using the right virtual hand (*M* = 41.6cm, *SD* = 11.5cm) were significantly larger than estimates using the left virtual hand (*M* = 39.5cm, *SD* = 10.8cm), *t*(21) = 2.1, *p* = .048, *d* = .45. However, when using the real left hand, there were no significant differences in reach estimates using the right virtual hand (*M* = 39.6cm, *SD* = 11.4cm) and the left virtual hand (*M* = 41.6cm, *SD* = 11.9cm), *t*(21) = 1.37, *p* = .19, *d* = .29.

Figure 3

Graph Showing Real and Virtual Hand Interaction



Note. Error bars represent standard error.

Additionally, there was a main effect of hysteresis, $F(1, 21) = 4.31$, $p = .05$, $\eta_p^2 = .17$, with longer estimates of reaching distance on near trials (M = 41cm, SD = 11.2cm) than far trials (M = 40.1cm, SD = 10.7cm). There was a main effect of direction, $F(2, 42) = 18.76$, $p < .001$, $\eta_p^2 = .47$, with Bonferroni post-hoc comparisons revealing that estimates of reach towards the centre (M = 39.2cm, SD = 10.6) were significantly lower than estimates to the left (M = 41.4cm SD = 11.2cm) and to the right (M = 41.1cm, SD = 10.9cm).

Three additional significant interactions were found. First, one between hysteresis and direction, $F(2, 42) = 5.18$, $p = .01$, $\eta_p^2 = .20$. When the target started near, reach estimates to the centre were significantly lower than reach estimates to the right and to the left, with no differences between reach estimates to the right and left. When the target started far away, reach estimates to the centre were significantly lower than reach estimates to the left and right, with no significant differences between estimates to the left and right.

Second, one between actual hand and direction, $F(2, 42) = 13.4$, $p < .001$, $\eta_p^2 = .39$. When estimating with the right hand, estimates to the centre were significantly lower than estimates to the left and right. Estimates to the right were also significantly higher than estimates to the left. When estimating with the left hand, estimates to the left were significantly higher than estimates to the centre and right, with no significant differences between estimates to the centre and right.

Third, one between actual hand, hysteresis and direction $F(2, 42) = 4.10$, $p = .024$, $\eta_p^2 = .16$. When participants estimated with their right hand and the target started near, reach estimates to the right were significantly higher than estimates to the left and centre, with no differences between centre and left. When the target started far away, estimates to the centre were significantly lower than estimates to both the left and right, with no differences between left and right estimates. For the left hand, when the target started near, estimates to the left were significantly higher than estimates to the centre, with no significant differences between the centre and right and left and right. When the target started far away, estimates to the left were significantly higher than estimates to the centre and right, with no significant differences between the centre and right. However, there were no significant interactions between hysteresis and real hand $F(1, 21) = 4.03$, $p = .06$, $\eta_p{}^2 = .16$; and virtual hand and hysteresis $F(1, 21) = 0.17$, $p = .69$, $\eta_p{}^2 = .008$;

Study 2

Findings from Study 1 showed that there were no significant differences in estimates of maximum reachability between the actual left and right hands or between the left and right virtual hands. Since previous research has highlighted how RHIs prefer to use their dominant hand more often when the task is more demanding (Gabbard et al., 2003; Mamolo et al., 2004; Mamolo et al., 2006), we conducted Study 2 to establish whether estimates of maximum reachability between the left and right hands could be further influenced by an additional, more complex, grasping task. Based on the findings of Study 1, our key hypotheses for study 2 were that estimations of reach would be significantly higher with the real right hand than the left, and that there would be no significant differences in estimates of reach between the right and left virtual hands.

Methods

Participants

A priori power analysis using MorePower 6.0 (Campbell & Thompson, 2012) was conducted with the real hand x virtual hand interaction being the key area of interest, with an effect size of ηp2 = .59, an alpha of 0.05 and desired power of 0.8. The effect size is based off the effect size of the main effect of arm found in RHIs in the reaching study in Linkenauger et al. (2009), on which this study is partly based. The results revealed a minimum sample size of eight is needed to achieve a power of 0.8. Therefore, we recruited 16 right-handed (4 male, 12 female) and one mixed-handed (1 male, laterality score = 57) individuals (age range: 19-31 years, *M* = 19.29, *SD* = 3.06) from Lancaster University. Two additional participants took part in the study (one 18 year old left-handed female and one 19 year old mixed-handed female), however these participants were not considered as part of the final sample as they did not meet the criteria for handedness. Handedness was assessed using the 10-item Edinburgh Handedness Inventory (Oldfield, 1971), with scores > +60 being assigned as right-handed, scores between +59 to -59 being assigned as mixed-handed, and scores < -60 being assigned as left-handed. The mixed-handed individual in the final sample was recruited as they stated a strong right-hand preference for writing, with writing being a key predictor of handedness (Bryden, 1977). Participants were recruited via Lancaster University SONA system and were offered two credits for their time. Data was collected in March 2023.

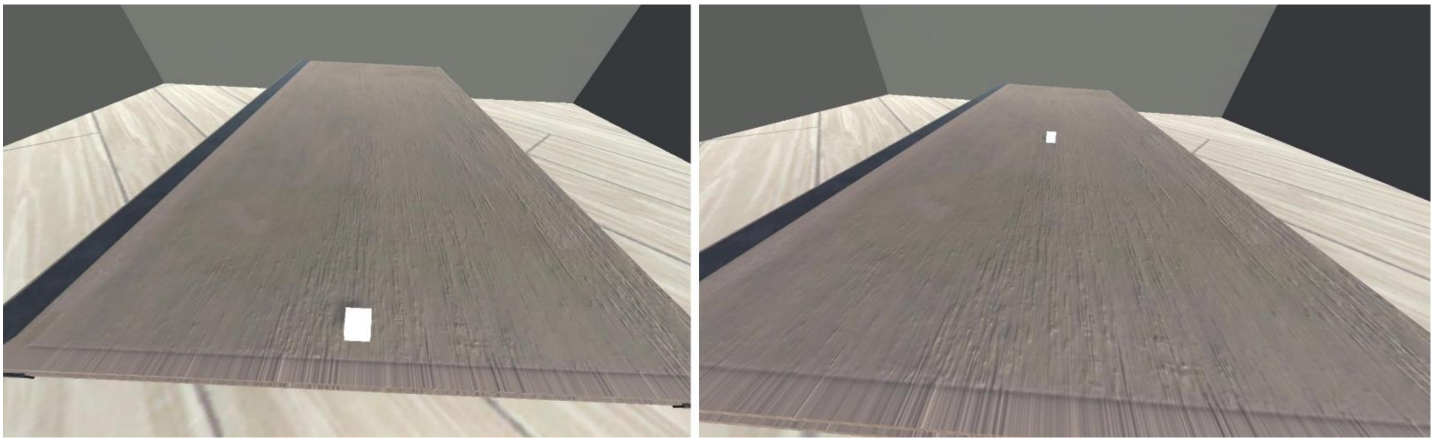
Materials

Virtual Environment

The virtual environment used in the precision reach study was almost the same as the environment used in Study 1. However, the small red circle known as the 'estimation dot' in the estimation trials was replaced by a white 'estimation box' (5 x 5 x 5 cm; see Figure 4).

Figure 4

The White Estimation Box, as Shown in 'Near' vs 'Far' Trials



Design

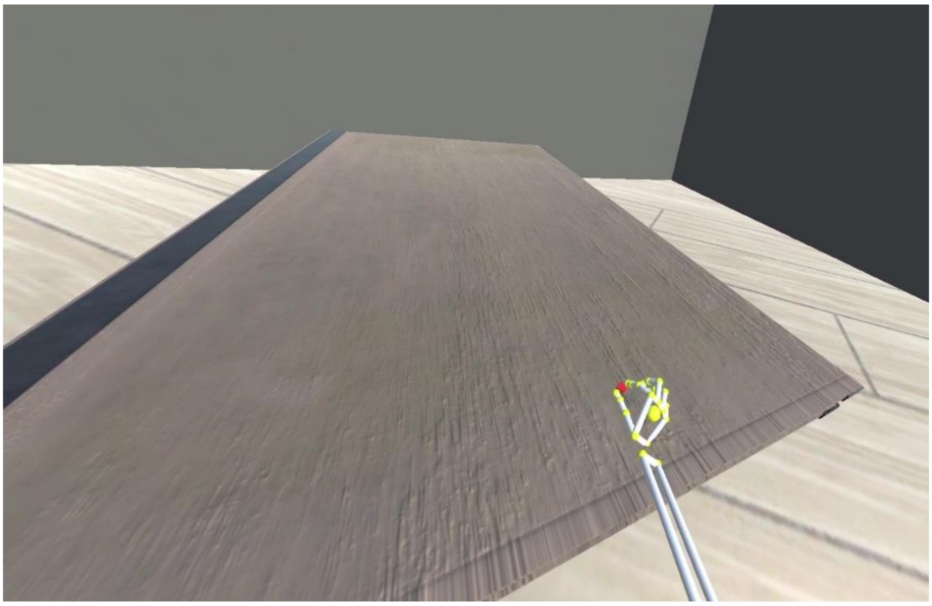
The design was identical to study 1.

Procedure

The procedure was very similar to study 1. However, there were two key differences. During the calibration, participants were required to reach and position their thumb and index finger around the calibration dot to simulate grasping it (see Figure 5). Additionally, during the estimation phase, participants were asked to estimate their maximum reaching distance by anticipating that they were attempting to reach and grasp the small white box using the thumb and index finger without bending or leaning forward at the hip. All study materials are available on the open science framework: https://osf.io/ut2gh/.

Figure 5

One of the Calibration Trials, shown using the Right Virtual Hand



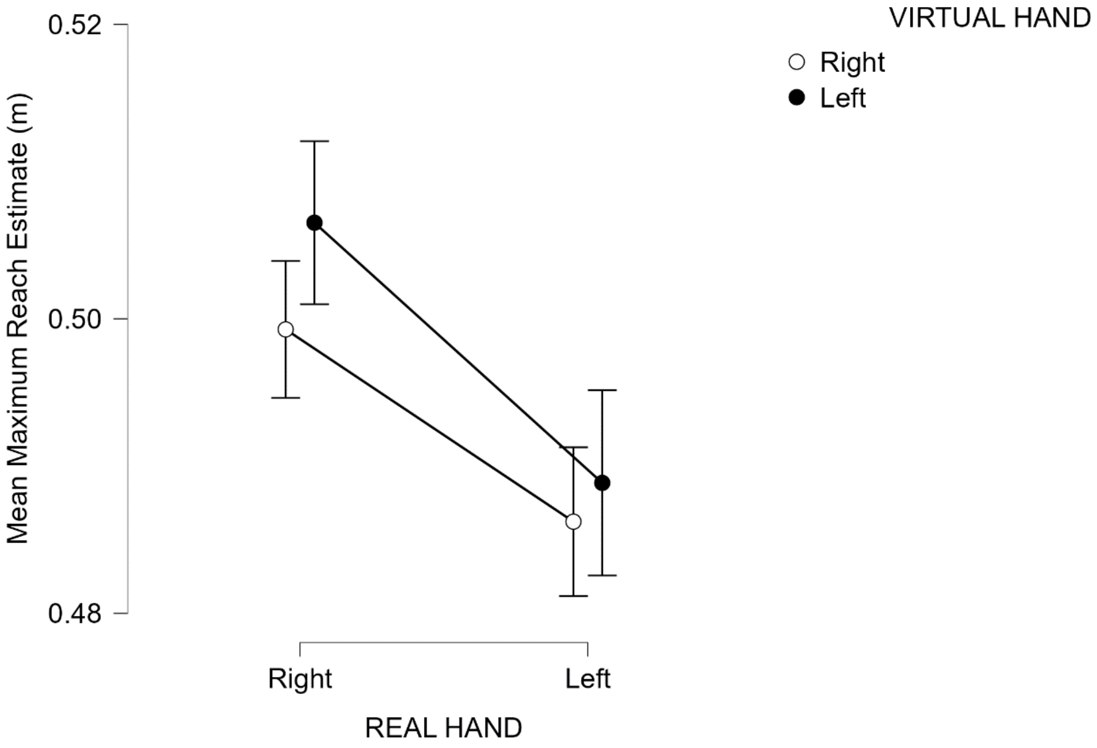
Results

A within-subjects ANOVA was conducted with actual hand (right vs left), virtual hand presented (right vs left), hysteresis (near vs far), and direction of reach (centre, left, right) as the independent variables and maximum reach estimate (as measured by the final position of the estimation block at the end of each trial) as the dependent variable. The key areas of interest are the main effect of real hand, main effect of virtual hand, and a real hand x virtual hand interaction.

There was a main effect of actual hand used, $F(1, 16) = 5.17$, $p = .037$, $\eta_p^2 = .24$, with estimates using the right hand ($M = 50.3$cm, $SD = 7.3$cm) being significantly further than the left ($M = 48.8$cm, $SD = 6.8$cm, see Figure 6). However, there was no main effect of virtual hand presented $F(1, 16) = 0.39$, $p = .54$, $\eta_p^2 = .02$, with no significant differences between the virtual right ($M = 49.3$cm, $SD = 7.3$cm) and virtual left ($M = 49.8$cm, $SD = 6.8$cm) hands. There was no significant interaction between the real and virtual hands, $F(1, 16) = .09$, $p = .76$, $\eta_p^2 = .006$.

Figure 6

Mean Maximum Reach Estimates for the Real and Virtual Right and Left Hands



Note. Error bars represent standard error.

However, there was a main effect of direction, $F(2, 32) = 12.98$, $p < .001$, $\eta_p^2 = .45$, with Bonferroni post-hoc comparisons revealing that estimates of reach towards the centre (M = 48cm, SD = 7cm) were significantly lower than estimates to the left (M = 50.5cm, SD = 6.1cm) and to the right (M = 50cm, SD = 7.9cm). There was also a significant interaction between real hand and direction, $F(2,32) = 21.14$, $p < .001$, $\eta_p^2 = .06$. When estimating reach with the real right hand, estimates to the right were significantly higher than estimates to the centre and left. Additionally, estimates to the left were significantly higher than reaches to the centre. When estimating reach with the real left hand, estimates to the left were significantly higher than estimates to the centre and right. However, there were no significant differences between estimates to the centre and to the right.

There was also a significant interaction between hysteresis and direction $F(2,32) = 11.72, p < .001, \eta_p^2 = .42$. When the target started near, estimates to the left were significantly higher than estimates to the centre, with no significant differences between estimates to the centre and right, and estimates to the left and right. When the target began far away, estimates to the centre were significantly lower than estimates to both the left and the right, with no significant differences in estimates to the left and right.

Additionally, there was no main effect of hysteresis, $F(1, 16) = .0007, p = .98, \eta_p^2 = .00004$, with no significant differences in estimates of reach between near trials ($M = 49.5$cm, $SD = 6.8$cm) and far trials ($M = 49.5$cm , $SD = 7.6$cm). There were no significant interactions between real hand and hysteresis ($F(1,16) = 1.21, p = .29, \eta_p^2 = .07$); virtual hand and hysteresis ($F(1,16) = .26, p = .62, \eta_p^2 = .02$); virtual hand and direction ($F(2,32) = .96, p = .39, \eta_p^2 = .06$); real hand, virtual hand and hysteresis ($F(1,16) = 1.57, p = .23, \eta_p^2 = .09$); real hand, virtual hand, and direction ($F(2,32) = .22, p = .80, \eta_p^2 = 0.1$); virtual hand, hysteresis, and direction ($F(2,32) = .98, p = .39, \eta_p^2 = .06$); and real hand, virtual hand, hysteresis, and direction ($F(2,32) = .61, p = .55, \eta_p^2 = .04$).

Discussion

In a set of two studies, we explored whether mirroring the presentation of the hands in a virtual environment would significantly impact RHIs perceptions of their maximum reaching ability with each hand. In Study 1, we found that when estimating the extent of a simple reaching action, there were no significant differences in estimates of maximum reach between the physical right and left hands. However, we did find that when the real and virtual hand was incongruent, estimates of reach were lower than when they were congruent. When the estimation task is adjusted so that it would require a greater level of skill to complete the action, as in Study 2, we find that RHIs estimate significantly greater capabilities using their real right hand than their left. However, there were no significant differences in reaching estimates between the right and left virtual hands. Overall, both studies provide evidence that proprioceptive laterality is more relevant when perceiving one's action boundaries for more demanding skills.

In Study 1, the lack of difference in estimates of maximum reach between the right and the left hands was surprising. Previous research has not only highlighted a perceptual bias that RHIs estimate their right arm to be longer than their left, but also that they estimate they can reach significantly further using their right hand even when simply anticipating pointing in studies outside of VR (Carello et al., 1989; Linkenauger et al., 2009). Additionally, we found that participants gave lower estimates of reach when the virtual hand was incongruent to the physical hand. Previous research shows that affordance perception can be impacted by various short-term changes to action capabilities (Smith & Pepping, 2010), such as fatigue (Bhalla & Profitt, 1999; Pijpers et al., 2007) and anxiety (Bootsma et al., 1992; Pijpers et al., 2006). It is possible that the difficulty of the mirrored calibration presented a short-term reduction in participant's normal capabilities, resulting in lower estimates of reach. Thus, mirroring visual feedback of the left hand to utilise the more efficient visual processing normally associated with the right side of the body (Flindall et al., 2013; Flindall et al., 2015) had the opposite of the intended effect by increasing the difficulty of the calibration. In contrast, in Study 2, the addition of a grasping component to the reach elicited the expected differences between the right and the left hand in RHIs. Unlike in Study 1, participants did not give lower estimates of maximum reach in the mirrored conditions. Thus, differences in the calibration task between Study 1 and Study 2 may account for this pattern of reaching estimates.

In Study 1, the calibration was a simple reach-to-point task; whereas, in Study 2 the calibration involved positioning the thumb and index finger precisely around the calibration dot to simulate grasping it. In Study 1, the more conservative estimates of reach when the real hand and virtual hand were incongruent likely reflects uncertainty of the ability of the mirrored hand due to the simple calibration task. The more complex calibration in Study 2 allowed participants to better map the movements of the actual hand to the virtual hand, generating a greater familiarity with their action capabilities within the virtual environment. Thus, participants did not experience the same degree of uncertainty when estimating the more complex reach-to-grasp action, hence why estimates of reach in Study 2 were not modulated by the congruency of the real and virtual hand. Moreover, a greater degree of calibration to the hands in Study 2 may account for the differences in reach estimates between the real right and left hands, since participants were better able to differentiate their skill level with each hand.

Differences in patterns of reaching estimates between Study 1 and Study 2 may also reflect the complexity of the estimation task itself. In Study 1, the estimation task was to simply imagine reaching the arm out. Reaching may not be a sophisticated enough action for handedness to be a relevant factor, indicating that RHIs base their perceptions of their action capabilities using their right hand on more than just the visual perception that their right arm and hand are larger. That is, the dexterity of each hand and the dexterity needed to complete a task are also key factors, especially as task complexity can influence the selection of which limb to use when picking up an object (Gabbard et al., 2003; Mamolo et al., 2004; Mamolo et al., 2006). Since simply reaching out the arm does not require a high degree of skill, it is a task that both the right and the left hands can do equally well. Indeed, various studies outlining the specialisation of the right hand in visually guided reaching tasks also include an additional component – grasping (Flindall et al., 2013; Flindall et al., 2015). Grasping is a specialised and complex action (Jeannerod, 1996), and has a higher cost-benefit ratio than simply reaching, since failure to complete the grasping portion of a reach-to-grasp action can result in dropping the target item (Readman et al., 2021). Hence, the more demanding reach-to-grasp estimation task in Study 2 differentiated the level of dexterity between the right and the left hand more than the simple estimation task in Study 1.

The main effect of real hand but non-significant effect of virtual hand in Study 2 indicates that participants were primarily relying on proprioceptive feedback during the calibration phase to direct their estimates. Previous research has demonstrated how the perceived action boundary for an array of actions can be altered through manipulating visual feedback about one's body. Notably, estimates of maximum reach can also change depending on the size of a virtual arm, with a longer virtual arm leading to significantly greater estimates of both horizontal and vertical reach (Lin et al., 2020; Lin & Linkenauger, 2021). However, in this instance, mirroring visual feedback to attempt to take advantage of pre-existing perceptual biases in hand size did not elicit significant adjustments in people's perceptions of their maximum reach. These findings suggest that the perceived right hand reaching advantage is a result of the feeling of proprioceptive movement of the right hand, not the visual perception of the hand. Thus, one could question previous assumptions that differences in visual perception of arm length result in differences in reaching perception (Linkenauger, Witt, Bakdash, et al., 2009). From these results, it is more likely that that differences in the perceived length of the right and left arm result from differences in perceived reaching ability, rather than the other way around.

Moreover, the real hand and direction interaction present in both studies provides more support for the claim that participants prioritised proprioceptive feedback over visual. Reach estimates ipsilateral to the real hand were higher than reach estimates to the centre or contralaterally. If participants calibrated to the visual location of the virtual hand, we should have expected the opposite pattern. This finding suggests that participants may not have fully calibrated to the visually changed location of the hand when it is mirrored, and instead take the visual perspective of their real hand during the estimation.

One key reason to prioritise proprioceptive feedback may be because, when estimating one’s action capabilities, a process called internal motor simulation may occur (Witt & Profitt, 2008). Motor simulation theory (MST) suggests that before an action occurs (motor execution, ME) there is a prior stage in which the action goal, how to achieve it, and the consequences are internally simulated (Jeannerod, 2001). During this internal simulation, many neural areas associated with executing the action are activated, including pre-motor cortex, primary motor cortex, and supplementary motor cortex (O’Shea & Moran, 2017). There are many cortical asymmetries that contribute to the right-hand bias in RHIs, such as greater cortical hand representation in the left motor cortex (Amunts et al., 1996; Volkmann et al., 1998) and greater cortical excitability (Triggs et al., 1999). Therefore, participants were likely utilising some of the same brain regions that underlie the right-hand bias in RHIs when estimating their maximum reach-to-grasp capability. Hence, participants would rely more on using cortical structures involved in motor imagery rather than the mirrored visual feedback they experienced during the calibration.

Overall, these two studies provide important insight into the nature of right-hand biases in RHIs. Estimates of maximum reaching ability using the real left and right hands varied depending on the task demand with RHIs estimating greater capability using their right hand than their left when estimating reach-to-grasp action. These findings suggest that RHIs’ perceptions of their action capabilities depend on the level of dexterity required to successfully execute the action. Previous assumptions that perceived morphological differences between the hands (Linkenauger, Witt, Bakdash, et al., 2009) lead to greater estimates of reach may in fact be inverse. That is, greater capabilities with the right hand result in the visual bias that the right arm is longer. Additionally, participants primarily used proprioceptive feedback to generate their reaching estimates and did not calibrate fully to the changed visual location of the hand during the mirrored calibration. Thus, a combination of underlying cortical asymmetries between the left and right hands, and enhanced sensory processing outside of vision (Flowers, 1975; Carson et al., 1990), primarily underlie the right-hand bias in RHIs, with visual feedback not necessarily enhancing this bias. However, more research should be conducted exploring online action rather than estimates to assess whether this methodology may be more effective using online visuomotor feedback.

Constraints on Generality

As all participants in these studies were healthy undergraduate university students aged between 19-34 years, it is possible that the findings would not generalise to differently aged populations, such as older adults. Reduced mobility associated with aging (Holt et al., 2013) could impact estimates of maximum reach, leading them to be lower than in these studies. Additionally, left-handed individuals do not experience the same perceptual biases towards the left side of their body as RHIs do towards their right (Linkenauger et al., 2009), and hence may respond differently to the manipulations in this study. Manipulating visual feedback specifying handedness in the way we have in these studies would not be possible in the real world. However, the presentation of stimuli in a virtual environment may affect estimates of maximum reach as egocentric distances in virtual reality are often underestimated (Renner et al., 2013). Overall, the results of this study would best generalise to young, healthy, right-handed adults who complete the procedure within an immersive virtual environment.

Data Accessibility Statement

The data used in analysis and study materials are publicly available on the Open Science Framework: https://osf.io/ut2gh/. Study analysis code is not available.

References

Amunts, K., Schlaug, G., Schleicher, A., Steinmetz, H., Dabringhaus, A., Roland, P., & Zilles, K. (1996). Asymmetry in the Human Motor Cortex and Handedness. *Neuroimage*, *4*(3), 216-222. https://doi.org/10.1006/nimg.1996.0073

Bhalla, M., & Proffitt, D. R. (1999). Visual–motor recalibration in geographical slant perception. *Journal of Experimental Psychology: Human Perception and Performance*, *25*(4), 1076–1096. https://doi.org/10.1037/0096-1523.25.4.1076

Bootsma, R. J., Bakker, F. C., van Snippenberg, F. E., & Tdlohreg, C. W. (1992). The effects of anxiety on perceiving the reachability of passing objects. *Ecological Psychology, 4*(1), 1–16. https://doi.org/10.1080/10407413.1992.10530790

Bryden, M. P. (1977). Measuring handedness with questionnaires. *Neuropsychologia*, *15*(4-5), 617–624. https://doi.org/10.1016/0028-3932(77)90067-7

Buckingham, G., & Carey, D. P. (2009). Rightward biases during bimanual reaching. *Experimental Brain Research*, 194(2), 197–206. https://doi.org/10.1007/s00221-008-1689-x

Buckingham, G., Main, J., & Carey, D. (2011). Asymmetries in motor attention during a cued bimanual reaching task: Left and right handers compared. *Cortex*, *47*(4), 432-440. https://doi.org/10.1016/j.cortex.2009.11.003

Campbell, J. I., & Thompson, V. A. (2012). MorePower 6.0 for anova with relational confidence intervals and bayesian analysis. *Behavior Research Methods*, *44*(4), 1255–1265. https://doi.org/10.3758/s13428-012-0186-0

Carello, C., Grosofsky, A., Reichel, F. D., Solomon, H. Y., & Turvey, M. T. (1989). Visually perceiving what is reachable. *Ecological Psychology*, *1*(1), 27–54. https://doi.org/10.1207/s15326969eco0101_3

Carson, R. G., Chua, R., Elliott, D., & Goodman, D. (1990). The contribution of vision to asymmetries in manual aiming. *Neuropsychologia*, *28*(11), 1215–1220. https://doi.org/10.1016/0028-3932(90)90056-t

Coelho, L., Zaninelli, G., & Gonzalez, C. (2016). A kinematic examination of hand perception. *Psychological Research*, *81*(6), 1224-1231. https://doi.org/10.1007/s00426-016-0815-9

Fajen, B. (2005). Perceiving Possibilities for Action: On the Necessity of Calibration and Perceptual Learning for the Visual Guidance of Action. *Perception*, *34*(6), 717-740. https://doi.org/10.1068/p5405

Fajen, B., Riley, M., & Turvey, M. (2009). Information, affordances, and the control of action in sport. *International Journal of Sport Psychology, 40*(1), 79–107.

Flindall, J. W., Doan, J. B., & Gonzalez, C. L. (2013). Manual asymmetries in the kinematics of a reach-to-grasp action. *Laterality: Asymmetries of Body, Brain and Cognition*, *19*(4), 489–507. https://doi.org/10.1080/1357650x.2013.862540

Flindall, J., Stone, K., & Gonzalez, C. (2015). Evidence for right-hand feeding biases in a left-handed population. *Laterality: Asymmetries of Body, Brain and Cognition*, *20*(3), 287-305. https://doi.org/10.1080/1357650x.2014.961472

Flowers, K. (1975). Handedness and controlled movement. *British Journal of Psychology, 66*(1), 39–52. https://doi.org/10.1111/j.2044-8295.1975.tb01438.x

Gabbard, C., Tapia, M., & Helbig, C. (2003). Task complexity and limb selection in reaching. *International Journal of Neuroscience*, *113*(2), 143-152. https://doi.org/10.1080/00207450390161994

Gibson, J. J. (1979). *The ecological approach to visual perception*. Boston,MA: Houghton Mifflin

Gonzalez, C., Whitwell, R., Morrissey, B., Ganel, T., & Goodale, M. (2007). Left handedness does not extend to visually guided precision grasping. *Experimental Brain Research*, *182*(2), 275-279. https://doi.org/10.1007/s00221-007-1090-1

Holt, R. J., Lefevre, A. S., Flatters, I. J., Culmer, P., Wilkie, R. M., Henson, B. W., Bingham, G. P., & Mon-Williams, M. (2013). Grasping the changes seen in older adults when reaching for objects of varied texture. *PLoS ONE, 8*(7). https://doi.org/10.1371/journal.pone.0069040

Jeannerod, M. (1996) Reaching and Grasping, Parallel Specification of Visuomotor Channels. In H. Heuer & S. W. Keele (Eds.), *Handbook of perception and action, vol. 2: Motor Skills* (pp. 405-460). London: Academic Press.

Jeannerod, M. (2001). Neural Simulation of Action: A Unifying Mechanism for Motor Cognition. *Neuroimage*, *14*(1), S103-S109. https://doi.org/10.1006/nimg.2001.0832

Jung, P., Baumgärtner, U., Bauermann, T., Magerl, W., Gawehn, J., Stoeter, P., & Treede, R. (2003). Asymmetry in the human primary somatosensory cortex and handedness. *Neuroimage*, *19*(3), 913-923. https://doi.org/10.1016/s1053-8119(03)00164-2

Kim, S.G., Ashe, J., Hendrich, K., Ellermann, J. M., Merkle, H., Uğurbil, K., & Georgopoulos, A. P. (1993). Functional magnetic resonance imaging of motor cortex:

Hemispheric asymmetry and handedness. *Science*, *261*(5121), 615–617. https://doi.org/10.1126/science.8342027

Lin, L., & Linkenauger, S. (2021). Perceiving action boundaries for overhead reaching in a height-related situation. *Attention, Perception, & Psychophysics*, *83*(5), 2331-2346. https://doi.org/10.3758/s13414-021-02293-2

Lin, L., McLatchie, N., & Linkenauger, S. (2020). The influence of perceptual–motor variability on the perception of action boundaries for reaching. *Journal of Experimental Psychology: Human Perception and Performance*, *46*(5), 474-488. https://doi.org/10.1037/xhp0000724

Linkenauger, S., Witt, J., Bakdash, J., Stefanucci, J., & Proffitt, D. (2009). Asymmetrical Body Perception. *Psychological Science*, *20*(11), 1373-1380. https://doi.org/10.1111/j.1467-9280.2009.02447.x

Linkenauger, S. A., Witt, J. K., Stefanucci, J. K., Bakdash, J. Z., & Proffitt, D. R. (2009). The effects of handedness and reachability on perceived distance. *Journal of Experimental Psychology: Human Perception and Performance, 35*(6), 1649–1660. https://doi.org/10.1037/a0016875

Mamolo, C., Roy, E., Bryden, P., & Rohr, L. (2004). The effects of skill demands and object position on the distribution of preferred hand reaches. *Brain and Cognition*, *55*(2), 349-351. https://doi.org/10.1016/j.bandc.2004.02.041

Mamolo, C., Roy, E., Rohr, L., & Bryden, P. (2006). Reaching patterns across working space: The effects of handedness, task demands, and comfort levels. *Laterality: Asymmetries of Body, Brain and Cognition*, *11*(5), 465-492. https://doi.org/10.1080/13576500600775692

Ocklenburg, S., Garland, A., Strockens, F., & Uber Reinert, A. (2015). Investigating the neural architecture of handedness. *Frontiers in Psychology*, *6*. https://doi.org/10.3389/fpsyg.2015.00148

O'Shea, H., & Moran, A. (2017). Does Motor Simulation Theory Explain the Cognitive Mechanisms Underlying Motor Imagery? A Critical Review. *Frontiers in Human Neuroscience*, *11*. https://doi.org/10.3389/fnhum.2017.00072

Pijpers, J. R., Oudejans, R. R., & Bakker, F. C. (2007). Changes in the perception of action possibilities while climbing to fatigue on a climbing wall. Journal of Sports Sciences, 25(1), 97–110. https://doi.org/10.1080/02640410600630894

Pijpers, J. R., Oudejans, R. R., Bakker, F. C., & Beek, P. J. (2006). The role of anxiety in perceiving and realizing affordances. *Ecological Psychology*, *18*(3), 131–161. https://doi.org/10.1207/s15326969eco1803_1

Readman, M., Cooper, D., & Linkenauger, S. (2021). It's in your hands: How variable perception affects grasping estimates in virtual reality. *Psychonomic Bulletin & Review*, *28*(4), 1202-1210. https://doi.org/10.3758/s13423-021-01916-x

Renner, R. S., Velichkovsky, B. M., & Helmert, J. R. (2013). The perception of egocentric distances in Virtual Environments - A Review. *ACM Computing Surveys*, *46*(2), 1–40. https://doi.org/10.1145/2543581.2543590

Roy, E. A., & Elliott, D. (1986). Manual asymmetries in visually directed aiming. *Canadian Journal of Psychology/Revue Canadienne De Psychologie*, *40*(2), 109–121. https://doi.org/10.1037/h0080087

Roy, E. A., & Elliott, D. (1989). Manual asymmetries in aimed movements. *The Quarterly Journal of Experimental Psychology Section A*, *41*(3), 501–516. https://doi.org/10.1080/14640748908402379

Roy, E. A., Kalbfleisch, L., & Elliott, D. (1994). Kinematic analyses of manual asymmetries in visual aiming movements. *Brain and Cognition*, *24*(2), 289–295. https://doi.org/10.1006/brcg.1994.1017

Smith, J., & Pepping, G.-J. (2010). Effects of affordance perception on the initiation and actualization of action. *Ecological Psychology*, *22*(2), 119–149. https://doi.org/10.1080/10407411003720080

Sörös P., Knecht S., Imai T., Gürtler S., Lütkenhöner B., Ringelstein E., et al. (1999). Cortical asymmetries of the human somatosensory hand representation in right- and left-handers. *Neuroscience Letters, 271*, 89–92.

Triggs, W. J., Calvanio, R., & Levine, M. (1997). Transcranial magnetic stimulation reveals a hemispheric asymmetry correlate of intermanual differences in motor performance. *Neuropsychologia*, *35*(10), 1355–1363. https://doi.org/10.1016/s0028-3932(97)00077-8

Triggs, W., Calvanio, R., Macdonell, R., Cros, D., & Chiappa, K. (1994). Physiological motor asymmetry in human handedness: evidence from transcranial magnetic stimulation. *Brain Research*, *636*(2), 270-276. https://doi.org/10.1016/0006-8993(94)91026-x

Triggs, W., Subramanium, B., & Rossi, F. (1999). Hand preference and transcranial magnetic stimulation asymmetry of cortical motor representation. *Brain Research*, *835*(2), 324-329. https://doi.org/10.1016/s0006-8993(99)01629-7

Technologies, U. (2018, April 19). Preparing assets for Unity. Unity. Retrieved January 26, 2023, from https://docs.unity3d.com/2019.3/Documentation/Manual/BestPracticeMakingBelievableVisuals1.html

Wagman, J. B. (2012). Perception of maximum reaching height reflects impending changes in reaching ability and improvements transfer to unpracticed reaching tasks. *Experimental Brain Research, 219*(4), 467–476. https://doi.org/10.1007/s00221-012-3104-x

Wagman, J. B., Cialdella, V. T., & Stoffregen, T. A. (2018). Higher order affordances for reaching: Perception and performance. *Quarterly Journal of Experimental Psychology, 72*(5), 1200–1211. https://doi.org/10.1177/1747021818784403

Walsh, A. S., Seifert, L., Button, C., & Croft, J. L. (2023). The effect of expertise upon perceived reach- and grasp-ability in rock climbers. *International Journal of Sport and Exercise Psychology*, 1–14. https://doi.org/10.1080/1612197x.2022.2161104

Witt, J., & Proffitt, D. (2008). Action-specific influences on distance perception: A role for motor simulation. *Journal Of Experimental Psychology: Human Perception and Performance*, *34*(6), 1479-1492. https://doi.org/10.1037/a0010781

Witt, J., Proffitt, D., & Epstein, W. (2005). Tool Use Affects Perceived Distance, But Only When You Intend to Use It. *Journal Of Experimental Psychology: Human Perception and Performance*, *31*(5), 880-888. https://doi.org/10.1037/0096-1523.31.5.880

Volkmann, J., Schnitzler, A., Witte, O., & Freund, H. (1998). Handedness and Asymmetry of Hand Representation in Human Motor Cortex. *Journal of Neurophysiology*, *79*(4), 2149-2154. https://doi.org/10.1152/jn.1998.79.4.2149

You, H., Meng, Y., Huan, D., & Wang, D.-H. (2011). The neural dynamics for hysteresis in visual perception. Neurocomputing, 74(17), 3502–3508. https://doi.org/10.1016/j.neucom.2011.06.004

Appendix: Coordinates of Calibration Circles

X-axis	Z-Axis
.05	.1
.05	.1
.05	.2
.05	.2
.0625	.1
.0625	.2
.075	.1
.075	.2
.0875	.1
.0875	.2
.1	.1
.1	.2
.1	.2
.125	.1
.125	.2
.15	.1
.15	.2
.175	.1
.175	.2
.2	.1
.2	.1
.2	.1
.2	.2
.2	.2
.225	.1
.225	.2
.25	.1
.25	.2
.275	.1
.275	.2

Note. The y-axis was kept constant at .47 across all trials. The x-axis was flipped (i.e. negative) when reaching to the left side of space.

Chapter 3

Embodiment of Mirrored Virtual Limbs in Action Estimates

Previous research into affordance perception has demonstrated that people can calibrate to visually specified changes to virtual hands and consider those changes in their perceptions of their action capabilities. This change in perception of action capabilities based on visual feedback suggests that people are embodying these virtual limbs. However, in this previous research the conditions for embodiment were optimal. The virtual limb provided visual feedback that matched the motor commands of the user, creating a sense of agency. The virtual hand models had realistic skin textures, helping to increase the sense of ownership over the virtual hand. Finally, visual and proprioceptive information specifying the hand being used were congruent.

In a set of four studies, I explored how participants can calibrate to changes in virtual hand size when visuo-proprioceptive information specifying hand use is incongruent. The aim of these studies was to provide further insight into the results of Chapter 2 by assessing whether participants can embody the characteristics of a virtual limb when there is visuo-proprioceptive incongruency.

Can the Left Hand Benefit from Being Right? Embodiment of Mirrored Virtual Hands in Grasping and Reaching Estimates

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We have no known conflict of interest to disclose.

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Data used in analysis are publicly available on the Open Science Framework: https://osf.io/mksxj/

Abstract

Previous research exploring affordance perception within virtual environments has found that people can readily calibrate to virtual bodies and consider changes to those virtual bodies in estimates of their action capabilities. This previous research presented these virtual bodies in a manner that is spatially congruent and morphologically like one’s real body. However, little research has explored whether people calibrate to virtual limbs when proprioceptive and visual information specifying the spatial location of the limb are incongruent. Therefore, we conducted four studies in which we manipulated both virtual hand size and the spatial location of the virtual hand. Participants from Lancaster University were placed in an immersive virtual environment, in which we presented a virtual hand as big or small. This virtual hand was either spatially congruent to the real hand, or mirrored so that it was on the opposite side of the real hand. Participants first completed a calibration to gain experience with the virtual hand, then completed various estimation tasks assessing their perceived grasping and reaching capabilities. Overall, the results demonstrate that people can calibrate to the size of the virtual hands and consider them in their estimates, regardless of whether the virtual hand is congruent to the real hand. However, participants do not calibrate to the spatial location of the virtual hand when it is incongruent when estimating their reaching capabilities. These results are discussed in context of wider embodiment literature, with suggestions for future research.

Keywords: affordances, grasping ability, reaching ability, virtual reality, embodiment

Can the Left Hand Benefit from Being Right? Embodiment of Mirrored Virtual Hands in Grasping and Reaching Estimates

The ability for an animal to accurately perceive their opportunities for action in the environment – also known as ‘affordances’ - is a vital part of survival. Affordances are highly varied, ranging from flat, rigid, horizontal surfaces that afford support for walking, or detached objects such as tools that afford manipulation with the hands (Gibson, 1979). To successfully interact with affordances, we must be able to accurately perceive the relationship between our bodies and environmental properties (Wagman, 2012). One key aspect is our morphology, which influences the action boundary of an action – that is, the maximum extent to which an action can be performed (Fajen, 2005; Linkenauger et al., 2013). People are generally very accurate at perceiving their action capabilities (Carello et al., 1989; Linkenauger et al., 2009) since they gain experience with a vast range of actions throughout actively exploring their capabilities throughout the lifespan (Fajen et al., 2009).

Since both aspects of our environment and our action capabilities are constantly changing, affordances are highly dynamic and can change from moment-to-moment (Turvey, 2004). Changes to our action capabilities can occur over both long and short timescales. Thus, being able to successfully perform an action requires our perception of affordances to reflect such changes (Wagman, 2012). Short-term changes can happen naturally, for example, as someone becomes fatigued (Pijpers et al., 2007) or changes their posture (Wagman, 2012). Additionally, changes to our action capabilities can occur through artificial means, such as holding a tool that can extend our reaching capabilities (Witt et al., 2005) or wearing a glove that increases the width of the hand (Ishak et al., 2008). People can attune to these changes to their body and update their perceptions of their action capabilities, in turn updating their affordance perception (Witt et al., 2005; Ishak et al., 2008).

Additionally, people can attune to changes not only to their real, physical body, but can also embody virtual limbs and consider changes to those virtual limbs when perceiving their environment. Linkenauger et al. (2013) manipulated the size of fully animated virtual hands that were tracked to the participant’s movements and found that perception of object size changed as the size of the virtual hands changed. That is, bigger virtual hands elicited smaller estimates of object size. Additionally, changes to object size perception did not occur when a familiar object was placed next to the target object, suggesting that people use their own body as a perceptual metric to scale the size of objects around them. Thus, changes to the dimensions of a virtual body can lead to changes in the perception of objects with which the virtual body could potentially interact (Linkenauger et al. 2013). If changes to a virtual body can elicit changes to object perception, it follows that changes to a virtual body will also elicit changes to one’s affordance perception, since successful execution of an action requires understanding the dynamic relationship between one’s body and their environment (Turvey, 2004; Wagman, 2012).

Indeed, various studies show that changes to a virtual body are reflected in people’s estimates of their own action capabilities. Readman et al. (2021) calibrated participants to a normal (100% of regular hand size), small (50% of regular hand size), and large (150% of regular hand size) virtual hand. Then, participants estimated their maximum grasping capability by adjusting the size of a virtual block until they believed it was the maximum size they could grasp. As expected, the larger virtual hand elicited significantly larger estimates of maximum grip than the normal and small virtual hands. Similar findings have also been found for reaching (Lin et al., 2020). Thus, people are capable of embodying virtual limbs to accommodate quite drastic and short-term changes to their action capabilities, resulting in changes to their affordance perception.

But what does it take to be able to embody a virtual body as our own? Firstly, we must understand what 'embodiment' means in this context. Sense of Embodiment (SoE) can be defined as the sense that the properties of an artificial body are processed as if they were the properties of one's own biological body (Kilteni et al., 2012). These properties can be split into three key aspects – sense of self-location, sense of agency, and sense of body ownership (Longo et al., 2008). Briefly speaking, one's sense of self-location refers to the experience of being inside a body and can be determined by the visuospatial perspective of the body, vestibular signals, and tactile input (Kilteni et al., 2012). Sense of agency refers to the sense of having motor control over one's actions, which can be elicited through the presence of synchronous visuomotor correlations when actively moving one's body (Kilteni et al., 2012). Finally, sense of body ownership refers to the implicit sense of possession over a body part, or that the body feels like one's own (Longo et al., 2008; Tsakiris, 2010). This ownership can be impacted by both bottom-up influences - such as visuo-tactile, visuomotor, and visuo-proprioceptive correlations - as well as top-down processes – for example, the degree of morphological similarity the artificial limb has to one's own body (Kilteni et al., 2012). Therefore, SoE is derived from these underlying subcomponents, the importance of which will be addressed further.

Various factors facilitate the process of embodying an artificial body as one's own. For example, viewing the body or limb from an egocentric perspective is critical for triggering the illusion of ownership (Petkova et al., 2011; Slater et al., 2010), since one's sense of self-location is normally rooted from an egocentric perspective (Kilteni et al., 2012). The sense of agency over a body is sensitive to any temporal discrepancies between the execution of an action and subsequent visual feedback (Kilteni et al., 2012), as well as discrepancies between predicted and actual sensory feedback (Sato & Asuda, 2005). Therefore, to experience agency over an artificial body it must elicit visuomotor correlations that preserve the time between executing and receiving visual feedback that one would normally experience with their own body (Kilteni et al., 2012). Finally, sense of ownership may be enhanced through maintaining the morphological similarity between one's own body and the artificial body, as well as personalising the artificial body to closely resemble one's own (e.g. skin colour) (Kilteni et al., 2012).

To elicit SoE over an artificial body, it would make sense that this body must move in real-time with one's own body, that it is presented from an egocentric perspective, and that it visually resembles one's own body. Interestingly, however, sense of location and sense of body ownership are dissociable entities, though they are highly correlated (Longo et al., 2008). That is, one can have the sense of experiencing the same sensory feedback as an artificial body without feeling that the body is their own. Furthermore, while discrepancies in predicted and actual sensory feedback from an action can reduce the sense of agency, this does not translate into a reduction in ownership (Sato & Yasuda, 2005). While the subcomponents of SoE are likely highly related, they may also be considered independent qualitative experiences, especially in the sense of agency and ownership (Tsakiris et al., 2010). Therefore, it may be that SoE over an artificial body can be elicited even when sensory feedback contributing to one's sense of location, agency, and bodily ownership are not optimal for all subcomponents.

As discussed before, various studies exploring people's capability to readily update their perceptions of their action boundaries (Lin et al., 2020; Readman et al., 2021) after calibrating to changes in a virtual body suggests that they embody these virtual bodies. In these studies (Lin et al., 2020; Readman et al., 2021), virtual arms and hands were presented from an egocentric perspective, in the same location as the real arm would be presented, thus preserving the sense of self-location that would ordinarily be experienced. Visual feedback from moving the virtual arms was delivered in real-time to actual arm movement -

maximising the visuomotor congruency between the real and virtual limb – and therefore enhancing sense of agency over the virtual arm. Finally, the virtual arms resembled real arms in terms of morphological structure and skin texture. All in all, the presentation of virtual limbs in previous affordance studies provides optimal conditions for embodiment of these virtual limbs, since there is a match between efferent motor commands, afferent proprioceptive signals, and visual feedback (Tsakiris et al., 2010).

One key question is whether people would be capable of embodying and calibrating to virtual limbs and considering them in their estimates of their action capabilities if the conditions were not so optimal. For example, if a virtual arm was mirrored so that the location of the arm was spatially incongruent to the actual arm, would participants be able to embody it? Would providing temporally synchronous visuomotor feedback that matches one's own movement in every sense but location be sufficient for people to overcome the discrepancy between the location of the virtual arm and the real arm? If so, will people consider changes to a virtual arm in their estimates of their action capabilities when this discrepancy exists, in much the same way that they have been shown to when the location of the real and virtual arm is congruent (e.g. Lin et al., 2020; Readman et al., 2021)?

To explore this question, we placed participants in an immersive virtual environment (VE) with hand tracking sensors that tracked and animated the hands in real time. We then either presented the right hand congruently to how it would be presented normally (as the right virtual hand) or mirrored it so that it both looked like and was in the same spatial location as the left (as the left virtual hand). In addition, we manipulated the size of the virtual hands, so that they appeared large, small, or varied in size during a calibration phase. After calibrating participants to this virtual limb, we then took participant's estimations of their maximum grasp and reaching ability in a series of studies. If the subcomponents of SoE are indeed their own individual entities, we would expect that disruption in normal processing of one component (sense of self-location) will not necessarily lead to a breakdown of embodiment if information for the other components (namely, sense of agency) is sufficient to elicit SoE. Therefore, we would not expect there to be any differences in how people calibrate to the virtual limbs, and therefore no differences in estimates of their action capabilities between the congruent and incongruent conditions. More specific hypotheses for each study will be addressed in detail as each study is introduced.

Study 1

In this study, we explored whether participants would update estimates of their action capabilities based on visual information on hand size if visual and somatosensory information specifying hand use were not congruent. We did this in the context of a maximum grasp estimation task. There were two key hypotheses for this study. Firstly, estimates of maximum grip would be significantly higher when the virtual hand was big than when the virtual hand was small. Secondly, we hypothesised that participants would use visual feedback specifying hand size in their grip estimates regardless of whether the visual presentation of the virtual hand was congruent to somatosensory information specifying hand use. Therefore, we anticipated would be no significant differences in estimates of grip between congruent and incongruent conditions, nor an interaction between virtual hand size and congruency.

Methods

Transparency and Openness

The study design, hypotheses and analysis plan were not preregistered. We report how we determined our sample size, all data exclusions (if any), all manipulations and all measures in the study. Data were analysed using JASP version 0.16.4.0 and R version 4.3.0. Analysis code for is not available for analyses using JASP as JASP does not have the functionality to export syntax. Data are publicly available on the Open Science Framework: [https://osf.io/mksxj/]. Study materials are available upon reasonable request.

Participants

We conducted a priori power analysis using MorePower 6.0 (Campbell & Thompson, 2012) with the real hand x virtual hand x hand size interaction being the key area of interest, with an effect size of $\eta_p^2 = .551$, an alpha of 0.05 and desired power of 0.8. The effect size is based off the results of the constricted, extended and variable grasping study in Readman et al., 2021. The analysis suggested an ideal sample size of 10. Therefore, we recruited 21 right-handed (13 female, 8 male) and 3 mixed-handed (3 female, laterality quotients were between +40 - +45.45) individuals from Lancaster University (age range: 20-34 years, *M* = 23.38, *SD* = 3.54). Handedness was assessed using the 10-item Edinburgh Handedness Inventory (Oldfield, 1971), with scores > +60 being assigned as right-handed, scores between +59 to -59 being assigned as mixed-handed, and scores < -60 being assigned as left-handed. The mixed-handed individuals were recruited as they all stated a strong right-hand preference for writing, with writing being a key predictor of handedness (Bryden, 1977; Rigal, 1992). Participants were recruited via Lancaster University SONA system, or by posters placed around the university campus, and were paid £8.50 for their time. Data was collected in July 2022.

Materials

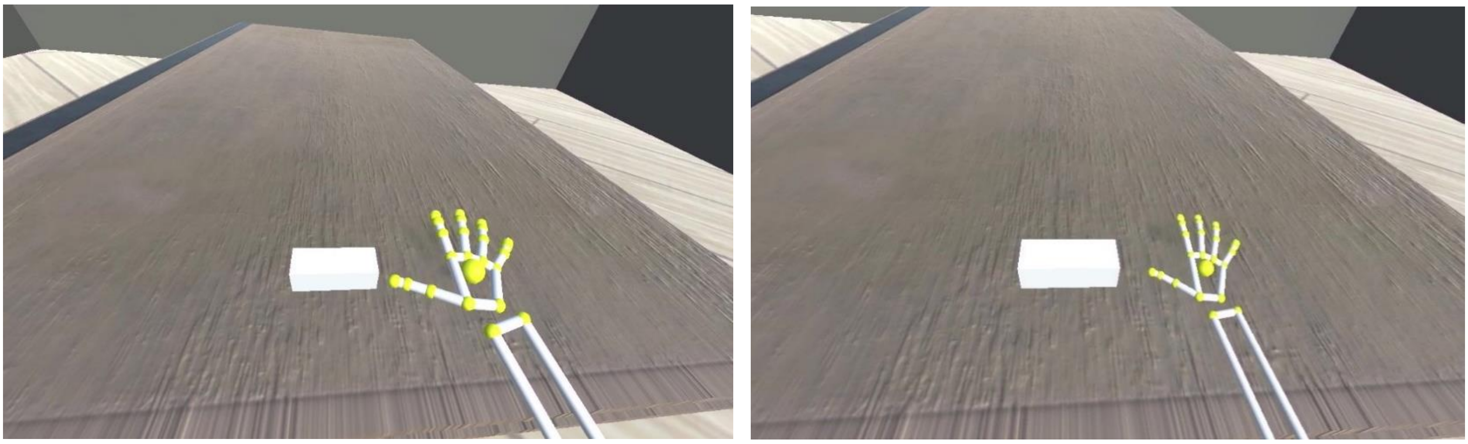
The environment was created using Unity Version 2021.1.24f1 (Unity Technologies, San Fransisco, California, United States). Unity uses unique scaling; therefore, descriptions of dimensions may differ to how they would appear in the real world. However, it is a standard assumption in Unity that 1 unit in Unity is equal to 1 real-world metre (Unity Technologies, 2018).

Virtual Environment

Participants wore an Oculus CV1 virtual reality (VR) headset which placed participants in an immersive virtual environment (VE). This environment was a room with three grey walls and a light wooden floor, with a wooden table (70cm height, 3m length) at which the participant sat. A pair of small red circles called ‘calibration dots’ (2cm in diameter, 2cm in depth) were placed on top of the virtual table to the left, right or centre of the participant during the calibration. A white block (6cm, 8cm, 10cm, 12cm, 14cm or 16cm in length, 5cm in length and 5cm in depth) was placed 20cm away from the participant on the virtual table during the estimation task. Eye height was set to 40cm from the top of the virtual table, and participants sat 17cm away from the virtual table. Attached to the front of the headset was a Leap Motion sensor that tracked the real hands and animated them to virtual hands. The virtual hands used were the Leap Motion ‘capsule hand’ models (Leap Motion, Inc., San Francisco, California, United States). These hand models are white with small, coloured spheres placed on the joints and fingertips. The sizes of these capsule hands changed depending on the condition the participant was in. When participants were using the ‘big’ virtual hand, the hand size was set to 125% of the size of the regular hand model. When using the ‘small’ virtual hand, the hand size was set to 75% of the size of the regular hand model (see Figure 1 for a visual comparison of the hands). The capsule hands were used because more realistic hand models we had tested became distorted when we attempted to mirror them. Therefore, these simplistic hands were the best option to ensure participants retained a good level of agency over the virtual hand.

Figure 1

The 'Big' versus 'Small' Capsule Hand Models



Design

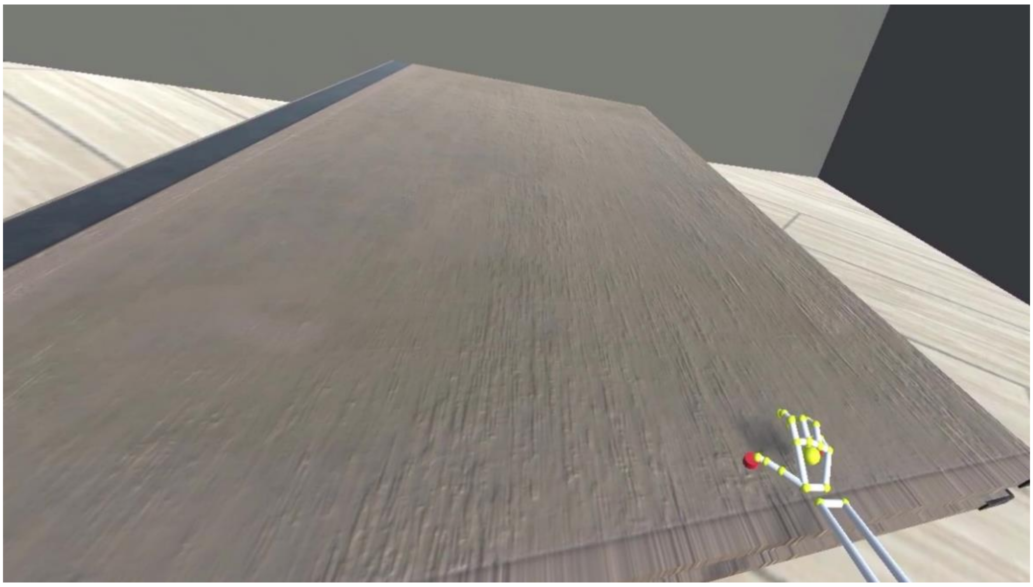
This was a 2 x 2 x 6 within-subjects design. There were three factors: first was whether the real hand and virtual hand were congruent in terms of laterality (congruent vs incongruent); second was the size of the virtual hand presented during the calibration (big vs small); third was the starting size of the white block during estimation trials. We varied the starting size of the estimation block to control for hysteresis, a phenomenon in which our estimations change based on initial experiences and can impact future judgements of action capabilities (You et al., 2011). The dependent measure was maximum estimated grip, as measured by the final length of the estimation block after adjustment.

Procedure

This study received ethical approval from the Faculty of Science and Technology ethics committee at Lancaster University. Participants gave full informed consent before participation. Participants sat a couple of feet away from a table so that they would not hit the table during the calibration. Before being placed in the virtual environment, participants were told that they would be using their right hand throughout all the conditions. Additionally, they were told whether they would be using the big or small virtual hands, as well as whether their hand would be presented as the right virtual hand (congruent) or mirrored to look like the left virtual hand (incongruent). The order of conditions was counterbalanced, with around half of the participants starting with the congruent condition, and half starting with the big hands. After being placed in the virtual environment, participants first completed a calibration phase. During the calibration, participants needed to stretch their hand out so that their thumb and little finger were each touching one of two red calibration dots positioned on the table (see Figure 2) and to move their hands to calibration dots as they changed position from trial to trial. The size of the virtual hand was kept consistently big or small throughout the calibration, depending on the condition the participant was assigned at the time. The positions of the calibration dots were presented in a randomised order (see Appendix A for exact positions of the calibration dots). The calibration dots were placed from the right to the centre of the participant when the right virtual hand was used, and placed from the centre to the left of the participant when the left virtual hand was used. This was so that participants could easily reach the calibration dots without needing to strain or bend over to reach across themselves. The calibration was for 60 trials, lasted between 5-7 minutes, with the incongruent calibration trials often taking longer than the non-mirrored trials due to the visuomotor adjustment needed to control the virtual hand.

Figure 2

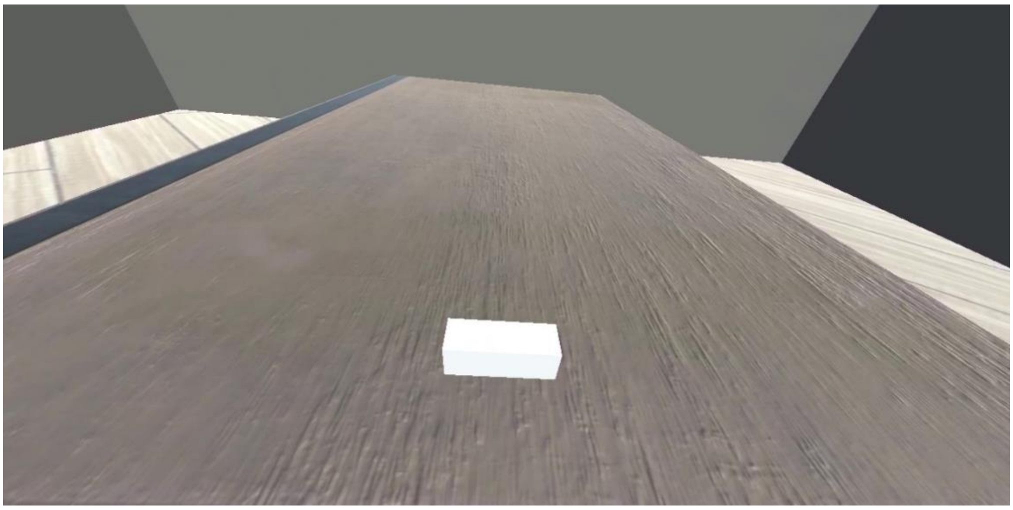
One of the Grasp Calibration Trials, as Shown when Using the Small Right Virtual Hand



After the calibration, participants were instructed to move their hand away from the hand sensor and place it in their lap so that they no longer received visual feedback from the virtual hand. Then, the white block appeared on the table in front of the participant (see Figure 3) to signify the start of the estimation phase. The researcher then increased or decreased the white block's length by 1mm – using the left and right arrow keys on the computer – until the participant told them to stop, at which point the participant felt that the length of the white block was at the maximum width that they could grip from the top using the thumb and index finger of the right hand. Participants could also request that no adjustment was made to the block. If participants questioned whether they should consider their actual hand or the virtual hand they had just used during the calibration in their estimates, they were told to use whichever they felt was most appropriate for them. The final size of the white block after adjustment was saved after each trial. The estimation phase lasted 12 trials, with 2 trials per starting length presented in a randomised order. The entire procedure was repeated four times, once for each condition. Overall, the study took around 30 minutes to complete.

Figure 3

The White Estimation Block used in the Estimation Phase



Results

A within-subjects ANOVA was conducted with real hand/virtual hand congruency (congruent vs incongruent), virtual hand size (big vs small), and white block starting length (6cm, 8cm, 10cm, 12cm, 14cm, 16cm) as the independent variables and maximum grip estimate (as measured by the length of the block after adjustment) as the dependent variable. The key areas of interest are the main effect of virtual hand size, main effect of congruency, and the interaction between congruency and hand size.

We report both Bayes factors and p-values for all one degree-of-freedom tests. Bayes factors are calculated as the ratio of probability of the data under one hypothesis (such as the alternative hypothesis, or H1) against the probability of data under another hypothesis (such as the null hypothesis, or H0). We calculated Bayes factors using the Dienes and McLatchie (2018) R script calculator and provide robustness regions (RR) to indicate the range of effect sizes that support our conclusions. Calculation of robustness regions follows the guidance of Dienes (2019).

Though Bayes factors are a continuous measure, Bayes factors greater than 3 and 10 are interpreted as moderate and strong evidence, respectively, in support of the alternative hypothesis. We interpret Bayes factors less than .33 and .10 as moderate and strong evidence, respectively, in support of the null hypothesis. Bayes factors between .33 and 3 are considered to provide weak or inconclusive evidence. These thresholds are designed to aid interpretation of the hypothesis that is most supported by the data. See Lakens et al. (2018) for discussion on comparison of Bayes factors and p values.

There was a main effect of virtual hand size, $F(1,23) = 40.24$, $p < .001$, $\eta_p^2 = .64$, $B_{H(0,2.5)} = 9.99$ x 10^7, *RR[.07, 836.48*[1]*]*, with estimates of maximum grip being significantly higher when the virtual hand was big (*M* = 12.2cm , *SD* = 3.1cm) versus small (*M* = 9.9cm , *SD* = 2.8cm). The Bayes factor indicates strong support for the alternative hypothesis. However, there was no main effect of congruency on grasping estimates, $F(1, 23) = 3.81$, p = .06, $\eta_p^2 = .14$, $B_{N(0, 2.3)} = .99$, *RR[0, 7.25*[2]*]*, with no significant differences in estimates of grasp between the congruent (*M* = 11.4cm, *SD* = 3.3cm) and incongruent (*M* = 10.7cm , *SD* = 2.5cm) presentation of virtual hand. The Bayes factor indicates inconclusive evidence for either hypothesis. Additionally, there was no significant interaction between congruency and hand size, $F(1, 23) = 2.56$, $p = .12$, $\eta_p^2 = .1$, $B_{N(0, 2.5} = 1.12$, *RR[0, 10.72*[3]*]*. The Bayes factor indicates inconclusive evidence for either hypothesis. See Figure 4 for a visual representation

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[1] H1 was specified from the main effect of virtual hand size in Readman et al. (2021). Readman et al. found a main difference of 5cm in maximum grasp estimates between virtual hand sizes that were 50% and 150% of normal hand size. As our manipulation used hand sizes that were 75% and 125% of normal hand size, we estimated the effect in our study to be roughly half of that from Readman et al. We assumed a half normal prior distribution with SD of 2.5.

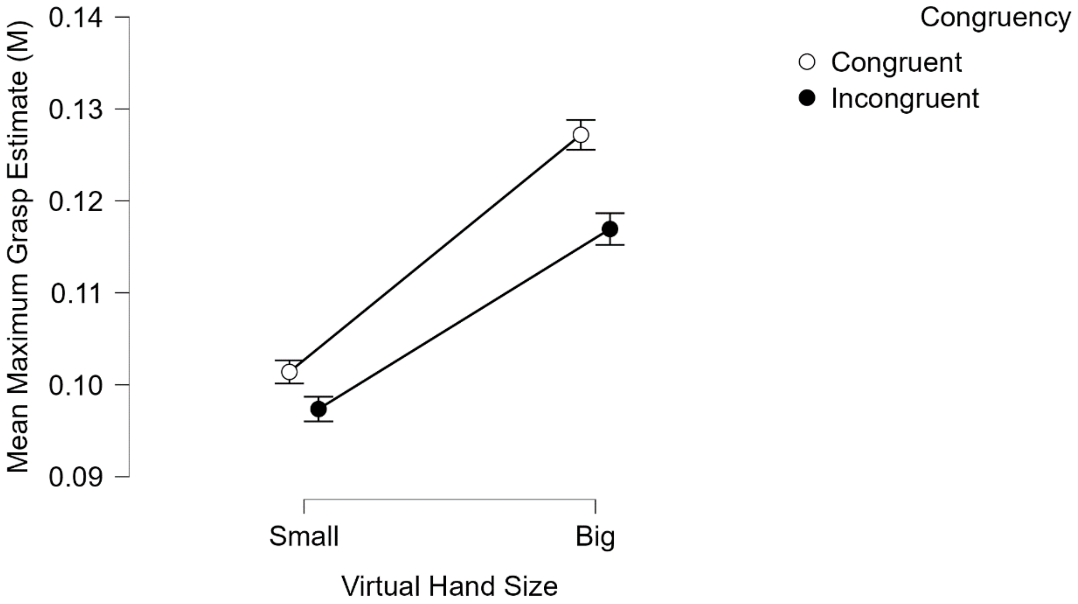
[2] H1 was specified from the obtained basic effect of virtual hand size in this study as we could not find previous research on congruency of visual feedback in grasp estimates to model H1. We assumed a normal prior with mode = 0 and SD = 2.3

[3] H1 was specified from half of the main effect of virtual hand size in Readman et al. to provide an approximate scale of effect for the interaction between virtual hand congruency and virtual hand size. We assumed a normal prior with mode = 0 and SD = 2.5.

of the impact of virtual hand size on maximum estimated grasp with respect to the congruency of the virtual hand.

Figure 4

Graph Showing the Effect of Hand Size with respect to Congruency on Grasp Estimates



Note. Error bars represent standard error.

Mauchly's test of sphericity found that the assumption of sphericity was violated for white block starting length and interactions between congruency and block starting length, hand size and block starting length, and congruency, hand size, and block starting length. Therefore, we report the Greenhouse-Geisser corrections for these tests. There was a main effect of block starting length, $F(2.482, 57.096) = 30.056$, $p < .001$, $\eta_p^2 = .57$, with larger starting lengths eliciting greater estimates of maximum grip. However, there were no significant interactions between congruency and block start length, $F(2.607, 59.954) = 2.07$, $p = .12$, $\eta_p^2 = .08$; between virtual hand size and block start length, $F(3.277, 75.381) = 1.12$, $p = .35$, $\eta_p^2 = .05$; nor between congruency, virtual hand size and block start length, $F(2.304, 54.002) = .76$, $p = .49$, $\eta_p^2 = .03$

Study 2

Findings from Study 1 demonstrated that participants could readily calibrate to different virtual hand sizes when estimating their maximum grasp ability, and that there were no significant differences in grasping estimates between the congruent and incongruent conditions. Additionally, there was no significant interaction between real hand/virtual hand congruency or object size. This suggests that people are capable of embodying virtual hands when visual information is incongruent to somatosensory information specifying hand use, and then using these in estimates of their action capabilities. However, one area of contention in affordance research is that changes to people's estimates of their action boundaries are due to demand characteristics, rather than a genuine change in their perception (Durgin et al., 2009). That is, the manipulations to hand size in this study were obvious, so it could be argued that participants simply changed their estimates equally across both congruent and incongruent conditions. Therefore, we used variable hand sizes to see whether there would be any differences in grasping estimates between congruent and incongruent hands when the intended outcome may not be so obvious.

Methods

Participants

We carried forward the same power analysis from Study 1, since Readman et al. (2021) also include a variable grasp condition in their study. Therefore, we recruited 13 right-handed (4 male, 9 female) and six mixed-handed (2 male, 4 female, with laterality quotients ranging from +33.33 to +53.84) individuals (age range: 18-23 years, *M* = 20.05, *SD* = 2.07) from Lancaster University. Handedness was assessed in the same way as in Study 1, with the same justification for retaining the mixed-handed participants. Participants were recruited via Lancaster University SONA system, or by posters placed around the university campus, and were either paid £8.50 or compensated with 2 SONA credits. Data was collected in November 2022.

Materials

Virtual Environment

The virtual environment used is almost identical to Study 1. However, rather than the virtual hands being consistently 125% or 75% the size of the normal hand model, the virtual hand size varied between 75%, 100%, or 125% the size of the normal hand model.

Design

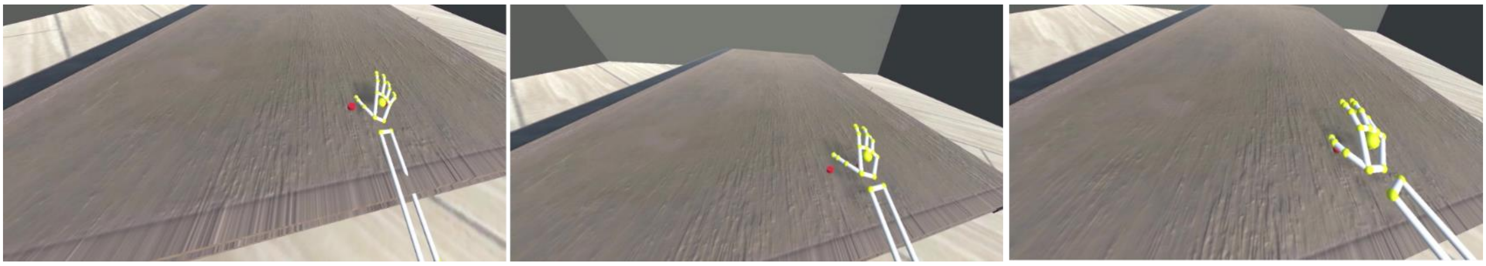
This was a 2 x 6 within-subjects design. There were two factors: first was whether the real hand and virtual hand were congruent (congruent vs incongruent); second was the starting size of the white block during estimation trials. The dependent measure was maximum estimated grip, as measured by the final length of the estimation block after adjustment.

Procedure

The procedure was very similar to study 1. However, during the calibration phase the virtual hand size varied for each trial between 75%, 100%, and 125% the size of the normal hand model (see Figure 5). Each hand size appeared equally but randomly throughout the calibration, for 20 trials each, for a total of 60 calibration trials. The procedure was repeated twice, once for each condition. The whole study lasted approximately 15 minutes.

Figure 5

The Calibration Task with the Small, Normal, and Big Hand sizes



Results

One participant was removed prior to analysis because they did not follow the instructions in the procedure properly. A within-subjects ANOVA was conducted with real hand/virtual hand congruency (congruent vs incongruent) and white block starting length (6cm, 8cm, 10cm, 12cm, 14cm, 16cm) as the independent variables and maximum grip estimate (as measured by the length of the block after adjustment) as the dependent variables. We report both Bayes factors and p-values for all one degree-of-freedom tests. The main factor of interest is real hand/virtual hand congruency.

There was no main effect of congruency, $F(1,17) = 1.79$, $p = .2$, $\eta_p^2 = 0.1$, $B_{N(0, 2.3)} = .08$, $RR[.54, \infty]$[4] with no significant differences in grasp ability estimates when the virtual hand was congruent (M = 11.2cm , SD = 1.7cm) or incongruent (M = 11.1cm , SD = 1.7cm) to the real hand being used (see Figure 6). The Bayes factor indicates that our data strongly support the null hypothesis. However, there was a main effect of block starting length $F(1.919, 32.631) = 26.220$, $p < .001$, $\eta_p^2 = .61$, with estimates of maximum grasp increasing as starting block size increased. Block starting length was reported with Greenhouse-Geisser corrections as this test violated sphericity assumptions. Finally, there was no significant interaction between congruency and block starting length, $F(5, 85) = .91$, $p = .48$, $\eta_p^2 = .05$.

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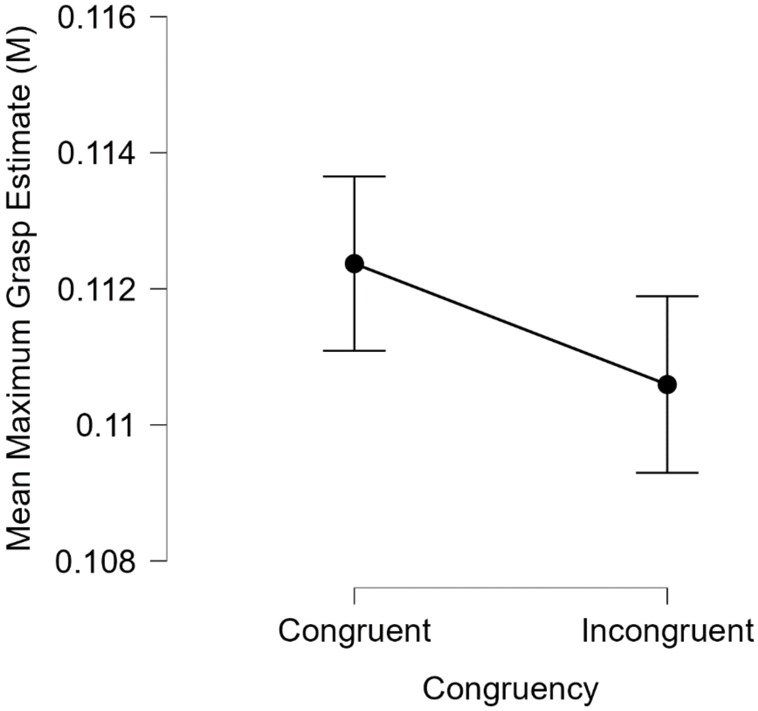
[4] We could not find previous research exploring the role of visuo-proprioceptive congruency of virtual hands on maximum grasp estimates. Therefore, H1 was modelled off the basic effect of hand size found in study 1. We assumed a normal prior with mode = 0 and SD = 2.3.

Figure 6

Graph Showing the Effect of Congruency on Grasp Estimates



Note. Error bars represent standard error.

Study 3

Study 2 demonstrated that there are no significant differences in estimates of grasp between congruent incongruent presentation of the hands when the hand size varied randomly throughout the calibration. This suggests that people consider changes to their action capabilities equally as well when visual feedback specifying hand use is incongruent to somatosensory information on the hand being used, and that the results from Study 1 are likely not due to demand characteristics. In Study 3, we extend the investigation into whether people would update estimates of their action capabilities based on visual information specifying hand size when visual and somatosensory information specifying hand are incongruent in the context of reaching.

There were two key hypotheses for this study. Firstly, estimates of maximum reach would be significantly higher when the virtual hand was big than when the virtual hand was small. Secondly, participants would use visual feedback specifying hand size in their reach estimates regardless of whether the visual presentation of the virtual hand was congruent to proprioceptive information specifying hand use. Therefore, there would be no significant differences in estimates of reach between congruent and incongruent conditions, nor an interaction between virtual hand size and congruency. Additionally, estimates to the ipsilateral side of the actual arm will be greater than estimates contralateral to the actual arm.

Methods

Participants

Using the effect size from the results of the constricted, extended and variable reach study in Lin et al. (2020), we conducted an a priori Power analysis using MorePower 6.0 (Campbell & Thompson, 2012) with the real hand x virtual hand x hand size interaction being the key area of interest, with an effect size of $\eta_p{}^2 = .42$, an alpha of 0.05 and desired power of 0.8. The analysis suggested an ideal sample size of 14.

Therefore, we recruited 14 right-handed (10 female, 5 male) and 5 mixed-handed (3 female, 2 male, laterality quotients were between +27.27 - +45.45) individuals from Lancaster University (age range: 18-32 years, *M* = 20.7, *SD* = 3.31). Handedness was ascertained using the same method as Study 1. Participants were recruited via Lancaster University SONA system, or by posters placed around the university campus, and were paid £8.50 for their time. Data was collected in July 2022.

Materials

Virtual Environment

The environment was like Study 1 and Study 2. However, during the calibration phase, a singular small red circle called a ‘calibration dot’ (2cm in diameter, 2cm in depth) was placed on top of the virtual table to the left, right or centre of the participant, instead of two placed parallel to each other. In the estimation phase, a small red circle known as the 'estimation target' (2cm in diameter, 2cm in depth) was placed on the virtual table 27.4cm away centrally from the participant on 'near' trials or centrally 90cm away or 100.6cm away to the left or right of the participant on 'far' trials.

Design

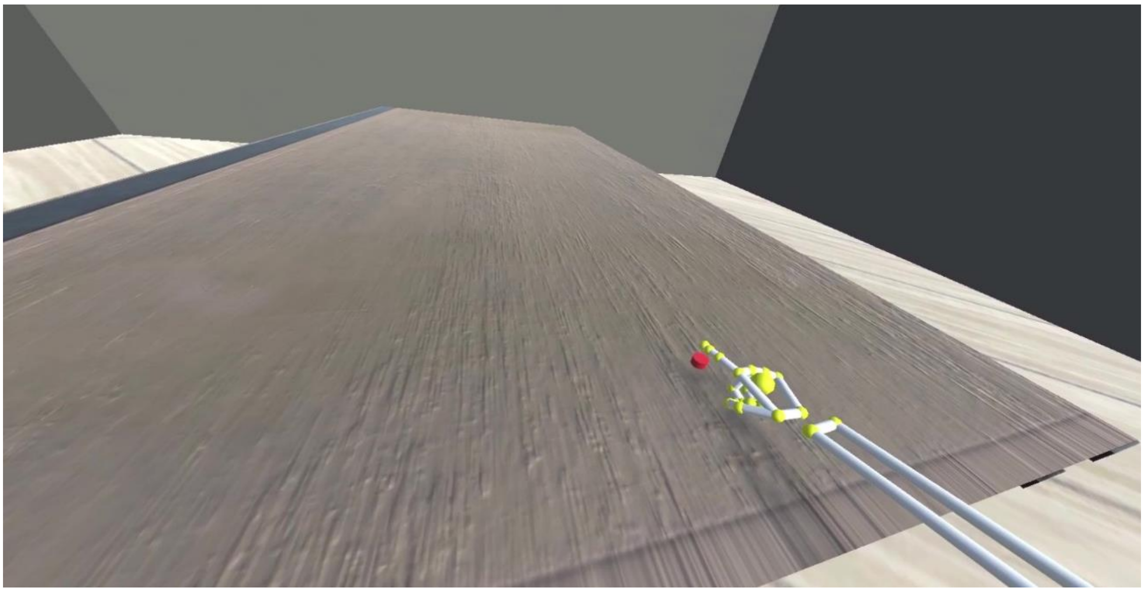
This was a 2 x 2 x 2 x 3 within-subjects design. There were four factors: first was the congruency between virtual hand and real hand (congruent vs incongruent); second was the size of the virtual arms (big vs small); third was the starting position of the estimation target, also known as hysteresis (near vs far); fourth was direction of reaching estimate (centre vs left vs right). We varied the starting position of the estimation target to control for hysteresis, a phenomenon in which our perception changes based on recent sensory experiences and can impact future judgements of action capabilities (You et al., 2011). The dependent measure was the maximum estimated reaching distance, as measured by the final position of the estimation target.

Procedure

The procedure of the study was very similar to Study 1, though there were key differences during the calibration and estimation task. During the calibration task, participants were instructed to use their index finger to control the virtual hand to point and touch a single calibration circle, which then changed position from trial to trial throughout the calibration phase (see Figure 7; see Appendix B for exact locations of the calibration dots). As in Study 1, the virtual hand was consistently presented as big or small depending on the condition the participant had been assigned.

Figure 7

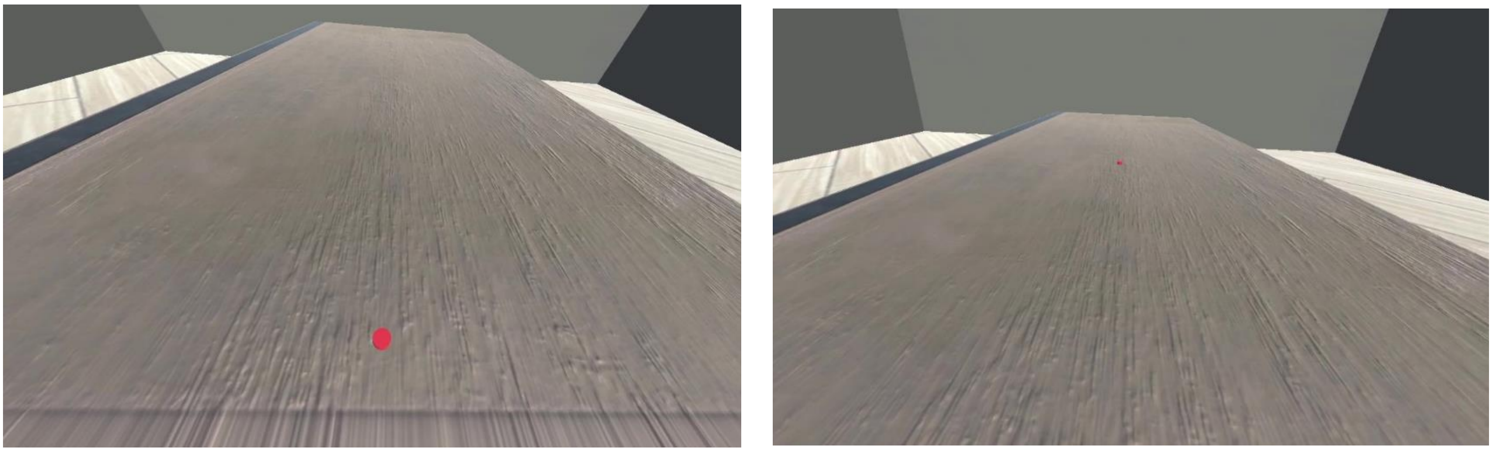
One of the Reach Calibration Trials, as Shown when Using the Small Right Virtual Hand



After completing the calibration, participants moved onto the estimation task (see Figure 8). Participants were told to imagine that they were estimating the maximum distance they could reach with the right arm, without bending forward at the hip. As in Study 1, visual feedback of the hands was removed at this stage. Then, the researcher would adjust the distance of the estimation dot by 2.25cm either away from the participant if it started close, or towards the participant if it started far away. The participant then told the researcher to stop moving the estimation dot when they believed it to be at the maximum distance they could reach with the previously described constraints. The estimation phase lasted 12 trials, with 2 trials per estimation target start position presented in a randomised order. This procedure was repeated four times, once for each condition. Overall, the study took around 30 minutes to complete.

Figure 8

The Reaching Estimation Task, shown as the Near Centre and Far Centre Trials



Results

Two participants were removed prior to analysis because they did not follow the instructions during the procedure correctly. One additional subject was removed prior to analysis as they stated that they found the calibration with the big virtual arm more difficult than the small virtual arm, a pattern that was not consistent with the rest of the participants. A within-subjects ANOVA was conducted with real hand x virtual hand congruency (congruent vs incongruent), virtual hand size (big vs small), hysteresis (near vs far), and direction of reach (centre, left, right) as the independent variables and maximum reach estimate (as measured by the final position of the estimation target at the end of each trial) as the dependent variable. Bayes factors are calculated for all one degree-of-freedom tests. The key areas of interest are the main effect of congruency, main effect of hand size, and a congruency x hand size interaction.

There was no main effect of congruency, $F(1, 16) = 0.91$, $p = .35$, $\eta_p^2 = .05$, $B_{N\{0, 3.8)} = .33$, *RR[0, 3.83*[5]*]*. We found no significant differences between congruent (M = 47.2cm, SD = 9.8cm) and incongruent (M = 48cm, SD = 11.4cm) hands, with the Bayes factor indicating weak support for the null or inconclusive evidence. However, there was a main effect of virtual hand size, $F(1, 16) = 10.86$, $p = .005$, $\eta_p^2 = .4$, $B_{H(0,8.5)} = 55.53$, *RR[0.42, 174.55*[6]*]*. There were significantly greater estimates of reach when the virtual hand was big (M = 49.5cm, SD = 9.8cm) versus small (M = 45.7cm , SD = 11.7cm), with the Bayes factor indicating strong support for the alternative hypothesis. There was no significant interaction between congruency and hand size, $F(1, 16) = 0.00008$, $p = .99$, $\eta_p^2 = 0.000005$, $B_{N\{0, 8.5)} = .99$, RR[0, 1470.75[7]]. The Bayes factor suggests that we do not have conclusive evidence on whether our data supports H1 or H0. See Figure 9 for a visual representation of the effect of virtual hand size on maximum reach estimates with respect to congruency.

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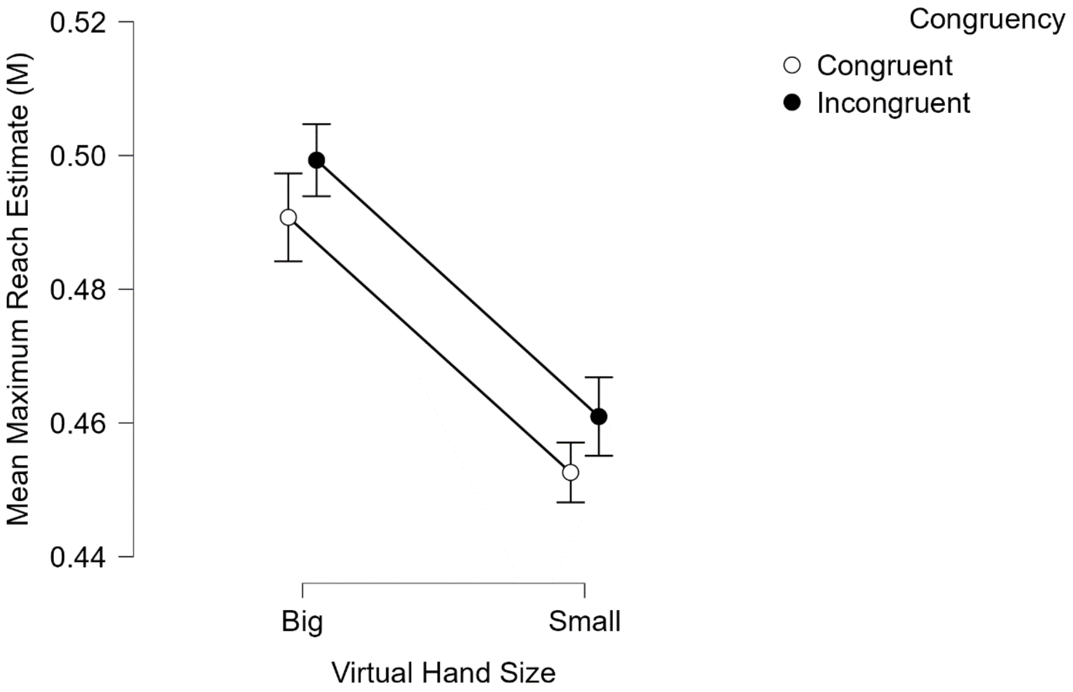
[5] We could not find previous research exploring the role of visuo-proprioceptive incongruency when calibrating to different virtual hand sizes. Therefore, we used the basic effect of hand size found in this study to model H1. We assumed a normal prior with mode = 0 and SD = 3.8.

[6] H1 was specified from the main effect of virtual hand size in Lin et al. (2020). Lin et al. found a main difference of 17cm in maximum reach estimates between virtual hand sizes that were 50% and 150% of normal hand size. As our manipulation used hand sizes that were 75% and 125% of normal hand size, we estimated the effect in our study to be roughly half of that from Lin et al. We assumed a half normal prior distribution with SD of 8.5.

[7] H1 was specified from half of the main effect of virtual hand size in Lin et al. to provide an approximate scale of effect for the interaction between virtual hand congruency and virtual hand size. We assumed a normal prior with mode = 0 and SD = 8.5.

Figure 9

Graph Showing the Effect of Hand Size with respect to Congruency on Reach Estimates

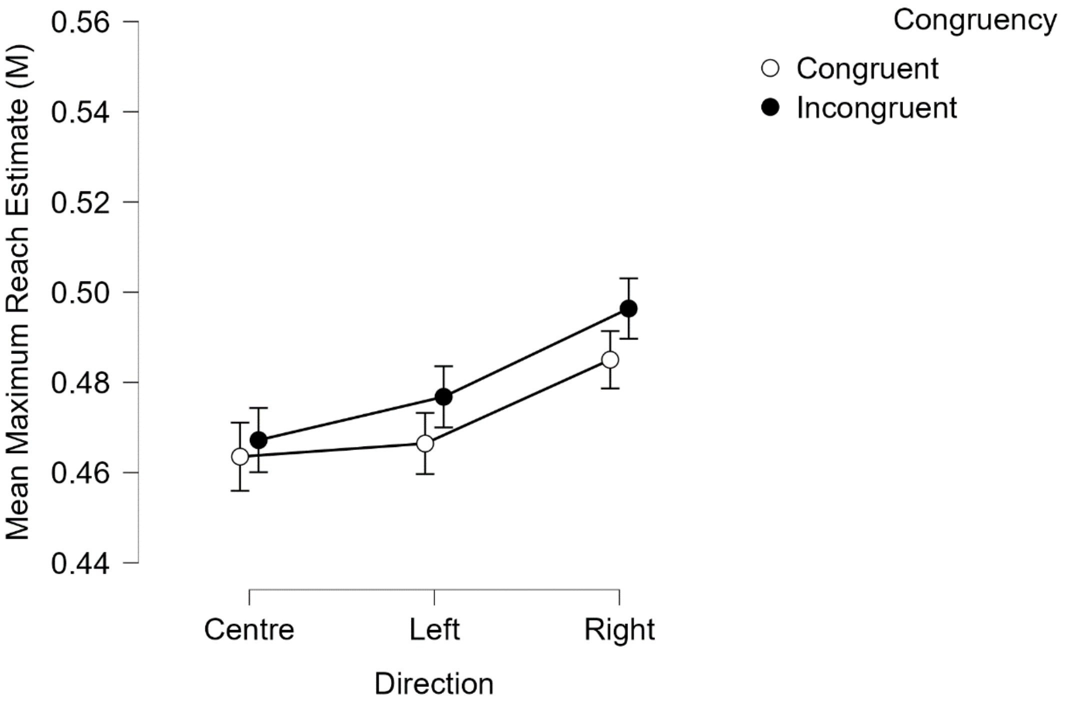


Note. Error bars show standard error.

There was a main effect of direction, $F(2, 32) = 20.95$, $p < .001$, $\eta_p^2 = .57$, with post-hoc t-tests with Bonferroni correction showing that reach estimates to the right (ipsilateral; $M = 49.1$cm, $SD = 10.5$cm) were significantly greater than estimates to the left (contralateral; $M = 47.2$cm, $SD = 10.3$cm) and centre ($M = 46.5$cm , $SD = 10.8$cm; see Figure 10). However, there were no significant differences in estimates of reach between the centre and left. Additionally, there was no main effect of hysteresis $F(1, 16) = 3.37$, $p = .09$, $\eta_p^2 = .17$, with no significant differences between estimates of reach when the estimation target started near ($M = 48.2$cm , $SD =10.4$cm) or far ($M = 47$cm , $SD = 10.8$cm) from the participant.

Figure 10

Effect of Reaching Direction on Maximum Reach Estimates with respect to Congruency



Note. Error bars represent standard error.

There was a significant interaction between hysteresis and direction $F(2, 32) = 3.46$, $p = .04$, $\eta_p^2 = .18$. When the target started near, estimates to the right were significantly higher than estimates to the centre and left, with no significant differences between estimates to the centre and left. When the target started far away, estimates to the centre were significantly lower than both estimates to the left and right. Estimates to the left were significantly lower than estimates to the right.

Furthermore, there was a significant interaction between size and hysteresis, $F(1, 16) = 4.9$, $p = .04$, $\eta_p^2 = .24$. With the big virtual hand, estimates when the target started near were significantly higher than when the target started far away. However, with the small virtual hand, hysteresis had no impact on reaching estimates.

However, there were no additional significant interactions between: congruency and hysteresis, $F(1, 16) = .11$, $p = .75$, $\eta_p^2 = .007$; congruency and direction, $F(2, 32) = .94$, $p = .4$,

η_p^2 = .06; size and direction, $F(2, 32) = 1.28$, $p = .29$, η_p^2 = .07; congruency, size and hysteresis, $F(1, 16) = .29$, $p = .59$, η_p^2 = .02; congruency, size, and direction, $F(2, 32) = 1.06$, $p = .36$, η_p^2 = .06; congruency, hysteresis, and direction, $F(2, 32) = 2.99$, $p = .06$, η_p^2 = .16; size, hysteresis, and direction, $F(2, 32) = 1.09$, $p = .35$, η_p^2 = .06; and finally, congruency, size, hysteresis, and direction $F(2, 32) = .36$, $p = .70$, η_p^2 = .02.

Study 4

Much like Study 1 with grasping, Study 3 demonstrates that people can embody a virtual hand and consider changes in hand size even when visual and somatosensory information specifying hand use are not congruent in the context of their maximum reaching capabilities. To address potential issues with demand characteristics that may occur when the virtual hands are obviously and consistently altered to either appear small or large, we explored whether estimates of maximum reach would be comparable between the congruent and incongruent presentation of the virtual hand when the size of the hand varied randomly throughout the calibration.

Methods

Participants

We carried forward the power analysis from Study 3, since Lin et al. (2020) included a variable reaching condition in their study. Therefore, we recruited 12 right-handed (8 female, 4 male) and 6 mixed-handed (4 female, 2 male, laterality quotients were between +27.27 - +53.84) individuals from Lancaster University (age range: 18-32 years, $M = 20.44$, $SD = 3.26$). Handedness was ascertained using the same method as Study 1. Participants were recruited via Lancaster University SONA system, or by posters placed around the university campus, and were paid £8.50 for their time. Data was collected in July 2022.

Materials

Virtual Environment

The virtual environment used is almost identical to Study 3. However, the virtual hand size varied between 75%, 100%, or 125% the size of the normal hand model, versus consistently being either 75% or 125% the size of the normal hand model.

Design

This was a 2 x 2 x 3 within-subjects design. There were three factors: first was the congruency between virtual hand and real hand (congruent vs incongruent); second was the starting position of the estimation target, also known as hysteresis (near vs far); fourth was direction of reaching estimate (centre vs left vs right). The dependent measure was the maximum estimated reaching distance, as measured by the final position of the estimation target.

Procedure

The procedure was almost identical to Study 3, except during the calibration the virtual hand would vary in size between 75%, 100%, and 125% the size of the normal hand model. Each hand size appeared with equal frequency, but in a random order, for the 60 calibration trials. The subsequent estimation phase was identical to Study 3. This procedure was repeated twice, once for each condition. Overall, the study took around 15 minutes to complete.

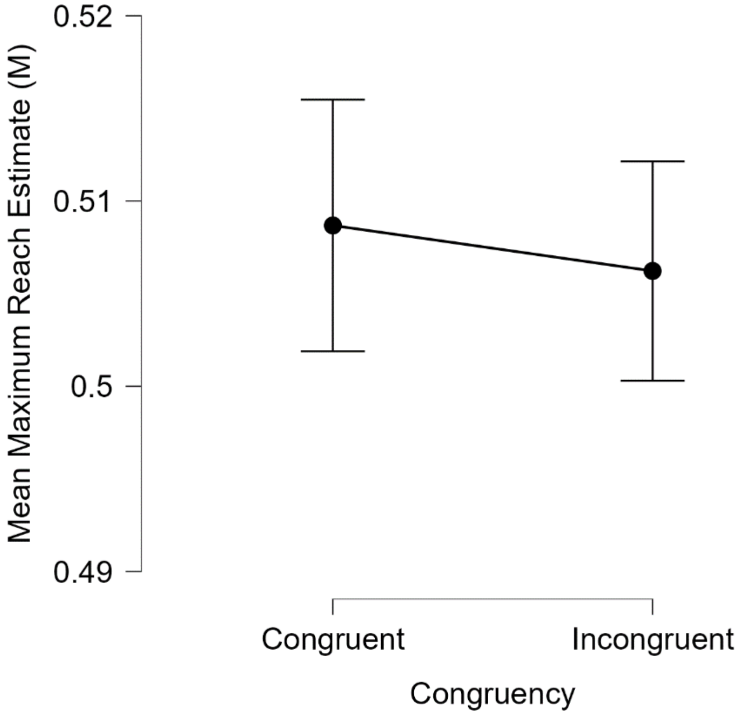
Results

Two participants were removed prior to analysis because they did not follow the instructions during the procedure correctly. A within-subjects ANOVA was conducted with real hand x virtual hand congruency (congruent vs incongruent), hysteresis (near vs far), and direction of reach (centre, left, right) as the independent variables and maximum reach estimate (as measured by the final position of the estimation target at the end of each trial) as the dependent variable. Bayes factors were calculated for all one degree-of-freedom tests. The main area of interest is the main effect of congruency.

There was no main effect of congruency, *F*(1, 15) = 0.09, *p* = .77, η_p^2 = .006, , $B_{N\{0, 3.8)}$ = .26, *RR[3,* ∞^{8}*]*. We found no significant differences between congruent (*M* = 50.9cm, *SD* = 8.1cm) and incongruent (*M* = 50.6cm, *SD* = 10.2cm) hands, with the Bayes factor suggesting moderate support for the null hypothesis (see Figure 11).

Figure 11

Graph showing the Effect of Congruency on Reach Estimates



Note. Error bars represent standard error.

However, there was a main effect of direction, *F*(2, 30) = 16.1, *p* < .001, η_p^2 = .52, with Bonferroni post-hoc t-tests showing that reach estimates to the right (ipsilateral; *M* = 52.9cm, *SD* = 9.3cm) were significantly greater than estimates to the left (contralateral; *M* = 50cm, *SD* = 8.4cm) and centre (*M* = 49.3cm , *SD* = 9.8cm). However, there were no significant differences in estimates of reach between the centre and left. Additionally, there was no main effect of hysteresis *F*(1, 15) = 1.37, *p* = .26, , η_p^2 = .08, with no significant

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[8] We could not find previous research exploring the role of visuo-proprioceptive congruency of virtual hands on maximum reach estimates. Therefore, H1 was modelled off the basic effect of hand size found in study 3. We assumed a normal prior with mode = 0 and SD = 3.8.

differences between estimates of reach when the estimation target started near (*M* = 51.4cm , *SD* = 8.7cm) or far (*M* = 50.1cm , *SD* = 9.9cm) from the participant.

There was a significant interaction between hysteresis and direction *F*(2, 30) = 5.43, *p* = .01, η_p^2 = .27. When the target started near, there were no significant differences in reach estimates to the centre and left. However, estimates to the right were significantly higher than estimates to the centre and left. When the target started far away, estimates to the centre were significantly lower than estimates to both the left and the right. In addition, estimates to the left were significantly lower than estimates to the right. However, there were no additional significant interactions between: congruency and hysteresis, *F*(1, 15) = 4.15, *p* = .06, η_p^2 = .22; congruency and direction, *F*(2, 30) = .54, *p* = .59, η_p^2 = .04; and lastly, congruency, hysteresis, and direction, *F*(2, 30) = 1.36, *p* = .27 η_p^2 = .08.

Discussion

In a set of four studies, we explored whether there would be significant differences in people's estimates of grasp and reach when we visually manipulated visual feedback about hand size. More specifically, we were interested in whether there would be differences in how people utilise visual feedback on hand size in estimates of their action boundaries when visual information specifying hand use was congruent or incongruent to somatosensory information specifying hand use. We used estimates of action capabilities as an indirect measure of embodiment. We investigated this issue because, to successfully interact with our environment, we must be able to adapt our action perception based on the dynamic relationship between our bodies and the world around us (Turvey, 2004). Thus, if changes to a virtual body are considered in people's estimates of their action capabilities, it stands to reason that those people consider the virtual body to be - to some degree – part of their own.

SoE is hypothesised to have three key subcomponents: sense of self-location, sense of agency, and sense of ownership (Longo et al., 2008; Kilteni et al, 2012; Tsakiris, 2010;

Tsakiris et al., 2010). Since these subcomponents can be considered dissociable and independent experiences (Tsakiris et al., 2010), we hypothesised that disruption to one's normal sense of self-location through mirroring the right hand to look like the left would not lead to a complete breakdown of embodiment if one's sense of agency over the virtual limb was preserved. Hence, there would be no significant differences in how visual feedback specifying hand size was used in estimates of reach and grasp when the virtual hand was congruent to the real hand being used versus when the virtual hand was incongruent.

In support of this hypothesis, in Study 1 we found that estimates of maximum grasp ability were significantly higher when the participant calibrated to the big virtual hand versus the small virtual hand. This finding replicates similar research done before by Readman et al. (2021). Additionally, in Study 1 we found no significant interaction between hand size and congruency, suggesting there were no significant differences in how participants calibrated to hand size regardless of the congruency of the hands. However, the Bayes factors on our data exploring both the effect of visuo-proprioceptive congruency and interactions between congruency and virtual hand sizes on maximum grasp estimates are not conclusive. Therefore, we can only tentatively suggest that people can calibrate to virtual hand sizes in the same way regardless of visuo-proprioceptive congruency.

We found the same pattern of results for Study 3, in which participants estimated their maximum reaching ability with respect to the big and small virtual hands, replicating and expanding on findings from Lin et al. (2020). Again, our data does not provide definitive support for either hypothesis for the effect of congruency nor the interaction between virtual hand size and congruency. From our current evidence, we suggest people can calibrate to different virtual hand sizes even when somatosensory and visual feedback specifying hand use is not congruent, particularly if the hand sizes are variable However, stronger evidence is needed to determine how the interaction between virtual hand size and visuo-proprioceptive congruency may impact estimates of reach and grasp.

While participants were able to calibrate to the sizes of the virtual hands and consider them in their estimates of maximum grasp and reach, they may not have calibrated to the changed location of the hand. In Study 3 and 4, there was a main effect of direction in that estimates to the right side of space were always further than estimates to the centre and to the left side. This effect persisted even when the virtual hand was presented to the left side of space, in which case it would be easier to reach to the left side than the right. There may be a couple of reasons for this finding. Firstly, mirroring the hand so that it appears visually on the opposite side of space may be too much of an adjustment for people to calibrate to, especially in the relatively short calibration phase experienced in Study 3 and 4. Thus, people would default to estimating their maximum reach with respects to where their real right arm would be in space, since this is the natural configuration that people have used throughout their lives.

Previous research has explored whether manipulating visual-proprioceptive spatial position offset – the distance between the proprioceptive cues and visual cues specifying hand position (Pritchard et al., 2016) – can impact ratings of embodiment. Pritchard et al. (2016) found that participants gave higher ratings of embodiment-location (that is, embodying the location of the virtual hand) when there was no spatial offset versus a 30cm spatial offset between the real and virtual hands. However, spatial offset did not have a significant impact on ratings of agency or ownership. The mirroring of the virtual hands in this current study would have created a considerable spatial offset between proprioceptive information specifying the location of the real hand and visual information specifying the location of the virtual hand, potentially lowering participant’s sense of being spatially present within the virtual body. Therefore, they would rely more on proprioceptive cues specifying location, and hence give estimates of reach that are consistent with the real right hand being used during the calibration.

Alternatively, the phrasing of the instructions for the estimation task may have inadvertently encouraged participants to view the estimation from the perspective of their real right hand. Since participants used their real right arm for the calibration, participants were asked to estimate their reach with ‘the right arm’. A key question of these studies was whether estimates of one’s action capabilities could change based on the visual presentation of virtual hands; therefore, it did not feel appropriate to lead participants to prioritise the properties of the virtual hand – such as location or size - if that were not a strategy they would ordinarily use. Indeed, if participants questioned whether they should consider their real arm or the virtual arm in their estimates, they were told to use whichever they deemed most appropriate. Changing the wording of the instructions for the estimation task to emphasise the virtual hand may, therefore, elicit different results in terms of reaching direction. Additionally, since the mirrored virtual hand visually becomes the left hand, this may have also influenced participants’ decisions to consider the position of their real right hand in their reaching estimates. Regardless of the reasoning, the lack of interaction between virtual hand congruency and reaching direction suggests that there is a dissociation between the participants’ abilities to update the representation of hand size and their ability to update the representation of the spatial location of the hand.

Since we used maximum grasp estimates and maximum reach estimates as indirect measures of embodiment, alternative direct measures of embodiment could be used with this paradigm for further research. For example, Longo et al. (2008) generated an embodiment questionnaire that separately investigated the impact of the rubber hand illusion regarding the subcomponents of self-location, agency, and ownership. Using such a questionnaire may be the next step to further understanding the degree to which certain aspects of embodiment may be affected by mirroring the hands in such a manner. Specifically, a more precise measure of sense of self-location after the calibration phase could inform us on whether the felt position of the actual hand changed at all. Thus, this would provide more insight into the finding that estimates of reach ipsilateral to the actual hand were always further than central or contralateral estimates. Currently, we cannot say for certain which subcomponents of SoE were satisfied to create a sense of embodiment that was sufficient for participants to at least calibrate to the size of the virtual hands and use them in their estimates of grasp and reach. However, from participants' action estimates, we can at least tentatively suggest that participants can calibrate to virtual hand sizes even when proprioceptive feedback is incongruent to visual feedback.

Overall, these four experiments provide some evidence that people can calibrate to different virtual hand sizes and consider changes to their action capabilities when estimating their maximum grasping and reaching abilities, even when proprioceptive and visual information specifying hand use are incongruent. Stronger evidence is needed, however, to generate more robust conclusions on the role of visuo-proprioceptive incongruency on calibration to different virtual hand sizes. In addition, people do not calibrate to extreme discrepancies in spatial location of the real and virtual hands. Further research should focus on using more direct measures of embodiment to tease apart why visual changes to hand size were considered in estimates, but not changes to the visually specified spatial location of the hand. Additionally, further research should carefully consider the wording of instructions when asking participants to estimate their action capabilities to assess whether the instructions themselves impact peoples' abilities to calibrate to different aspects of the virtual hand.

References

Carello, C., Grosofsky, A., Reichel, F. D., Solomon, H. Y., & Turvey, M. T. (1989). Visually perceiving what is reachable. *Ecological Psychology*, *1*(1), 27–54. https://doi.org/10.1207/s15326969eco0101_3

Dienes, Z. (2019). How do I know what my theory predicts? *Advances in Methods and Practices in Psychological Science*, *2*(4), 364–377. https://doi.org/10.1177/2515245919876960

Dienes, Z., & Mclatchie, N. (2018). Four reasons to prefer bayesian analyses over significance testing. Psychonomic Bulletin & Review, 25(1), 207–218. https://doi.org/10.3758/s13423-017-1266-z

Durgin, F. H., Baird, J. A., Greenburg, M., Russell, R., Shaughnessy, K., & Waymouth, S. (2009). Who is being deceived? the experimental demands of wearing a backpack. *Psychonomic Bulletin & Review*, *16*(5), 964–969. https://doi.org/10.3758/pbr.16.5.964

Fajen, B. (2005). Perceiving Possibilities for Action: On the Necessity of Calibration and Perceptual Learning for the Visual Guidance of Action. *Perception*, *34*(6), 717-740. https://doi.org/10.1068/p5405

Fajen, B., Riley, M., & Turvey, M. (2009). Information, affordances, and the control of action in sport. *International Journal of Sport Psychology*, *40*(1), 79–107.

Gibson, J. J. (1979). The ecological approach to visual perception. Boston,MA: Houghton Mifflin

Ishak, S., Adolph, K., & Lin, G. (2008). Perceiving affordances for fitting through apertures. *Journal Of Experimental Psychology: Human Perception and Performance*, *34*(6), 1501-1514. https://doi.org/10.1037/a0011393

Kilteni, K., Groten, R., & Slater, M. (2012). The sense of embodiment in virtual reality. *Presence: Teleoperators and Virtual Environments*, *21*(4), 373–387. https://doi.org/10.1162/pres_a_00124

Lakens, D., McLatchie, N., Isager, P. M., Scheel, A. M., & Dienes, Z. (2018). Improving inferences about null effects with Bayes factors and equivalence tests. The Journals of Gerontology: Series B, 75(1), 45–57. https://doi.org/10.1093/geronb/gby065

Lin, L., McLatchie, N., & Linkenauger, S. (2020). The influence of perceptual–motor variability on the perception of action boundaries for reaching. *Journal of Experimental Psychology: Human Perception and Performance*, *46*(5), 474-488. https://doi.org/10.1037/xhp0000724

Linkenauger, S. A., Leyrer, M., Bülthoff, H. H., & Mohler, B. J. (2013). Welcome to wonderland: The influence of the size and shape of a virtual hand on the perceived size and shape of virtual objects. *PLoS ONE*, *8*(7). https://doi.org/10.1371/journal.pone.0068594

Linkenauger, S. A., Witt, J. K., Stefanucci, J. K., Bakdash, J. Z., & Proffitt, D. R. (2009). The effects of handedness and reachability on perceived distance. *Journal of Experimental Psychology: Human Perception and Performance*, *35*(6), 1649–1660. https://doi.org/10.1037/a0016875

Longo, M. R., Schüür, F., Kammers, M. P. M., Tsakiris, M., & Haggard, P. (2008). What is embodiment? A psychometric approach. *Cognition*, *107*(3), 978–998. https://doi.org/10.1016/j.cognition.2007.12.004

Petkova, V. I., Khoshnevis, M., & Ehrsson, H. H. (2011). The Perspective Matters! multisensory integration in ego-centric reference frames determines full-body ownership. *Frontiers in Psychology*, *2*. https://doi.org/10.3389/fpsyg.2011.00035

Pijpers, J. R., Oudejans, R. R., & Bakker, F. C. (2007). Changes in the perception of action possibilities while climbing to fatigue on a climbing wall. Journal of Sports Sciences, 25(1), 97–110. https://doi.org/10.1080/02640410600630894

Pritchard, S. C., Zopf, R., Polito, V., Kaplan, D. M., & Williams, M. A. (2016). Non-hierarchical influence of visual form, touch, and position cues on embodiment, agency, and presence in virtual reality. *Frontiers in Psychology*, *7*. https://doi.org/10.3389/fpsyg.2016.01649

Readman, M., Cooper, D., & Linkenauger, S. (2021). It's in your hands: How variable perception affects grasping estimates in virtual reality. *Psychonomic Bulletin & Review*, *28*(4), 1202-1210. https://doi.org/10.3758/s13423-021-01916-x

Sato, A., & Yasuda, A. (2005). Illusion of sense of self-agency: Discrepancy between the predicted and actual sensory consequences of actions modulates the sense of self-agency, but not the sense of self-ownership. *Cognition*, *94*(3), 241–255. https://doi.org/10.1016/j.cognition.2004.04.003

Slater, M., Spanlang, B., Sanchez-Vives, M. V., & Blanke, O. (2010). First person experience of body transfer in virtual reality. *PLoS ONE*, *5*(5). https://doi.org/10.1371/journal.pone.0010564

Tsakiris, M. (2010). My body in the brain: A neurocognitive model of body-ownership. *Neuropsychologia*, *48*(3), 703–712. https://doi.org/10.1016/j.neuropsychologia.2009.09.034

Tsakiris, M., Longo, M. R., & Haggard, P. (2010). Having a body versus moving your body: Neural signatures of agency and body-ownership. *Neuropsychologia*, *48*(9), 2740–2749. https://doi.org/10.1016/j.neuropsychologia.2010.05.021

Turvey, M. T. (2004). Space (and its perception): The first and final frontier. *Ecological Psychology*, *16*(1), 25–29. https://doi.org/10.1207/s15326969eco1601_3

Wagman, J. B. (2012). Perception of maximum reaching height reflects impending changes in reaching ability and improvements transfer to unpracticed reaching tasks. *Experimental Brain Research, 219*(4), 467–476. https://doi.org/10.1007/s00221-012-3104-x

Witt, J., Proffitt, D., & Epstein, W. (2005). Tool Use Affects Perceived Distance, But Only When You Intend to Use It. *Journal Of Experimental Psychology: Human Perception and Performance*, *31*(5), 880-888. https://doi.org/10.1037/0096-1523.31.5.880

Appendix A: Coordinates of Calibration Circles for the Grasping Calibration

Calibration circle 1 (x-axis)	Calibration circle 2 (x-axis)	Both calibration circles (z-axis)
.05	.22	.1
.05	.1	.1
.05	.12	.2
.05	.1	.2
.0625	.175	.1
.0625	.175	.2
.075	.25	.1
.075	.15	.2
.0875	.225	.1
.0875	.125	.2
.1	.28	.1
.1	.2	.2
.1	.28	.2
.125	.275	.1
.125	.275	.2
.15	.25	.1
.15	.25	.2
.175	.225	.1
.175	.225	.2
.2	.38	.1
.2	.3	.1
.2	.3	.1
.2	.3	.2
.2	.38	.2
.225	.375	.1
.225	.375	.2
.25	.35	.1
.25	.35	.2
.275	.325	.1
.275	.325	.2

Note. The y-axis was kept constant at .47 across all trials. The x-axis was flipped (i.e. negative) when reaching to the left side of space.

Appendix B: Coordinates of Calibration Circles for the Reaching Calibration

X-axis	Z-Axis
.05	.1
.05	.1
.05	.2
.05	.2
.0625	.1
.0625	.2
.075	.1
.075	.2
.0875	.1
.0875	.2
.1	.1
.1	.2
.1	.2
.125	.1
.125	.2
.15	.1
.15	.2
.175	.1
.175	.2
.2	.1
.2	.1
.2	.1
.2	.2
.2	.2
.225	.1
.225	.2
.25	.1
.25	.2
.275	.1
.275	.2

Note. The y-axis was kept constant at .47 across all trials. The x-axis was flipped (i.e. negative) when reaching to the left side of space.

Chapter 4

The Effect of Mirrored Virtual Hands in Actions Towards Visual Illusions

Previous research using visual illusions suggests that there is a double dissociation between visual processing used for perception and action. The magnitude of size-contrast illusions, such as the Ebbinghaus Illusion, is consistently higher when using perceptual measures versus action measures, such as grasping. In addition, the right hand may be more resistant to the illusion than the left, with grasps towards objects embedded in visual illusions using the right hand showing a significantly lower magnitude than grasps using the left hand. The greater resistance to the illusion in the right hand may suggest that mechanisms for visuomotor control are lateralised to the left hemisphere.

In a set of two studies, I investigated how people interact with the Ebbinghaus illusion in virtual reality. In the first study I attempted to see whether manipulating visual feedback specifying handedness when grasping would impact susceptibility to the illusion in each hand. In a follow-up study, I explored potential differences in grasping behaviours towards real and virtual objects embedded in the Ebbinghaus illusion.

Can the Left Hand Benefit from Being Right? Overcoming Visual Illusions

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Author note:

On behalf of all authors, the corresponding author states that there is no conflict of interest.

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Study data used in analysis are publicly available on the Open Science Framework: https://osf.io/n74bs/ Study analysis code is not available. Study materials are available upon reasonable request.

Abstract

Previous research into motor asymmetries suggest a left-hemisphere advantage for visually guided actions. Specifically, when grasping objects whose perceived size are influenced by size-contrast illusions, the right hand's grip aperture the actual metrics of the object rather than its perceived size. In contrast, the grip aperture left hand can be affected by size-contrast illusions. To investigate the origin of the right-hand advantage for visually guided actions, this study aimed to see if mirroring the left hand to take advantage of the visual information associated with moving the right hand could enable it to develop accurately scaled grips to objects affected by size-contrast illusions. Twenty-five participants made precision grip movements towards the centre circle of various Ebbinghaus display in a virtual environment. In two conditions, the seen virtual hand would be congruent with the physical moving hand while in the other two conditions, the seen virtual hand would be incongruent with the physical moving hand. We found that maximum grip aperture was influenced by the illusion except the condition when the right hand animated the right virtual hand. These results are discussed in the context of interacting in virtual versus real worlds, and the visual processing used to direct actions in these different environments.

Keywords: right-handed individuals, mirror visual feedback, virtual reality, two-streams hypothesis

Public Significance Statement – Results of this study revealed that participants experienced a significant impact of the Ebbinghaus illusion on maximum grip aperture when using their left hand, and when their right hand was mirrored to look like the left. However, these results are not conclusive. This study provides insight into the nature of interacting with virtual objects, and how visual processing directing action may differ between the real world and immersive virtual environments.

Can the Left Hand Benefit from Being Right? Overcoming Visual Illusions

The two-streams hypothesis, proposed by Goodale and Milner (1992), suggests that two distinct neural pathways process visual information regarding either conscious identification or action. The ventral stream processes visual information associated with identification, which computes the size, location, shape and orientation of an object primarily in relation to other objects. In contrast, the dorsal stream processes visual information for action performance by using body centric metrics, rather than relative to environmental context, so that movements towards target objects are scaled accurately with respect to movement (Westwood & Goodale, 2003).

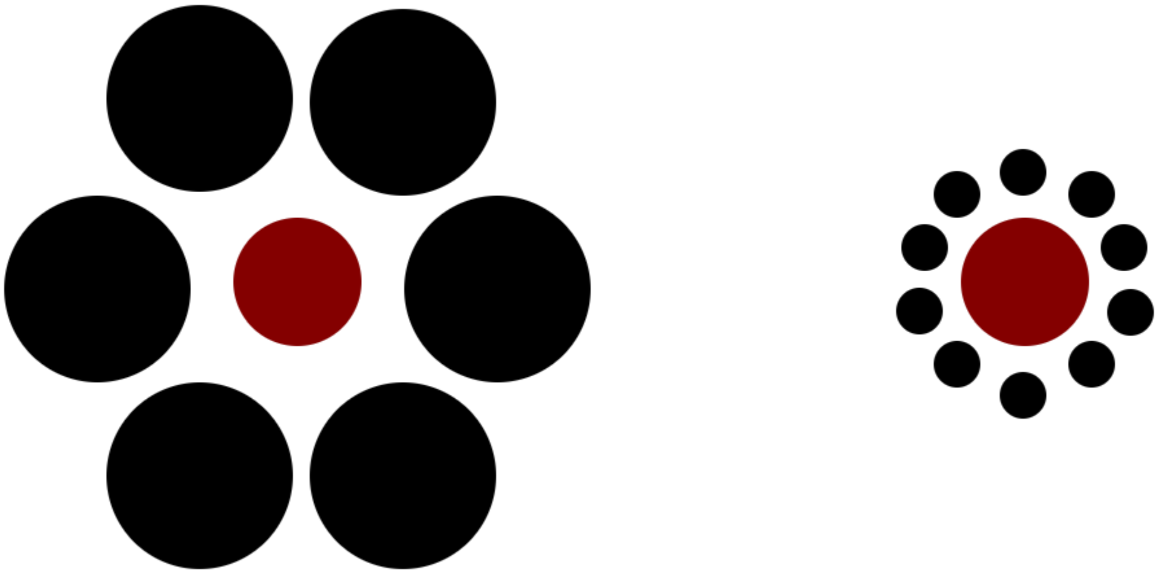
Evidence for this hypothesis - and therefore a dissociation in the processing of visual information for identification and action – was first found in patients with brain lesions. Goodale et al (1991) conducted a single case study with patient DF, who suffers with visual apperceptive agnosia due to bilateral lesions to the lateral occipital cortex. Despite showing severe deficits in discriminating the shape and orientation of objects, patient DF could accurately orient her hand to fit through an aperture or shape her fingers appropriately for the size of an object she was about to pick up. In contrast, other cases involving bilateral parietal damage demonstrate impairments in action while shape processing and visual recognition remain intact (Ellis & Young, 1996). However, the problem with evidence from lesion case studies is that it is unclear whether the ventral stream would process visual information for object recognition in the same way if the dorsal stream was not damaged (and vice versa).

Fortunately, evidence for a dissociation between action and identification can be found in the neurotypical population through exploring perceptual and motoric responses to objects affected by size-contrast illusions. A key example is the Ebbinghaus (or Titchener) Illusion, an illusion in which a target circle is surrounded by either larger or smaller circles.

Small surrounding circles induce larger perceptions of the target circle's size and large surrounding circles induce smaller perceptions of the target's circle size (see Figure 1). This illusion is robust perceptually with past research consistently finding a large magnitude of the illusion across several psychophysical measures. Despite the perceived differences in centre circle size, precision grasp measurements - specifically the maximum grip aperture (MGA) - have been shown to be either unaffected or significantly less impacted than perceptual measures, such as verbal estimates and visual matching (Aglioti et al., 1995; Haffenden & Goodale, 2000). This difference suggests that grips are scaled to the actual metrics of the object, rather than being influenced by adjacent objects (Aglioti et al., 1995; Haffenden & Goodale, 2000). As such, vision for action and vision for perception are two distinct processes (Goodale & Milner, 1992).

Figure 1

An Example of the Ebbinghaus (or Titchener) Illusion



However, controversy exists surrounding whether evidence from visual illusions and lesion case studies is sufficient support for the two-streams hypothesis. Critics suggest that, during perceptual estimates of target circle size in previous studies (see Aglioti et al., 1995; Haffenden & Goodale, 1998), study designs typically require people make direct comparisons between the two target circles, thereby increasing the magnitude of the illusion (Franz et al., 2000). Conversely, during tasks involving grasping the centre circles, even if the composite version of the illusion is presented to participants during prehension, they are focusing on only one target circle and not making a direct comparison. When the perceptual and motor tasks are modified by presenting only one set of circles (out of the two in the Ebbinghaus figure) at a time (single context versions) to reduce this discrepancy, no evidence was found for a difference between perceptual and motoric estimates of target circle size (Franz et al., 2000).

The authors suggest that the Ebbinghaus illusion, therefore, does not provide evidence for two distinct visual pathways for perception and action (Franz et al., 2000). However, this finding can still be reconciled within the two-streams hypothesis. Perceptual estimates of object size in the Ebbinghaus illusion can be explained by a relative-size scaling mechanism, in which an object that is smaller than its surroundings is judged to be smaller than an object that is larger than its surroundings. However, when it comes to prehension, rather than making a comparison between the two objects, the focus is on calculating the metrics of the target itself (Aglioti et al., 1995). Additionally, a direct comparison between the two objects is necessary to maximise the magnitude of the illusion – if the stimuli being used does not elicit a perceptual illusion, it is questionable how it can provide the means to make conclusions on the two-streams hypothesis (Jacob & Jeannerod, 1999). Thus, Franz et al (2000) do not provide convincing evidence that contradicts the mechanisms proposed by Aglioti et al. (Carey, 2001).

More uncertainty arises when exploring the effect of size-contrast illusions on manual prehension. Some studies show that left hand prehension is impacted by the Ebbinghaus and Ponzo illusions, while the right hand scaled grips are less or not affected (Gonzalez et al., 2006). Others demonstrate no effect of the illusion in prehension of either hand when the action is simple to execute or well-practiced (Gonzalez et al., 2008). If the action is unfamiliar or difficult, such as prehension using the thumb and ring finger, both hands are initially impacted by the illusion. After a few sessions of training however, the illusion of the magnitude decreases for the right hand but not the left (Gonzalez et al., 2008). This raises the question of whether there is an inherent advantage in the right hand due to hemispheric specialisation of visuomotor mechanisms in the left hemisphere which allows the right hand to pick up skilled actions more quickly and easily (Fisk & Goodale, 1998; Flindall et al., 2014) or whether mere practice with the action leads to changes in visual processing of the information directing the action.

One question that has not been explored is how the left hand may be trained to overcome the illusion and accurately scale grips to the actual target size. Repetitive training seems to be ineffective in reducing illusion magnitude in the left hand, but what if it took advantage of some of the information and visual motor processing normally associated with moving the right? A left hemisphere advantage is not only shown in this task, but to a range of other tasks as well. A study exploring hand preference across the lifespan found a strong right-hand preference for grasp-to-eat tasks (even in the left-handed population, see Flindall et al., 2015), and the authors suggest a left-hemisphere specialisation for grasping on a more general scale (Gonzalez et al., 2015). Furthermore, in a simple reach-to-point task in which the target abruptly moved to the left or right, RHIs were faster at acquiring the new target location with their right hand than their left (Elliott et al., 1995).

Additionally, evidence from lesion studies demonstrate that patients with left-hemisphere lesions took significantly longer to complete the reaching stage of a reach-to-grasp movement. Conversely, those with right-hemisphere lesions performed comparably to neurotypical controls, being able to update trajectory during reach (Fisk & Goodale, 1998). This suggests the left hemisphere is heavily involved in using visual and proprioceptive information when making visually guided movements, and is key for quickly updating movement trajectory to meet the correct end-point (Elliott et al., 1995). Whether this advantage is primarily due to more efficient proprioceptive processing, more efficient visual processing, or an equal combination of both, is unclear. Based on the evidence that more efficient visuomotor processing in the left hemisphere controlling the right hand exists in grasping movements (Fisk & Goodale, 1998; Flindall et al., 2014; Gonzalez et al., 2008; Gonzalez et al., 2015) perhaps allowing the left hand to utilise the visual information associated with moving the right hand will help its actions become resistant to visual illusions when engaging in target directed movements, such as grasping.

To explore this possibility, we used virtual reality and motion tracking to animate and mirror the hands in real time, so that movements of the actual left hand are mapped as movements of the right hand in the virtual environment from an egocentric perspective and vice versa. Thus, we isolated the visual feedback associated with moving the right hand from other types of sensory feedback that would normally be experienced. Please note that we were **not** attempting to alter the neuroanatomical setup of the left hand being controlled by the right hemisphere using this methodology. We are simply exploring whether visual feedback associated with moving the right hand when using the left is sufficient to elicit the improved performance of the right hand in visually guided tasks.

In this study, participants made precision grip and reaching movements towards target objects affected by the Ebbinghaus illusion, and we compared maximum grip aperture

(MGA) between the handedness conditions. Based on previous research, we expect that in normal viewing conditions, the right hand will demonstrate no effect of the illusion on MGA, while the left hand may show an effect. If visual processing plays a key role in the right-hand advantage, we may see a reduction in the illusion in the left hand when it is mirrored to look like the right. Conversely, it is also possible that the right hand may show an increased magnitude of the illusion during prehension when viewed as the left if less efficient visual processing to the left side of the body impairs performance in this task.

Additionally, this study also explores the how virtual reality affects the visual control of action and dorsal processing. A key distinction must be made in the cognitive processes associated with interacting with a real object, versus 'pantomiming' an action. For example, reach-to-grasp movements towards target objects are considerably different when performed in real-time or performed with a delay (so that the target object is no longer visible), and the latter may be mediated by the ventral stream rather than the dorsal stream (Goodale et al., 1994; Westwood et al., 2000). Thus, actions towards 'real' objects differ to actions towards 'non-real' or imagined objects due to reliance on different visual streams. A key question is to what extent objects in virtual reality are considered 'real' as, while visually present, cannot elicit haptic feedback. Therefore, it is possible that due to the nature of the virtual objects used in this study that no difference will be found in MGA between the hand conditions due to reliance on the ventral visuomotor processing.

Methods

Transparency and Openness

The study design, hypotheses and analysis plan were not preregistered. We report how we determined our sample size, all data exclusions (if any), all manipulations and all measures in the study. Data were analysed using SPSS version 28.0. Analysis code is not available as

SPSS does not have the functionality to export syntax. Data are publicly available at: https://osf.io/n74bs/

Participants

A priori power analysis using MorePower 6.0 (Campbell & Thompson, 2012) was conducted using information on the sample size and F-values from a previous study by Gonzalez et al. (2006), which investigated illusion magnitude in grasping with the Ebbinghaus illusion. Using a sample of 26, Gonzalez et al., found a main effect of hand on illusion magnitude, achieving an F-value of 16.29. According to the power analysis, they would have achieved a power of .97, which is more than sufficient. Therefore, we recruited 17 right-handed (13 female, 4 male), 2 left-handed (1 female, 1 male), and 6 mixed-handed (4 female, 2 male) individuals from Lancaster University (age range: 18 – 39 years, *M* = 20.65, *SD* = 4.33). Handedness was assessed using the 10-item Edinburgh Handedness Inventory (Oldfield, 1971), with scores >+60 being assigned as right-handed, scores between +59 - -59 being assigned as mixed-handed, and scores <-60 being assigned as left-handed. Participants were recruited from Lancaster University SONA system. Participants of all types of handedness were recruited as previous research suggests that the hemispheric specialisation of motor control, specifically precision grasping, that underlies the right-hand resistance to grasping visual illusions is independent of handedness (Gonzalez et al., 2006). However, the majority of our participants were right-handed. They were either awarded 2 credits as part of their undergraduate psychology course or £7.00 for their participation. All participants first gave written informed consent before participating. Data was collected in January - March 2019.

Materials

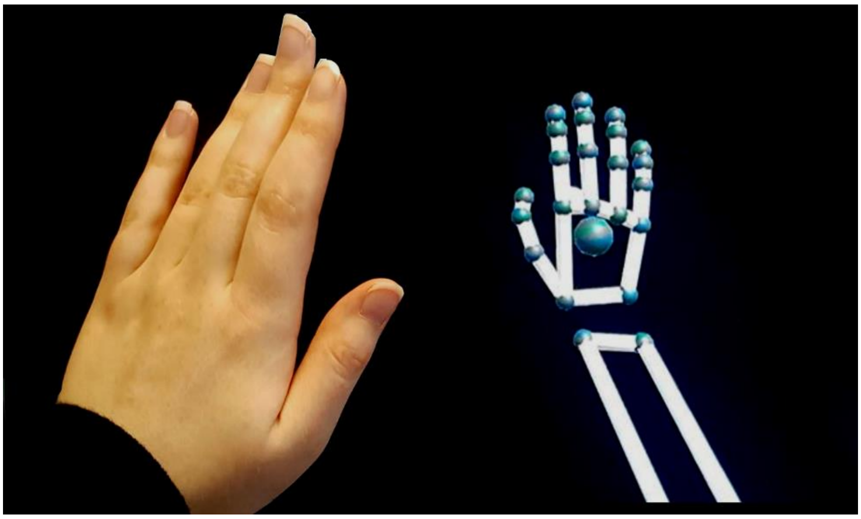
For descriptions of specific objects in the virtual environment, it is difficult to give exact real-world dimensions as Unity Version 2018.2.8f1 (Unity Technologies, San Fransisco, California, United States) uses unique scaling. However, descriptions will assume that 1 unit in Unity is equal to 1 real-world metre as specified by the specs provided by unity. Coordinates of where virtual objects are placed are specific to the virtual environment and will not reflect any real-world coordinates.

Virtual Environment

Participants wore an Oculus CV1 virtual reality (VR) headset which placed participants in a virtual environment (VE) that consisted of a table (70cm height, 3m length) and a black screen (1.5m x 1.5m) placed at a 90-degree angle on the table. Eye height was standardised for all participants at 1.085m from the virtual floor. A LEAP motion sensor was attached to the front of the headset that tracked participants' hand movements in real time. Hand movements were animated using Leap Motion 'capsule hand' models (Leap Motion, Inc., San Francisco, California, United States). When the virtual hands were mirrored, both the spatial layout and representation of the hand itself were flipped (i.e. if the right hand was controlling the left virtual hand, participants would see a left virtual hand in the left-side of space, see Figure 2).

Figure 2

Visual Representation of the Left Hand Mirrored as Right

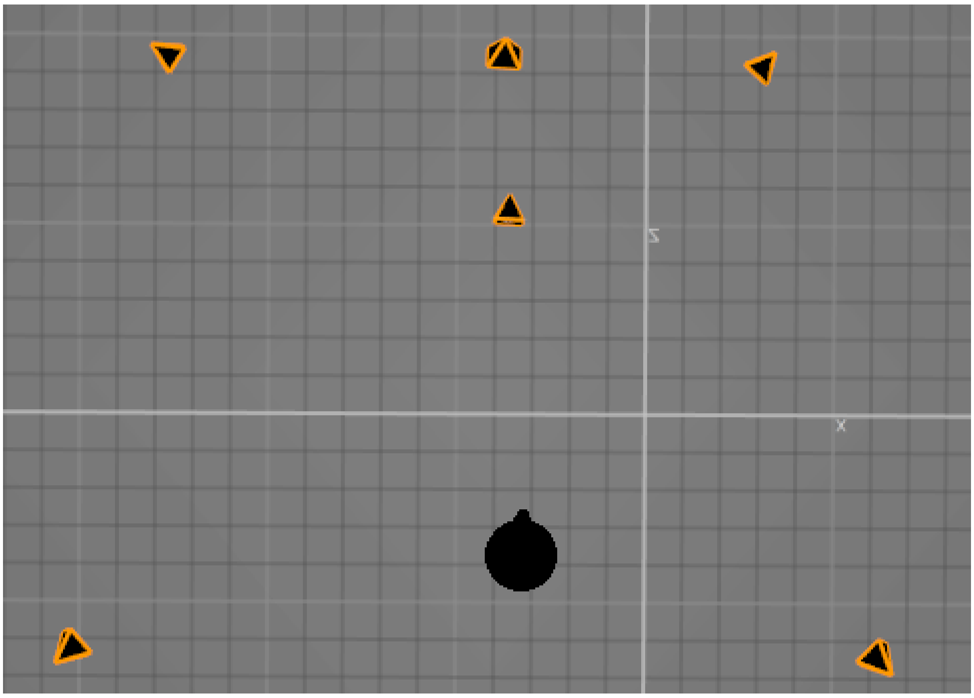


Motion Tracking

Maximum grip aperture was recorded using six OptiTrack (NaturalPoint, Inc., Corvallis, Oregon, United States) Flex-13 motion capture cameras (see Figure 3 for the configuration of the Optitrack cameras as shown in the OptiTrack motion software). The OptiTrack cameras tracked the 3d position of 1cm diameter reflective markers that were attached as close as possible to the tip of the thumb and index fingers of both hands (see Figure 4).

Figure 3

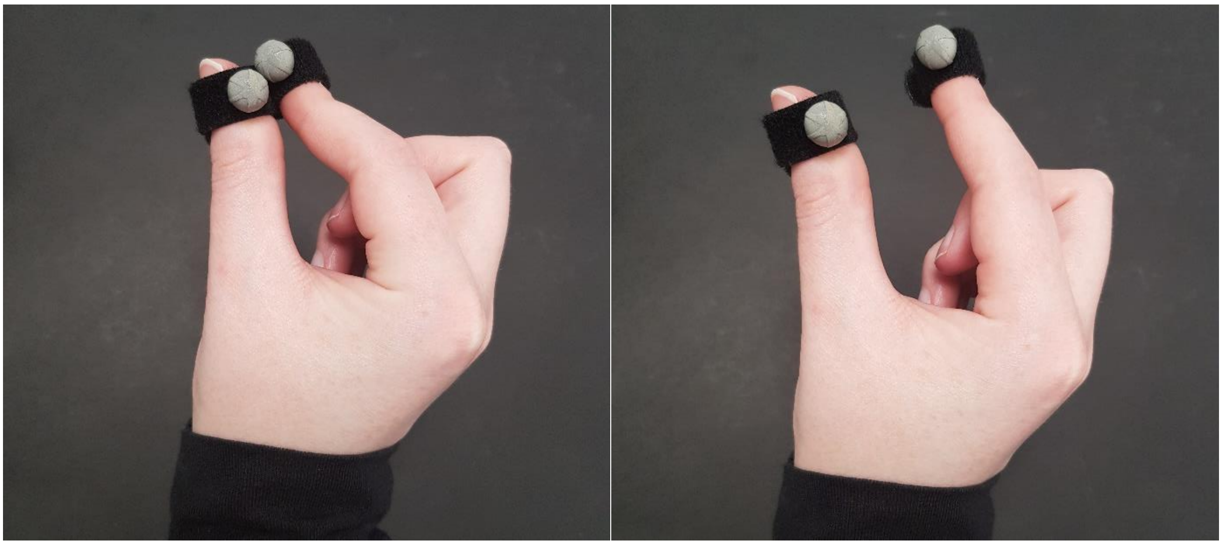
Configuration of OptiTrack Cameras from Birds-eye View



Note. Participant position and orientation is represented by the black circle

Figure 4

Positions of 3D Reflective Markers Worn by Participants

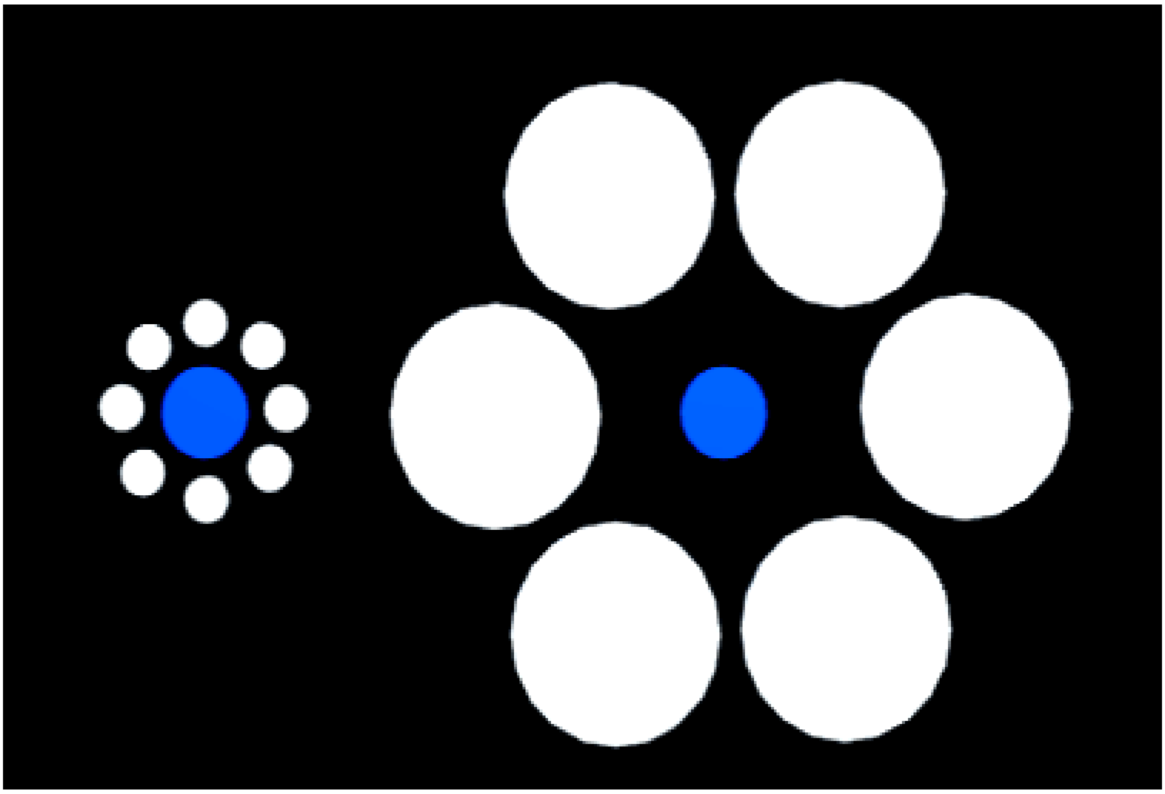


Visual Stimulus

The main stimuli used were various Ebbinghaus illusion displays. Each configuration was one blue target circle (5cm in diameter, 1cm depth) surrounded by white outer circles. These white outer circles would either be smaller (2.5cm in diameter, 1cm depth) or larger (12cm in diameter, 1cm depth) than the blue target circle (see Figure 5). The distance between the centre of the blue centre circles and the centre of 'large' outer circles was approximately 13.8cm. The distance between the centre of the blue centre circles and the centre of the 'small' outer circles was approximately 4.7cm. The distance between the centre of the two blue centre circles was approximately 19.9cm The Ebbinghaus illusion was presented directly in front of participants on the black screen at a 90-degree angle perpendicular to the virtual table.

Figure 5

An Example of the Visual Stimulus Shown to Participants



Design

There were two factors: first was the condition that participants performed the action in (RR = right hand presented as right, LL = left hand presented as left, RL = right hand presented as left, LR = left hand presented as right); second was the illusory size of the inner circles in the Ebbinghaus illusion (big vs small). The dependent variable was maximum grip aperture (MGA) in millimetres when gripping towards one of the target circles.

Procedure

Before participation, participants provided informed consent and had the task explained to them. Participants then sat on a chair surrounded by the Optitrack motion cameras (as shown in Figure 3) and wore the head-mounted display to put them in the virtual environment where they completed the calibration and main task. For each condition, participants first completed a calibration phase consisting of 50 trials. The hand the participant used and on which they received visual feedback during calibration was dependent on the condition they were assigned: the physical right hand was used in RR and RL, and the physical left hand in LL and LR. During the calibration, participants were instructed to simply reach and point to a red circle (2cm in diameter and 2cm in depth) that would alternate between 10 different positions on the black screen (see Appendix A for exact positions of the calibration circles). The calibration was designed to get participants used to the visual feedback they would receive when moving their hand in the VE. Then, participants moved onto the main trial phase, using the same hand as the calibration.

For each trial, participants would first see a small white circle (1cm in diameter and 1cm in depth) that appeared for 1000ms either to the left ($X = -0.949$, $Y = -0.019$) or right ($X = 1.038$, $Y = -0.019$) of the black screen to act as a cue to which target circle the participant should reach towards. Then 1000ms after the cue had disappeared, the Ebbinghaus Illusion appeared for 1000ms, with the blue centre circles placed in the same position as the preceding cues. Participants were instructed to keep their thumb and index fingers pressed together with their hand placed in their lap until they saw the Ebbinghaus Illusion. As soon as the Ebbinghaus Illusion appeared, participants would reach and grip towards the cued inner circle using their thumb and index finger, scaling their grip to the width of the inner circle. Once they had completed this movement, the participant would place their thumb and index finger together with their hand in their lap ready for the next trial. Reach direction and target circle size were randomized. All possible conditions of trials were each repeated for 60 trials for each condition for a total of 240 trials.

Results

Two participants were removed from analysis as they did not follow the procedure correctly. Two further participants were removed from analysis due to errors in the motion tracking that led to more than 20% of missing data values. This left 21 participants as the final sample.

A univariate ANOVA split by condition, with illusory circle size as the fixed factor and participant as a random factor, was conducted to assess differences in mean MGA for target circles surround by large versus small circles in the different conditions (right as right (RR) vs left as left (LL) vs left as right (LR) vs right as left (RL))[1]. There was a main effect of illusory circle size on MGA in LL ($F(1, 20.04) = 6.18$, $p = .022$, $\eta_p^2 = .24$) with significantly larger grips with the ‘larger’ circle (*M* = 56.59mm, *SD* = 1.29mm) than the ‘smaller’ circle (*M* = 54.22mm, *SD* = 1.30). There was a main effect of illusory circle size on MGA in LR ($F(1, 20.01 = 4.4$, $p = .049$, $\eta_p^2 = .18$) with significantly larger grips with the

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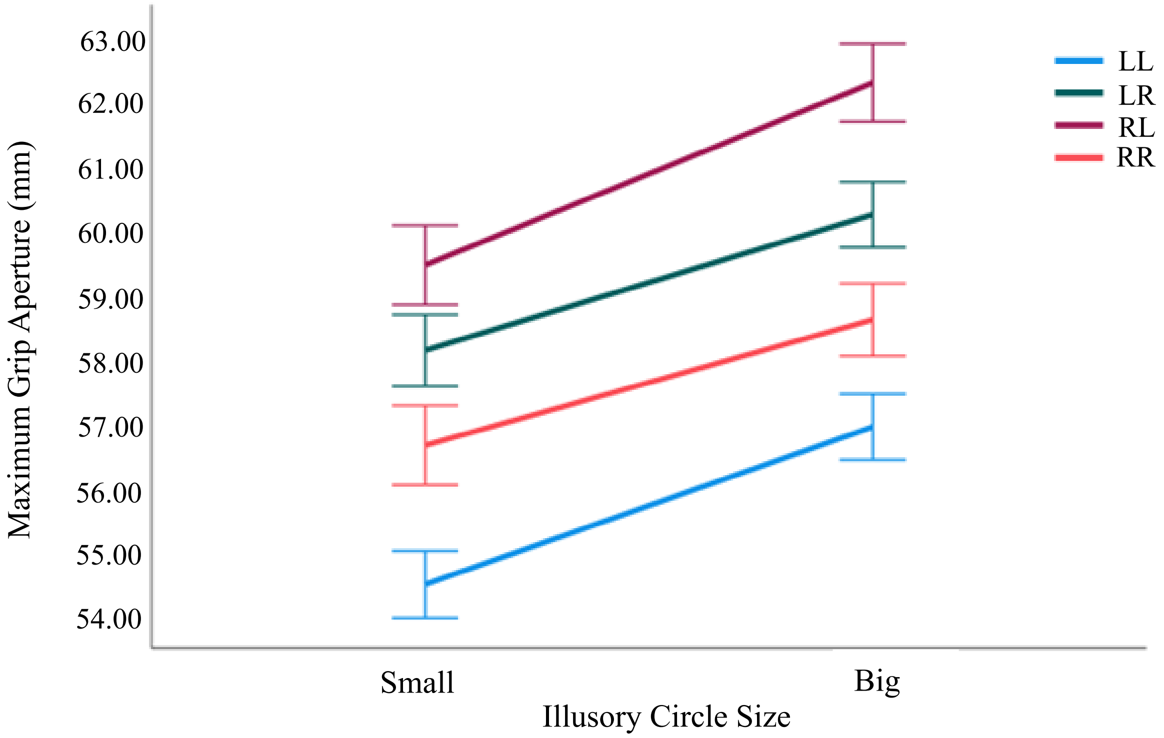
[1] A univariate ANOVA split by condition was used in place of a repeated measures ANOVA as there were a variable number of missing data points in each condition. This was due to errors in the Optitrack software used to collect MGA.

‘larger’ circle (*M* = 60.04mm, *SD* = 1.49mm) than the ‘smaller’ circle (*M* = 58.08, *SD* = 1.48mm). There was a main effect of illusory circle size on MGA in RL (*F*(1, 20.01) = 7.5, *p* = .013, η_p^2 = .27) with significantly larger grips with the ‘larger’ circle (*M* = 62.17mm, *SD* = 1.66mm) than the ‘smaller’ circle (*M* = 59.36mm, *SD* = 1.65mm). However, there was no main effect of illusory circle size in RR (*F*(1, 20.03) = 4.002, *p* = .059, η_p^2 = .17) with no significant differences in MGA between the ‘larger’ circle (*M* = 58.46 mm, *SD* = 1.29mm) and the ‘smaller’ circle (*M* = 56.346mm, *SD* = 1.29mm). We did not find any significant interactions. See Figure 6 for a visual representation of the effect of illusory object size in each condition.

Another Univariate ANOVA, with congruency as the fixed factor and participant as a random factor, was conducted to assess differences in mean MGA between ‘congruent’ (‘RR’ and ‘LL’) and ‘incongruent’ (‘RL’ and ‘LR’) conditions. We found a main effect of congruency *F*(1, 20.001) = 4.80, *p* = .40, η_p^2 = .19), with grips made with incongruent visual and proprioceptive information being significantly larger (*M* = 59.95mm, *SD* = 0.84mm) than grips made with congruent visual and proprioceptive information (*M* = 56.51mm, *SD* = 0.85mm).

Figure 6

The effect of the Ebbinghaus Illusion on MGA in Each Condition



Note. Error bars represent standard error.

Discussion

We hypothesized that in normal viewing conditions, the right hand will show no difference in MGA between the ‘small’ and ‘large’ circles, whereas the left hand will show an effect of the illusion. We also anticipated that if more efficient visuomotor feedback underlies the right-hand advantage in resisting size-contrast illusions, mirroring the left hand to look like the right may result in a decrease in illusion magnitude on MGA with training, and mirroring the right hand to look like the left may result in an increase in illusion magnitude on MGA. However, in this study, we found a main effect of perceived object size in that the ‘larger’ centre circle elicited significantly larger MGAs, on average, than the ‘smaller’ centre circle, in all conditions except RR. That is, the MGA of the right hand, under normal viewing conditions, appeared to be uninfluenced by the surrounding circles (illusion). Therefore, our findings do not support the hypothesis that the left hand can benefit from the visual processing of the right side of the body to overcome visual illusions in the context of grasping the Ebbinghaus illusion.

The findings of this study do not provide a clear picture into the underlying mechanisms behind the right-hand resistance to grasping of visual illusions demonstrated in some previous research due to ambiguity of our results in replicating original research. It is unclear whether this right-hand advantage existed in this study, although the differences in MGA between the large and small circle were not statistically significant in the RR condition. This lack of significance was borderline (marginally significant) and visual inspection of the data suggests all conditions experienced a similar degree of illusion magnitude. Hence, this lack of finding in the RR condition should be approached with extreme scepticism.

Although the answer to our main research question remains unclear, our results do provide some interesting insights into the nature of interacting with virtual objects and the potential implications this has into using VR as a tool for researching motor control. Firstly, the findings suggest there may be inherent differences in performing actions in VR and real life (Chessa et al., 2019; Harris et al., 2019). Most previous research into the impact of size-contrast illusions on manual prehension is done with real objects in the real world; whereas, this study was done completely in a VE. Hence, participants interacted with objects that were simulated and therefore not physically present and did not provide haptic feedback. Therefore, it is possible that participants' actions may have been more akin to pantomiming rather than directly interacting with the object in the same way as they would in the real world through goal-directed actions (Freud et al., 2018).

Consistent with this speculation, previous research has shown differences in the kinematic execution of goal directed versus pantomimed actions. When performing a reach-to-grasp towards an imagined object, peak velocity was consistently slower and the action took significantly longer in comparison to natural grasping to real objects (Goodale et al., 1994b). Interestingly, individuals with visual form agnosia, a deficit associated with disrupted ventral processing, can perform successfully goal directed grasping actions towards targets; however, their grasping movements become completely disrupted when asked to pantomime the same action (Goodale et. al, 1994). Additionally, previous research has found that when individuals are asked to grasp, pantomime the grasp, or make verbal size judgements, MGA in the pantomime condition tend to show the illusion in a similar magnitude as in the verbal judgements, while MGA in the goal directed grasp did not show evidence of the illusion (Westwood, Chapman & Roy, 2000).

As a result, these findings suggest that pantomimed actions rely largely on ventral stream processing rather than dorsal stream processing (Goodale et al., 1994). Removing haptic feedback from the goal objects in this study may have induced a switch from typical motor control in real grasping - which relies primarily on dorsal processes - and instead encouraged participants to use a more cognitively driven strategy that relies more on ventral processes (Whitwell et al., 2015). Since the ventral stream processes visual information of an object (such as size) in relation to other objects (Goodale & Milner, 1992), we likely found differences in MGA in this study for the perceptually larger circle (but not physically larger), because participants were using ventral stream processing to direct their actions similar to previous research in pantomiming. Hence, our results suggest that grasping movements in VR may be similar to pantomiming and engage **ventral** rather than dorsal processing. This finding highlights a problematic issue for the use of VR for training scenarios which involve motor control. This evidence suggests training in VR for physical rehabilitation and even user interface training (such as driving and piloting), may not generalise to the real world, at least for grasping movements that require a good deal of precision or on objects in the context of other objects. Some evidence exists that certain motor elements are extremely similar in VR as in the real world and can transfer well (Levac et al., 2019). So, these differences beg the question as to which actions are similar and dissimilar in real and VEs and what can this difference tell us about dorsal and ventral processing for different actions.

In addition, the visual display presented in virtual reality subtly differs from visual displays in the real world, primarily due to artificial presentation of depth in VEs as well as resolution of the virtual scene. The presentation of objects at varying depths on a screen placed at a fixed depth close to the eyes means that vergence, an important binocular depth cue for dorsal processing (Mon-Williams et al., 2001), is disrupted. As such, the visual system may rely more on ventral processes when guiding actions in VEs than in the real world (Harris et al., 2019). Finally, a study by Mann and Van der Kamp (2014) found that scaling of grip to objects placed against an illusory background in a VE is altered more than if this grip is performed in a real environment, suggesting that visually guided actions are more sensitive to visual illusions in a VE. Therefore, a combination of differences in visuomotor processing between actions performed in the real world (that relies primarily on egocentric processing mediated by the dorsal stream) and in VEs (that may rely on allocentric processing mediated by the ventral stream; Foley et al., 2015) may account for the differences we see in this study in comparison to real-world studies (Mann & Van der Kamp, 2014).

Despite these concerns about whether action in a virtual environment is comparable to the real world, this study demonstrates how people **can** effectively recalibrate to these virtual mirrored hands in the context of grasping. Although MGA was larger when the hands were mirrored, the illusion magnitude is very similar to when the hands are presented with congruent visual and proprioceptive information. This indicates that people were able to effectively adjust their grip to the perceived differences in the sizes of the objects when proprioceptive and visual information were incongruent, in much the same way as they would in normal viewing conditions. Also, the variability in MGA in the mirrored and non-mirrored conditions were extremely similar. In other words, these results clearly show that participants could adapt to and effective use the virtual hands even when they were mirrored. Thus, this mirror technique in VR could potentially be developed as a tool to enhance mirror visual feedback (MVF) therapy, although more research would need to be done to see if different types of action aside from grasping are as successful during this visuomotor recalibration.

Overall, the aim of this study was to assess whether mirroring the left hand to exploit the visual feedback associated with moving the right hand could allow the left hand to develop resistance to size-contrast illusions when performing reach-to-grasp movements. We found a main effect of illusory object size on MGA except in the RR condition, although this is uncertain. Therefore, in this instance mirroring the left hand did not generate any improvement in the accuracy of MGAs. More research should be conducted further exploring the effects of mirror training in VEs to assess whether differences in visual processing between VEs and real-world environments negatively impacts transferability of skills developed in VEs.

Constraints on Generality

As all participants in this study were healthy undergraduate university students aged between 18-39 years (with a mean age of 20.65 years), it is possible that the findings would not generalise to differently aged populations, such as older adults. This is because old age is associated with reduced mobility of the hand (Holt et al., 2013), hence reduced mobility could impact the ability to adjust MGA accurately to the target object size. Additionally, children may elicit different results as some evidence suggests children are less susceptible to the Ebbinghaus illusion (Doherty et al., 2010). The experimental stimuli are all presented in a virtual environment; however, manipulating sensory feedback in the way we have done in this study is not easily achieved in the real-world. Overall, the results of this study would best generalise to healthy, young adults who complete this study within an immersive virtual environment.

Data Accessibility Statement

The data used in analysis are publicly available on the Open Science Framework: https://osf.io/n74bs/ Study analysis code is not available. Study materials are available upon reasonable request.

References

Aglioti, S., DeSouza, J., & Goodale, M. (1995). Size-contrast illusions deceive the eye but not the hand. *Current Biology*, *5*(6), 679-685. https://doi.org/10.1016/s0960-9822(95)00133-3

Carey, D. P. (2001). Do action systems resist visual illusions? *Trends in Cognitive Sciences*, *5*(3), 109–113. https://doi.org/10.1016/s1364-6613(00)01592-8

Chessa, M., Maiello, G., Klein, L., Paulun, V., & Solari, F. (2019). Grasping objects in immersive Virtual Reality. In IEEE Conference on Virtual Reality and 3D User Interfaces (VR) (pp. 1749-1754), https://doi.org/10.1109/VR.2019.8798155. IEEE; IEEE. Retrieved 18 August 2022, from https://ieeexplore.ieee.org/abstract/document/8798155.

Doherty, M. J., Campbell, N. M., Tsuji, H., & Phillips, W. A. (2010). The ebbinghaus illusion deceives adults but not young children. Developmental Science, 13(5), 714–721. https://doi.org/10.1111/j.1467-7687.2009.00931.x

Elliott, D., Lyons, J., Chua, R., Goodman, D., & Carson, R. (1995). The Influence of Target Perturbation on Manual Aiming Asymmetries in Right-Handers. *Cortex*, *31*(4), 685-697. https://doi.org/10.1016/s0010-9452(13)80020-2

Ellis, A., & Young, A. (1996). *Human cognitive neuropsychology*. Hove: Psychology Pr.

Flindall, J., Stone, K., & Gonzalez, C. (2015). Evidence for right-hand feeding biases in a left-handed population. Laterality: Asymmetries of Body, Brain and Cognition, *20*(3), 287-305. https://doi.org/10.1080/1357650x.2014.961472

Foley, R., Whitwell, R., & Goodale, M. (2015). The two-visual-systems hypothesis and the perspectival features of visual experience. Consciousness And Cognition, 35, 225-233. https://doi.org/10.1016/j.concog.2015.03.005

Franz, V., Gegenfurtner, K., Bülthoff, H., & Fahle, M. (2000). Grasping Visual Illusions: No Evidence for a Dissociation Between Perception and Action. *Psychological Science*, *11*(1), 20-25. https://doi.org/10.1111/1467-9280.00209

Freud, E., Macdonald, S. N., Chen, J., Quinlan, D. J., Goodale, M. A., & Culham, J. C. (2018). Getting a grip on reality: Grasping movements directed to real objects and images rely on dissociable neural representations. Cortex, 98, 34–48. https://doi.org/10.1016/j.cortex.2017.02.020

Furmanek, M., Schettino, L., Yarossi, M., Kirkman, S., Adamovich, S., & Tunik, E. (2019). Coordination of reach-to-grasp in physical and haptic-free virtual environments. *Journal Of Neuroengineering and Rehabilitation*, *16*(1). https://doi.org/10.1186/s12984-019-0525-9

Gonzalez, C., Ganel, T., & Goodale, M. (2006). Hemispheric Specialization for the Visual Control of Action Is Independent of Handedness. *Journal Of Neurophysiology*, *95*(6), 3496-3501. https://doi.org/10.1152/jn.01187.2005

Gonzalez, C., Ganel, T., Whitwell, R., Morrissey, B., & Goodale, M. (2008). Practice makes perfect, but only with the right hand: Sensitivity to perceptual illusions with awkward grasps decreases with practice in the right but not the left hand. *Neuropsychologia*, *46*(2), 624-631. https://doi.org/10.1016/j.neuropsychologia.2007.09.006

Gonzalez, C. L. R., Flindall, J. W., & Stone, K. D. (2015). Hand preference across the lifespan: Effects of end-goal, task nature, and object location. *Frontiers in Psychology, 5,* Article 1579. https://doi.org/10.3389/fpsyg.2014.01579

Goodale, M., Jakobson, L., & Keillor, J. (1994b). Differences in the visual control of pantomimed and natural grasping movements. *Neuropsychologia*, *32*(10), 1159-1178. https://doi.org/10.1016/0028-3932(94)90100-7

Goodale, M., Meenan, J., Bülthoff, H., Nicolle, D., Murphy, K., & Racicot, C. (1994). Separate neural pathways for the visual analysis of object shape in perception and prehension. *Current Biology*, 4(7), 604-610. https://doi.org/10.1016/s0960-9822(00)00132-9

Goodale, M., Milner, A., Jakobson, L., & Carey, D. (1991). A neurological dissociation between perceiving objects and grasping them. *Nature*, *349*(6305), 154-156. https://doi.org/10.1038/349154a0

Goodale, M., & Milner, A. (1992). Separate visual pathways for perception and action. *Trends In Neurosciences*, *15*(1), 20-25. https://doi.org/10.1016/0166-2236(92)90344-8

Haffenden, A.M., & Goodale, M.A. (1998). The effect of pictorial illusion on prehension and perception. *Journal of Cognitive Neuroscience, 10*(1), 122–136. https://doi.org/10.1162/089892998563824

Haffenden, A., & Goodale, M. (2000). Independent effects of pictorial displays on perception and action. *Vision Research*, *40*(10-12), 1597-1607. https://doi.org/10.1016/s0042-6989(00)00056-0

Harris, D., Buckingham, G., Wilson, M., & Vine, S. (2019). Virtually the same? How impaired sensory information in virtual reality may disrupt vision for action. *Experimental Brain Research*, *237*(11), 2761-2766. https://doi.org/10.1007/s00221-019-05642-8

Holt, R. J., Lefevre, A. S., Flatters, I. J., Culmer, P., Wilkie, R. M., Henson, B. W., Bingham, G. P., & Mon-Williams, M. (2013). Grasping the changes seen in older adults when reaching for objects of varied texture. PLoS ONE, 8(7). https://doi.org/10.1371/journal.pone.0069040

Jacob, P. and Jeannerod, M. (1999) Consciousness and the visuomotor transformation. *CNRS Institute of Cognitive Science* (http://www.isc.cnrs.fr/wp/wp99–13.htm)

Levac, D. E., Huber, M. E., & Sternad, D. (2019). Learning and transfer of complex motor skills in virtual reality: A perspective review. Journal of NeuroEngineering and Rehabilitation, 16(1). https://doi.org/10.1186/s12984-019-0587-8

Mann, D., & van der Kamp, J. (2014). Visually-guided interceptive actions performed in virtual environments [Abstract]. Journal Of Vision, 14(10), 842-842. https://doi.org/10.1167/14.10.842 Abstract retrieved from https://jov.arvojournals.org/article.aspx?articleid=2144719

Mon-Williams, M., Tresilian, J., McIntosh, R., & Milner, D. (2001). Monocular and binocular distance cues: insights from visual form agnosia I (of III). *Experimental Brain Research*, *139*(2), 127-136. https://doi.org/10.1007/s002210000657

Roy, E., Kalbfleisch, L., & Elliott, D. (1994). Kinematic Analyses of Manual Asymmetries in Visual Aiming Movements. *Brain And Cognition*, *24*(2), 289-295. https://doi.org/10.1006/brcg.1994.1017

Westwood, D., Chapman, C., & Roy, E. (2000). Pantomimed actions may be controlled by the ventral visual stream. *Experimental Brain Research*, *130*(4), 545-548. https://doi.org/10.1007/s002219900287

Westwood, D., & Goodale, M. (2003). A haptic size-contrast illusion affects size perception but not grasping. *Experimental Brain Research*, *153*(2), 253-259. https://doi.org/10.1007/s00221-003-1599-x

Whitwell, R., Ganel, T., Byrne, C., & Goodale, M. (2015). Real-time vision, tactile cues, and visual form agnosia: removing haptic feedback from a “natural” grasping task induces pantomime-like grasps. *Frontiers In Human Neuroscience*, *9*. https://doi.org/10.3389/fnhum.2015.00216

Appendix A

Positions of Calibration Circles on the Black Screen in the Virtual Environment

Circle Number	X position on black screen	Y position on black screen
1	0.031	-1.806
2	1.037	-0.766
3	0.691	-1.173
4	-1.062	-0.686
5	-1.415	-2.866
6	-1.348	-1.646
7	1.464	-3.180
8	0.851	-2.120
9	-0.888	-2.413
10	-0.448	-0.079

Note. Coordinates are presented to 3 decimal places and are therefore not exact.

Getting to Grips with the Ebbinghaus Illusion: Grasping in Virtual Reality versus the Real World

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Word Count: 5,795

Abstract

Virtual reality (VR) is a tool that is becoming rapidly popular for motor control research. However, differences in visual processing in VR as well as the lack of haptic feedback present when interacting with virtual objects, may have consequences on the transferability of skills assessed in VR versus the real world. To assess how differences in visual processing may impact actions performed in VR, we had 24 participants from Lancaster University perform grasps towards objects embedded in the Ebbinghaus illusion. We compared maximum grip aperture (MGA) when participants grasped objects in both the real world and in VR. We found that MGA when grasping the perceptually larger object was smaller than when grasping the perceptually smaller object. The results suggest that participants demonstrated a strategy of obstacle avoidance and were not affected by any perceptual effects of the illusion when grasping. The results are discussed in the context of obstacle avoidance when interacting with objects embedded in the Ebbinghaus illusion, as well as differences between interacting in VR and the real world more generally.

Keywords: Ebbinghaus illusion, Virtual Reality, Grasping

Getting to Grips with the Ebbinghaus Illusion: Grasping in Virtual Reality versus the Real World

Virtual reality (VR) is a tool that is rapidly becoming popular for physical and motor control research (Keshner, 2004) due to its ability to generate an immersive and engaging environment that is comparable to the real world (Levin et al., 2015). VR has many strengths for rehabilitation versus performing motor research within the real world. These include precise stimulus control and consistency, real-time feedback, the ability to easily modify the training environment and increased motivation for the user (Keshner, 2004). Users can interact with objects directly via hand gestures and body movements (Levin et al., 2015) using software that tracks and animates hand movements in real time, such as the Leap Motion Controller (Leap Motion, Inc., San Francisco, California, United States).

While practice of motor tasks within VR can offer benefits for users seeking rehabilitation, researchers and practitioners should consider the transferability of skills developed within virtual environments (VEs) to the real world (Levac et al., 2019). One advantage of VR rehabilitation programs is their ability to present any scenario within a VE, allowing patients undergoing rehabilitation to perform very similar behaviours as would be experienced in the real world (Howard, 2017). For example, researchers could develop an immersive VE in which patients need to grasp an object from a shelf in a supermarket, a task that is commonly done in real life. These research designs contrast with many typical real-world rehabilitation programs which develop activities through repetitive, abstract tasks that do not resemble typical activities and may be limited by the clinical environment in which the rehabilitation takes place (Howard, 2017). Thus, VR may be an extremely beneficial tool for rehabilitation and development of motor skills, particularly for the upper limbs.

However, one aspect of VR rehabilitation to consider is how visual feedback for action may be processed differently to visual feedback delivered from movement in the real world. Specifically, we will focus on natural grasping movements moving forward. In natural grasping movements, grasping is directed at the goal object and executed with online visual feedback (Whitwell et al., 2015). This grasping action is mediated by the dorsal stream, which processes visual feedback to generate the appropriate sensorimotor transformations to successfully grasp the object (Goodale & Milner, 1992). Vitally, the goal object will also provide haptic feedback once contact has been made. However, when haptic feedback on the target object is not given, the grasp no longer resembles a natural grasp but becomes more ‘pantomimed’, with increases in grip aperture and slower movement velocity (Whitwell et al., 2015). Thus, removing haptic feedback of the target object induces a switch from real-time visual control mediated by dorsal processes towards a grasping strategy that relies more on visual perception mediated by ventral processes (Westwood et al., 2000; Whitwell et al., 2015). Additionally, fMRI of natural and pantomimed grasping movements reveals that brain regions typically activated by real actions may not be activated through pantomimed actions (Króliczak et al., 2007). Thus, pantomimed actions performed towards virtual objects have different kinematics and neural activations to the real action.

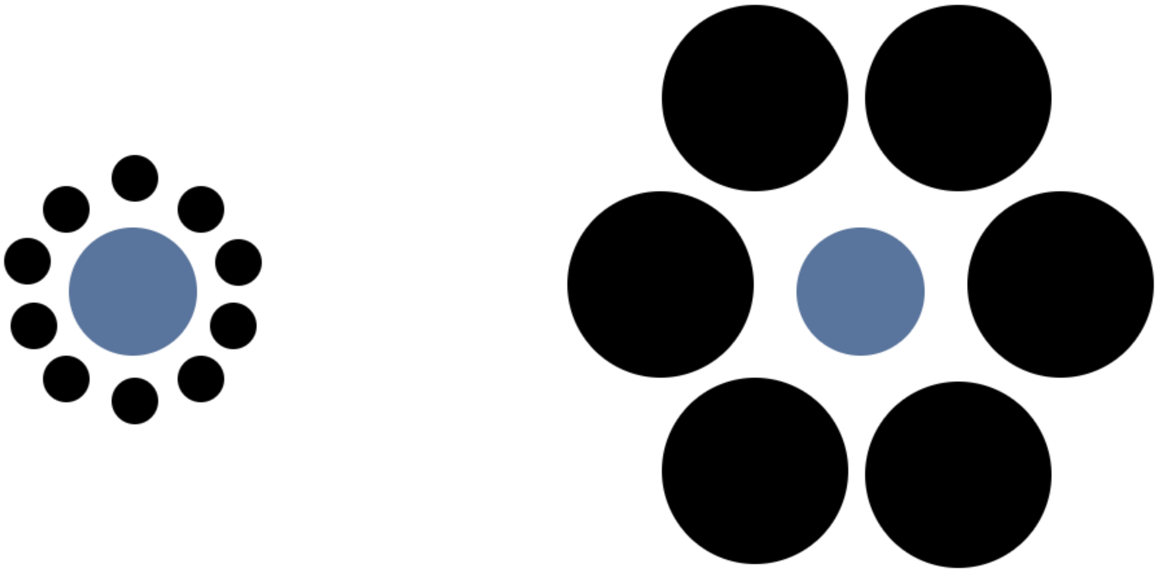
Moreover, viewing objects within an immersive VE has important differences to viewing them within the real world. More specifically, depth cues used within the real world and in VEs can differ quite dramatically. In the real world, a variety of different depth cues - such as binocular disparity and vergence – are used to construct perceived depth. However, when there is a conflict between vergence and other depth cues, vergence becomes much less reliable (Harris et al., 2019; Mon-Williams & Tresilian, 1999). In the case of head-mounted displays, the screen presenting the VE is placed at a fixed depth from the eyes. This means vergence, an important binocular depth cue for dorsal processing (Mon-Williams et al., 2001) is disrupted when processing objects at varying depths within the VE (Harris et al., 2019). Furthermore, a lack of prior experience with interacting with virtual objects may make retinal image size – another effective depth cue – less reliable (Harris et al., 2019). Therefore, more weight may be afforded to ventral visual processing, rather than dorsal, when interacting with virtual objects (Harris et al., 2019).

Previous research has explored differences in grasping behaviours towards virtual and real objects (see Chessa et al., 2019 and Furmanek et al., 2019 for examples). However, this research focused on exploring the differences in grasping behaviours towards virtual objects in the context of them lacking haptic feedback. Therefore, more research is needed to consider differences in visual processing that may underlie differences in grasping behaviours between real life and VR. One way to explore dorsal and ventral processing in VR may be to utilise visual illusions, such as the Ebbinghaus (or Titchener) illusion. The Ebbinghaus illusion has previously been used to provide evidence of the double dissociation between vision-for-perception and vision-for-action in neurologically healthy people (Aglioti et al., 1995; Haffenden & Goodale, 2000). Therefore, it would be a beneficial tool to use to explore differences in dorsal and ventral visual processing when performing actions in VR versus real life.

The Ebbinghaus Illusion is a size contrast illusion in which two target circles are surrounded by smaller or larger circles (see Figure 1). The perceived size of the target circles varies depending on whether the surrounding circles are smaller or larger than the target circles. Using perceptual measures, such as manual or verbal estimation, elicits a strong magnitude of illusory differences in target circle size. Despite these perceived differences, maximum grip aperture (MGA) when performing precision grasps towards the target circles elicit a far lower magnitude of the illusion (Aglioti et al., 1995; Haffenden & Goodale, 1998). Therefore, precision grasps to the target circles are scaled to actual metrics of the object, rather than being influenced by adjacent objects (Aglioti et al., 1995; Haffenden & Goodale, 1998). Thus, the Ebbinghaus illusion is a useful tool for exploring whether action in VR may be mediated more by dorsal or ventral processing, due to its previous use in differentiating vision-for-action and vision-for-perception (Goodale & Milner, 1992).

Figure 1

An Example of the Ebbinghaus Illusion



The purpose of this current study is not to provide support for nor contradict the two-streams hypothesis. However, it is important to at least acknowledge a key alternative account for the discrepancy between perceptual estimates and grip scaling in the Ebbinghaus illusion to appropriately justify its implementation in this study. Some critics suggest that during perceptual estimation tasks people make direct comparisons between the two target circles, thereby increasing the magnitude of the illusion (Franz et al., 2000). However, during grasping tasks, attention is focused on just one target circle and people fail to attend to the surrounding context, hence the magnitude of the illusion is decreased (Franz et al., 2000). However, more recent evidence contests this account. Whitwell et al. (2023) replicated the classic dissociation between action and perception with the Ebbinghaus illusion. Importantly, they found that the percentage of fixation time or fixations directed at the target circles during grasping or manually estimating the target circles did not explain this dissociation (Whitwell et al., 2023). Therefore, with this most recent evidence and other empirical studies consistently demonstrating the dissociation between action and perception in the Ebbinghaus illusion (Aglioti et al., 1995; Haffenden & Goodale, 1998; Pavani et al., 1999), we consider it an appropriate tool to explore potential differences in dorsal and ventral visual processing when performing actions in VR.

The main goal of this study was to explore whether grasping actions performed in virtual reality may rely more on ventral visual processing than similar actions performed in the real world. To do this, we created two versions of the Ebbinghaus illusion – one in the real world and one in VR. Within VR, we used motion tracking to animate hand movements in real time so that people could see their hands in a way they would be able to in the real world. We then had participants reach and grasp target circles embedded within the Ebbinghaus illusion in both the real world and VR whilst measuring MGA. If grasping within VR does indeed rely on more ventral visual processes, we would expect that the magnitude of the Ebbinghaus illusion reflected by differences in MGA between the ‘big’ and ‘small’ target circles would be greater than the magnitude found in the real world. When the illusion does impact MGA, we expect that grasps to the perceptually larger object will be larger than grasps to the perceptually smaller object. Additionally, we predict that grasping with the right hand will elicit a smaller magnitude of the illusion than grasping with the left, based on previous research that suggests visuomotor mechanisms within the left hemisphere play a vital role in the visual control of action (Gonzalez et al., 2006).

Methods

Participants

Sample size and F-values from a previous study by Gonzalez et al. (2006) – which investigated the impact of the Ebbinghaus illusion on maximum grip aperture between the right and left hands – was used as a reference to generate the sample size for this study. With a sample of 26, Gonzalez et al. (2006) found a main effect of hand on illusion magnitude, with an F-value of 16.29. According to power analysis using MorePower 6.0 (Campbell & Thompson, 2012), this would have achieved a power of .97. Since the aim of the present study is to aim for .80 power, we aimed for a sample size between 20-25.

Therefore, we recruited 21 right-handed (17 female, 4 male) and 3 mixed-handed (1 female, 2 male, with laterality quotients between -50 to + 6.66) students from Lancaster University (age range: 18-24 years, *M* = 19.08, *SD* = 1.41). Handedness was assessed using the 10-item Edinburgh Handedness Inventory (Oldfield, 1971), with laterality scores > +60 being assigned as right-handed, scores between +59 and -59 considered mixed-handed, and scores <-60 assigned as left-handed. All the mixed-handed participants stated a strong right-hand preference for writing, a key predictor of handedness (Bryden, 1977; Rigal, 1992). Participants were recruited via the Lancaster University SONA system and were either compensated with 3 credits or paid £10 for their time. Data was collected in February and March 2023.

Materials

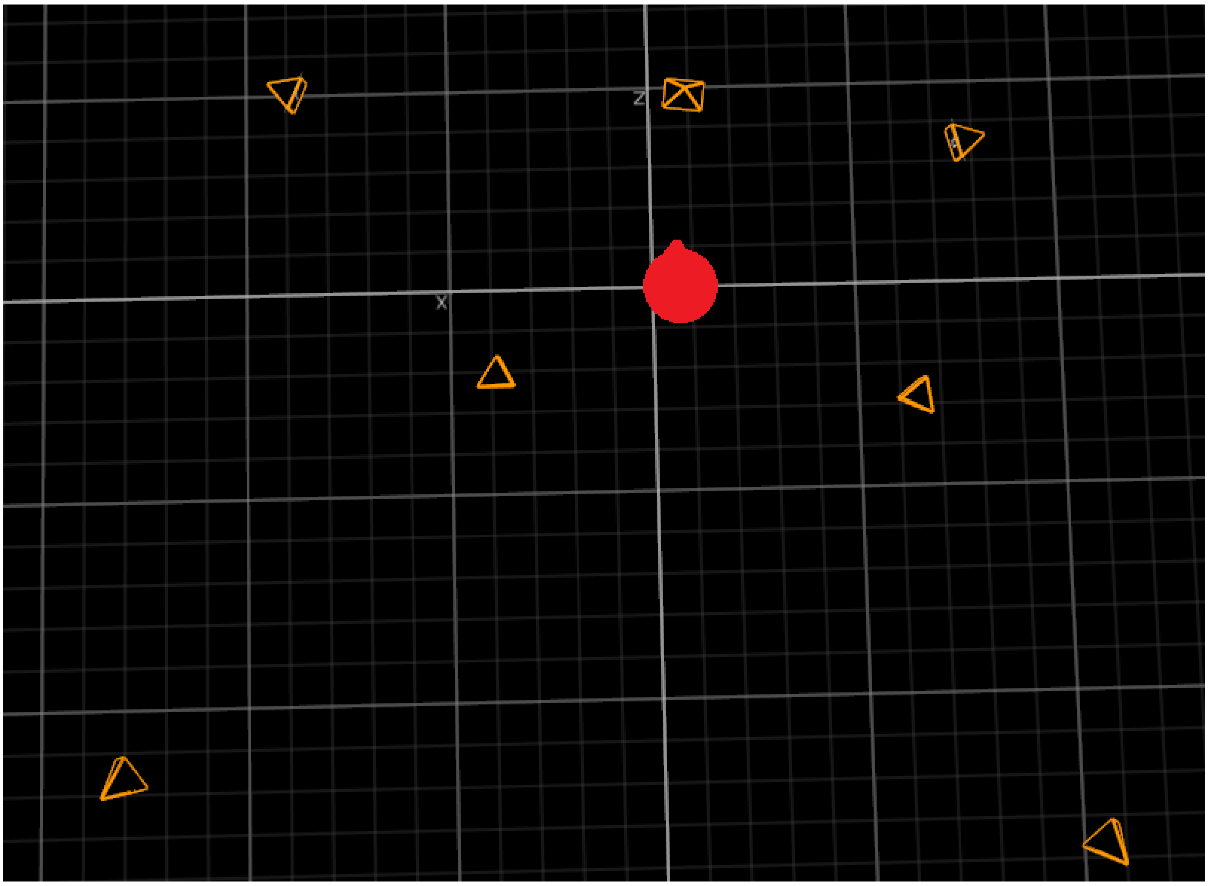
The materials section will be split into three main sub-sections. Firstly, outlining the setup of the motion capture cameras. Secondly, outlining the virtual environment created for the virtual reality conditions. Thirdly, outlining the stimuli created for the real-world conditions.

Motion Tracking

Maximum grip aperture (MGA) was recorded using seven OptiTrack (NaturalPoint, Inc., Corvallis, Oregon, United States) Flex-13 motion capture cameras. See Figure 2 for the configuration of the Optitrack cameras as shown in the OptiTrack motion software, and Figure 3 for the configuration of the motion cameras within the real-world environment. The OptiTrack cameras tracked the 3d position of 1cm diameter reflective markers that were attached as close as possible to the tip of the thumb and index fingers of both hands.

Figure 2

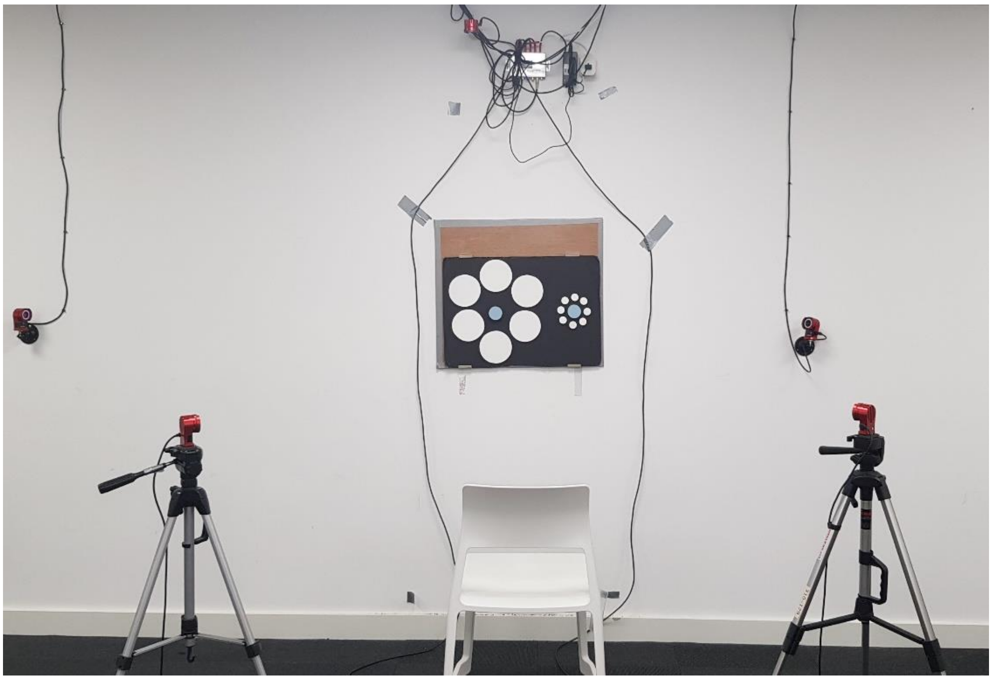
The Position of the Optitrack Motion Capture Cameras in Optitrack



Note. This is a bird's eye view, with the location of the participant signified by the red circle.

Figure 3

The Configuration of the Optitrack Cameras within the Real World



Note. Five of the seven cameras are visible in this photo. Two cameras are on the ceiling and not visible.

Virtual Environment

The virtual environment (VE) used for the virtual reality (VR) conditions of the study was created using Unity Version 2021.1.24f1 (Unity Technologies, San Fransisco, California, United States). For descriptions of specific objects in the virtual environment, descriptions will assume that 1 unit in Unity is equal to 1 real-world metre as specified by the Unity documentation (Unity Technologies, 2018). Coordinates of where virtual objects are placed are specific to the virtual environment and will not reflect any real-world coordinates.

The VE was presented through an Oculus CV1 VR headset. Participants were placed within a simple immersive VE that contained a wooden table (70cm height, 3m length) with a black screen (1.5m x 1.5m) placed perpendicularly on top of the table. Eye height was set to approximately 125cm from the virtual floor for all participants - though slight variations would occur based on the height of the participant – and participants were approximately 25cm away from the black screen. Attached to the front of the VR headset was a LEAP motion sensor (Leap Motion, Inc., San Francisco, California, United States) that tracked and animated participants' hand movements in real time. Leap Motion 'capsule hand' models were used to animate the participants' hand movements. These capsule hand models are primarily white, with coloured spheres signifying the joints in the fingers and wrists.

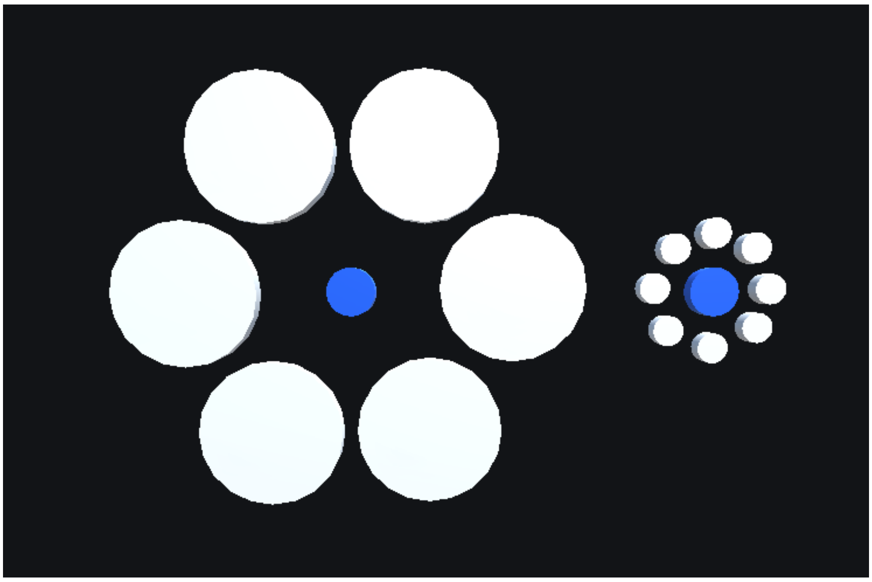
Visual Stimuli. The visual stimuli used in the VE for the calibration and Ebbinghaus grasping task are described in the following sections.

Calibration. For the calibration task, red cylinders (3cm diameter, 1.5cm depth) were placed in various positions on the black screen in front of participants (see Appendix for exact coordinates of the calibration cylinders).

Ebbinghaus Illusion. Various configurations of the Ebbinghaus illusion were used as the visual stimuli for the VR conditions in study. The Ebbinghaus illusion contained two blue target circles of the same size (either 4cm or 5cm in diameter, 1cm depth), placed approximately 29.7cm apart (measured from the centre of the blue circles), at around eye-height. Each blue circle was surrounded by white outer circles, henceforth called 'flankers'. The flankers would either be smaller (2.5cm diameter, 1cm depth) or larger (12cm diameter, 1cm depth) than the blue target circle. The large flankers were approximately 13.2cm away from the blue target circle, while the small flankers were approximately 4.7cm away from the blue target circle. The Ebbinghaus illusion was presented directly in front of participants at a 90-degree angle on the black screen described in the previous section. See Figure 4 for an example of the Ebbinghaus illusion presented in VR.

Figure 4

An Example of the Ebbinghaus Illusion in VR



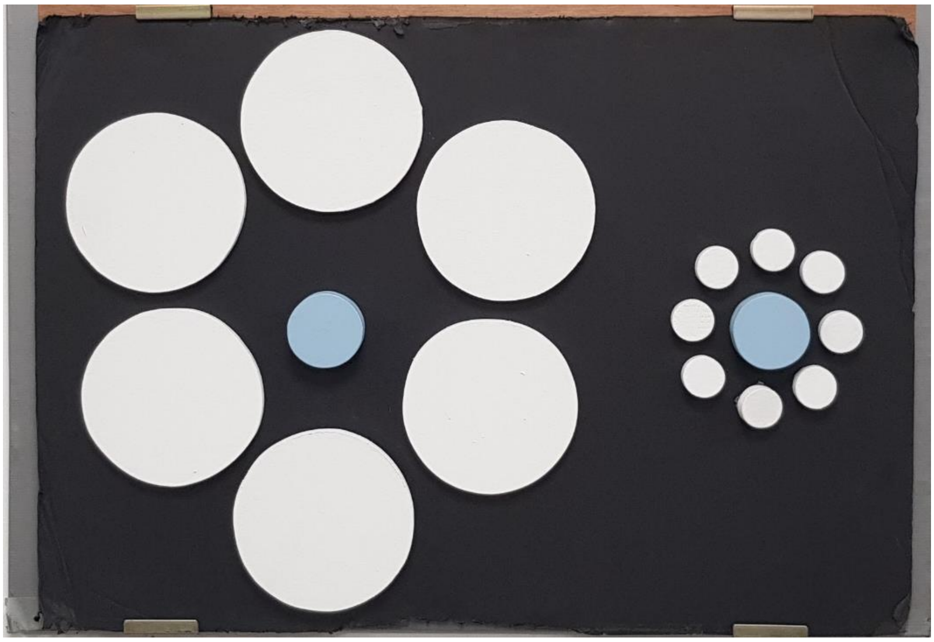
Real-world Environment

The real-world presentation of the Ebbinghaus illusion was designed to be as similar as possible to the virtual environment, though slight differences did occur. Participants were sat in a chair directly in front of a board holding the Ebbinghaus illusion, with the front of the chair being approximately 35cm away from the board.

Ebbinghaus Illusion. Again, various configurations of the Ebbinghaus illusion were used as visual stimuli for the real-world conditions in this study. The dimensions of the blue target circles and flankers were identical to the VR Ebbinghaus illusion. The two blue target circles were placed approximately 30cm apart (measured from the centre of the blue circles). The large flankers were approximately 8.5cm away from the blue target circle, and the small flankers were approximately 3.5cm away from the blue target circles. The blue centre circles were approximately 125cm from the floor, coinciding with the approximate eye-height set in the VR Ebbinghaus illusion. The blue and white circles were placed on a black board that was 58cm x 41cm. The blue circles were attached to the board magnetically, allowing them to be removed and replaced easily. The white circles were glued to the board so that they could not be moved. The entire board holding the Ebbinghaus illusion was placed on a wooden board (63cm x 56cm) with hooks attached that allowed the black board to be moved. See Figure 5 to see how the board looked with the 5cm blue target circles.

Figure 5

The Ebbinghaus Illusion Board used for the Real-World Conditions



Design

This was a 2x2x2x2 repeated measures study. There were four factors: first was the real hand used to grasp the blue target circle (left vs right); second was the setting in which participants interacted with the Ebbinghaus illusion (real world vs VR); third was the real size of the target circle (4cm vs 5cm); finally, the last was the illusory size of the target circle (big vs small). The dependent measure was maximum grip aperture (MGA) in millimetres when grasping one of the target circles.

Procedure

This study was approved by Lancaster University Faculty of Science and Technology Ethics Committee. All participants provided informed consent before participation, as well as completed a questionnaire to assess demographic information such as age, sex, and handedness. Before beginning the first condition the participant was assigned, the 3D reflective markers were attached to both hands. The order of conditions in which participants interacted with the Ebbinghaus illusion was counterbalanced.

VR study

Before participants put on the VR headset, they were told which hand to use throughout the calibration and Ebbinghaus grasping task. Participants wore the VR headset, sat in a chair surrounded by the Optitrack motion cameras, and were placed directly in front of the black screen within the VE described in the materials section. For each hand, participants first completed a short calibration phase to give them experience interacting with virtual objects. During the calibration, participants were instructed to reach and grasp a red calibration cylinder using their thumb and index finger and simply move it to another location (see Figure 6). Once this had successfully been done, the next calibration cylinder was presented in a new position. The calibration lasted for 10 trials, with the starting position of the calibration cylinder changing each trial.

Figure 6

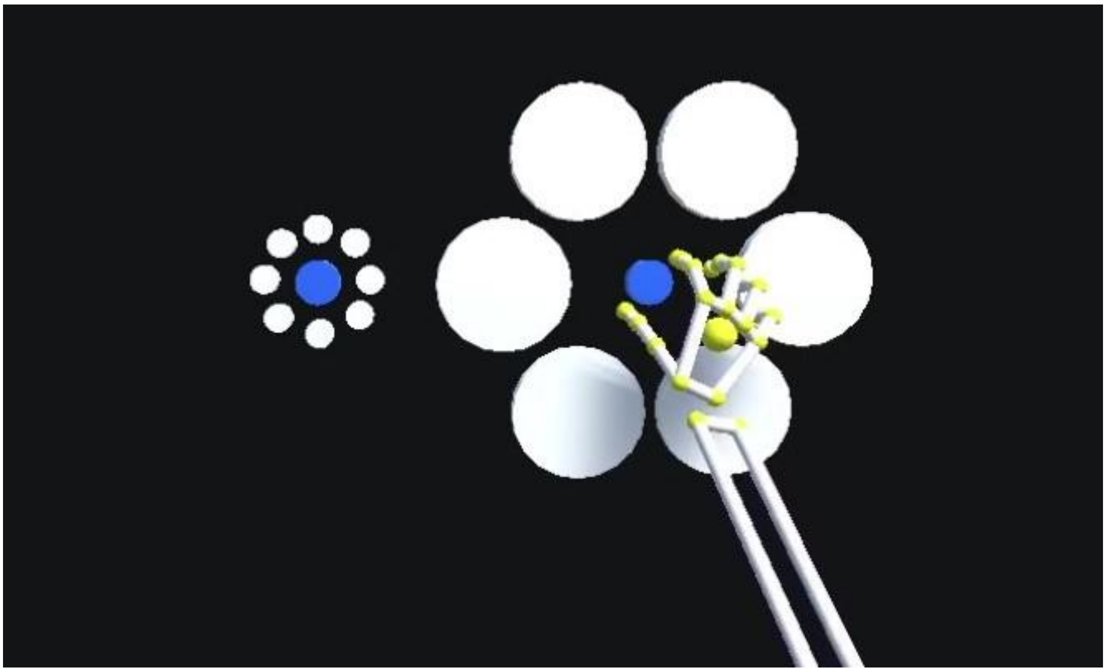
One of the Calibration Trials using the Right Hand

After the calibration was completed, participants moved onto practice trials of the main Ebbinghaus grasping task. Between trials, participants were instructed to hold their hand between chin and chest height and keep their thumb and index finger together. For each practice trial, the researcher counted from three to one to prepare participants for the trial. Participants would first see a small white circle (1cm diameter, 1cm depth) appear for 1000ms either to the left or right of the black screen to act as a cue for which target circle they should grasp. 1000ms after the cues had disappeared, the full Ebbinghaus illusion appeared and remained on the screen for 4000ms. The blue target circles appeared in the same position as the preceding cues. As soon as participants saw the Ebbinghaus illusion, they were instructed to reach, grasp, and pick off the blue target circle from the black screen that had been preceded by the cue using their thumb and index finger (see Figure 7). After the participant successfully picked off the blue circle, they simply let it go to allow the researcher to reset its position for the next trial. The participant then placed their hand back in the default position to prepare for the next trial. The practice lasted for 8 trials, with an equal number of trials towards the left and right, and an equal number of trials towards the ‘big’ and ‘small’ target circles. The size of the target circles was consistent at 5cm for every trial. The purpose of the practice was to give participants experience with the Ebbinghaus grasping task before any measurement of MGA took place.

Once the practice trials were done, participants moved onto the real Ebbinghaus grasping task. The real task was almost identical to the practice. The main difference was that during half of the trials the blue target circles were 5cm in diameter and for the other half they were 4cm in diameter. Additionally, MGA was recorded for every trial using the Optitrack motion cameras. The main task lasted for 24 trials, with the trials presented in a random order. The entire procedure was repeated twice, once for each hand. The entire VR task took approximately 20-25 minutes.

Figure 7

One of the Ebbinghaus Illusion Grasping Trials using the Right Hand



Real-world Study

Before participants began each condition, they were told which hand they would be using. Participants were sat in a chair surrounded by the Optitrack motion cameras, directly in front of the board holding the Ebbinghaus illusion. First, participants completed 8 practice trials to get them adjusted to the procedure of the study. During these practice trials, participants were instructed to hold their hand between chin and chest height, to keep their thumb and index finger together, and to keep their eyes closed until the trial began. The researcher would verbally state whether the participant should grasp the blue target circle on the left or on the right. Then, the researcher would count from three to one to prepare participants for the trial. After the countdown, participants would hear a short beep to signify that they can open their eyes to reach and grasp the specified blue target circle using their thumb and index finger. After 4000ms had elapsed, a short beep played again to tell participants that they needed to close their eyes once again. These audio cues were used to control for stimulus presentation time with the presentation time of 4000ms being the same as the VR condition. Once a trial was complete, the researcher would manually adjust the Ebbinghaus illusion by flipping the board if needed. Participants were told that they may hear the researcher making adjustments, but to please keep their eyes closed between trials. An equal number of trials towards the left and right and an equal number of trials towards the ‘big’ and ‘small’ target circles were included. The size of the target circles was consistent at 5cm for every trial. The practice allowed participants to get used to the procedure before any measurement of MGA took place.

Once the practice was complete, participants moved onto the main Ebbinghaus grasping task. This task was almost identical to the practice trials. The main differences were that during half of the trials the blue target circles were 5cm in diameter, and in the other half they were 4cm in diameter. Additionally, MGA was measured for all trials. The size of the blue target circles was adjusted by simply removing the target circles of one size and replacing them with the target circles of the other size, using the magnets attached to the board and the circles themselves. The main task lasted for 24 trials, with the trial order being predetermined but randomised. The entire procedure was repeated twice, once for each hand. The entire real-world procedure took between 35-40 minutes.

Results

Two subjects were removed prior to analysis due to technical issues that meant they did not complete the entire study. To assess the relative influence of each variable (hand, environment, illusory object size, real object size) on MGA, we first performed linear mixed modelling. We first generated the null model, only including the random effect of participant on MGA. The Akaike information criterion (AIC; a measure of model quality that considers fit and complexity, in which a lower score is better; Akaike, 1973) for the null model was 16488. The single addition of hand as a fixed factor to the null model did not significantly improve model fit $\chi(1)^2 = 1.05$, $p = .30$, AIC = 16489. However, single addition of environment as a fixed factor to the null model did improve model fit $\chi(1)^2 = 307.79$, $p < .001$, AIC = 16182.

The addition of real object size as a fixed factor to the environment model improved model fit $\chi(1)^2 = 85.32$, $p < .001$, AIC = 16098. However, the addition of the real object size and environment interaction did not improve model fit, $\chi(1)^2 = 0.77$, $p = .38$, AIC = 16100. The addition of illusory object size to the model with environment and real object size improved model fit $\chi(1)^2 = 160.03$, $p < .001$, AIC = 15940. The addition of the environment and illusory object size interaction further improved model fit $\chi(1)^2 = 9.01$, $p < .01$, AIC = 15933. However, adding the three-way interaction between environment, real object size and illusory object size did not significantly improve model fit $\chi(3)^2 = 2.06$, $p = .56$, AIC = 15937.

The addition of hand to the model with environment, real object size, illusory object size and illusory object size and environment interaction did not improve model fit $\chi(4)^2 = 3.30$, $p = .51$, AIC = 16000, nor did adding any hand interactions $\chi(11)^2 = 11.627$, $p = .39$, AIC = 15944. Therefore, the best quality model to explain MGA is the model with environment, illusory object size, the environment and illusory object size interaction, and real object size as fixed factors, and participant as the random factor. This model had an AIC of 15933.

We then conducted an ANOVA on the model generated with all factors. There was a significant effect of environment on MGA, $F(1, 2067) = 375.23$, $p < .001$, $\eta_p^2 = 0.15$, with grasps in the real world ($M = 63.82$mm, $SD = 10.77$mm) being significantly smaller than grasps in VR ($M = 72.59$mm, $SD = 15.78$mm). There was a main effect of real object size, $F(1, 2067) = 93.85$, $p < .001$, $\eta_p^2 = .04$, with grasps to the 5cm object ($M = 70.4$mm , $SD = 14.03$mm) being significantly larger than grasps to the 4cm object ($M = 66$mm, $SD = 14.03$mm). There was a main effect of illusory object size, $F(1, 2067) = 166.73$, $p <. 001$, $\eta_p^2 = .07$ with grasps to the ‘small’ object ($M = 71.1$mm, $SD = 13.54$mm) being significantly larger than grasps to the ‘large’ object ($M = 65.31$mm, $SD = 14.27$mm). However, there was no main effect of hand used, $F(1, 2067) = 1.244$, $p = .27$, $\eta_p^2 = .0006$, with no significant differences in MGA between the left ($M = 67.82$mm , $SD = 13.89$mm) or right ($M = 68.49$, $SD = 14.5$mm) hands.

There was a significant interaction between hand and environment, $F(1, 2067) = 6.21$, $p = .013$, $\eta_p^2 = 0.002$. Analysis of simple main effects suggests that, when in VR, there was no significant difference in MGA between the right ($M = 72.3$mm, $SE = 1.76$mm) and left hand

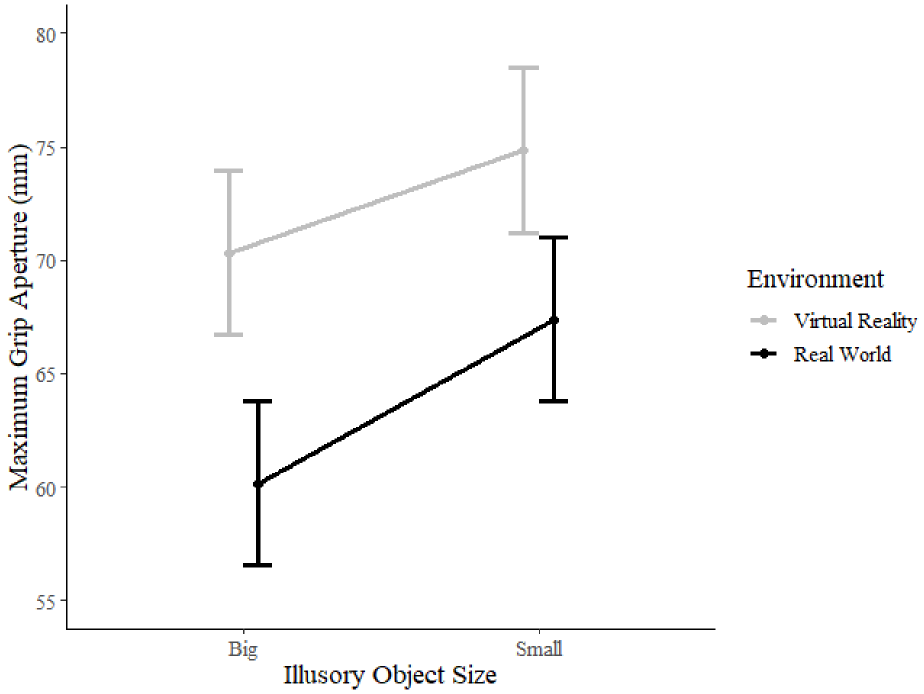
(*M* = 72.9mm, *SE* = 1.76mm), $t(2067) = -.97$, $p = .33$, $d = .06$. However, when in the real world, MGA with the right hand (*M* = 64.6mm, *SE* = 1.76) was significantly larger than MGA with the left hand (*M* = 63mm, *SE* = 1.76), $t(2067) = 2.55$, $p = .011$, $d = .16$.

There was also a significant interaction between environment and illusory object size, $F(1, 2067) = 8.96$, $p = .003$, $\eta_p^2 = .004$ Analysis of simple main effects suggests that, when the centre circle was 'big', MGA in VR (*M* = 70.3mm, SE = 1.76) was significantly larger than in the real world (*M* = 60.2mm, SE = 1.76), $t(2067) = 15.81$, $p < .001$, $d = .96$. In addition, when the centre circle was 'small', MGA in VR (*M* = 74.8mm, SE = 1.76) was significantly larger than MGA in the real world (*M* = 67.4mm, SE = 1.76), $t(2067) = 11.59$, $p < .001$, $d = .71$ (see Figure 8).

However, there were no significant interactions between: hand and real object size, F(1, 2067) = 0.99, $p = .32$, $\eta_p^2 = .0005$; environment and real object size, $F(1, 2067) = .79$, $p = .37$, $\eta_p^2 = .0004$; hand and illusory object size, $F(1, 2067) = .41$, $p = .52$, $\eta_p^2 = .0002$; real object size and illusory object size, $F(1, 2067) = .39$, $p = .53$, $\eta_p^2 = 0.0002$; hand, environment, and real object size, $F(1, 2067) = .14$, $p = .7$, $\eta_p^2 = .00007$; hand, environment, and illusory object size, $F(1, 2067) = .22$, $p = .64$, $\eta_p^2 = .0001$; hand, real object size, and illusory object size, $F(1, 2067) = .31$, $p = .58$, $\eta_p^2 = .0001$; environment, real object size, and illusory object size, $F(1, 2067) = .86$, $p = .35$, $\eta_p^2 = .0004$; hand, environment, real object size, and illusory object size $F(1, 2067) = .0007$, $p = .98$, $\eta_p^2 = .0000003$.

Figure 8

Interaction between Environment and Illusory Object Size



Note. Error bars represent 95% CI.

Discussion

In this study, we explored whether the impact of the Ebbinghaus illusion on MGA would differ between real and virtual environments. Specifically, we were interested in how the lack of haptic feedback when interacting with virtual objects may encourage actions that are more akin to pantomiming and, hence, more susceptible to perceptual illusions. Furthermore, the nature of head-mounted displays means that important depth cues for vision-for-action are disrupted (Harris et al., 2019; Mon-Williams & Tresilian, 1999), thus people may use more ventral visual processing to direct their actions. Various studies provide evidence for a dissociation between grasping and perceptual estimates. Grasps towards objects embedded in the Ebbinghaus illusion are scaled to the absolute metrics of the object and thus do not show the same magnitude as perceptual estimates (Aglioti et al., 1995; Haffenden & Goodale, 1998; Pavani et al., 1999).

Thus, our key hypotheses were as follows: we expected that grasps towards objects embedded in the Ebbinghaus illusion in virtual environments would show a greater magnitude of the illusion when compared to grasps performed in the real world. We expected that, when the effect of the illusion is present, grasps towards the perceptually larger object would elicit significantly larger MGA than grasps to the perceptually smaller object. Moreover, we expected that grasps using the right hand would show a lower magnitude of the illusion than grasps using the left hand, based on previous research that suggests the left hemisphere is specialised for the visual control of action (Gonzalez et al., 2006).

We found a main effect of illusory object size. However, the direction of the illusion magnitude was inverse to what would be expected. The target circle surrounded by the large flankers, which should appear perceptually smaller, elicited significantly larger MGA compared to the target circle surrounded by the small flankers. This inverse effect of the illusion was present in both the real-world and VR. Notably, there was a significant interaction between illusory object size and environment. Contrary to our hypothesis, the illusion magnitude appeared to be greater in the real world versus VR. Based on both the inverse effect of the illusion and the greater impact of illusory object size on MGA in the real world versus in VR, we believe that this effect may be due to factors independent of the perceptual differences in size between the target circles. A similar view is held by Haffenden et al. (2001) who suggest that previous effects of the illusion found on grasping are due to non-illusory effects of the Ebbinghaus displays. Haffenden et al suggest that obstacle avoidance explains patterns of MGA that are consistent with the perceptual effects of the illusion. When the distance between the target and the flankers is equal across the different perceptual conditions, the effect of the illusion on grasp scaling no longer occurs.

The distance between the flankers for the ‘small’ and ‘large’ target circles was not equal in that the small flankers were closer to the target circle than the large flankers. This difference in flanker distance is consistent with the displays used in previous studies (Aglioti et al., 1995; Gonzalez et al., 2006; Haffenden & Goodale, 1998; Haffenden & Goodale, 2000); therefore, we did not expect the distance of the flankers to impact the results of this study. However, it is possible that the closer flankers to the ‘large’ target circle acted as an obstacle when grasping, encouraging participants to reduce their MGA. This explanation would be consistent with the interaction effect that showed that the difference in MGA between the ‘big’ versus ‘small’ target circles was greater in the real world versus in VR. In the real world the flankers act as a greater obstacle since they would physically limit the extent to which people can grasp the target circle, whereas in VR the virtual hand can simply phase through the flankers. However, the fact that the inverse effect of the illusion also existed in VR suggests that even purely visual obstacles can impact MGA in the context of grasping towards the Ebbinghaus Illusion. Haffenden & Goodale (2000) suggest that even two-dimensional edges can form part of the input for programming visually guided movements, meaning that the most efficient strategy when performing a grasp towards the Ebbinghaus illusion would be to consider any visual contours surrounding the target that could interfere with the grasp.

Two different explanations for how the position of the flankers in the Ebbinghaus illusion influences grasping via obstacle avoidance have been proposed (Chen et al., 2021). There may be a positive relationship between flanker-target distance and grip size, meaning that grip size would be reduced if the distance between the flanker and the target is small to avoid collision with the flankers (Franz et al., 2003). Alternatively, Haffenden and Goodale (2000) propose a negative relationship between flanker-target distance and grip size. When the flanker-target distance is very small, flankers are grouped together with the central target and are only considered obstacles when they are further away. The explanation proposed by Haffenden and Goodale would predict patterns of MGA in line with the perceptual effects of the illusion, but this explanation does not appear to be the case for our study.

Chen et al. (2021) manipulated both flanker size, flanker-target distance, and flanker density to assess their impacts on MGA and found that these factors had effects on grasping that could not be fully attributed to the size illusion. When the flankers were sparse and the perceptual effect of the Ebbinghaus illusion was weak, reducing flanker distance caused MGA to decrease. This effect would not be explained by the size illusion but would be consistent with obstacle avoidance (Chen et al., 2021). Thus, the pattern of MGA in this study could be attributed to a combination of a weak perceptual effect of the Ebbinghaus Illusion in combination with differences in the distance of the small and large flankers from the target. Further investigation into the perceptual effect of the illusion from our specific stimulus would provide more insight into why MGA for the target surrounded by the large flankers was larger than MGA for the target surrounded by small flankers.

Comparison of MGA between the real-world environment and the VE reveal that, on average, MGA was larger when grasping objects in VR than in the real world. This pattern is consistent with other research exploring grasping movements between real-world objects and virtual objects. For example, Magdalon et al. (2011) found that MGA towards virtual objects was larger than MGA to equivalent physical objects, even when haptic feedback was provided through a use of a haptic glove. Therefore, larger MGAs in VR do not appear to be from lack of haptic feedback. Larger MGAs in the VE could instead reflect lack of experience interacting with virtual objects, leading participants to be more liberal with their grasp scaling to ensure they could pick up the virtual target circle. Thus, larger MGA in VR could be due to unfamiliarity with interacting with virtual objects.

Though MGA between the real world and VR was different, participants were able to scale their grips in response to real differences in object size equally well in both environments. Thus, people are equally as capable of considering changes to the dimensions of both virtual objects and real objects. Furthermore, participants were indeed scaling their grasps to changes in object size rather than employing the same grasp-programme repeatedly for every object. In terms of the hand being used, we found no significant differences in MGA between the right and the left hand. Unlike in Gonzalez et al. (2006), MGAs in this study did not follow the pattern consistent with the perceptual effects of the Ebbinghaus illusion, which may account for the difference in results. However, other research has not found any differences in MGA between the left and right hand when performing precision grasps (Grosskopf & Kuhtz-Buschbeck, 2005). Thus, right-hand advantages in precision grasp may be specific to grasps that are affected by size-contrast illusions or may be best reflected in measures outside of MGA.

Overall, this study provides insight into subtle differences that may occur when interacting with virtual and real objects embedded in visual illusions. Though participants performed grasps consistent with obstacle avoidance in both environments, this was more apparent in the real world versus VR. Thus, although even non-physical 2D elements can impact the programming of a grasp (Haffenden & Goodale, 2000), physical obstacles seem to play a larger role in influencing MGA than purely visual ones. Conclusions on differences in visual processing in VR versus the real world cannot be made as participants' grasping behaviour was driven by obstacle avoidance rather than any perceptual impact of the Ebbinghaus illusion itself.

References

Aglioti, S., DeSouza, J., & Goodale, M. (1995). Size-contrast illusions deceive the eye but not the hand. *Current Biology*, *5*(6), 679-685. https://doi.org/10.1016/s0960-9822(95)00133-3

Akaike, H. (1973). Information theory and an extension of the maximum likelihood principle. In E. Parzen, K. Tanabe, & G. Kitagawa (Eds.), Selected papers of Hirotugu Akaike (pp. 199 –213). New York: Springer. http://dx.doi.org/10.1007/978-1-4612-1694-0_15

Chen, Z., Zhang, N., & Saunders, J. A. (2021). Dual processes underlie the effect of the Ebbinghaüs illusion on control of grasping. *Journal of Experimental Psychology: Human Perception and Performance, 47*(11), 1472–1492. https://doi.org/10.1037/xhp0000819

Chessa, M., Maiello, G., Klein, L., Paulun, V., & Solari, F. (2019). Grasping objects in immersive Virtual Reality. In IEEE Conference on Virtual Reality and 3D User Interfaces (VR) (pp. 1749-1754), https://doi.org/10.1109/VR.2019.8798155. IEEE; IEEE. Retrieved 03 July 2023, from https://ieeexplore.ieee.org/abstract/document/8798155.

Franz, V. H., Bülthoff, H. H., & Fahle, M. (2003). Grasp effects of the ebbinghaus illusion: Obstacle avoidance is not the explanation. *Experimental Brain Research, 149*(4), 470–477. https://doi.org/10.1007/s00221-002-1364-6

Furmanek, M., Schettino, L., Yarossi, M., Kirkman, S., Adamovich, S., & Tunik, E. (2019). Coordination of reach-to-grasp in physical and haptic-free virtual environments. *Journal Of Neuroengineering and Rehabilitation*, *16*(1). https://doi.org/10.1186/s12984-019-0525-9

Gonzalez, C. L., Ganel, T., & Goodale, M. A. (2006). Hemispheric specialization for the visual control of action is independent of handedness. *Journal of Neurophysiology*, *95*(6), 3496–3501. https://doi.org/10.1152/jn.01187.2005

Goodale, M., & Milner, A. (1992). Separate visual pathways for perception and action. *Trends In Neurosciences*, *15*(1), 20-25. https://doi.org/10.1016/0166-2236(92)90344-8

Grosskopf, A., & Kuhtz-Buschbeck, J. P. (2005). Grasping with the left and right hand: A Kinematic Study. Experimental Brain Research, 168(1–2), 230–240. https://doi.org/10.1007/s00221-005-0083-1

Haffenden, A. M., & Goodale, M. A. (1998). The effect of pictorial illusion on prehension and perception. *Journal of Cognitive Neuroscience*, *10*(1), 122–136. https://doi.org/10.1162/089892998563824

Haffenden, A. M., & Goodale, M. A. (2000). Independent effects of pictorial displays on perception and action. *Vision Research*, *40*(10–12), 1597–1607. https://doi.org/10.1016/s0042-6989(00)00056-0

Haffenden, A. M., Schiff, K. C., & Goodale, M. A. (2001). The dissociation between perception and action in the ebbinghaus illusion. *Current Biology*, *11*(3), 177–181. https://doi.org/10.1016/s0960-9822(01)00023-9

Harris, D., Buckingham, G., Wilson, M., & Vine, S. J. (2019). *Virtually the Same? How Impaired Sensory Information in Virtual Reality May Disrupt Visually-Guided Action.* https://doi.org/10.31234/osf.io/68cnj

Howard, M. C. (2017). A meta-analysis and systematic literature review of Virtual Reality Rehabilitation Programs. *Computers in Human Behavior*, *70*, 317–327. https://doi.org/10.1016/j.chb.2017.01.013

Keshner, E. A., & Kenyon, R. V. (2004). Using immersive technology for postural research and Rehabilitation. *Assistive Technology*, *16*(1), 54–62. https://doi.org/10.1080/10400435.2004.10132074

Króliczak, G., Cavina-Pratesi, C., Goodman, D. A., & Culham, J. C. (2007). What does The brain do when you fake it? an fmri study of pantomimed and real grasping. *Journal of Neurophysiology*, *97*(3), 2410–2422. https://doi.org/10.1152/jn.00778.2006

Levac, D. E., Huber, M. E., & Sternad, D. (2019). Learning and transfer of complex motor skills in virtual reality: A perspective review. *Journal of NeuroEngineering and Rehabilitation*, *16*(1). https://doi.org/10.1186/s12984-019-0587-8

Levin, M. F., Weiss, P. L., & Keshner, E. A. (2015). Emergence of virtual reality as a tool for upper limb rehabilitation: Incorporation of Motor Control and Motor Learning principles. *Physical Therapy*, *95*(3), 415–425. https://doi.org/10.2522/ptj.20130579

Magdalon, E. C., Michaelsen, S. M., Quevedo, A. A., & Levin, M. F. (2011). Comparison of grasping movements made by healthy subjects in a 3-dimensional immersive virtual versus physical environment. Acta Psychologica, 138(1), 126–134. https://doi.org/10.1016/j.actpsy.2011.05.015

Mon-Williams, M., & Tresilian, J. R. (1999). Some recent studies on the extraretinal contribution to distance perception. Perception, 28(2), 167–181. https://doi.org/10.1068/p2737

Mon-Williams, M., Tresilian, J., McIntosh, R., & Milner, D. (2001). Monocular and binocular distance cues: insights from visual form agnosia I (of III). *Experimental Brain Research*, *139*(2), 127-136. https://doi.org/10.1007/s002210000657

Pavani, F., Boscagli, I., Benvenuti, F., Rabuffetti, M., & Farnè, A. (1999). Are perception and action affected differently by the Titchener circles illusion? *Experimental Brain Research*, *127*(1), 95–101. https://doi.org/10.1007/s002210050777

Westwood, D., Chapman, C., & Roy, E. (2000). Pantomimed actions may be controlled by the ventral visual stream. Experimental Brain Research, 130(4), 545-548. https://doi.org/10.1007/s002219900287

Whitwell, R. L., Ganel, T., Byrne, C. M., & Goodale, M. A. (2015). Real-time vision, tactile cues, and visual form agnosia: Removing haptic feedback from a “natural” grasping task induces pantomime-like grasps. *Frontiers in Human Neuroscience*, *9*. https://doi.org/10.3389/fnhum.2015.00216

Whitwell, R. L., Garach, M. A., Goodale, M. A., & Sperandio, I. (2022). Looking at the ebbinghaus illusion: Differences in neurocomputational requirements, not gaze-mediated attention, explain a classic perception-action dissociation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *378*(1869). https://doi.org/10.1098/rstb.2021.0459

Appendix: Coordinates of Calibration Circles

X-axis	Y-Axis
.006	.996
.157	1.152
.105	1.091
-.158	1.164
-.211	.837
-.201	1.02
.221	.79
.129	.949
-.132	.905
-.066	1.255

Note. The Z-axis was kept constant at -1.1 across all trials.

Chapter 5

General Discussion

The primary goal of this thesis was to explore whether visual feedback on handedness is sufficient to elicit biases in action perception normally associated with moving the right hand when moving the left in right-handed individuals (RHIs). If the perceptual bias that the right hand is visually larger enhances the right hand bias present in RHIs, manipulating visual feedback so that the left hand takes on the perceptually larger properties of the right hand may lead to larger estimates of one’s action capabilities than when the left hand is presented normally. However, if these biases originate purely from asymmetries in sensorimotor representation of the right and left hands, it is more likely that action estimates will reflect these cortical asymmetries. That is, manipulating visual feedback would not lead to significant changes in one’s perceptions of their action capabilities, since inherent biases favouring the right hand derive from cortical asymmetries rather than asymmetries in visual feedback.

5.1 Summary of Research

In Chapter 2, three affordance experiments were conducted using the VR methodology described earlier. For each of the three experiments, participants performed a simple calibration task in which either congruent or incongruent visual feedback was paired with movement of the real left or right hand. After calibration, participants estimated the maximum extent of their grasping, reaching, and precision reaching abilities. The aim of these experiments was to assess whether manipulating visual feedback specifying hand use could significantly alter RHIs perceptions of their action boundaries, on the basis that previous research suggests visual distortions that the right hand is larger than the left may contribute to the perception of greater capabilities with the right hand (Linkenauger et al., 2009).

The experiments in Chapter 2 found that differences in action estimates between the left and the right hands was contingent on the action being performed. For both grasping and precision reaching, which are more complex actions that have greater consequences if not performed correctly (Readman et al., 2021; Jeannerod, 1996), participants estimated greater capabilities using their real right hand than their left. When it came to a simple reaching task in which there was no grasping component, participants estimated both hands to be equally capable. The results of these experiments suggests that participants estimated their action capabilities using the somatosensory feedback that was received during the calibration, rather than visual feedback. Specifically, when participants estimated greater maximum extents of reach and grasp with their right hand, they did this regardless of the visual feedback specifying hand use. Overall, these experiments suggest that visual feedback on the hands does not enhance biases towards the right hand in RHIs in the context of action estimation.

Chapter 3 investigated how people embody virtual limbs when there are incongruencies between visual and somatosensory feedback when moving the hands. In two experiments, participants calibrated to either a large or small virtual arm – which was either presented congruently or incongruently to the real arm being moved – and then estimated their action boundary for grasping and reaching. These two experiments revealed that there were no significant differences in participants' capabilities to update their action estimates between congruent or incongruent visual feedback after calibrating to differently sized virtual arms. Whether the virtual arm was presented congruently or incongruently to the physical hand, participants estimated the extent of their grasp and reach to be greater when the virtual hand was large than when it was small. Thus, the results of Chapter 3 suggest that dramatic changes to one's sense of self-location does not hinder their ability to embody visually specified changes in hand size and consider them in their estimates of their action capabilities.

An additional two experiments in which the size of the virtual hand varied randomly, so that the intended consequence of the virtual manipulation is not so obvious, further supports the data from the previous embodiment studies. Participants gave similar estimates of reach and grasp in both the incongruent and congruent conditions, suggesting that they calibrated to the varying size of the hands in a similar manner regardless of the congruency of visual feedback to somatosensory feedback from moving their hands.

Chapter 4 explored whether visual biases in processing of visual feedback from visually guided actions could be exploited within the context of visual illusions. Previous research has found that people perform grasps with their right hand that are resistant to the perceptual size difference between targets created by the Ebbinghaus illusion. However, when grasping with the left hand, grasps show an effect of the illusion (Gonzalez et al., 2006). Gonzalez et al. interpret this effect as evidence of a left hemisphere advantage in visuomotor control. The first study in this chapter investigated whether presenting the left hand as the right would reduce the magnitude of the illusion when grasping with the left hand. Participants calibrated to either congruent or mirrored virtual hands and performed grasps towards objects embedded in the Ebbinghaus illusion. I found that, contrary to expectations, both the left and the right hands showed maximum grip aperture (MGA) that reflected the perceptual size difference between the targets. In this case, presenting the left hand as the right did not lead to any significant reductions in illusion magnitude as reflected in MGA.

A follow-up study was conducted to explore potential differences in the visual processing of action that may occur between real environments and VEs. In this study participants performed grasps towards targets embedded in the Ebbinghaus illusion with their right and left hand under normal viewing conditions. Participants performed these grasps either within an immersive VE or in the real world. Based on prior research that suggests that action performed in VR may use more ventral visual processing (Harris et al., 2019; Whitwell et al., 2015) I hypothesised that grasps in VR would show a greater magnitude of the illusion than grasps in the real world. Contrary to these expectations, grasps performed both in VR and in the real world had MGAs inverse to the normal effect of the illusion. That is, grasps towards the perceptually smaller object were larger than grasps to the perceptually larger object. This pattern of MGA likely reflects a strategy of obstacle avoidance, rather than any pictorial effects of the illusion.

5.2 Implications for Action Perception in RHIs

Previous research by Linkenauger et al. (2009) found that RHIs overestimated the length and span of their right hand and arm in comparison to their left. This perceptual distortion in the size of the right arm likely originates from cortical and functional asymmetries that lead to an enlarged sensorimotor representation of the right arm relative to the left (Amunts et al., 1996; Buchner et al., 1995; Jung et al., 2003; Sörös et al., 1999; Volkmann et al., 1998). The perceptual distortion that the right hand is larger was thought to have consequences on the perception of RHIs' action capabilities with each hand. Consistent with this view, Linkenauger et al. found that RHIs estimated their action boundaries for reaching and grasping to be significantly greater using their right hand than their left.

The experiments in chapter 2 provide further insight into the impact of that the visual perception of the arms may have on RHIs perceptions of their action capabilities. For grasping and precision reaching, participants estimated their capabilities with their real right hand to be greater than their real left hand. This finding was regardless of the visual information specifying hand use. A couple of possibilities could account for these results.

One is that for the perceptual bias that the right hand is larger to be present it must be paired with the somatosensory feedback associated with moving the right hand. Since this somatosensory feedback would activate the enlarged left somatosensory cortex that contributes to the right hand bias, visual feedback on handedness alone may not be sufficient to elicit biases in the perception of hand size. Thus, the left hand would not benefit from the visual feedback normally reserved for moving the right hand because of the reliance on cortical structures needed to elicit the visual bias in the first place.

Another related but slightly different explanation is that the estimation tasks used in the experiments in Chapter 2 do not prioritise the visual feedback experienced in the calibration phases. Estimating one’s action capabilities may involve internal motor simulation, in which simulating an action shares the same mechanisms as real action with overlapping neural activation (O’Shea & Moran, 2017; Witt & Profitt, 2008). As the estimation tasks involve imagining the action being executed rather than relying on online visual feedback, it is likely that some of the cortical areas associated with the right hand bias in RHIs are activated during the estimation task. Thus, participants would estimate their abilities to be greater using their right hand regardless of visual feedback specifying hand use because visual feedback is not needed for this estimation to take place. This interpretation is supported by the fact that in the reaching experiments participants gave larger estimates of maximum reach in the direction ipsilateral to the real hand being used, rather than the virtual hand being presented.

The results from the reaching experiments in Chapter 2 provide further insight into how the visual perception of hand size may or may not impact RHIs’ perceptions of their action capabilities. Based on the results of Linkenauger et al (2009), one may assume that greater estimations of grasp and reach using the right arm are a consequence of the visual bias that the right arm is larger than the left. When we perceive our opportunities for action (our affordances; Gibson, 1979), we consider the dynamic relationship between our bodies and the aspects of the environment with which we want to interact (Profitt & Linkenauger, 2013). One aspect of our body we consider with respect to our spatial layout is our morphology, which will limit the extent to which we can perform an action (Fajen, 2005). If RHIs perceive their right arm to be longer than their left, they would consider this aspect of their morphology that would be directly relevant when estimating their action boundary for reaching. However, when participants were asked to estimate their maximum extent of reach (without grasping) in the second study of Chapter 2, I found no significant differences in estimates between the real left and real right arms. Rather, it was not until participants were required to estimate reaching with the intent of grasping an object (precision reach) that differences in reaching estimates between the real left and right hands became apparent.

Reaching on its own is a relatively simple skill, hence both arms can perform it equally well. However, grasping requires greater dexterity and has a greater cost if the action fails when compared to reaching (Jeannerod, 1996; Readman et al., 2021). Differences in estimates of maximum reach between the left and right arms only became apparent with the precision reach task. This finding suggests that differences in estimates of RHIs' action capabilities between their left and right hands is not a consequence of the visual bias that the right arm is larger. If this finding were the case, we would expect to see differences in estimates of simple reach between the real left and right arms. Thus, the dexterity of each hand and the skill needed to successfully complete a task are more important factors when considering the action boundaries of each hand. Both the grasping and precision reach experiments differentiated the dexterity between the left and right hands more than the simple reaching experiment, hence why participants estimated greater capabilities with their right hand in these highly skilled tasks. From these results, perception of greater capabilities with the right arm likely further enhances the visual bias that the right arm is larger than the left in

RHIs, rather than the visual bias that the right arm is larger fuelling the perception that the right arm is more capable than the left.

Overall, the experiments in Chapter 2 offer important insight into the role of visual feedback on handedness on RHIs' perceptions of their action capabilities. Participants estimated greater capabilities when grasping and precision reaching using their real right hand versus their real left hand. The real right hand was estimated as more capable regardless of the visual feedback specifying handedness during the calibration phases. Differences in estimates between the real hands strongly suggests that visual feedback on handedness does not enhance the bias that the right hand is more capable. **Rather, the perception of greater capability with the right hand likely helps drive the bias that the right hand is larger than the left.** One important factor to consider when making these conclusions is whether participants embodied the virtual hands well enough to consider the visual feedback experienced in the calibration phases. Heinrich et al. (2020) demonstrated that healthy participants can embody mirrored, low-fidelity virtual hands. Further evidence for people's ability to embody virtual hands comes from the experiments in Chapter 3.

5.3 Implications for Embodiment of Mirrored Virtual Limbs

Sense of Embodiment (SoE) refers to the sense that properties of an artificial body are processed as if they were one's own body (Kilteni et al., 2012). This sense of embodiment has three underlying components – sense of self-location, sense of agency, and sense of body ownership (Longo et al., 2008). For someone to experience changes to a virtual body and consider those changes in their estimates of their action capabilities, they must consider that virtual body as their own to some degree. The key question regarding the results of Chapter 2's experiments is whether participants were able to embody the virtual hands when they were mirrored to consider them in their estimates of their action capabilities. If participants did not embody the virtual hands when they were mirrored, this inconsistency would prove problematic when concluding that participants prioritised somatosensory feedback over visual feedback when estimating their action capabilities. However, participants can

Previous research into affordance perception in VEs consistently supports the assertion that people are capable of embodying virtual limbs and considering the properties of those virtual limbs in estimates of their action boundaries. For example, both Lin et al. (2020) and Readman et al. (2021) found that participants estimated greater maximum reach and grasp when calibrated to a large virtual hand versus a small virtual hand. Thus, changes to participants' estimates of their action capabilities are a direct consequence of not only the visual feedback they received that altered the perceived size of the hands, but also their ability to embody those changes. However, the conditions for embodiment in these studies were optimal because the hand models were of a higher fidelity than those used in my own studies and a regular sense of self-location was maintained.

Despite these potential barriers to embodiment, the results of the four experiments in Chapter 3 provide evidence that people can embody virtual limbs even when the sense of self-location is altered to a dramatic degree. The results suggest that participants were able to calibrate to the different sizes of the virtual hands even when visuo-proprioceptive feedback specifying hand use were incongruent. Therefore, the results from the studies in Chapter 2 cannot be explained by a lack of embodiment of the mirrored virtual hands. Rather, the findings of Chapter 3 suggest that participants were indeed prioritising the somatosensory feedback over the visual feedback experienced in the calibration phase of the experiments of Chapter 2. Thus, subsequent estimates of reach and grasp would reflect the felt position of the hands as opposed to visual feedback specifying the location of the hands.

While participants could calibrate well to the changed sizes of the virtual hands, they did not calibrate to the changed location. In the reaching studies in both Chapter 2 and Chapter 3, participants gave greater estimates of reach when estimating ipsilateral to the actual hand that moved. This effect persisted even when the virtual hand was visually incongruent to the actual hand being moved. Hypothetically speaking, if the virtual arm was mirrored and participants attempted to reach to the right side of space using their right arm, they would need to reach across their body for the virtual arm to visually be in the right side of space. In this situation they should find it more difficult to reach in the direction ipsilateral to the real hand because doing so would require them to reach across their body. Again, this could be a consequence of the estimation task itself relying on cortical areas associated with the sensorimotor representation of the hands, rather than visual feedback experienced during the calibration phase.

Some cortical areas associated with action execution are activated during action estimation (O’Shea & Moran, 2017; Witt & Profitt, 2008). During the calibration, the participant would need to direct attention to the visually specified spatial location of the hand to position it in the correct location for each trial. However, no visual feedback is received during the estimation phase. Activation of some sensorimotor areas associated with performing the reaching action when estimating would therefore mean that participants prioritise the felt location of the hand but not where it appeared visually. Consequently, participants would estimate greater reaching capabilities in the direction ipsilateral to the real hand.

Alternatively, a dissociation between one’s ability to calibrate to changes in hand size and to calibrate to changes in the spatial location of the arms may exist. Previous research into embodiment has found that introducing a spatial offset between the real and artificial arm can lead to lower ratings of embodying the spatial location of the artificial limb, though this did not reduce ratings of agency or ownership (Pritchard et al., 2016). Therefore, changing the spatial location of the arms dramatically by mirroring the virtual limbs could reduce the sensation of being spatially present within the virtual body, but not reduce the sense of agency or ownership over those virtual limbs. Thus, people could still easily embody changes in hand size but not dramatic changes to spatial location.

Overall, Chapter 3 provides evidence of people's ability to calibrate to visually specified changes to mirrored virtual limbs and consider those changes in their estimates of their action capabilities. The experiments in Chapter 3 extend on previous research finding that people can embody mirrored virtual arms (Heinrich et al., 2020) by demonstrating that not only do people embody these virtual arms, but that they can also consider changes to the morphology of virtual limbs when estimating their action capabilities. Chapter 3 additionally strengthens the conclusions made in Chapter 2 by showing that embodiment is not a barrier to participants using visual feedback specifying hand use in their estimates of their action capabilities.

5.4 Implications for Actions Towards Visual Illusions

Chapter 2 and Chapter 3 both explored the effect of manipulating visual feedback specifying hand use on estimates of action capabilities. The first study in Chapter 4 attempted to explore whether visual feedback specifying hand use would impact the control of visually guided actions. Specifically, I wanted to explore the role of visual feedback specifying handedness when interacting with objects embedded in visual illusions.

Previous research has consistently found that visually guided actions, such as grasping, towards objects embedded in visual illusions show a significantly lower magnitude of the illusion than perceptual estimates of object size (Aglioti et al., 1995; Haffenden & Goodale, 1998; Milner & Goodale, 1992; Pavani et al., 1999). Gonzalez et al. (2006)

expanded on these findings by showing that grasps towards objects embedded in the Ebbinghaus and Ponzo illusion with the right hand demonstrated a significantly lower magnitude of the illusion than grasps using the left hand, even in left-handed individuals (LHIs). Gonzalez et al. interpret this finding as evidence of visuomotor mechanisms being lateralised in the left hemisphere, providing an advantage to the right hand in the control of visually guided actions more generally. Therefore, allowing the left hand to utilise the more efficient visual feedback associated with moving the right hand may lead to lower sensitivity to the perceptual effects of visual illusions when grasping.

However, the right hand advantage in grasping towards objects embedded in visual illusions has not been replicated well in other studies. Both Dewar and Carey (2006) and Radoeva et al. (2005) found no differences in the magnitude of visual illusions when grasping with the left and the right hand. Furthermore, critics argue that the proposal that visuomotor mechanisms for the online control of action are lateralised within the left hemisphere would mean that the left hand would be unable to use the advantages of the vision-for-action system (Franz & Gegenfurtner, 2010). Movements of the dominant left hand in LHIs would therefore be seriously disadvantaged leading to question the plausibility of conclusion that the vision-for-action system is lateralised in the left hemisphere (Franz & Gegenfurtner, 2010). Therefore, the conclusions made by Gonzalez et al. (2006) are not without controversy.

The results of the first experiment in Chapter 4 are interpreted within the context of performing actions in VEs more generally. When participants wear a head-mounted display (HMD), objects are presented at a fixed depth on a screen close to their eyes. This means that depth cues ordinarily used for dorsal processing when executing actions in real life are not as reliable (Harris et al., 2019). Additionally, participants received no haptic feedback, making their actions more akin to pantomime. These factors when interacting in VEs may result in more ventral visual processing being used to direct action in VR (Westwood et al., 2000;

Whitwell et al., 2015). Various studies have shown that perceptual estimates of size contrast illusion magnitude, mediated by the ventral stream, are significantly greater than action-based estimates of illusion magnitude (Aglioti et al., 1995; Haffenden & Goodale, 1998; Pavani et al., 1999). Hence, a dissociation exists for perception and action for the Ebbinghaus illusion. Since I found a consistent significant effect of illusory object size from the MGA measures in my study, this suggests that participants were using ventral visual processing to direct their actions towards the virtual Ebbinghaus illusion.

The final study in Chapter 4 was a direct follow-up to assess differences in actions performed in real environments versus VEs by using the Ebbinghaus illusion as a tool. Based on the results of the previous study and the possibility of actions in VR being directed by more ventral visual processing, I expected that grasps performed in VR would show a significantly greater magnitude of the illusion than grasps performed in the real environment. Additionally, based on the finding that the right hand is less sensitive to visual illusions, I expected the magnitude of the illusion to be lower when using the right hand. However, participants grasped in a manner that was inverse to the expected direction of the Ebbinghaus illusion in both environments. I found no significant difference in MGA between the left and right hand. Since participants did not grasp in a manner consistent with the perceptual effects of the illusion, it is unclear whether the left hand would be more susceptible to illusion based on the findings of this study. The main difference in MGA in the real environment versus the VE is that grasps in the VE were larger, likely due to participants employing a more liberal grasping strategy due to their relative lack of experience in VR.

The results of the final study of Chapter 4 likely reflect a strategy of obstacle avoidance. As the distance between target object and the flankers was not equal between the two illusory circle sizes, participants would have had less room to grasp the perceptually larger object than the perceptually smaller one. Therefore, participants reduced their grip aperture for the perceptually larger object to avoid collision with the close flankers. While this finding was an unexpected result, it does support the notion that actions performed towards objects embedded in the Ebbinghaus illusion are resistant to the perceived differences in object size (Aglioti et al., 1995; Haffenden & Goodale, 1998; Milner & Goodale, 1992; Pavani et al., 1999), even within VEs.

One question is why the results of the first and second study of Chapter 4 tell different stories. One factor may have been the nature of the actions performed in these studies. Notably, a key difference between the first and second study is that participants could actually interact with the objects in VR during the second study. That is, grasping the target object caused it to move, unlike in the first study where the object would stay stationary and not respond to user input. Possibly the lack of interaction in the first study meant that the grasps performed towards the target objects were more akin to pantomime, which does not activate the same brain regions as real actions (Króliczak et al., 2007). Additionally, the ‘grasp’ performed in the first study may have acted more as a manual estimate, with manual estimates demonstrating a high illusion magnitude in line with perceptual judgements (Whitwell et al., 2023). Once the target object became interactive the grasping would become more goal-directed and driven by more dorsal visual processing, and hence resistant to the perceptual effects of the illusion.

Overall, Chapter 4 provides insight into the nature of interacting with objects in VR and important considerations such that researchers should ensure that target objects can be moved by the participant with hand input. Though lack of haptic feedback in VR can create actions that are more akin to pantomime than the real action (Westwood et al., 2000; Whitwell et al., 2015) what appears to be most important is that the action performed in VR serves a specific goal. Explicitly, if objects in both the real world and VR are relatively equal in their manipulability, people will direct actions in a similar manner in both environments.

5.5 Limitations and Further Research

While the studies in this thesis provide important insight into how handedness may impact RHIs' estimates of their action capabilities, further research should be conducted looking at online action. The nature of the visual biases discussed in the introduction appear to be more relevant during execution of visually guided actions rather than during estimates of one's action capabilities. For example, Flowers (1975) suggests that differences in skill between the preferred and non-preferred hand is because sensory feedback is transmitted more quickly back to the motor system to correct online movement with the preferred hand. Evidence for this theory comes from visually guided aiming tasks in which people are actively monitoring and correcting their movement trajectories. Thus, further research should explore whether allowing the left hand to use the visual feedback normally associated with the right hand would improve the efficiency of the sensorimotor feedback loop, or whether other types of sensory feedback are more important in correcting skilled movements.

Furthermore, the role of attentional biases that show favoured monitoring of the right hand in RHIs would again be more apparent during online action. RHIs demonstrate attentional biases that prime movement of the right hand (Buckingham et al., 2011; Buckingham & Carey, 2009; Buckingham & Carey, 2015). Additionally, RHIs show greater visual monitoring of the right hand (Honda, 1982, 1984) with directing attention away from the right hand impairing its performance (Peters, 1981). If the left hand could visually appear as the right, possibly the visual monitoring normally reserved for moving the right hand would be used for movement of the left hand instead. Again, future studies should explore this question by using online action rather than action estimates.

5.6 Key Conclusions

Overall, this thesis provides new insight into why RHIs perceive their action capabilities to be greater using their right arm than their left. Notably, I found no significant effect of visual hand presented on participants' action estimates, suggesting that biases in action perception are not due to the visual bias that the right hand is larger than the left. **Rather, the results of my thesis suggest that greater skill with the right hand contributes to the bias that the right hand is larger than the left.** This finding is most evident when exploring actions requiring different levels of dexterity. When people are tasked with a simple action, such as reaching forward, the simplicity of the action means that both hands are equally as capable of completing the task. The length of the arms would therefore be the most directly relevant aspect of someone's morphology when they would consider then estimating their reach. If RHIs' perceptions of their reaching ability were impacted by the distorted visual perception that the right arm is longer, I would expect that they estimate their action boundary for reach to be further using their right arm. However, I did not find any differences in estimates of maximum reach between the hands.

When people estimate their ability for a more complex task, such as reach-to-grasp, they consider the dexterity needed to complete it (Bryden et al., 2003; Gabbard et al., 2003; Gonzalez et al., 2007; Mamolo et al., 2004). In RHIs, the right hand would have a greater skill than the left due to more use throughout the lifespan, greater sensorimotor representation, and greater neural activation when using the right hand (Amunts et al., 1996; Buchner et al., 1995; Dassonville et al., 1997; Jung et al., 2003; Volkmann et al., 1998). Thus, RHIs would estimate greater capabilities with the right hand in a manner that is independent of the visual feedback they receive on handedness. The subsequent perceptual bias that the right hand is larger is adaptive, because it encourages continued use of the more skilled right hand (Linkenauger et al., 2009)

Moreover, this thesis demonstrates that people are capable of embodying and calibrating to visual changes to virtual bodies even when the hand being moved is incongruent to the hand being seen. The findings have potential implications for neurorehabilitation research in which researchers may want to assess the efficacy of mirror visual feedback (MVF) therapy treatments using VR. MVF, first developed by Ramachandran et al. (1995) has been used in a variety of clinical scenarios, such as alleviating phantom limb pain or promoting motor recovery in paretic limbs after stroke (see Deconinck et al., 2014, for a review). Embodiment of mirrored virtual limbs would be a key part the recovery process. Phantom limb pain is hypothesised to be a consequence of conflicting visual and proprioceptive signals from the limb (Ramachandran & Altschuler, 2009). Relief of these conflicting signals would therefore require visual feedback to match proprioceptive signals, which would only be effective if the patient embodied the limb providing this visual feedback. Thus, evidence from this thesis that people can embody mirrored virtual limbs shows the potential of mirrored visual feedback in VR in neurorehabilitation scenarios.

Consolidated References

Aglioti, S., DeSouza, J., & Goodale, M. (1995). Size-contrast illusions deceive the eye but not the hand. *Current Biology*, *5*(6), 679-685. https://doi.org/10.1016/s0960-9822(95)00133-3

Akaike, H. (1973). Information theory and an extension of the maximum likelihood principle. In E. Parzen, K. Tanabe, & G. Kitagawa (Eds.), Selected papers of Hirotugu Akaike (pp. 199 – 213). New York: Springer. http://dx.doi.org/10.1007/978-1-4612-1694-0_15

Amunts, K., Schlaug, G., Schleicher, A., Steinmetz, H., Dabringhaus, A., Roland, P. E., & Zilles, K. (1996). Asymmetry in the human motor cortex and handedness. *NeuroImage*, *4*(3), 216–222. https://doi.org/10.1006/nimg.1996.0073

Bhalla, M., & Proffitt, D. R. (1999). Visual–motor recalibration in geographical slant perception. *Journal of Experimental Psychology: Human Perception and Performance*, *25*(4), 1076–1096. https://doi.org/10.1037/0096-1523.25.4.1076

Bootsma, R. J., Bakker, F. C., van Snippenberg, F. E., & Tdlohreg, C. W. (1992). The effects of anxiety on perceiving the reachability of passing objects. *Ecological Psychology, 4*(1), 1–16. https://doi.org/10.1080/10407413.1992.10530790

Bryden, M. P. (1977). Measuring handedness with questionnaires. *Neuropsychologia*, *15*(4-5), 617–624. https://doi.org/10.1016/0028-3932(77)90067-7

Bryden, P. J., Roy, E. A., & Mamolo, C. M. (2003). The effects of skill demands and object characteristics on the distribution of preferred hand reaches in working space. *Brain and Cognition*, *53*, 111–112.

Buchner, H., Ludwig, I., Waberski, T., Wilmes, K., & Ferbert, A. (1995). Hemispheric asymmetries of early cortical somatosensory evoked potentials revealed by topographic analysis. *Electromyogr Clin Neurophysiol*, *35*(4), 207–215.

Buckingham, G., & Carey, D. P. (2009). Rightward biases during bimanual reaching. *Experimental Brain Research*, 194(2), 197–206. https://doi.org/10.1007/s00221-008-1689-x

Buckingham, G., & Carey, D. P. (2015). Attentional asymmetries - cause or consequence of human right handedness? *Frontiers in Psychology, 5*. https://doi.org/10.3389/fpsyg.2014.01587

Buckingham, G., Main, J., & Carey, D. (2011). Asymmetries in motor attention during a cued bimanual reaching task: Left and right handers compared. *Cortex*, *47*(4), 432-440. https://doi.org/10.1016/j.cortex.2009.11.003

Calvert, G. A. (1998). Quantifying hand preference using a behavioural continuum. *Laterality: Asymmetries of Body, Brain and Cognition, 3*(3), 255–268. https://doi.org/10.1080/713754307

Campbell, J. I., & Thompson, V. A. (2012). MorePower 6.0 for anova with relational confidence intervals and bayesian analysis. *Behavior Research Methods*, *44*(4), 1255–1265. https://doi.org/10.3758/s13428-012-0186-0

Carello, C., Grosofsky, A., Reichel, F. D., Solomon, H. Y., & Turvey, M. T. (1989). Visually perceiving what is reachable. *Ecological Psychology*, *1*(1), 27–54. https://doi.org/10.1207/s15326969eco0101_3

Carey, D. P. (2001). Do action systems resist visual illusions? *Trends in Cognitive Sciences*, *5*(3), 109–113. https://doi.org/10.1016/s1364-6613(00)01592-8

Carson, R. G., Chua, R., Elliott, D., & Goodman, D. (1990). The contribution of vision to asymmetries in manual aiming. *Neuropsychologia*, *28*(11), 1215–1220. https://doi.org/10.1016/0028-3932(90)90056-t

Chen, R., Gerloff, C., Hallett, M., & Cohen, L. G. (1997). Involvement of the ipsilateral motor cortex in finger movements of different complexities. *Annals of Neurology*, *41*(2), 247–254. https://doi.org/10.1002/ana.410410216

Chen, Z., Zhang, N., & Saunders, J. A. (2021). Dual processes underlie the effect of the Ebbinghaüs illusion on control of grasping. *Journal of Experimental Psychology: Human Perception and Performance*, *47*(11), 1472–1492. https://doi.org/10.1037/xhp0000819

Chessa, M., Maiello, G., Klein, L., Paulun, V., & Solari, F. (2019). Grasping objects in immersive Virtual Reality. In IEEE Conference on Virtual Reality and 3D User Interfaces (VR) (pp. 1749-1754), https://doi.org/10.1109/VR.2019.8798155. IEEE; IEEE. Retrieved 18 August 2022, from https://ieeexplore.ieee.org/abstract/document/8798155.

Civardi, C., Cavalli, A., Naldi, P., Varrasi, C., & Cantello, R. (2000). Hemispheric asymmetries of cortico-cortical connections in human hand motor areas. *Clinical Neurophysiology*, *111*(4), 624-629. https://doi.org/10.1016/s1388-2457(99)00301-6

Coelho, L., Zaninelli, G., & Gonzalez, C. (2016). A kinematic examination of hand perception. *Psychological Research*, *81*(6), 1224-1231. https://doi.org/10.1007/s00426-016-0815-9

Dassonville, P., Zhu, X.-H., Ugurbil, K., Kim, S.-G., & Ashe, J. (1997). Functional activation in motor cortex reflects the direction and the degree of handedness. *Proceedings of the National Academy of Sciences*, *94*(25), 14015–14018. https://doi.org/10.1073/pnas.94.25.14015

Deconinck, F. J., Smorenburg, A. R., Benham, A., Ledebt, A., Feltham, M. G., & Savelsbergh, G. J. (2014). Reflections on mirror therapy. *Neurorehabilitation and Neural Repair*, *29*(4), 349–361. https://doi.org/10.1177/1545968314546134

Dewar, M., & Carey, D. (2006). Visuomotor ‘immunity’ to perceptual illusion: A mismatch of attentional demands cannot explain the perception–action dissociation. *Neuropsychologia, 44*(8), 1501–1508. https://doi.org/10.1016/j.neuropsychologia.2005.11.010

Dienes, Z. (2011). Bayesian versus Orthodox statistics: Which side are you on? Perspectives on Psychological Science, 6(3), 274–290. https://doi.org/10.1177/1745691611406920

Dienes, Z., & Mclatchie, N. (2018). Four reasons to prefer bayesian analyses over significance testing. Psychonomic Bulletin & Review, 25(1), 207–218. https://doi.org/10.3758/s13423-017-1266-z

Doherty, M. J., Campbell, N. M., Tsuji, H., & Phillips, W. A. (2010). The ebbinghaus illusion deceives adults but not young children. Developmental Science, 13(5), 714–721. https://doi.org/10.1111/j.1467-7687.2009.00931.x

Durgin, F. H., Baird, J. A., Greenburg, M., Russell, R., Shaughnessy, K., & Waymouth, S. (2009). Who is being deceived? the experimental demands of wearing a backpack. Psychonomic Bulletin & Review, 16(5), 964–969. https://doi.org/10.3758/pbr.16.5.964

Elliott, D., Lyons, J., Chua, R., Goodman, D., & Carson, R. (1995). The Influence of Target Perturbation on Manual Aiming Asymmetries in Right-Handers. *Cortex*, *31*(4), 685-697. https://doi.org/10.1016/s0010-9452(13)80020-2

Ellis, A., & Young, A. (1996). *Human cognitive neuropsychology*. Hove: Psychology Pr.

Fagard, J., & Lockman, J. J. (2005). The effect of task constraints on infants’ (BI)manual strategy for grasping and exploring objects. *Infant Behavior and Development*, *28*(3), 305–315. https://doi.org/10.1016/j.infbeh.2005.05.005

Fajen, B. (2005). Perceiving Possibilities for Action: On the Necessity of Calibration and Perceptual Learning for the Visual Guidance of Action. *Perception*, *34*(6), 717-740. https://doi.org/10.1068/p5405

Fajen, B., Riley, M., & Turvey, M. (2009). Information, affordances, and the control of action in sport. *International Journal of Sport Psychology, 40*(1), 79–107.

Flindall, J. W., Doan, J. B., & Gonzalez, C. L. (2013). Manual asymmetries in the kinematics of a reach-to-grasp action. *Laterality: Asymmetries of Body, Brain and Cognition*, *19*(4), 489–507. https://doi.org/10.1080/1357650x.2013.862540

Flindall, J., Stone, K., & Gonzalez, C. (2015). Evidence for right-hand feeding biases in a left-handed population. *Laterality: Asymmetries of Body, Brain and Cognition*, *20*(3), 287-305. https://doi.org/10.1080/1357650x.2014.961472

Flowers, K. (1975). Handedness and controlled movement. *British Journal of Psychology*, *66*(1), 39–52. https://doi.org/10.1111/j.2044-8295.1975.tb01438.x

Foley, R., Whitwell, R., & Goodale, M. (2015). The two-visual-systems hypothesis and the perspectival features of visual experience. Consciousness And Cognition, 35, 225-233. https://doi.org/10.1016/j.concog.2015.03.005

Franz, V. H., Bülthoff, H. H., & Fahle, M. (2003). Grasp effects of the ebbinghaus illusion: Obstacle avoidance is not the explanation. *Experimental Brain Research*, *149*(4), 470–477. https://doi.org/10.1007/s00221-002-1364-6

Franz, V. H., & Gegenfurtner, K. R. (2008). Grasping visual illusions: Consistent data and no dissociation. Cognitive Neuropsychology, 25(7–8), 920–950. https://doi.org/10.1080/02643290701862449

Franz, V. H, , Gegenfurtner, K., Bülthoff, H., & Fahle, M. (2000). Grasping Visual Illusions: No Evidence for a Dissociation Between Perception and Action. *Psychological Science*, *11*(1), 20-25. https://doi.org/10.1111/1467-9280.00209

Freud, E., Macdonald, S. N., Chen, J., Quinlan, D. J., Goodale, M. A., & Culham, J. C. (2018). Getting a grip on reality: Grasping movements directed to real objects and images rely on dissociable neural representations. Cortex, 98, 34–48. https://doi.org/10.1016/j.cortex.2017.02.020

Furmanek, M., Schettino, L., Yarossi, M., Kirkman, S., Adamovich, S., & Tunik, E. (2019). Coordination of reach-to-grasp in physical and haptic-free virtual environments. *Journal Of Neuroengineering and Rehabilitation*, *16*(1). https://doi.org/10.1186/s12984-019-0525-9

Gabbard, C., Iteya, M., & Rabb, C. (1997). A lateralized comparison of handedness and object proximity. *Canadian Journal of Experimental Psychology / Revue Canadienne de Psychologie Expérimentale, 51*(2), 176–180. https://doi.org/10.1037/1196-1961.51.2.176

Gabbard, C., Tapia, M., & Helbig, C. R. (2003). Task Complexity and limb selection in reaching. *International Journal of Neuroscience, 113*(2), 143–152. https://doi.org/10.1080/00207450390161994

Gibson, J. J. (1979). *The ecological approach to visual perception*. Boston,MA: Houghton Mifflin

Gooderham, S. E., & Bryden, P. J. (2013). Does your dominant hand become less dominant with time? the effects of aging and task complexity on hand selection. *Developmental Psychobiology*, *56*(3), 537–546. https://doi.org/10.1002/dev.21123

Gonzalez, C. L., Flindall, J. W., & Stone, K. D. (2015). Hand preference across the lifespan: Effects of end-goal, task nature, and object location. *Frontiers in Psychology, 5,* Article 1579. https://doi.org/10.3389/fpsyg.2014.01579

Gonzalez, C. L., Ganel, T., & Goodale, M. A. (2006). Hemispheric specialization for the visual control of action is independent of handedness. *Journal of Neurophysiology*, *95*(6), 3496–3501. https://doi.org/10.1152/jn.01187.2005

Gonzalez, C., Ganel, T., Whitwell, R., Morrissey, B., & Goodale, M. (2008). Practice makes perfect, but only with the right hand: Sensitivity to perceptual illusions with awkward grasps decreases with practice in the right but not the left hand. Neuropsychologia, 46(2), 624-631. https://doi.org/10.1016/j.neuropsychologia.2007.09.006

Gonzalez, C., Whitwell, R., Morrissey, B., Ganel, T., & Goodale, M. (2007). Left handedness does not extend to visually guided precision grasping. *Experimental Brain Research*, *182*(2), 275-279. https://doi.org/10.1007/s00221-007-1090-1

Goodale, M., Jakobson, L., & Keillor, J. (1994b). Differences in the visual control of pantomimed and natural grasping movements. *Neuropsychologia*, *32*(10), 1159-1178. https://doi.org/10.1016/0028-3932(94)90100-7

Goodale, M., Meenan, J., Bülthoff, H., Nicolle, D., Murphy, K., & Racicot, C. (1994). Separate neural pathways for the visual analysis of object shape in perception and prehension. *Current Biology*, 4(7), 604-610. https://doi.org/10.1016/s0960-9822(00)00132-9

Goodale, M., Milner, A., Jakobson, L., & Carey, D. (1991). A neurological dissociation between perceiving objects and grasping them. *Nature*, *349*(6305), 154-156. https://doi.org/10.1038/349154a0

Goodale, M., & Milner, A. (1992). Separate visual pathways for perception and action. *Trends In Neurosciences*, *15*(1), 20-25. https://doi.org/10.1016/0166-2236(92)90344-8

Grouios, G. (2006). Right hand advantage in visually guided reaching and aiming movements: Brief review and comments. *Ergonomics, 49*(10), 1013–1017. https://doi.org/10.1080/00140130600665349

Grosskopf, A., & Kuhtz-Buschbeck, J. P. (2005). Grasping with the left and right hand: A Kinematic Study. Experimental Brain Research, 168(1–2), 230–240. https://doi.org/10.1007/s00221-005-0083-1

Haffenden, A.M., & Goodale, M.A. (1998). The effect of pictorial illusion on prehension and perception. *Journal of Cognitive Neuroscience, 10*(1), 122–136. https://doi.org/10.1162/089892998563824

Haffenden, A., & Goodale, M. (2000). Independent effects of pictorial displays on perception and action. *Vision Research*, *40*(10-12), 1597-1607. https://doi.org/10.1016/s0042-6989(00)00056-0

Haffenden, A. M., Schiff, K. C., & Goodale, M. A. (2001). The dissociation between perception and action in the ebbinghaus illusion. *Current Biology*, *11*(3), 177–181. https://doi.org/10.1016/s0960-9822(01)00023-9

Hardyck, C., & Petrinovich, L. F. (1977). Left-handedness. *Psychological Bulletin*, *84*(3), 385–404. https://doi.org/10.1037/0033-2909.84.3.385

Harris, D., Buckingham, G., Wilson, M., & Vine, S. (2019). Virtually the same? How impaired sensory information in virtual reality may disrupt vision for action. *Experimental Brain Research*, *237*(11), 2761-2766. https://doi.org/10.1007/s00221-019-05642-8

Heinrich, C., Cook, M., Langlotz, T., & Regenbrecht, H. (2020). My hands? importance of personalised virtual hands in a neurorehabilitation scenario. Virtual Reality, 25(2), 313–330. https://doi.org/10.1007/s10055-020-00456-4

Helsen, W. F., Starkes, J. L., Elliott, D., & Buekers, M. J. (1998). Manual asymmetries and saccadic eye movements in right-handers during single and reciprocal aiming movements. *Cortex*, *34*(4), 513–530. https://doi.org/10.1016/s0010-9452(08)70511-2

Holt, R. J., Lefevre, A. S., Flatters, I. J., Culmer, P., Wilkie, R. M., Henson, B. W., Bingham, G. P., & Mon-Williams, M. (2013). Grasping the changes seen in older adults when reaching for objects of varied texture. *PLoS ONE, 8*(7). https://doi.org/10.1371/journal.pone.0069040

Honda, H. (1982). Rightward superiority of eye movements in a bimanual aiming task. *The Quarterly Journal of Experimental Psychology Section A*, *34*(4), 499–513. https://doi.org/10.1080/14640748208400833

Honda, H. (1984). Functional between-hand differences and outflow eye position information. *The Quarterly Journal of Experimental Psychology Section A*, *36*(1), 75–88. https://doi.org/10.1080/14640748408401504

Howard, M. C. (2017). A meta-analysis and systematic literature review of Virtual Reality Rehabilitation Programs. *Computers in Human Behavior*, *70*, 317–327. https://doi.org/10.1016/j.chb.2017.01.013

Ishak, S., Adolph, K., & Lin, G. (2008). Perceiving affordances for fitting through apertures. Journal Of Experimental Psychology: Human Perception and Performance, 34(6), 1501-1514. https://doi.org/10.1037/a0011393

Jacob, P. and Jeannerod, M. (1999) Consciousness and the visuomotor transformation. *CNRS Institute of Cognitive Science* (http://www.isc.cnrs.fr/wp/wp99–13.htm)

Jeannerod, M. (1996) Reaching and Grasping, Parallel Specification of Visuomotor Channels. In H. Heuer & S. W. Keele (Eds.), *Handbook of perception and action, vol. 2: Motor Skills* (pp. 405-460). London: Academic Press.

Jeannerod, M. (2001). Neural Simulation of Action: A Unifying Mechanism for Motor Cognition. *Neuroimage*, *14*(1), S103-S109. https://doi.org/10.1006/nimg.2001.0832

Jung, P., Baumgärtner, U., Bauermann, T., Magerl, W., Gawehn, J., Stoeter, P., & Treede, R.-D. (2003). Asymmetry in the human primary somatosensory cortex and handedness. *NeuroImage*, *19*(3), 913–923. https://doi.org/10.1016/s1053-8119(03)00164-2

Kawashima, R., Yamada, K., Kinomura, S., Yamaguchi, T., Matsui, H., Yoshioka, S., & Fukuda, H. (1993). Regional cerebral blood flow changes of cortical motor areas and prefrontal areas in humans related to ipsilateral and contralateral hand movement. *Brain Research*, *623*(1), 33–40. https://doi.org/10.1016/0006-8993(93)90006-9

Keshner, E. A., & Kenyon, R. V. (2004). Using immersive technology for postural research and Rehabilitation. *Assistive Technology*, *16*(1), 54–62. https://doi.org/10.1080/10400435.2004.10132074

Kilteni, K., Groten, R., & Slater, M. (2012). The sense of embodiment in virtual reality. *Presence: Teleoperators and Virtual Environments*, *21*(4), 373–387. https://doi.org/10.1162/pres_a_00124

Kilteni, K., Normand, J.-M., Sanchez-Vives, M. V., & Slater, M. (2012). Extending body space in immersive virtual reality: A very long arm illusion. *PLoS ONE*, *7*(7). https://doi.org/10.1371/journal.pone.0040867

Kim, S., Ashe, J., Hendrich, K., Ellermann, J., Merkle, H., Ugurbil, K., & Georgopoulos, A. (1993). Functional magnetic resonance imaging of motor cortex: hemispheric asymmetry and handedness. *Science*, *261*(5121), 615-617. https://doi.org/10.1126/science.8342027

Kokkinara, E., & Slater, M. (2014). Measuring the Effects through Time of the Influence of Visuomotor and Visuotactile Synchronous Stimulation on a Virtual Body Ownership Illusion. *Perception*, *43*(1), 43-58. https://doi.org/10.1068/p7545

Króliczak, G., Cavina-Pratesi, C., Goodman, D. A., & Culham, J. C. (2007). What does The brain do when you fake it? an fmri study of pantomimed and real grasping. *Journal of Neurophysiology*, *97*(3), 2410–2422. https://doi.org/10.1152/jn.00778.2006

Lakens, D., McLatchie, N., Isager, P. M., Scheel, A. M., & Dienes, Z. (2018). Improving inferences about null effects with Bayes factors and equivalence tests. *The Journals of Gerontology: Series B, 75*(1), 45–57. https://doi.org/10.1093/geronb/gby065

Levac, D. E., Huber, M. E., & Sternad, D. (2019). Learning and transfer of complex motor skills in virtual reality: A perspective review. Journal of NeuroEngineering and Rehabilitation, 16(1). https://doi.org/10.1186/s12984-019-0587-8

Levin, M. F., Weiss, P. L., & Keshner, E. A. (2015). Emergence of virtual reality as a tool for upper limb rehabilitation: Incorporation of Motor Control and Motor Learning principles. *Physical Therapy*, *95*(3), 415–425. https://doi.org/10.2522/ptj.20130579

Lin, L., & Linkenauger, S. (2021). Perceiving action boundaries for overhead reaching in a height-related situation. *Attention, Perception, & Psychophysics*, *83*(5), 2331-2346. https://doi.org/10.3758/s13414-021-02293-2

Lin, L., McLatchie, N., & Linkenauger, S. (2020). The influence of perceptual–motor variability on the perception of action boundaries for reaching. *Journal of Experimental Psychology: Human Perception and Performance*, *46*(5), 474-488. https://doi.org/10.1037/xhp0000724

Linkenauger, S., Witt, J., Bakdash, J., Stefanucci, J., & Proffitt, D. (2009). Asymmetrical Body Perception. *Psychological Science*, *20*(11), 1373-1380. https://doi.org/10.1111/j.1467-9280.2009.02447.x

Linkenauger, S. A., Witt, J. K., & Proffitt, D. R. (2011). Taking a hands-on approach: Apparent grasping ability scales the perception of object size. *Journal of Experimental Psychology: Human Perception and Performance*, *37*(5), 1432–1441. https://doi.org/10.1037/a0024248

Longo, M. R., Schüür, F., Kammers, M. P. M., Tsakiris, M., & Haggard, P. (2008). What is embodiment? A psychometric approach. *Cognition*, *107*(3), 978–998. https://doi.org/10.1016/j.cognition.2007.12.004

Macdonell, R. A. L., Shapiro, B. E., Chiappa, K. H., Helmers, S. L., Cros, D., Day, B. J., & Shahani, B. T. (1991). Hemispheric threshold differences for motor evoked potentials produced by magnetic coil stimulation. *Neurology*, *41*(9), 1441–1441. https://doi.org/10.1212/wnl.41.9.1441

Magdalon, E. C., Michaelsen, S. M., Quevedo, A. A., & Levin, M. F. (2011). Comparison of grasping movements made by healthy subjects in a 3-dimensional immersive virtual versus physical environment. Acta Psychologica, 138(1), 126–134. https://doi.org/10.1016/j.actpsy.2011.05.015

Mamolo, C. M., Roy, E. A., Bryden, P. J., & Rohr, L. E. (2004). The effects of skill demands and object position on the distribution of preferred hand reaches. *Brain and Cognition*, *55*(2), 349–351. https://doi.org/10.1016/j.bandc.2004.02.041

Mamolo, C. M., Roy, E. A., Rohr, L. E., & Bryden, P. J. (2006). Reaching patterns across working space: The effects of handedness, task demands, and comfort levels. *Laterality: Asymmetries of Body, Brain and Cognition*, *11*(5), 465–492. https://doi.org/10.1080/13576500600775692

Mann, D., & van der Kamp, J. (2014). Visually-guided interceptive actions performed in virtual environments [Abstract]. Journal Of Vision, 14(10), 842-842. https://doi.org/10.1167/14.10.842 Abstract retrieved from https://jov.arvojournals.org/article.aspx?articleid=2144719

McManus, I. C., Sik, G., Cole, D. R., Mellon, A. F., Wong, J., & Kloss, J. (1988). The development of handedness in children. *British Journal of Developmental Psychology*, *6*(3), 257–273. https://doi.org/10.1111/j.2044-835x.1988.tb01099.x

Mon-Williams, M., & Tresilian, J. R. (1999). Some recent studies on the extraretinal contribution to distance perception. Perception, 28(2), 167–181. https://doi.org/10.1068/p2737

Mon-Williams, M., Tresilian, J., McIntosh, R., & Milner, D. (2001). Monocular and binocular distance cues: insights from visual form agnosia I (of III). *Experimental Brain Research*, *139*(2), 127-136. https://doi.org/10.1007/s002210000657

Normand, J.-M., Giannopoulos, E., Spanlang, B., & Slater, M. (2011). Multisensory stimulation can induce an illusion of larger belly size in immersive virtual reality. *PLoS ONE*, *6*(1). https://doi.org/10.1371/journal.pone.0016128

Nelson, E. L., Campbell, J. M., & Michel, G. F. (2013). Unimanual to bimanual: Tracking the development of handedness from 6 to 24 months. *Infant Behavior and Development*, *36*(2), 181–188. https://doi.org/10.1016/j.infbeh.2013.01.009

Netelenbos, N., & Gonzalez, C. (2015). Is that graspable? Let your right hand be the judge. *Brain and Cognition*, *93*, 18-25. https://doi.org/10.1016/j.bandc.2014.11.003

Ocklenburg, S., Garland, A., Strockens, F., & Uber Reinert, A. (2015). Investigating the neural architecture of handedness. *Frontiers in Psychology*, *6*. https://doi.org/10.3389/fpsyg.2015.00148

Ogawa, N., Narumi, T., & Hirose, M. (2019). Virtual hand realism affects object size perception in body-based scaling. *2019 IEEE Conference on Virtual Reality and 3D User Interfaces (VR)*. https://doi.org/10.1109/vr.2019.8798040

O'Shea, H., & Moran, A. (2017). Does Motor Simulation Theory Explain the Cognitive Mechanisms Underlying Motor Imagery? A Critical Review. *Frontiers in Human Neuroscience*, *11*. https://doi.org/10.3389/fnhum.2017.00072

Pavani, F., Boscagli, I., Benvenuti, F., Rabuffetti, M., & Farnè, A. (1999). Are perception and action affected differently by the Titchener circles illusion? *Experimental Brain Research*, *127*(1), 95–101. https://doi.org/10.1007/s002210050777

Peters, M. (1981). Attentional asymmetries during concurrent bimanual performance. *The Quarterly Journal of Experimental Psychology Section A*, *33*(1), 95–103. https://doi.org/10.1080/14640748108400772

Petkova, V. I., Khoshnevis, M., & Ehrsson, H. H. (2011). The Perspective Matters! multisensory integration in ego-centric reference frames determines full-body ownership. *Frontiers in Psychology*, *2*. https://doi.org/10.3389/fpsyg.2011.00035

Pijpers, J. R., Oudejans, R. R., & Bakker, F. C. (2007). Changes in the perception of action possibilities while climbing to fatigue on a climbing wall. Journal of Sports Sciences, 25(1), 97–110. https://doi.org/10.1080/02640410600630894

Pijpers, J. R., Oudejans, R. R., Bakker, F. C., & Beek, P. J. (2006). The role of anxiety in perceiving and realizing affordances. Ecological Psychology, 18(3), 131–161. https://doi.org/10.1207/s15326969eco1803_1

Pritchard, S. C., Zopf, R., Polito, V., Kaplan, D. M., & Williams, M. A. (2016). Non-hierarchical influence of visual form, touch, and position cues on embodiment, agency, and presence in virtual reality. Frontiers in Psychology, 7. https://doi.org/10.3389/fpsyg.2016.01649

Proffitt, D. R., & Linkenauger, S. A. (2013). Perception viewed as a phenotypic expression. In W. Prinz, M. Beisert, & A. Herwig (Eds.), *Action science: Foundations of an emerging discipline*, (pp. 171-197). MIT Press.

Proffitt, D. R., Linkenauger, S. A., Lin, L. P., & Taylor, R. L. (2022). Body scaling of visually perceived metric space. In *The Routledge Handbook of Bodily Awareness* (pp. 427-458). Routledge.

Radoeva, P. D., Cohen, J. D., Corballis, P. M., Lukovits, T. G., & Koleva, S. G. (2005). Hemispheric asymmetry in a dissociation between the visuomotor and visuoperceptual streams. *Neuropsychologia*, *43*(12), 1763–1773. https://doi.org/10.1016/j.neuropsychologia.2005.02.005

Ramachandran, V. S., & Altschuler, E. L. (2009). The use of visual feedback, in particular mirror visual feedback, in restoring brain function. *Brain*, *132*(7), 1693–1710. https://doi.org/10.1093/brain/awp135

Ramachandran, V. S., Rogers-Ramachandran, D., & Cobb, S. (1995). Touching the phantom limb. *Nature*, *377*(6549), 489–490. https://doi.org/10.1038/377489a0

Ramsay, D. S. (1980). Onset of unimanual handedness in infants. *Infant Behavior and Development*, *3*, 377–385. https://doi.org/10.1016/s0163-6383(80)80045-2

Ramsay, D. S., & Weber, S. L. (1986). Infants' hand preference in a task involving complementary roles for the two hands. *Child Development*, *57*(2), 300. https://doi.org/10.2307/1130585

Readman, M., Cooper, D., & Linkenauger, S. (2021). It's in your hands: How variable perception affects grasping estimates in virtual reality. *Psychonomic Bulletin & Review*, *28*(4), 1202-1210. https://doi.org/10.3758/s13423-021-01916-x

Rigal, R. A. (1992). Which handedness: Preference or performance? *Perceptual and Motor Skills*, *75*(3), 851–866. https://doi.org/10.2466/pms.1992.75.3.851

Roy, E. A., & Elliott, D. (1986). Manual asymmetries in visually directed aiming. *Canadian Journal of Psychology/Revue Canadienne De Psychologie*, *40*(2), 109–121. https://doi.org/10.1037/h0080087

Roy, E. A., & Elliott, D. (1989). Manual asymmetries in aimed movements. *The Quarterly Journal of Experimental Psychology Section A*, *41*(3), 501–516. https://doi.org/10.1080/14640748908402379

Roy, E. A., Kalbfleisch, L., & Elliott, D. (1994). Kinematic analyses of manual asymmetries in visual aiming movements. *Brain and Cognition, 24*(2), 289–295. https://doi.org/10.1006/brcg.1994.1017

Sanchez-Vives, M., Spanlang, B., Frisoli, A., Bergamasco, M., & Slater, M. (2010). Virtual Hand Illusion Induced by Visuomotor Correlations. *Plos ONE*, *5*(4), e10381. https://doi.org/10.1371/journal.pone.0010381

Sato, A., & Yasuda, A. (2005). Illusion of sense of self-agency: Discrepancy between the predicted and actual sensory consequences of actions modulates the sense of self-agency, but not the sense of self-ownership. *Cognition, 94*(3), 241–255. https://doi.org/10.1016/j.cognition.2004.04.003

Slater, M., Perez-Marcos, D., Ehrsson, H., & Sanchez-Vives, M. (2008). Towards a digital body: The virtual arm illusion. *Frontiers In Human Neuroscience*, *2*. https://doi.org/10.3389/neuro.09.006.2008

Slater, M., & Sanchez-Vives, M. V. (2014). Transcending the self in immersive virtual reality. *Computer, 47*(7), 24–30. https://doi.org/10.1109/mc.2014.198

Slater, M., Spanlang, B., Sanchez-Vives, M. V., & Blanke, O. (2010). First person experience of body transfer in virtual reality. *PLoS ONE, 5*(5). https://doi.org/10.1371/journal.pone.0010564

Smith, J., & Pepping, G.-J. (2010). Effects of affordance perception on the initiation and actualization of action. *Ecological Psychology*, *22*(2), 119–149. https://doi.org/10.1080/10407411003720080

Sörös, P., Knecht, S., Imai, T., Gürtler, S., Lütkenhöner, B., Ringelstein, E. B., & Henningsen, H. (1999). Cortical asymmetries of the human somatosensory hand representation in right- and left-handers. *Neuroscience Letters*, *271*(2), 89–92. https://doi.org/10.1016/s0304-3940(99)00528-5

Steenhuis, R. E. (1999). The relation between hand preference and hand performance: What you get depends on what you measure. *Laterality: Asymmetries of Body, Brain and Cognition*, *4*(1), 3–26. https://doi.org/10.1080/713754324

Stone, K., Bryant, D., & Gonzalez, C. (2013). Hand use for grasping in a bimanual task: evidence for different roles? *Experimental Brain Research*, *224*(3), 455-467. https://doi.org/10.1007/s00221-012-3325-z

Technologies, U. (2018, April 19). Preparing assets for Unity. Unity. Retrieved January 26, 2023, from https://docs.unity3d.com/2019.3/Documentation/Manual/BestPracticeMakingBelievableVisuals1.html

Tsakiris, M. (2010). My body in the brain: A neurocognitive model of body-ownership. *Neuropsychologia*, *48*(3), 703–712. https://doi.org/10.1016/j.neuropsychologia.2009.09.034

Tsakiris, M., Longo, M. R., & Haggard, P. (2010). Having a body versus moving your body: Neural signatures of agency and body-ownership. *Neuropsychologia*, *48*(9), 2740–2749. https://doi.org/10.1016/j.neuropsychologia.2010.05.021

Turvey, M. T. (2004). Space (and its perception): The first and final frontier. *Ecological Psychology*, *16*(1), 25–29. https://doi.org/10.1207/s15326969eco1601_3

Triggs, W. J., Calvanio, R., & Levine, M. (1997). Transcranial magnetic stimulation reveals a hemispheric asymmetry correlate of intermanual differences in motor performance. *Neuropsychologia, 35*(10), 1355–1363. https://doi.org/10.1016/s0028-3932(97)00077-8

Triggs, W., Calvanio, R., Macdonell, R., Cros, D., & Chiappa, K. (1994). Physiological motor asymmetry in human handedness: evidence from transcranial magnetic stimulation. *Brain Research*, *636*(2), 270-276. https://doi.org/10.1016/0006-8993(94)91026-x

Triggs, W., Subramanium, B., & Rossi, F. (1999). Hand preference and transcranial magnetic stimulation asymmetry of cortical motor representation. *Brain Research*, *835*(2), 324-329. https://doi.org/10.1016/s0006-8993(99)01629-7

Wagman, J. B. (2012). Perception of maximum reaching height reflects impending changes in reaching ability and improvements transfer to unpracticed reaching tasks. *Experimental Brain Research, 219*(4), 467–476. https://doi.org/10.1007/s00221-012-3104-x

Wagman, J. B., Cialdella, V. T., & Stoffregen, T. A. (2018). Higher order affordances for reaching: Perception and performance. Quarterly Journal of Experimental Psychology, 72(5), 1200–1211. https://doi.org/10.1177/1747021818784403

Walsh, A. S., Seifert, L., Button, C., & Croft, J. L. (2023). The effect of expertise upon perceived reach- and grasp-ability in rock climbers. *International Journal of Sport and Exercise Psychology*, 1–14. https://doi.org/10.1080/1612197x.2022.2161104

Westwood, D., Chapman, C., & Roy, E. (2000). Pantomimed actions may be controlled by the ventral visual stream. *Experimental Brain Research*, *130*(4), 545-548. https://doi.org/10.1007/s002219900287

Westwood, D., & Goodale, M. (2003). A haptic size-contrast illusion affects size perception but not grasping. *Experimental Brain Research*, *153*(2), 253-259. https://doi.org/10.1007/s00221-003-1599-x

Witt, J., & Proffitt, D. (2008). Action-specific influences on distance perception: A role for motor simulation. *Journal Of Experimental Psychology: Human Perception and Performance*, *34*(6), 1479-1492. https://doi.org/10.1037/a0010781

Witt, J., Proffitt, D., & Epstein, W. (2005). Tool Use Affects Perceived Distance, But Only When You Intend to Use It. *Journal Of Experimental Psychology: Human Perception and Performance*, *31*(5), 880-888. https://doi.org/10.1037/0096-1523.31.5.880

Whitwell, R. L., Garach, M. A., Goodale, M. A., & Sperandio, I. (2023). Looking at the ebbinghaus illusion: Differences in neurocomputational requirements, not gaze-mediated attention, explain a classic perception-action dissociation. *Philosophical Transactions of the Royal Society B: Biological Sciences, 378*(1869). https://doi.org/10.1098/rstb.2021.0459

Whitwell, R., Ganel, T., Byrne, C., & Goodale, M. (2015). Real-time vision, tactile cues, and visual form agnosia: removing haptic feedback from a “natural” grasping task induces pantomime-like grasps. *Frontiers In Human Neuroscience*, *9*. https://doi.org/10.3389/fnhum.2015.00216

van Doorn, R. R. A. (2008). Manual asymmetries in the temporal and spatial control of aimed movements. *Human Movement Science*, *27*(4), 551–576. https://doi.org/10.1016/j.humov.2007.11.006

Volkmann, J., Schnitzler, A., Witte, O., & Freund, H. (1998). Handedness and Asymmetry of Hand Representation in Human Motor Cortex. *Journal Of Neurophysiology*, *79*(4), 2149-2154. https://doi.org/10.1152/jn.1998.79.4.2149

You, H., Meng, Y., Huan, D., & Wang, D.-H. (2011). The neural dynamics for hysteresis in visual perception. Neurocomputing, 74(17), 3502–3508. https://doi.org/10.1016/j.neucom.2011.06.004