

The Role of Visual and Proprioceptive Feedback for Motor Imagery Tasks

By

Stephen Wood

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Abstract

Motor imagery refers to the internal simulation or rehearsal of movements without physical execution. These internal action simulations are thought to evoke the same cognitive and neuronal processes involved in motor performance. One significant difference between motor imagery and motor execution is the availability of online sensory feedback for performance. The present study evaluated whether online sensory feedback systems are involved in motor imagery. Fifty participants completed the *Hand Laterality Judgement Task* (HLJT) in four conditions that altered the availability of visual and proprioceptive feedback from participants' hands during task performance (control, no vision, disrupted proprioception, no vision + disrupted proprioception). The results indicate: 1) Online sensory feedback is used to simulate actions effectively; 2) implicit motor imagery continues to be used to identify the laterality of hands when sensory feedback is disrupted; 3) both visual and proprioceptive feedback contribute to motor imagery performance in the HLJT, which indicates that participants use both internal and kinesthetic imagery to make hand laterality judgements.

Introduction

Imagine yourself swinging a golf club, lifting a heavy weight off the ground, or sprinting as fast as possible; in each situation, you can vividly picture how it would look and feel to execute these movements. These action simulations, known as motor imagery, enable us to rehearse and refine our motor skills without executing them (Dickstein & Deutsch, 2007; Jeannerod, 2001; Ladda et al., 2021). Motor imagery can be performed using internal, external, or kinesthetic techniques. Internal motor imagery refers to the simulation of actions from a first-person perspective, requiring one to imagine how a given movement would appear from the perspective of the person performing it. External motor imagery refers to the simulation of movements from a third-person perspective, imagining how a movement would look if observing someone else perform it (Hardy & Callow, 1999; Mahoney & Avenier, 1977). Alternatively, kinesthetic motor imagery—despite the name—does not necessarily refer to *imagery* at all, rather, it refers to the simulation of expected kinesthetic sensations associated with performing a movement (Hardy & Callow, 1999; Jongsma et al., 2013). Although kinesthetic motor imagery represents a third distinct category of motor imagery, it is linked to, and can be coactivated by, the performance of internal or external motor imagery (Callow & Hardy, 2004; Hardy & Callow, 1999; Klatzky, 2010). For example, if asked to imagine swinging a golf club, you would likely imagine the visual and kinesthetic sensations associated with the action, such as watching the head of the club as it is pulled back, the transferring of weight in your legs, the stretching of the shoulder at the top of the backswing, and making contact with the ball.

Motor imagery can be further divided and categorized by the precursors eliciting its performance. Explicit motor imagery refers to the performance of motor imagery in situations where one is instructed to imagine performing a task (Jeannerod & Frak, 1999; Vries et al.,

2013). Such situations may include being asked to imagine making a free throw by your basketball coach before taking your shot. Additionally, motor imagery questionnaires such as the Movement Imagery Questionnaire (MIQ; Williams et al., 2012) measure explicit motor imagery when they require participants to simulate a movement and rate the ease or vividness of their imagery experience. Alternatively, implicit motor imagery refers to action simulations completed without instruction and often without conscious awareness (Jeannerod & Frak., 1999).

Implicit motor imagery may be involved in action-planning processes, observational learning, and is used in perceptual tasks aided by motor processing (Jeannerod, 2001; Miall & Wolpert, 1996; Monaco et al., 2020; Parsons, 1987a; Schwartz & Black, 1999; Toussaint et al., 2013; Wolpert & Flanagan, 2001). For example, implicit motor imagery may be used in action planning to assess the feasibility of various grips for grabbing and holding a pair of scissors or a mug with a handle before initiating a reaching movement toward the object (Klein et al., 2023). Action observations evoke implicit motor imagery through a process of perspective-taking in which an individual attempts to understand the behaviour and action-related goals of others by simulating the performance of the observed actions (Jeannerod, 2001; Gallese & Goldman, 1998). Indeed, observing goal-related movements can activate a mirror neuron network that functionally represents the action being viewed as if it were being performed by the observer (Pellegrino et al., 1992; Rizzolatti et al., 1988). Finally, perceptual tasks, such as laterality judgements, can evoke implicit motor imagery as people tend to solve them by simulating movements toward the object to identify its laterality. For example, a hockey player might assess whether a particular stick is for right- or left-handed players by imagining themselves grabbing and holding the stick to make their evaluation. Furthermore, people tend to judge whether body parts such as hands or feet belong to the right or left side of the body by imagining moving their

own hand or foot into the same orientation (Coslett et al., 2010; Parsons, 1987a). This use of motor imagery will be discussed in more detail below.

Motor Simulation Theory

Motor simulation theory suggests that motor imagery relies on the same cognitive and neuronal processes that facilitate motor execution (Jeannerod, 1994, 2001). Research supports this by highlighting many similarities between imagining and performing the same tasks. For example, motor imagery is subject to the same biomechanical constraint effects that limit motor performance (Parsons, 1987a). This means that as we internally simulate a given movement, we are constrained by the same physical limitations that would be present if we were to execute the same action. To illustrate this point, Decety and Jeannerod (1995) conducted a study in which participants were to imagine performing the Fitts task. The Fitts task is a simple task in which participants make pointing movements from a starting position to targets that vary in size and distance from the starting position. Movement time on the Fitts task is a function of the movement's index of difficulty (the distance of the movement and the size of the target), such that as a target becomes smaller or farther away, movement time to the target increases (Fitts, 1954). Accordingly, Decety and Jeannerod found that when participants are asked to imagine performing the Fitts task, their imagined movement time to the target is related to the movement's index of difficulty, just as it is when participants physically complete the task. Biomechanical constraints in motor imagery have also been demonstrated in situations ranging from walking to writing and drawing by altering the demands of the task being simulated (Decety et al., 1989; Decety & Michel, 1989).

Motor imagery not only considers the presence of biomechanical constraints inherent in a given movement, but it also accounts for the constraints imposed by our body's current position

or orientation in the environment. For example, imagined movement times during simulated walking tasks are longer when participants imagine the movements from a seated position compared to a standing position (Saimpont et al., 2011). Furthermore, participants take longer to identify the laterality of hands rotated outward when their own hands are rotated toward their body than when their hands are straight in front of them (DeLang et al., 2006).

Physiological findings also support the notion that imagining and executing actions share many similarities. For example, heart and respiratory rates increase when participants are asked to simulate strenuous exercise such as walking, running, and weightlifting (Decety et al., 1991; Decety et al., 1993). Moreover, the recorded elevations in heart and respiratory rates, as well as participants' perceived level of fatigue, are proportional to the intensity of the exercise being simulated (Decety et al., 1991; Decety et al., 1993). A study conducted by Wang and Morgan (1992) found that blood pressure was increased by weight training to the same extent when participants performed or imagined weight training from internal or external perspectives. Lastly, simulating self-touch actions has been shown to habituate tactile sensation similarly to executed self-touch movements (Kilteni et al., 2018).

The similarities between action simulation and execution are also represented neurologically. Motor imagery involves activating cortical regions similar to those involved in motor performance, including the premotor cortex, supplementary motor cortex, basal ganglia, and the cerebellum (Gerardin et al., 2000; Jeannerod & Decety, 1995; Kosslyn et al., 2003). Notably, primary motor cortex activation has been reported inconsistently throughout motor imagery literature, and its contribution to action simulation remains under debate (Decety, 1996; Lotze et al., 1999; Sharma et al., 2008; Sirigu et al., 1995). Functional Magnetic Resonance Imaging studies have recently shown that motor imagery not only activates the same cortical

regions as motor performance but also engages many of the same cortical networks. For example, Sharma and Barron (2013) identified networks in the contralateral primary motor cortex, the dorsal premotor area, and the supplementary motor area that were similarly activated when performing and imagining hand movements. The use of similar neural regions and networks during motor imagery and motor execution is one aspect of Jeannerod's motor simulation theory, which proposes that performing and simulating movements are functionally equivalent (Jeannerod, 1994, 2001).

Research involving clinical populations with neurological damage to motor systems has provided additional support for the idea that motor imagery and execution are functionally equivalent. For example, hemiparkinsonism is a rare form of Parkinson's Disease characterized by an asymmetric deterioration of motor control across the body (Tessitore et al., 2010). A study conducted by Dominey et al. (1995) demonstrated that patients with hemiparkinsonism simulate actions more slowly when imagining movements on the side of their body with higher symptom severity compared to their less affected side. Additionally, Fiorio et al. (2005) found that patients with focal dystonia in the hand/wrist performed worse than healthy controls when mentally rotating hand, but not foot stimuli. Taken together, these results support the notion that there is a functional equivalence between motor imagery and execution, demonstrating that damage to neurological systems controlling the movement of specific limbs or body parts creates similar motor limitations when simulating movements of the affected regions.

Due to the similarities between motor imagery and execution, researchers have hypothesized that motor imagery may offer an opportunity to improve or practice motor abilities without the need to execute movements (Hinshaw, 1991; Jeannerod & Pacherie, 2004; Sharma et al., 2006). In many clinical populations with motor impairments, physiotherapy is considered an

extremely effective rehabilitation tool and may be used alone or in combination with other pharmacological interventions (Taylor et al., 2007). Unfortunately, in cases of extreme disability, performing physiotherapy may be dangerous, if not impossible. This is often the case for stroke patients, advanced-stage Parkinson's disease patients, or amputees with phantom limb pain who no longer have the limb requiring therapy. In these situations, motor imagery may offer a unique opportunity to exercise and strengthen the neural pathways used to effectively execute movements, without requiring the patient to physically complete the actions being practiced (Ladda et al., 2021). Motor imagery-based therapies may be particularly beneficial at the beginning of a rehabilitation program or immediately after injury when patients have their most extreme mobility limitations (Ladda et al., 2021). Additionally, motor imagery may be effective when combined with typical physiotherapy programs, providing patients with a safe and effective way to practice exercises at home or when supervision or guidance is not feasible.

Motor imagery training has been shown to increase maximum strength output when executing internally rehearsed movements (Reiser, 2015; Yue & Cole, 1992). Additionally, it has been utilized in older adults to improve balance, mobility, and time to stand (Goudarzian et al., 2017). Incorporating motor imagery training into physiotherapy programs has also been shown to significantly enhance mobility following stroke compared to physiotherapy alone (Page, 2000; Page et al., 2001). Despite the benefits of motor imagery-based therapies across many populations, their clinical significance has been questioned by the relatively small effect sizes observed (for a meta-analysis, see Nicholson et al., 2019).

Hand Laterality Judgement Task

The *Hand Laterality Judgement Task* (HLJT) is a common measure of motor imagery that evokes implicit motor imagery by requiring participants to identify the laterality of hands

presented to them in various orientations (Parsons, 1987a; Parsons, 1994). The HLJT's use of embodied hand stimuli encourages participants to use motor imagery to complete the task; specifically, participants imagine themselves moving their own hands to match the orientation of the hand they are presented with to make their judgements (Parsons, 1987b; Parsons, 1994). This reliance on motor imagery in the HLJT is unique among mental rotation tasks, which typically involve visual or third-person rotation strategies. For example, in the same/different judgement task—another mental rotation task that often utilizes hand stimuli—participants are shown two hands side by side and are instructed to identify if the hands are the same (e.g., two right hands/two left hands) or different (e.g., one right hand and one left hand). In the same/different judgement task, participants imagine rotating the hands to match the orientation of each other from a third-person perspective (Hoyek et al., 2013). This third-person strategy recruits visual processing centers in the occipital and parietal cortices and results in reaction times (RTs) that are based on the angle of rotation effect—as the angular difference between the two hands or objects increases, so do participants' RTs (Alivisatos & Petrides, 1997; Harris & Miniussi, 2003; Hoyek et al., 2013; Kosslyn et al., 2003). In contrast, RTs on the HLJT are based on biomechanical constraint effects, meaning they reflect the time it would take participants to match their own hand to the orientation of the hand stimulus they are presented with (Parsons, 1987).

Biomechanical constraints are represented in the HLJT through increased RTs and lower accuracy scores when identifying hands at physically awkward orientations (Parsons, 1987a). For instance, participants respond faster and more accurately to hands rotated 90° medially than to hands rotated 90° laterally (refer to Table 1 for examples of hand orientations; Bek et al., 2022; Conson et al., 2021; Parsons, 1994; Saran & Marotta, 2024). This phenomenon, known as

the medial over lateral advantage, occurs due to the ease with which we can rotate our own hands medially compared to the difficulty we have rotating our hands laterally. The medial over lateral advantage is especially prominent when participants are presented with the palm view of a hand, which elicits implicit motor imagery strategies significantly more than viewing the back of a hand. (Bek et al., 2022; Conson et al., 2021; Mibu et al., 2020; Zapparoli et al., 2014). In many studies, when participants are presented with the palm of a hand, they respond faster to hands rotated 90° medially than they do to unrotated hands, and they respond faster to 180-degree rotations than they do to 90° lateral rotations (Bek et al., 2022; Brady et al., 2011; Choidealbha et al., 2011). These results emphasize the importance of biomechanical constraints when viewing palm stimuli in the HLJT, as they are directly opposite to the expected RT relationship in mental rotation tasks subject to angle of rotation effects. Biomechanical constraints are also reflected in the HLJT by repeated findings that right-handed participants respond faster to right-hand stimuli than they do to left-hand stimuli (Jones et al., 2021).

The use of motor imagery strategies to complete the HLJT activates motor planning and execution regions of the brain, such as the supplementary motor cortex, the premotor cortex, and regions of the parietal lobe known for their role in sensorimotor integration and reaching tasks (Kosslyn et al., 2003; Wraga et al., 2003). Furthermore, activity in the parietal lobe and the frontoparietal network is dependent on the position of the participant's hands while performing the HLJT (DeLang et al., 2006). Position-dependent activation in these regions indicates that the motor plans being created and simulated during HLJT performance consider the participant's current position and the feasibility of the movement in their current environment. Some studies have reported activation in the primary motor and somatosensory cortices during HLJT performance, albeit to a lesser extent than during movement execution (Kosslyn et al., 2003;

Porro et al., 1996). The relative lack of primary motor cortex excitation during motor imagery compared to motor execution may result from inhibitory signals from the supplementary motor cortex and the parietal lobe, which prevent us from performing movements intended to be imagined (Kasess et al., 2008; Schwoebel et al., 2002). In accordance with the increased biomechanical constraint effects observed in the HLJT when viewing palm stimuli, motor system recruitment in HLJT performance is significantly stronger when viewing the palm of a hand compared to the back of a hand. According to Zapparoli et al. (2014), viewing palm stimuli significantly increases activity in premotor and parietal regions, while back-of-hand stimuli increase activity in the occipital cortex during HLJT performance.

Sensory Feedback in Motor Execution

For motor imagery to be an effective motor assessment or rehabilitation tool, it relies on recreating the cognitive and neurological processes that underly motor learning and execution as closely as possible. One significant difference between motor imagery and motor performance is the availability of online sensory feedback for their execution. Movements rely heavily on online visual and proprioceptive feedback in situations ranging from skilled motor tasks such as reaching and grasping to automatic processes, including gait control and postural corrections (Kasuga et al., 2022; Simoneau et al., 1995). According to optimal feedback control theory, motor performance uses sensory information to monitor ongoing actions and correct for errors that may interfere with the desired movement outcome (Todorov & Jordan, 2002). In contrast, motor imagery does not produce the actions that would be required to receive and use online sensory feedback. Because motor imagery is proposed as a tool to measure or rehabilitate motor impairments or pain in clinical populations with high rates of sensory deficits (e.g., stroke patients, Parkinson's patients, phantom limb pain patients), it is essential to understand how

sensory systems are involved in motor imagery, motor execution, and how these processes may be affected by sensory limitations in various clinical populations. If disruptions to online sensory systems discourage the use of implicit motor imagery, the rationale for using implicit motor imagery training tasks in populations with sensory deficits could be significantly weakened. Furthermore, reduced reliance on or use of implicit motor imagery due to sensory limitations may affect motor planning processes that rely on it to evaluate the feasibility of various actions to complete a given task.

Visual feedback is crucial for performing everyday movements and tasks, as it enables us to judge distances, navigate spaces, and interact with objects effectively. Consider the simple act of making breakfast in the morning. Visual feedback guides the positioning of your hand to open the fridge door by determining the correct angle and verticality needed to grasp the handle. It also ensures that your grasp is wide enough for the door handle to fit into your hand without being so wide that you stub your fingers directly into the fridge door. Similarly, when reaching for your cup of coffee, visual feedback helps you grasp the mug by the handle, keep the mug level as you bring it to your mouth, and place it back down gently on the table.

Tasks requiring accuracy rely on visual feedback to monitor and reduce movement-related errors (Desmurget & Grafton, 2000; Schmidt, 1975). This is especially true for movements of a longer duration, as the added time allows one to process and incorporate information from sensory sources into the movement before it is completed (Keele & Posner, 1968; Saunders & Knill, 2005). Visual feedback aids locomotion by providing information about terrain, obstacles, and our body's position relative to them (Gibson, 1958; Marigold, 2008). In fact, the absence of visual feedback has been shown to alter stride length, stride time, walking velocity, and base width during treadmill walking (Wuehr et al., 2012). Additionally, visual

impairments can affect locomotion even when navigating uncluttered environments (Hallemans et al., 2010). Although visual feedback is considered the most influential source of online feedback in motor control, it is often used in combination with proprioception to obtain the most accurate representations of our body's position in the environment (Cameron et al., 2014; Ernst & Banks, 2002; Patla, 1997).

Proprioception refers to our sense of our body's movement and position in space (Bastian, 1887; Han et al., 2016). Proprioceptive signals come from a variety of sources, including mechanoreceptors that can provide information about the stretch present in our joints or skin, as well as muscle spindles, which provide information about the relative length of our muscles (Macefield, 2021). Afferent information from mechanoreceptors and muscle spindles is then incorporated with efferent knowledge of outgoing motor commands to create an accurate representation of our body's position in space (Bhanpuri et al., 2013; Proske & Gandevia, 2012). The role of proprioception is relatively obvious in some motor tasks, such as postural control and locomotion, which rely on proprioceptive signals to respond to postural disturbances, enabling us to maintain balance. Evidence for the role of proprioception in these situations was presented by Simoneau et al. (1995), who found that diabetic patients with somatosensory deficits exhibited reduced postural control compared to typical diabetics and healthy controls. However, others have also demonstrated the importance of proprioception in goal-directed motor performance such as reaching, grasping, or tracking tasks, especially when visual feedback is limited or unavailable (Fleishman & Rich, 1963; Glazebrook et al., 2019; Gordon et al., 1995; Kasuga et al., 2022; Notterman & Page, 1962).

Proprioception disruptions are common in a variety of clinical populations, such as stroke and Parkinson's disease patients. One analysis by Connel et al. (2008) found that 34-64% of

stroke patients exhibit some loss of proprioception, and this loss of proprioceptive feedback has been shown to contribute to the motor impairments experienced after a stroke (Turville et al., 2017). Furthermore, research has suggested that recovering proprioceptive feedback is crucial in rehabilitating motor abilities after a stroke (Zandvleit et al., 2020). In patients with Parkinson's disease, proprioceptive feedback limitations have been associated with balance difficulty and an increased rate of fall incidence (Gorst et al., 2019). Moreover, the misalignment between outgoing motor commands and incoming visual and proprioceptive feedback in Parkinson's disease patients is thought to contribute to the development of other debilitating symptoms, such as freezing of gait (Beck et al., 2015; Martens et al., 2013).

Clinical populations tend to rely more on visual feedback to perform motor tasks when proprioceptive feedback is limited. For example, Herter et al. (2019) found that many stroke patients can fully or partially compensate for a lack of proprioception with visual feedback in limb positioning tasks. Others have demonstrated that stroke patients increasingly rely on visual feedback to perform a variety of motor tasks, and the correlation between their somatosensory abilities and motor function is stronger for tasks with visual deprivation (Scalha et al., 2011). The use of visual feedback as a compensatory mechanism for faulty or lacking proprioception is also evident in Parkinson's disease patients, who rely on vision of limbs during gait to maintain posture and balance (Beck et al., 2015).

Proprioceptive feedback can be manipulated in healthy participants using a variety of methods, ranging from virtual reality environments that systematically misalign visual and somatosensory feedback to mechanical stimulation of muscles or electrical stimulation of cutaneous nerves that transmit proprioceptive feedback from the extremities to the central nervous system. For example, a study conducted by Mortaza et al. (2023) used a Digitimer

constant current stimulator to stimulate the median nerve, which disrupted somatosensory feedback from the thumb and pointer finger in healthy participants during pointing tasks. Much like the results obtained from clinical populations described above, this study found that participants can compensate for proprioceptive feedback disruptions by relying on visual feedback to control their movements. However, when visual feedback is unavailable, proprioceptive disruptions significantly impair movement accuracy. Research utilizing virtual reality environments has shown that visual feedback has a strong influence over motor control when signals from visual and proprioceptive systems are conflicting (Kasuga et al., 2022). Together, these findings suggest that increased use of visual information to compensate for proprioceptive feedback disruptions does not need to be learned or adapted over a long period, as could be the case in clinical populations with chronic proprioception difficulties. Instead, our sensory integration systems rapidly adjust to the incoming sensory information available to facilitate the motor action being performed. Indeed, Ernst and Banks (2002) demonstrated that sensory integration systems selectively use and combine visual and proprioceptive feedback in a statistically optimal manner to reduce the variability of our judgements for a given task. Therefore, when the variability or noise associated with one sensory source is increased, we rely on other sensory modalities more to guide our judgements.

Sensory Feedback in Motor Learning

Much like motor execution, sensory feedback plays a crucial role in motor learning. Schema theory posits that motor learning involves executing a movement and comparing its outcome with the intended outcome at the time the movement was initiated (Schmidt, 1975). The discrepancy between the executed and intended action is then used to adjust our motor commands for similar movements in similar conditions in the future. Sensory feedback would

therefore be essential for gaining knowledge of how to improve movement for future situations according to schema theory. Neurologically, motor learning is characterized by a strengthening of pathways associated with successful motor execution, which facilitates an easier flow of information across networks involved in performing the action being practiced (Dayan & Cohen, 2011). According to Hebb (2002), when neurons are repeatedly activated together, the connections between them strengthen over time. In this way, practicing movements serves a Hebbian function by repeatedly activating and strengthening neural circuits associated with motor commands (Hebb, 2002; Ladda et al., 2021). Given our reliance on sensory feedback for motor execution, the ability to strengthen networks in both motor and sensory processing or integration regions may be essential for movement rehabilitation, especially in clinical populations with sensory deficits (Takeuchi & Izumi, 2013; Richards et al., 2008). Therefore, for motor imagery to be maximally beneficial to motor learning or rehabilitation in these populations, it should activate sensorimotor systems similarly to motor performance. This process would be beneficial for strengthening neural pathways that integrate sensory information for motor production.

Sensory Feedback in Motor Imagery

Given that motor imagery involves imagining how it would *look* or *feel* to perform a given action, it is unsurprising that action simulations and sensory systems are connected in multiple ways. For example, Porro et al. (1996) found that motor imagery practice increased somatosensory cortex activity compared with visual imagery practice and rest conditions. It is worth noting, however, that this activity increase was less than that observed when participants executed actions in the same experiment. Activity in the somatosensory cortex has also been shown to significantly correlate with motor imagery ability, indicating that the ease with which

one can imagine movements may be related to their ability to activate sensory systems (Confalonieri et al., 2012). Moreover, research has demonstrated that simulating a movement followed by positive imagined sensory feedback (feedback associated with successful motor performance) improves motor performance on the imagined task more than simulating the same movement followed by negative imagined sensory feedback (feedback associated with unsuccessful motor performance; Ashraf et al., 2023). Therefore, the type of feedback simulated during motor imagery practice influences its effectiveness in training protocols.

The relationship between motor imagery and sensory systems is interesting, given that motor imagery does not produce changes to the environment that can be observed using sensory feedback. To better understand how sensory systems are utilized in action simulations, it may be beneficial to consider a type of action that is also performed without feedback—rapid movements. It takes time to process and incorporate sensory feedback into our actions; therefore, rapid movements, which are terminated before the performer has had enough time to process the feedback associated with the movement, are performed without the use of visual or proprioceptive feedback (Keele & Posner, 1968; Chernikoff & Taylor, 1952). According to Schema theory, these rapid actions are governed solely by the motor program created before initiating the action, and sensory feedback is only used after the movement is complete to evaluate its quality and enhance the motor schema for future situations (Schmidt, 1975). This view, however, has been challenged by the finding that participants begin to correct for movement-related errors before enough time has passed for the error to be identified using sensory information (Higgins & Angel, 1970). Findings such as these indicate the presence of forward models, which predict the sensory feedback associated with outgoing motor commands and use this predicted feedback to rapidly adjust movements. Forward models have been used to

address the shortcomings of previous motor control theories and have led to the development of models that recognize feedforward information as a significant factor in motor control. For example, Desmurget and Grafton (2000) proposed a hybrid model of motor control in which actions are initiated with a motor program which is then monitored and adjusted using internal feedback loops comprised of top-down sensory expectations and bottom-up sensory feedback.

Evidence of forward models has also been reported in research on visual information processing and the coordination of eye movements. When we move through our environment, the visual information entering our retinas changes in the same way it would if objects in the environment were moving around us. In theory, this should make it impossible to interpret whether objects are stationary or moving when we shift our body or gaze. To make sense of the visual information being received, knowledge of outgoing motor commands and predictions about how these actions would influence the position of objects on our retina is required to accurately interpret our visual scene (Erickson & Thier, 1992). Regarding eye movements, forward modelling and knowledge of outgoing motor commands are essential for coordinating simultaneous movements of the eyes and head. Indeed, animal research has shown that even when visual and proprioceptive feedback are experimentally eliminated during oculomotor tasks, the performer can respond to saccadic perturbations to bring their gaze back to the intended location (Guthrie et al., 1983; Pelisson et al., 1995).

The research described above is intended to demonstrate how sensory processing does not necessarily require the presence of bottom-up sensory feedback. Motor imagery may therefore activate sensory systems by simulating the expected feedback associated with imagined movements. Motor imagery's ability to simulate feedback has been well documented in the literature on motor planning, where it is believed that the performer uses motor imagery to

simulate the outcome of various actions before initiating a movement (Klein et al., 2023; Miall & Wolpert, 1996; Monaco et al., 2020; Wolpert & Flanagan, 2001). Unlike motor performance, however, it is not known whether simulated movements utilize feedback received from sensory sources, or if their relationship with sensory systems is purely predictive. According to motor simulation theory, simulated movements are functionally equivalent to executed ones (Jeannerod, 1994, 2001). Therefore, motor imagery, like motor performance, should use both top-down and bottom-up sensory processes to generate internal feedback loops that guide actions (Desmurget & Grafton, 2000; Todorov & Jordan, 2002). Because motor imagery is used in motor planning processes and has been proposed as a therapeutic tool for alleviating motor limitations in clinical populations with high rates of sensory impairments, understanding how online feedback is or is not used in action simulations is important. Research involving clinical populations with sensory deficits suggests that online sensory feedback aids motor imagery performance, however, these findings are often confounded by motor impairments that accompany sensory deficits (Haslam et al., 2023; Helmich et al., 2007). Due to this limitation, it is necessary to study the impact of sensory feedback on motor imagery performance in a healthy population.

To date, there have been two studies that manipulated sensory feedback in healthy participants during HLJT performance. One study, conducted by McCormick et al. (2007), used mechanical vibration to disrupt proprioceptive feedback and create the illusion of wrist flexion in participants' left (experimental) hand while their right (control) hand was unaffected. This study found that proprioceptive disruptions significantly increased participants' RTs while accuracy remained unchanged. Notably, in McCormick's experiment, participants could see their control hand while their experimental hand was out of view. The researchers suggest this is not an issue, as there were no differences between experimental and control hands when a sham vibration

stimulus was applied, and the effect was only observed during proprioceptive disruption.

However, given that people tend to rely more on vision in motor control tasks when variability from proprioceptive feedback signals is increased, it is possible that having sight of one's hand(s) only becomes important to HLJT performance once proprioception is disrupted (Beck et al., 2015; Ernst & Banks, 2002; Herter et al., 2019; Mortaza et al., 2023).

Building on this study, Silva et al. (2011) examined HLJT performance in a group of preoperative patients receiving anesthesia for upper-limb surgery. This study compared participants' performance in a control condition (without anesthesia), a deafferented condition in which they could not see their deafferented hand, and a deafferented condition in which they could see both of their hands. This study found that both RTs and accuracy scores were affected by upper limb anesthesia, and the impact of proprioceptive feedback loss was largely reduced once participants could see their deafferented hand.

Overall, these studies suggest that proprioceptive feedback plays a role in HLJT performance. However, they both suffer from limitations that reduce the conclusions that can be drawn from them. For instance, both experiments only manipulated feedback from one hand, leaving the other completely unaffected. This method may have influenced the strategies participants used to complete the HLJT. For example, participants may have compared the hand presented to them with their control hand first, therefore increasing RTs when responding to stimuli of the experimental hand—even if sensory disruptions did not impact how quickly they could simulate movements of their experimental hand. Second, neither study evaluated the effect of vision on HLJT performance in conditions with and without proprioceptive disruptions. This limits the ability to determine how sensory feedback from different sources were integrated and utilized during task performance. Third, the study conducted by Silva and colleagues recruited

participants scheduled to undergo upper limb surgery, which raises the question of whether those recruited had pain or motor impairments in the experimental arm at the time of the study.

Perhaps most importantly, these studies did not use appropriate stimuli or analyses to determine the strategies participants used to solve the HLJT. In the study conducted by McCormick et al. (2007), RT and accuracy scores were averaged across all hand orientations. This analysis showed that RTs increased with disruptions to proprioceptive feedback, but it did not provide information on which hand orientations or views were most affected. In contrast, Silva et al. (2011) did separate RT and accuracy analyses across different views (palm, back, pinky, thumb) and orientations (easy vs difficult). However, in this experiment, *easy* orientations consisted entirely of hands presented upright at 0° while *difficult* orientations consisted of hands presented in lateral and 180° orientations. The failure to include hands rotated medially makes it impossible to determine whether the observed RT and accuracy changes for *difficult* orientations are due to increased difficulty simulating actions or increased difficulty mentally rotating the hand stimuli using visual imagery.

The Present Study

To build on the results reported by McCormick et al. (2007) and Silva et al. (2011) this study was designed to assess the following questions: 1) Does motor imagery recruit online visual and proprioceptive feedback systems to simulate movements? 2) Do participants compensate for disruptions to one sensory system by increasing their reliance on the other? 3) Do participants continue to employ motor imagery strategies to the HLJT when visual and/or proprioceptive feedback is limited? To address these questions, participants were asked to complete the HLJT in four different sensory feedback conditions. These conditions included a control condition with no sensory feedback disruptions, a condition in which the participants do

not have sight of their hands (no vision; NV), a condition where participants' proprioceptive feedback from their hands is disrupted (disrupted proprioception; DP), and a condition in which both proprioceptive *and* visual feedback from participants' hands is disrupted (NV-DP).

Hypotheses

Does motor imagery recruit online visual and proprioceptive feedback systems to simulate movements?

To operationalize this research question, this study tested two specific hypotheses.

Hypothesis 1a: A significant main effect of *condition* was expected, where RTs increase, and accuracy scores decrease in the NV-DP condition compared to the control condition. This would indicate that disrupting online feedback sources negatively impacted participants' ability to complete the HLJT. **Hypothesis 1b:** Because palm view stimuli are thought to elicit motor imagery strategies more than back-of-hand stimuli, increased RTs and decreased accuracy scores when viewing the palm, but not the back of the hand, were expected and would suggest sensory feedback disruptions specifically impacted participants' ability to simulate actions. This hypothesis would be supported by a significant *condition* x *view* interaction effect, in which RT increases and accuracy decreases in the NV, DP, or NV-DP condition are larger when participants view the palm than when they view the back of the hand.

Do participants compensate for disruptions to one sensory system by increasing their reliance on the other?

Studies have shown that visual feedback becomes more essential when proprioceptive feedback is disrupted in overt motor performance (Beck et al., 2015; Herter et al., 2019; Mortaza et al., 2023; Scalha et al., 2011). Furthermore, Ernst and Banks (2002) showed that people tend

to use sensory feedback based on the accuracy of estimates from each source at a given time. This study aimed to assess whether participants compensate for disruptions to one source of feedback by increasing their reliance on the other during motor imagery tasks. To address this question, **Hypothesis 2** predicted that participants would perform better on the HLJT in the NV and DP conditions than in the NV-DP condition. This hypothesis would be supported if post hoc comparisons revealed a significant reduction in RTs and an increase in accuracy scores in the NV and DP conditions compared to the NV-DP condition.

Do participants continue to employ motor imagery strategies to complete the HLJT when visual and/or proprioceptive feedback is limited?

Hypothesis 3: If disruptions to visual and/or proprioceptive feedback influence participants to shift from motor to visual imagery strategies, a significant *condition x view x orientation* interaction would be expected. Specifically, strategy changes would be represented by an increase in RTs and a decrease in accuracy scores when identifying palm stimuli presented in 90°M and 180° orientations. I would also expect a decrease in RTs and an increase in accuracy for palm stimuli rotated 90°L. This response profile would more closely resemble that which we see when participants respond to hand stimuli using visual imagery strategies. Alternatively, a consistent *orientation x view* interaction across all four sensory feedback conditions, including a strong medial over lateral advantage for palm view stimuli, would indicate participants continued to use motor imagery to complete the task when sensory feedback was disrupted.

Methods

Participants

An a priori power analysis using G*Power version 3.1 indicated that 48 participants were required to achieve 80% power, assuming an effect size of $f = 0.20$ and an $\alpha = .05$ significance threshold (Faul et al., 2009). This experiment recruited 63 participants from introductory psychology classes. Of the 63 participants recruited, 13 were excluded from the analyses, resulting in a final sample size of 50 (33 female, 17 male; age range: 17-35; mean = 19.4, SD = 3.12; exclusion criteria are provided below). All participants submitted informed consent before beginning the study and received a brief debriefing form after participation. This research complies with the American Psychological Association ethical standards in the treatment of participants and was approved by the Research Ethics Board at the University of Manitoba, Fort Garry campus. All participants were compensated with three credits toward their class grade for participation, regardless of whether they completed the study. After providing informed consent, participants completed a short demographic information questionnaire and a 12-item MIQ, which will be described below.

Procedures

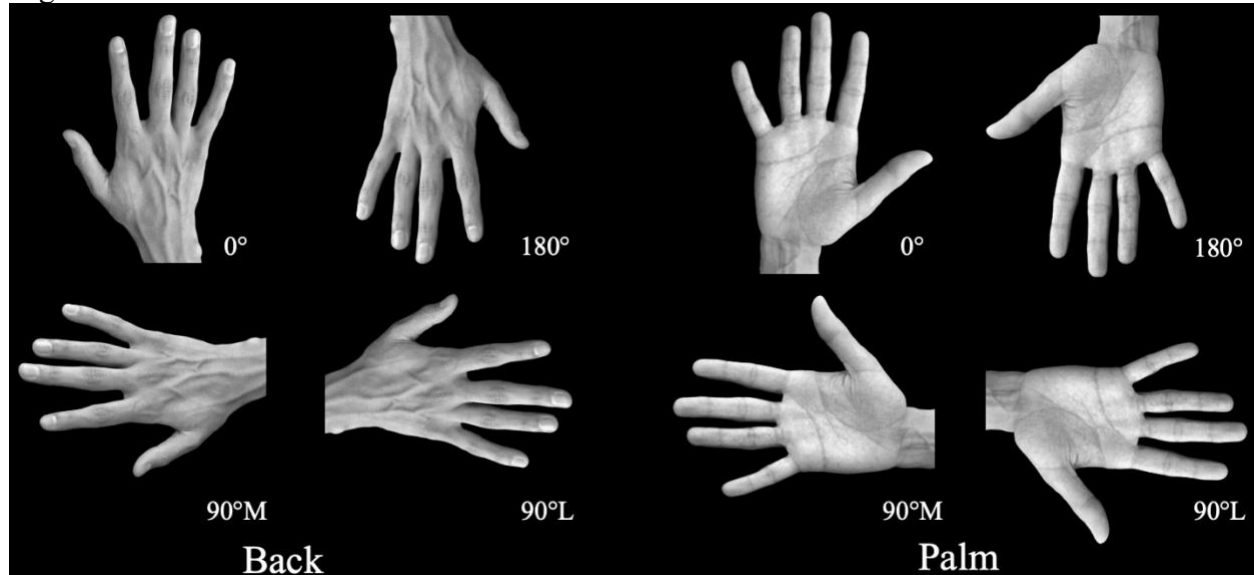
Stimuli and Materials

The HLJT used in this experiment consisted of 16 black-and-white photos of hands positioned in the center of a black background. The 16 hand orientations consisted of the palm and back of left and right hands presented in four different orientations (upright, 180° rotated, 90° medially rotated [90° M], or 90° laterally rotated [90° L]; Figure 1). The hands measure 578

x 447 pixels and will be presented immediately after a 1500ms fixation cross in the middle of the screen.

Figure 1

Right-Hand Stimuli



Note. Right-hand stimuli used in the hand laterality judgement task presented in palm and back views at 0°, 90° medial, 90° lateral, and 180° orientations.

Participants were seated in front of a computer screen with an Ikkegol triple-switch foot pedal (IKKEGOL, Nanshan District, Shenzhen, China) at their feet (Figure 2a). Participants completed a simple reaction time (SRT) test and two training phases before beginning the experiment. SRTs were measured by having participants respond as quickly as possible to the presentation of a red circular stimulus in the centre of the computer screen, using their left or right foot, 20 times each. In the first training phase, participants were instructed to physically match their hands to the hand stimulus presented on the computer screen and to identify whether they could match its orientation. Participants responded to each stimulus by pressing the ‘Y’ key to indicate that they could match the orientation on the screen, and the ‘N’ key to indicate that they could not. The hand stimuli were presented one at a time and included all 16 hand

orientations used in the HLJT once. In the second training phase, participants were presented with each of the 16 hand stimuli once more; however, this time their task was to identify whether the hand being presented was a left or right hand. Participants were instructed not to move their hands during the second training phase and to indicate the laterality of the presented hand using the corresponding left and right foot pedals.

After finishing both training phases, participants were connected to the Digitimer constant current stimulator (DS7AH; Digitimer, Welwyn Garden City, Hertfordshire, UK), underwent sensory threshold testing, and reported their perceived level of numbness or tingling in their hands using a modified item from the Patient Neurotoxicity Questionnaire (PNQ; Hausheer et al., 2006; these processes will be outlined further below). Following sensory detection threshold testing, participants were assigned to one of the four conditions (control, NV, DP, NV-DP) in a counterbalanced block fashion and began the experiment. Each experimental condition consisted of 64 HLJT trials, presenting each of the 16 hand stimuli to participants four times. Stimuli were sampled randomly without replacement, ensuring that participants responded to all 16 hand stimuli once before being presented with any of them a second time. Experimental conditions were split into two equal blocks of 32 trials. Participants completed each experimental condition once and responded to a total of 256 HLJT trials across the four experimental conditions.

Vision

Vision was manipulated by placing a 35cm x 30cm x 12 cm box over the participant's hands during 'no vision' experimental conditions (Figure 2b). The box has an opening on the side facing participants, allowing it to be comfortably placed over their forearms/wrists without

touching them. Furthermore, the box was thin enough to ensure it did not block the participant's view of the computer screen during the experiment.

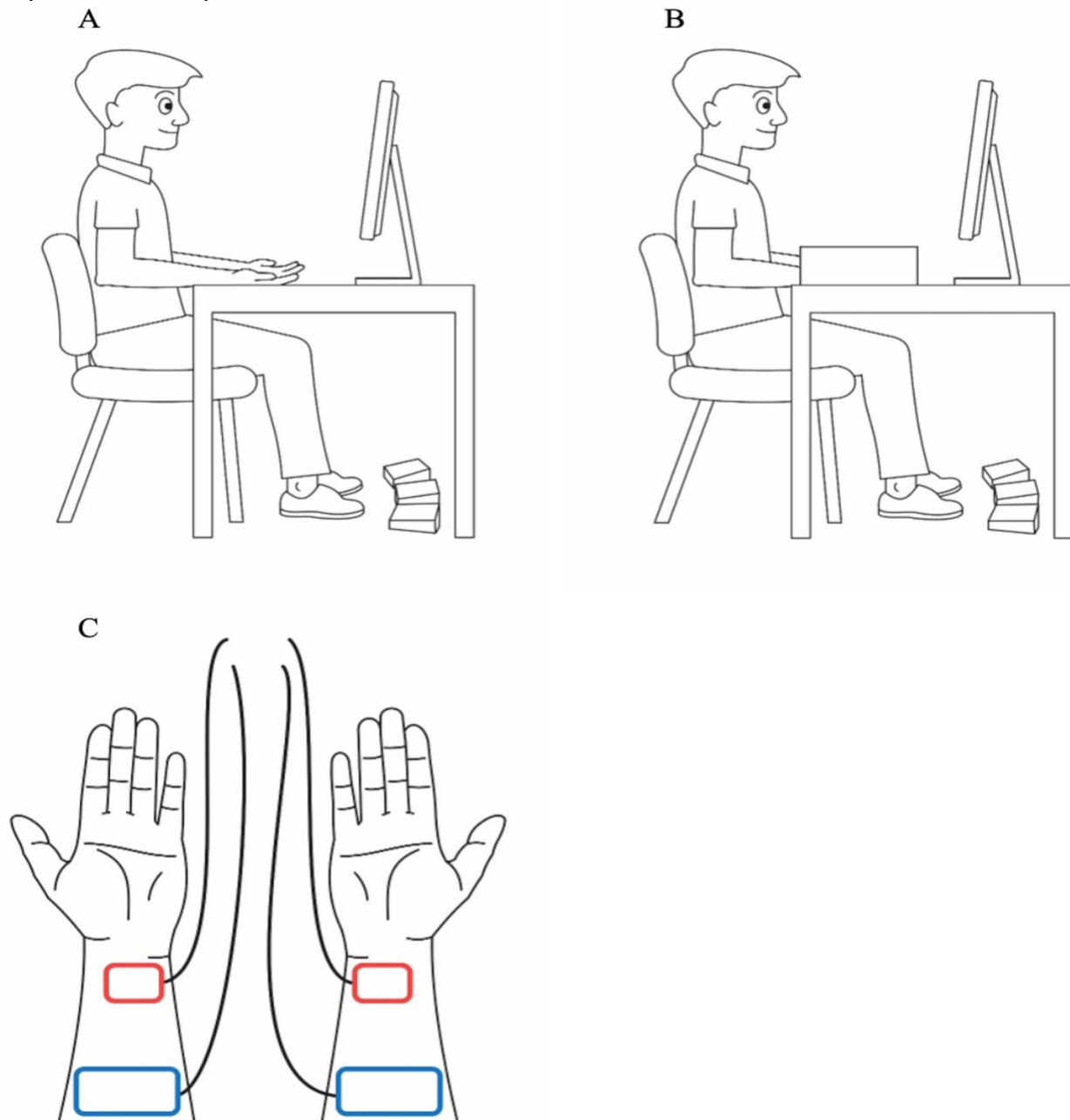
Proprioception

Proprioceptive feedback was manipulated using a Digitimer constant current stimulator. The Digitimer was connected to participants by placing two Axelgaard Ultrastim electrodes (Axelgaard, Fallbrook, California, U.S.A) on the anterior portion of the participant's right and left forearms (Figure 2c). The positive electrode (5cm x 5cm, square) was placed 2 cm proximal to the carpal line along the predicted course of the median and ulnar nerve, while the negative electrode (5cm x 10cm, rectangle) was placed 2 – 5 cm proximal to the positive one. Once the Digitimer was turned on, participants received brief electrical pulses transcutaneously (a 200 μ s square-wave pulse for a duration of 0.2 ms, with an interstimulus interval of 10 ms), which disrupts proprioceptive feedback by adding noise to cutaneous nerves that carry afferent information from mechanoreceptors. According to a study conducted by Kurukuti et al. (2025), participants perform significantly worse on wrist position-matching tasks when transcutaneous stimulation is applied to nerves in the forearm, indicating a decrease in proprioceptive abilities resulting from ongoing transcutaneous stimulation. During stimulation, participants experienced paresthesia in their hands. The experimenter determined the level of stimulation needed to induce this sense of paresthesia in each participant by identifying their sensory threshold (lowest level of stimulation that the participant reports feeling), radiating threshold (lowest level of stimulation that the participant reports feeling radiate through the hand), motor threshold (lowest level of stimulation that causes participants to involuntarily contract muscles in their hand), and premotor threshold (highest level of stimulation the participant can handle without involuntarily

contracting muscles in their hand or wrist). The premotor threshold was the level of stimulation used to create paresthesia and disrupt proprioceptive feedback throughout this experiment.

Figure 2

Experimental Setup



Note. **A)** Depicts the experimental setup when participants complete the hand laterality judgement task in conditions with vision of their hands. **B)** Depicts the experimental setup when

participants complete the hand laterality judgement task without vision of their hands. C)

Illustrates the location of electrode placement used to disrupt proprioceptive information from the median and ulnar nerve. Red outlines represent positive electrodes while blue outlines represent negative electrodes.

Measures

Movement Imagery Questionnaire

Motor imagery abilities were measured using the Movement Imagery Questionnaire 3 (MIQ-3; Williams et al., 2012). According to a recent systematic review of motor imagery measures, the MIQ-3 is among the most reliable and valid measures of motor imagery ability in use (Suica et al., 2022). Additionally, this 12-item questionnaire is designed to measure *internal* visual motor imagery, *external* visual motor imagery, and kinesthetic motor imagery abilities. Each item of the MIQ-3 instructs participants to assume a starting position and complete a specific movement. Following movement completion, participants are instructed to return to the starting position and rate the ease with which they can imagine themselves completing the same movement again. Items measuring kinesthetic motor imagery asked participants to “attempt to *feel* yourself making the movement just observed without actually doing it. Now rate the ease/difficulty with which you were able to do this mental task.” These items are rated using a 7-point Likert-type scale ranging from 1 (*very hard to feel*) to 7 (*very easy to feel*). Alternatively, items designed to measure internal or external visual imagery abilities ask participants to “attempt to *see* yourself making the movement just observed from an *internal/external* perspective. Now rate the ease/difficulty with which you were able to do this mental task.” These items are similarly rated using a 7-point Likert-type scale, which ranged from 1 (*very hard to see*) to 7 (*very easy to see*).

Sensory Detection Thresholds

To ensure that the Digitimer was having the desired effect on the participant's proprioceptive feedback, monofilament pressure sensitivity testing was recorded on the hypothenar and thenar eminence as well as the distal palmar surface of the thumb and little finger. Sensory detection thresholds were measured using Touch-Test Sensory Evaluators (Northcoast Medical), which can produce 0.07 to 300 grams of force. During testing, participants were instructed to close their eyes or look away from their hands and verbally indicate to the experimenter when and where they felt the stimulus. The experimenter began by touching each region of the hand with the smallest monofilament fibre (0.07 grams). If the monofilament fibre went undetected, the experimenter increased to the next smallest fibre and retested the location(s) where participants did not report sensation.

Sensory detection threshold testing was completed once before beginning the experiment to establish a baseline level and again at the beginning, middle, and end of each experimental condition. Repeated detection threshold testing was used to ensure that Digitimer stimulation remained effective throughout the experiment when participants completed trials in the DP and NV-DP conditions. This process also allowed the experimenter to adjust stimulation levels throughout the experiment to maintain an adequate level of proprioceptive disruption of the hands. Sensory detection threshold increases during Digitimer stimulation, compared to baseline recordings, indicated that the Digitimer was effectively disrupting sensory feedback of the participant's hands. Detection threshold increases in the thumb and thenar eminence indicated that the Digitimer was adequately stimulating the median nerve, while detection threshold increases in the little finger and the hypothenar eminence indicated that the Digitimer was adequately stimulating the ulnar nerve.

Patient Neurotoxicity Questionnaire

To further evaluate the effectiveness of Digitimer stimulation, participants were asked to self-report their perceived level of *numbness* or *tingling* in their hands using a single test item from the PNQ, which was slightly adapted for this study. The PNQ is a two-item questionnaire used to assess chemotherapy-induced Peripheral Neuropathy (Hausheer et al., 2006). Item 1 of this questionnaire is presented as a 5-point Likert-type scale asking patients to report the level of numbness, pain, or tingling they are experiencing in their hands or feet from 1 (*I have no numbness, pain or tingling in my hands or feet.*) to 5 (*I have severe tingling, pain or numbness in my hands or feet. It completely prevents me from doing most activities of daily living.*) In this study, item 1 of the PNQ was adapted to focus exclusively on the sensation of numbness or tingling in the participant's hands. Furthermore, the response options did not include statements about how these sensations factor into participants' ability to complete activities in daily living. The adapted PNQ used in this experiment was still presented as a 5-point Likert-type scale, and responses ranged from 1 (*I have no numbness or tingling in my hands*) to 5 (*I have severe tingling or numbness in my hands*). Like detection threshold recordings, PNQ scores were evaluated at the beginning, middle, and end of each experimental condition.

Hand Laterality Judgement Task

As described above, the HLJT used in this study presented participants with photos of black and white hands, including the palm and back of left and right hands in various orientations (0°, 90°M, 90°L, 180°). Participants completed 256 trials of the HLJT, including 16 trials for all 16 hand orientations split across the four sensory feedback conditions. The primary measures of interest in the HLJT are participants' RT and accuracy scores. RTs were measured as the length of time between the presentation of a hand stimulus and the participant's subsequent

pedal press, indicating the laterality of the hand presented. Accuracy was measured as the proportion of correct responses for each hand stimulus in each condition. Participants indicated their laterality judgements to left and right hands by pressing down on the corresponding left or right foot pedal. Participants' hands were placed on the desk in front of them with their palms facing up in each experimental condition.

Data Processing and Analysis

Data Cleaning and Exclusion Criteria

Participant Exclusion Criteria

Participants were excluded from further analyses if the Digitimer could not satisfactorily disrupt sensory feedback coming from a participant's hands during the experiment ($N = 5$). The Digitimer's success was determined by comparing monofilament fibre detection thresholds and participants' self-reported PNQ scores in conditions with and without Digitimer stimulation. Some participant data was discarded due to exceedingly high error rates while completing the HLJT ($N = 8$). See Appendix for a more detailed description of exclusion criteria.

Data Cleaning

Data cleaning began by removing extreme outlier trials which were defined as any trial with RTs $< 500\text{ms}$ or $> 8,000\text{ms}$. These trials were removed as they are likely to reflect anticipatory errors or a failure to attend to the task on a given trial. After removing these outliers, the data were further cleaned by removing the top and bottom 10% of trials, calculated for each condition, view, hand, and orientation combination separately. The bottom cutoff for RT's ranged from 603ms to 959ms, while the top RT cutoff ranged from 1,737ms to 3,700ms. The decision to trim data using percentiles was based on the observation that the data were positively skewed.

Therefore, standard deviation-based trimming would result in asymmetric data cleaning and could artificially reduce mean RTs in this experiment. Additionally, data cleaning using percentiles is thought to be effective for positively skewed data According to Wilcox (1995).

Data Analyses

After data cleaning was complete, data analysis was conducted using JAMOV (Version 2.6.26.0) software. RT analyses were performed using a generalized linear mixed model (GLMM) with a gamma distribution and log link function from the GAMLj package. This model was chosen based on the observation that the RT data remained positively skewed after the data cleaning process, which can be troublesome for analysis of variance (ANOVA) models and other linear regressions. The GLMM used in this study is as follows: $\text{Reaction Time} \sim 1 + \text{Condition} * \text{View} * \text{Hand} * \text{Orientation} + (1 | \text{ID})$. This model predicts RTs using four categorical IVs (condition, control vs. NV vs. DP vs. NV-DP; view, palm vs. back; hand, right vs. left; orientation, 0° vs. 90°M vs. 90°L vs. 180°) and their interaction terms as fixed effects variables while controlling for participant ID as a random effects variable. Accuracy analyses were also performed with JAMOV software and the GAMLj package. Accuracy was analyzed using a logistic GLMM, which predicts the probability of identifying the correct hand in each HLJT trial based on the same predictor variables and interaction terms used for RT analyses. Accuracy analyses also controlled for participant ID as a random effects variable. The final model used to analyze accuracy scores was as follows: $\text{Accuracy} \sim 1 + \text{Condition} * \text{View} * \text{Hand} * \text{Orientation} + (1 | \text{ID})$.

Results

Movement Imagery Questionnaire 3

Participants reported being able to perform internal, external, and kinesthetic imagery tasks with relative ease. The average MIQ-3 score for each category fell between 5.45 to 5.78, indicating that, on average, participants could imagine the sensations associated with each movement somewhat easily to easily (Table 1). Additionally, all participants reported having some ability to perform visual and kinesthetic imagery, indicating this sample did not include anyone with aphantasia.

Table 1

MIQ-3 Scores

	Total	Internal Visual Imagery	External Visual Imagery	Kinesthetic Imagery
Mean	5.64	5.78	5.70	5.45
Standard deviation	0.938	1.05	1.09	1.09
Minimum	3.50	3.50	3.00	1.75
Maximum	7.00	7.00	7.00	7.00

Note. This table provides the mean, standard deviation, minimum, and maximum MIQ-3 scores obtained in this experiment. The Total column represents participants scores across each of the three subcategories of the questionnaire.

Simple Reaction Time

A paired-samples t-test was performed to determine whether participants' SRTs differed when responding to stimuli using either their right or left foot. This analysis found that participants responded similarly to the presentation of the SRT stimulus when using their right ($M = 354$ ms, $SD = 126$ ms) and left feet ($M = 366$ ms, $SD = 125$ ms), $t(49) = -0.748$, $p > .05$. RT differences between feet should therefore not confound the RT results presented below.

Effect of Digitimer Stimulation

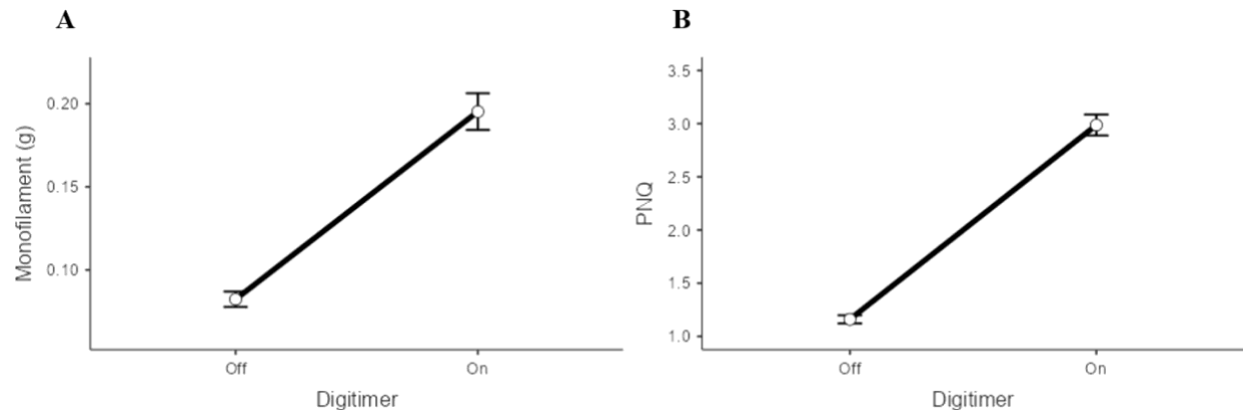
To assess the effectiveness of Digitimer stimulation and its ability to disrupt proprioceptive feedback, detection thresholds from each hand, testing site, and assessment time (beginning, middle, and end) were averaged to create a mean detection threshold score for each condition. Likewise, PNQ scores were averaged across each hand and assessment time to create an average PNQ rating. Detection thresholds and PNQ scores were then compared between each experimental condition using a GLMM with a gamma distribution and log link function. These analyses predicted participants monofilament fibre detection thresholds and PNQ scores using 2 categorical variables (Digitimer: on vs. off; box: on vs. off) while controlling for participant ID as a random effects variable.

The results of these analyses showed that Digitimer stimulation significantly increased both sensory detection threshold and PNQ scores. The analysis of monofilament fibre detection thresholds found a significant main effect of Digitimer ($X^2(1) = 676.860, p < .001$) with significantly higher detection thresholds in Digitimer-On (DP, NV-DP) compared to Digitimer-Off (control, NV) conditions (Figure 3a). Likewise, the analysis of participants PNQ scores detected a significant main effect of Digitimer ($X^2(1) = 2125.889, p < .001$) with participants reporting significantly more numbness and tingling in Digitimer-On compared to Digitimer-Off conditions. As illustrated in Figure 3b, PNQ scores rose from 1.16 in Digitimer-Off conditions to 2.99 in conditions with the Digitimer on. For reference, a score of 1 on the PNQ corresponds to the statement *I have no numbness or tingling in my hands* while reporting a score of 3 is represented by the statement *I have moderate tingling or numbness in my hands*. Together, these results suggest that Digitimer stimulation had a meaningful and significant effect on participants' detection thresholds and their subjective experience of sensations in their hands. Therefore,

Digitimer stimulation effectively disrupted sensory feedback from participants' hands and created the desired effect of paresthesia in this experiment.

Figure 3

Effect of Digitimer Stimulation



Note. **A)** depicts participants' average monofilament fibre detection threshold in grams of force during conditions where the Digitimer was turned off vs. turned on. **B)** Plots participants' average PNQ scores in conditions where the Digitimer was turned off vs. turned on. Error bars represent standard error scores.

Hand Laterality Judgement Task

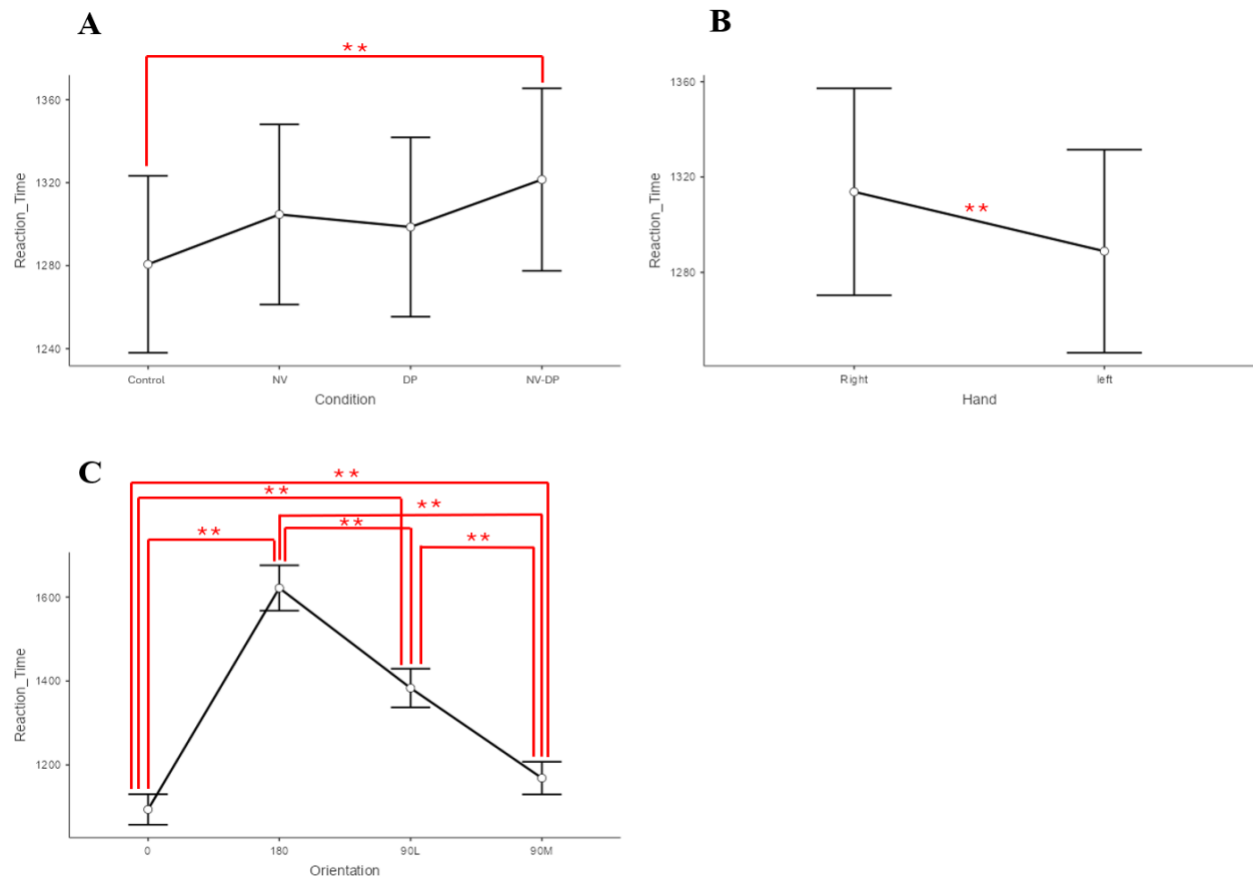
Reaction Time

Main Effects. RT analyses revealed a significant main effect of condition ($X^2(3) = 15.523, p = .001$). As expected, post hoc comparisons using Bonferroni corrections indicated that participants responded significantly faster in the control condition than they did in the NV-DP condition ($p < .001$; Figure 4a). A significant main effect of hand was identified ($X^2(1) = 11.363, p < .001$), with participants responding faster to images of left than right hands ($p < .001$, Figure 4b). Lastly, this experiment observed a significant main effect of orientation ($X^2(3) = 484.096, p < .001$; Figure 4c). Participants responded significantly faster to hands presented at 0° than to

those presented at 90°M ($p < .001$), 90°L ($p < .001$), or 180° ($p < .001$) orientations. Hands rotated 180° resulted in significantly longer RTs than any other orientation ($p < .001$). This study also found that participants responded faster to hands rotated 90°M than to those rotated 90°L ($p < .001$); this result aligns with prior research and indicates that participants used motor imagery strategies to complete the task.

Figure 4

RT Main Effects



Note. Figure 4 depicts the three significant main effects identified by reaction time analyses. In each graph, the Y axis represents participants' reaction times (in milliseconds). **A)** Depicts participants' average reaction times during each of the four experimental conditions. **B)** Depicts average reaction times for right vs left hand stimuli. **C)** Depicts reaction times over the four hand orientations used in this study. Error bars represent standard error scores. Significant differences were calculated using Bonferroni corrections for multiple comparisons.

* $p < .05$; ** $p < .01$.

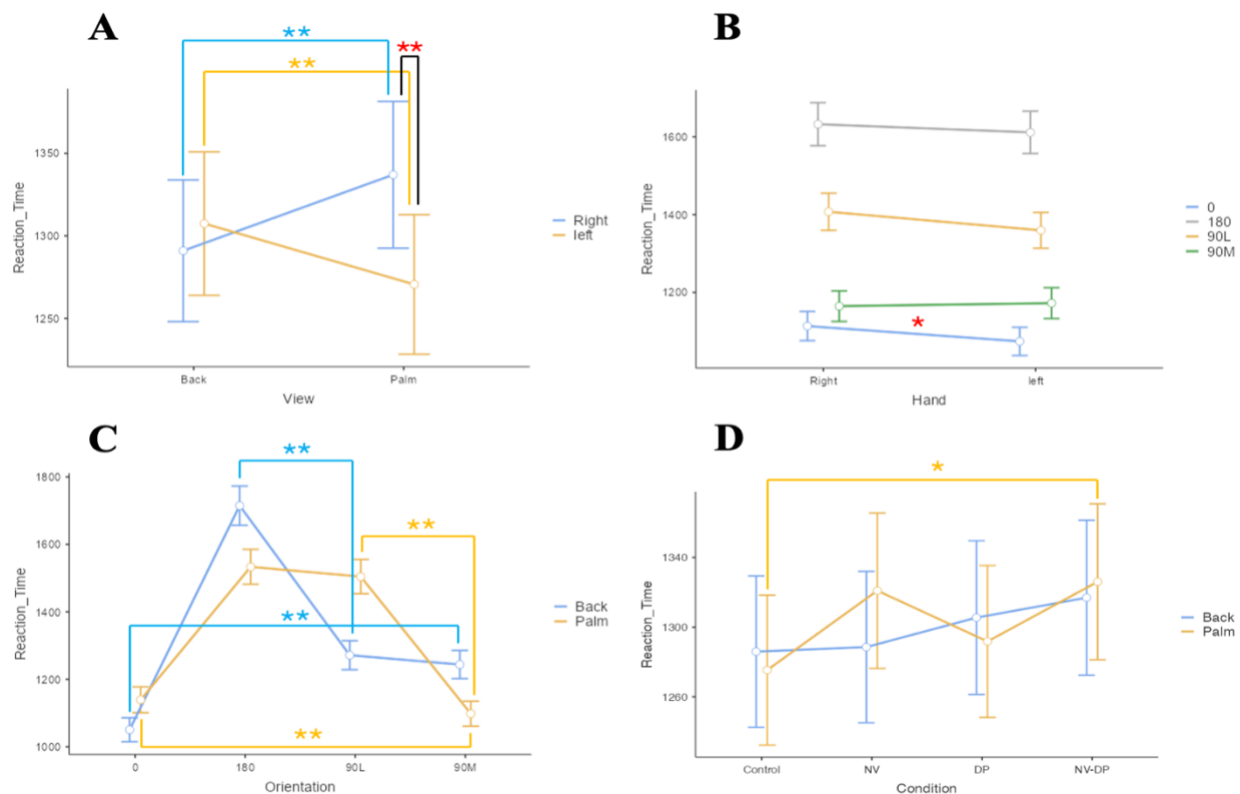
Interaction Effects. A significant view x hand interaction effect was identified ($X^2(1) = 31.398, p < .001$). Post hoc comparisons using Bonferroni corrections revealed that participants responded significantly faster to the palm than to the back of the hand when viewing left-hand

stimuli ($p < .05$), while the opposite was true when viewing right-hand stimuli ($p < .001$; Figure 5a). Additionally, participants responded significantly faster to images of left hands than to right hands when viewing the palm ($p < .001$), but not when viewing the back of the hand ($p > .05$). There was a significant hand x orientation interaction ($X^2(3) = 9.715, p < .05$), with post hoc analyses indicating that participants responded faster to left than right hands at 0° ($p < .05$) but no other orientation ($p > .05$; Figure 5b). Finally, there was a significant view x orientation interaction ($X^2(3) = 484.144, p < .001$). Participants responded significantly faster to hands rotated 90°M than 90°L when viewing the palm ($p < .001$), but not the back ($p = 1.000$) of the hand. Conversely, participants were faster to identify 90°L than 180° orientations when viewing the back ($p < .001$) but not the palm ($p > .05$) of the hand. Participants were also faster to identify 90°M than 0° orientations when viewing the palm of the hand ($p < .05$), whereas the opposite was true when viewing the back of the hand ($p < .001$; Figure 5c). Overall, this interaction effect shows that RTs are more closely related to biomechanical constraints when participants respond to palm-view stimuli. This finding is consistent with previous literature on the subject, which suggests that people tend to use motor imagery strategies more for palm than for back-of-hand stimuli.

Contrary to the hypotheses of this study, initial analyses did not find a significant condition x view interaction effect; however, after adjusting for multiple comparisons using Bonferroni corrections, this interaction term became significant. Post-hoc comparisons found that RTs were significantly longer in the NV-DP condition than in the control condition when viewing palm stimuli ($p < .05$), but not when viewing back-of-hand stimuli ($p > .05$; Figure 5d). These results are consistent with this study's hypotheses, which stated that the effect of sensory disruption should be larger when viewing the palm compared to the back of the hand.

Figure 5

RT Interaction Effects



Note. Figure depicts the four interaction effects identified by reaction time analyses that were significant after using Bonferroni corrections for multiple comparisons. In each graph, the Y axis represents participants' reaction times (in milliseconds). **A)** depicts average reaction times for palm and back views of left and right hands. **B)** depicts reaction time scores for right and left hands at each orientation. **C)** Plots average reaction times to stimuli in each orientation across palm and back views separately. **D)** Average reaction times to palm and back stimuli are shown for each condition. Error bars represent standard error scores. Significant differences were calculated using Bonferroni corrections for multiple comparisons.

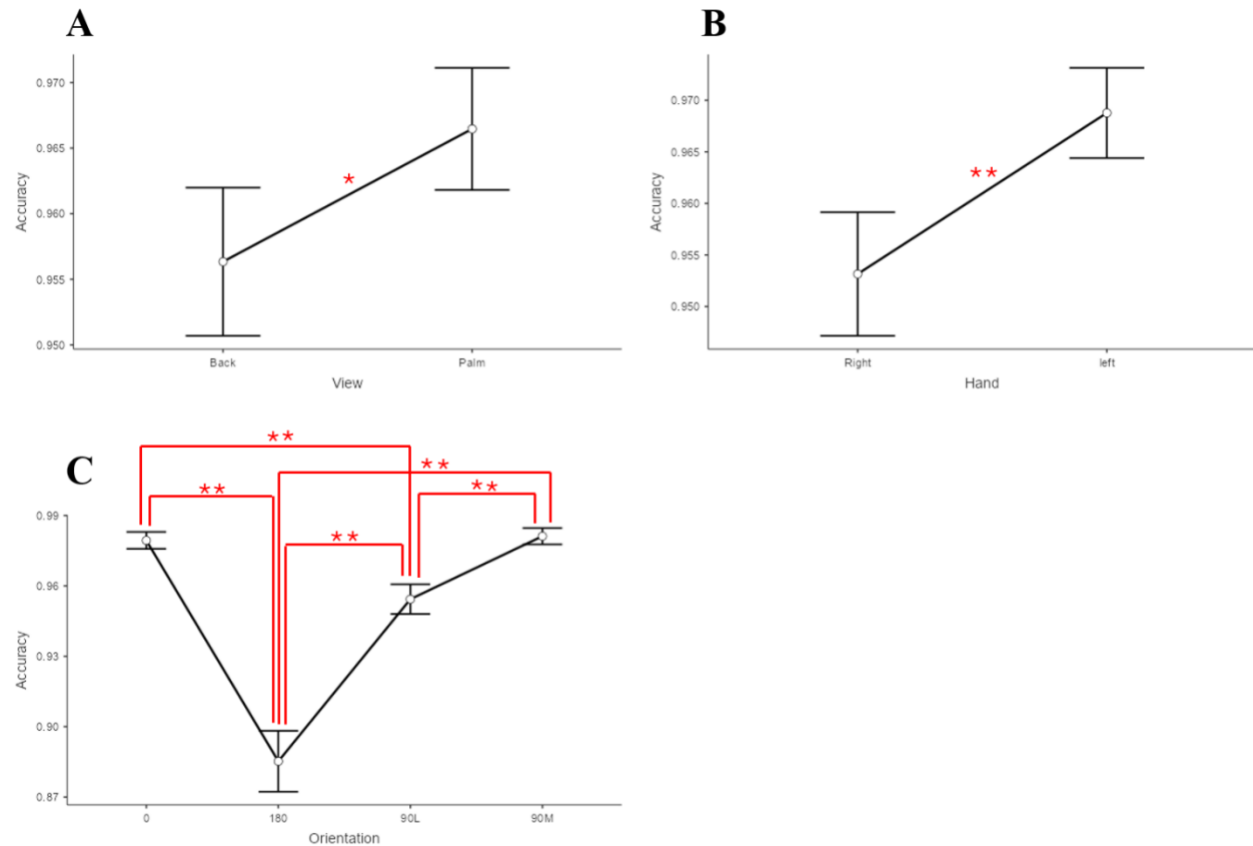
* $p < .05$; ** $p < .01$.

Accuracy

Main Effects. Accuracy analyses revealed a significant main effect of View ($\chi^2(1) = 5.705, p < .05$). Parameter estimates indicate that participants made significantly fewer errors when viewing palm compared to back-of-hand stimuli ($\beta = 0.274, SE = 0.115, Z = 2.389, p < .05$; Figure 6a). There was a significant effect of hand $X^2(1) = 13.507, p < .001$, with participants making significantly less errors when viewing left compared to right-hand stimuli ($\beta = 0.422, SE = 0.115, Z = 3.675, p < .001$; Figure 6b). Finally, there was a significant main effect of orientation $X^2(3) = 270.699, p < .001$. Participants made significantly fewer errors when viewing hands presented at 0° compared to when hands were presented in $90^\circ L$ ($\beta = -0.820, SE = 0.164, Z = 4.993, p < .001$) or 180° orientations ($\beta = -1.817, SE = 0.150, Z = 12.091, p < .001$; Figure 6c).

Figure 6

Accuracy Main Effects



Note. Figure 6 depicts the three significant main effects identified by accuracy analyses. In each graph, the Y axis represents participants accuracy with a score of 1 indicating 100% accuracy. **A)** Depicts participants accuracy when identifying back and palm view stimuli separately. **B)** Depicts participants accuracy when responding to the presentation of right and left hands. **C)** Depicts accuracy scores over the four hand orientations used in this study. Error bars represent standard error scores. Significant differences were calculated using Bonferroni corrections for multiple comparisons.

* $p < .05$; ** $p < .01$.

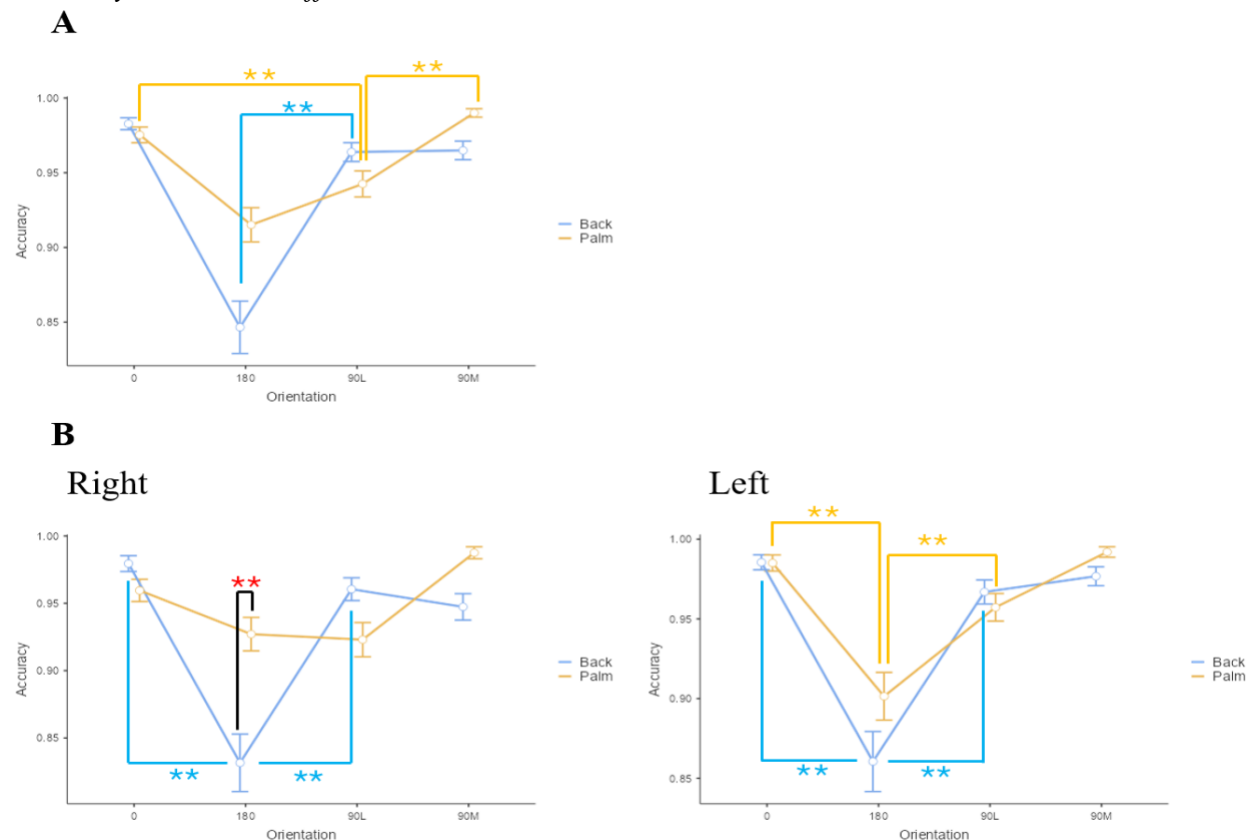
Interaction effects. Accuracy analyses revealed multiple significant interaction effects, including a View x Orientation interaction $X^2(3) = 44.727, p < .001$, a Hand x Orientation interaction $X^2(3) = 11.068, p < .05$, and a View x Hand x Orientation interaction $X^2(3) = 7.810, p = .05$. Regarding the View x Orientation interaction, post hoc analyses using Bonferroni corrections showed that participants were significantly more accurate when responding to hands presented 90°M compared to 90°L when viewing the palm ($p < .001$) but not the back of the hand ($p > .05$; Figure 7a). Viewing the palm of a hand also resulted in significantly higher accuracy when responding to 0° orientations compared to 90°L orientations ($p = .001$), this difference did not exist when viewing back-of-hand stimuli ($p > .05$). Viewing back-of-hand stimuli lead to a significant increase in accuracy when viewing 90°L hands compared to 180° ($p < .001$) whereas there was no significant difference between 90°L and 180° when viewing palm stimuli ($p > .05$). Finally, participants were significantly more accurate at identifying palm than back-of-hand stimuli in 90°M, 90°L, and 180° orientations ($p < .05$), however, no significant differences existed for hands presented in 0° orientations ($p > .05$). As with the view x orientation interaction identified in RT analyses, these results suggest that participants tend to identify the laterality of palm hand stimuli using motor imagery strategies while back-of-hand stimuli are identified using more visual imagery strategies.

Post hoc analyses of the View x Hand x Orientation interaction added additional information to the view x orientation interaction effects described above. For example, this interaction term shows that although participants are more accurate at responding to palm than back-of-hand stimuli at 180°, this effect reaches significance only for right-hand stimuli ($p < .001$), and no such differences were observed for left-hand stimuli ($p > .05$; Figure 7b). In fact, right-hand palm stimuli seem to be specifically resilient to the difficulties of identifying 180°

orientations. In this experiment, participants could more accurately identify hands presented in 0° and 90° orientations compared to 180° orientations for the back of left and right hands ($p < .001$), the palm of left hands ($p < .05$) but not the palm of right hands ($p > .05$). Regarding the Hand x Orientation interaction, post hoc analyses suggest that participants were more accurate when responding to left hands than to right hands at each orientation, except for 180° . However, after applying Bonferroni corrections for multiple comparisons, these differences were no longer significant.

Figure 7

Accuracy Interaction Effects



Note. Figure 6 depicts the two interaction effects identified by accuracy analyses that remained significant after using Bonferroni corrections for multiple comparisons. In each graph, the Y axis represents participants' accuracy, with a score of 1 indicating 100% accuracy. **A)** Shows participants' accuracy scores for each orientation, separated by palm and back view stimuli. **B)** Depicts the view x hand x orientation interaction. The graph on the left illustrates participants' accuracy scores when responding to palm and back views of right-hand stimuli in each orientation. The graph on the right illustrates accuracy scores for palm and back views of left-hand stimuli in each orientation. Error bars represent standard error scores. Significant differences were calculated using Bonferroni corrections for multiple comparisons.

* $p < .05$; ** $p < .01$.

Discussion

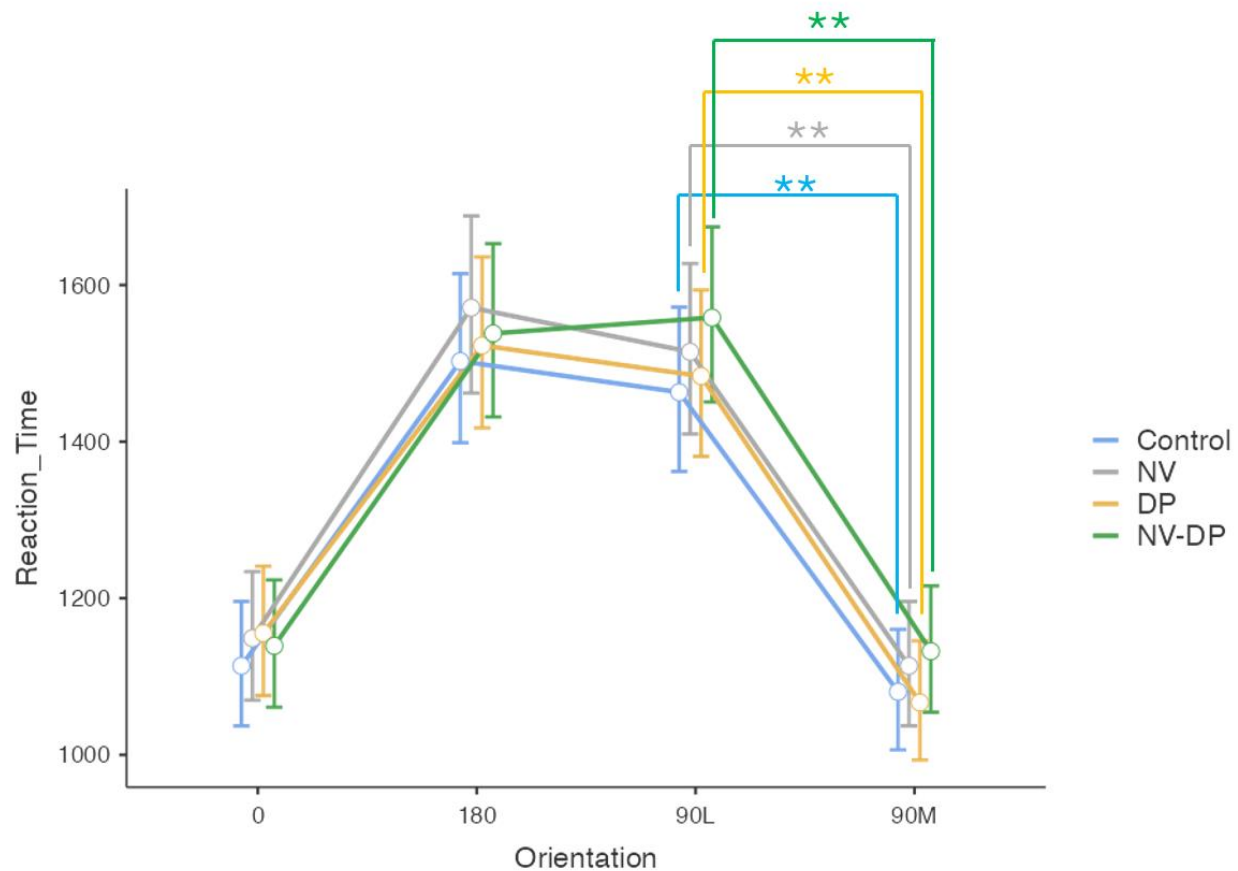
The present study examined whether online sensory feedback is involved in motor imagery performance. In this study, participants completed the HLJT while a box and a Digitimer constant current stimulator were used to disrupt visual and proprioceptive feedback, respectively. According to sensory detection thresholds and self-reported PNQ data, Digitimer stimulation was effective at disrupting proprioception and creating a sense of paresthesia in participants' hands. The results of this study are in line with past research using the HLJT, as participants demonstrated a strong medial-over-lateral advantage, especially when presented with palm-view stimuli.

Use of Motor Imagery in Conditions of Limited Sensory Feedback

Implicit motor imagery can be elicited by a variety of situations and tasks we encounter on any given day. These situations include action observations, motor planning, and perceptual tasks such as laterality judgements (Jeannerod, 2001; Miall & Wolpert, 1996; Monaco et al., 2020; Parsons, 1987a; Schwartz & Black, 1999; Toussaint et al., 2013; Wolpert & Flanagan, 2001). Laterality judgements can be completed using visual or motor imagery strategies, with people imagining objects rotating in space or imagining themselves interacting with the object to identify its laterality, respectively (Alivisatos & Petrides, 1997; Harris & Miniussi, 2003; Hoyek et al., 2013; Parsons, 1987b; Parsons, 1994). Past research has reported that individuals with chronic sensory or motor limitations continue to show biomechanical constraints effects when performing motor imagery tasks (Dominey et al., 1995; Fiorio et al., 2005; Helmich et al., 2007; Lyu et al., 2016). However, the duration and severity of sensory limitations may also influence motor imagery abilities (Imbiriba et al., 2006; Schott et al., 2021). Because participants experienced acute sensory disruptions in this study, it was essential to evaluate whether the

cognitive strategies used to complete the task were influenced by sensory disruptions in any of the experimental conditions.

This experiment found that participants demonstrated a strong medial-over-lateral advantage when responding to palm-view stimuli in all four sensory feedback conditions (Figure 8). Given that the use of motor imagery in the HLJT manifests itself in the form of biomechanical constraint effects, this finding indicates that participants continued to employ motor imagery strategies to identify palm-view stimuli, regardless of the sensory feedback disruptions they experienced at the time. This result is noteworthy as it rules out the possibility that the differences observed between conditions are due to changes in the strategy used to identify stimuli.

Figure 8*Medial Over Lateral Advantage for Each Experimental Condition*

Note. This figure depicts participants average reaction time to identify palm-view stimuli in each orientation separated by each sensory feedback condition. The Y axis represents reaction times in milliseconds, and error bars represent standard error scores. Significant differences were calculated using Bonferroni corrections for multiple comparisons.

* $p < .05$; ** $p < .01$.

Use of Online Sensory Feedback in Motor Imagery

According to motor simulation theory, simulated movements are functionally equivalent to executed ones (Jeannerod, 1994, 2001). One difference between motor imagery and motor performance is that motor imagery does not generate online sensory feedback, while motor

performance generates and heavily relies on feedback to facilitate precise movements (Kasuga et al., 2022; Simoneau et al., 1995). Despite its inability to create sensory feedback, research suggests motor imagery activates sensory networks and simulates the sensory consequences of imagined actions (Kilteni et al., 2018; Klein et al., 2023; Miall & Wolpert, 1996; Monaco et al., 2020; Wolpert & Flanagan, 2001).

Due to the interconnected nature of motor imagery and sensory feedback systems, I hypothesized that disrupting sources of online feedback would negatively affect participants' ability to perform motor imagery tasks, such as the HLJT. Specifically, it was hypothesized that RTs would increase, and accuracy would decrease when visual and proprioceptive feedback were disrupted in the NV-DP condition compared to when participants completed the task in the control condition. This hypothesis was partially supported by the experiment's results. In line with the experiment's predictions, RT analyses show that participants took significantly longer to identify the laterality of hands presented to them in the NV-DP condition compared to the control condition. Interestingly, neither visual nor proprioceptive disruptions alone were sufficient to significantly affect participants' RTs, and the effect was only observed when both forms of sensory feedback were disrupted simultaneously.

In contrast with the results obtained from RT analyses, this study did not find evidence to suggest that participants were any more or less accurate in identifying the laterality of hands across the four sensory feedback conditions. This outcome was unexpected as people generally compromise both speed and accuracy when task difficulty increases to prevent either from being overly affected (Bek et al., 2022; Fitts, 1954; Saran & Marotta, 2024). Given that the experiment yielded relatively high accuracy scores across all four conditions (min: 95.7%, max: 96.5%), it is possible that certain aspects of the experimental setup (e.g., completing the task next to the

experimenter) led participants to prioritize accuracy over speed during the task. Overall, the results presented here suggest that sensory feedback disruptions impaired participants' ability to complete the HLJT, as indicated by an increase in the time required to correctly identify hand laterality in the NV-DP condition compared to the control condition.

As mentioned previously, the HLJT can be completed by using visual or motor imagery strategies. Research has consistently shown that the decision to use either strategy is largely determined by the hand stimuli presented on a given trial. Participants tend to favour motor imagery when identifying palm-view stimuli, while visual imagery is more commonly used to identify back-of-hand stimuli (Bek et al., 2022; Conson et al., 2021; Mibu et al., 2020; Saran & Marotta, 2024; Zapparoli et al., 2014). For this reason, the present study hypothesized that if sensory disruptions were limiting participants' ability to perform motor imagery, then the effect they have on HLJT performance should be greater when participants view palm compared to back-of-hand stimuli. This hypothesis was supported by the significant condition x view interaction, which showed that the increase in RTs observed in the NV-DP condition was significant for palm, but not for back-of-hand views.

Past research has demonstrated that acute sensory feedback disruptions negatively affect HLJT performance, resulting in increased RTs and, in some cases, reduced accuracy scores (McCormick et al., 2007; Silva et al., 2011). However, to my knowledge, this is the first study to show that disrupting sensory feedback in healthy participants specifically affects their performance when identifying palm-view stimuli. Prior to this observation, it was reasonable to conclude that the performance deficits associated with sensory disruptions could have been due to increased noise or distraction present when completing the HLJT under conditions of disrupted sensory feedback. If this were the case, however, one would expect all hand stimuli—

eliciting motor or visual imagery strategies—to be equally affected by sensory manipulations. The results of this experiment show that sensory disruptions selectively increase RTs on trials requiring motor imagery, while visual-based (back-of-hand) trials remain relatively unaffected. This selective effect suggests that participants took longer to identify stimuli in the HLJT when sensory feedback was disrupted because they were unable to simulate movements as effectively as they could in the control condition.

The results presented here suggest that motor imagery engages both top-down and bottom-up sensory processing systems, and that disruptions to online feedback reduce one's ability to simulate actions, just as it would reduce one's ability to execute them (Desmurget & Grafton, 2000; Hallemans et al., 2010; Simoneau et al., 1995; Todorov & Jordan, 2002). These findings indicate that motor imagery does not just simulate the expected feedback of imagined actions, rather, it incorporates this expected feedback with incoming sensory information to create an internal feedback model that is representative of the one used to execute movements. These findings are in line with motor simulation theory and its proposition that simulated movements are functionally equivalent to executed ones (Jeannerod, 1994, 2001). Moreover, the results presented here contribute to our understanding of the computational processes involved in motor imagery and emphasize the importance of visual and proprioceptive feedback in motor control.

Sensory Integration Systems in Motor Imagery

In perceptual tasks and overt motor performance, people tend to rely on different sources of sensory feedback depending on the reliability or variability coming from each source at a given time (Beck et al., 2015; Ernst & Banks, 2002; Mortaza et al., 2023; Herter et al., 2019). This study aimed to explore whether sensory integration processes are involved in motor

simulations, as they are in motor performance. I hypothesized that RTs would be significantly higher and accuracy would be significantly lower when visual and proprioceptive feedback were disrupted concurrently, compared to when either modality was disrupted independently.

The results of this experiment did not support this hypothesis, as there were no significant differences in RT or accuracy scores across the three experimental conditions. Despite failing to support this hypothesis, it is worth noting that neither visual nor proprioceptive disruptions, applied in the NV and DP conditions, respectively, had a significant impact on participants' RTs on their own. RT increases were exclusively observed when both vision and proprioception were disrupted in the NV-DP condition. Therefore, while this study did not find evidence that participants performed better in the NV or DP conditions than in the NV-DP condition, it also did not find evidence that participants performed worse in either of these conditions than in the control condition. This result may suggest that participants were compensating for disruptions to one sensory modality by relying on the other, since they only needed uninterrupted feedback from a single sensory modality to reduce RTs back to a level similar to that of the control condition. However, it is also possible that disrupting feedback from a single sensory system is not meaningful enough to significantly affect participants' RTs on its own, and that participants did not need to compensate for sensory disruptions to complete the task effectively under these conditions.

Any cognitive or neuronal process involved in motor performance that is not accurately replicated by motor imagery is of importance, given that much of our understanding of motor imagery—and the justification of its use in rehabilitative or performance-based contexts—relies on its functional equivalence to motor execution. Therefore, understanding how processes, such as sensory integration, differ between motor imagery and execution is important to our

theoretical understanding of motor imagery and may provide valuable information for designing motor imagery training protocols or enhancing our knowledge of the contexts in which motor imagery training is or is not suitable. It is possible that this study was unable to find evidence for sensory integration and compensation processes in motor imagery because of the task that was chosen. Tasks requiring more precision, such as imagined pointing tasks, may be better suited to assess how different forms of sensory feedback are utilized in motor imagery. Overall, more research is needed to understand how sensory information from different sources is integrated to simulate movements.

Despite failing to obtain significant differences between the three experimental conditions, the observation that RTs only significantly increased in the NV-DP condition indicates that both visual and proprioceptive feedback are involved in performing action simulations in the HLJT. Past research has suggested that motor imagery strategies used in the HLJT are primarily kinesthetic, meaning participants imagine the kinesthetic sensations associated with moving their hands into the orientation of the presented hand rather than visualizing what the movement would look like. This suggestion primarily stems from the observation that the position of participants' own hands during HLJT performance facilitates faster responses to hand stimuli in congruent orientations (Jongsma et al., 2013). However, in the studies used to justify this claim, participants are typically positioned with their hands directly in front of them, meaning they can feel and see the position of their hands and use information from either sensory source to facilitate responses to congruent hand stimuli (Funk et al., 2005; Jongsma et al., 2013). Additionally, altering participants' hand position during task performance shifts the starting point of their action simulations, therefore influencing RTs regardless of the sensory information being used after the simulated action is initiated. According to Sober and

Sabes (2005), visual and proprioceptive feedback are used differently depending on the sensory modality of the target being acted on. Since HLJT performance requires participants to identify the laterality of a visually presented stimulus, it is unlikely that they would solve the task exclusively using proprioceptive feedback and kinesthetic motor imagery. Indeed, the results of this study indicate that participants likely use a combination of internal and kinesthetic motor imagery techniques that simulate feedback from both visual and proprioceptive sources to identify palm-view stimuli in the HLJT.

Comparison to Past Research

Past research examining the role of sensory feedback in motor imagery has often focused on clinical populations with sensory deficits, such as stroke, Parkinson's disease, and patients with phantom limbs (Dominey et al., 1995; Haslam et al., 2023; Helmich et al., 2007; Lyu et al., 2016). These studies typically suggest that performance on motor imagery tasks, such as the HLJT, is impaired by disruptions to online feedback; however, attributing these results to sensory limitations can be difficult, as many of these clinical populations have comorbid motor impairments.

As previously mentioned, two studies conducted by McCormick, Silva, and their respective colleagues examined the effect of proprioceptive deficits on HLJT performance in healthy individuals prior to this experiment. These studies concluded that disruptions to proprioceptive feedback negatively impacted HLJT performance. However, various limitations, including inconsistencies between the availability of visual feedback in control and experimental conditions, the manipulation of only one hand, and the disregard for how different views/orientations may be differentially affected by sensory disruptions, limit the conclusions that can be drawn from them.

The results obtained by this experiment replicate and support some of the broader takeaways reported by McCormick et al. (2007) and Silva et al. (2011). For example, the present experiment found that participants' RTs are increased when online sensory feedback of their hands was disrupted during HLJT performance. Furthermore, this RT increase diminished when participants could see their hands during task performance, which is consistent with the results reported by Silva et al. (2011). This study also found that sensory disruptions did not significantly affect participants' accuracy scores, which matches the results reported by McCormick et al. (2007) but not Silva et al. (2011).

Despite supporting some of the main conclusions reported previously, this study differs from these earlier works in several significant ways. For instance, McCormick et al. (2007) concluded that proprioceptive disruptions alone were sufficient to influence RTs on the HLJT, despite failing to account for visual differences between the experimental and control conditions when proprioceptive feedback was manipulated. In contrast, the present study found that proprioceptive disruptions only affect motor imagery performance when the imaged limb is out of sight. When participants could see the limb being simulated, their motor imagery performance returned to a level comparable to that of the control condition. Another key difference between this study and those done prior is that this study presented participants with palm and back views of hands rotated 90° in medial and lateral directions. The use of medial and lateral hand orientations rotated equally from an upright position was essential, as it allowed this study to analyze how participants respond to stimuli that differ in biomechanical difficulty but require the same spatial rotation to identify. RT analyses revealed that participants were quicker to identify palm-view stimuli rotated 90° medially compared to 90° laterally in each experimental condition. This indicates that participants used motor imagery to identify palm-view stimuli throughout the

experiment, which strengthens the interpretation of this study and those done previously, that sensory disruptions limit participants' ability to simulate movements of the affected limbs efficiently.

One final difference between this experiment and those done by McCormick et al. (2007) and Silva et al. (2011) is that this study found that disrupting sensory feedback produced a relatively modest RT increase of about 4%. For comparison, the studies conducted by Silva, McCormick, and their colleagues reported much larger increases of approximately 25% and 50%, respectively. Part of this discrepancy likely reflects methodological differences between the present study and those done prior. In Silva et al. (2011), proprioceptive signals from the entire arm were disrupted with anesthesia. In contrast, the present study specifically manipulated feedback of the hands. Given that hand location can be partly determined by the positions of the elbow and shoulder joints, it is not surprising that this technique would yield a larger effect size than that observed in the present experiment. Another explanation stems from the decision to manipulate feedback from both hands in this experiment, rather than from just one hand as in the previous studies. According to Choisdealbha et al. (2011), each hand contributes differently to laterality judgements; in their experiment, disrupting feedback from one hand not only increased RTs to the manipulated hand, but also decreased RTs to the unmanipulated hand. These findings suggest that single-hand manipulations alter each hand's contribution to task performance, such that the "control" hand may benefit from manipulating the opposite hand. Comparing RTs for disrupted vs undisrupted hands, as was done by McCormick et al. (2007), may therefore artificially inflate the observed effect. Overall, while the present study supports the general conclusions reported by McCormick and Silva, the results indicate that the impact of sensory disruptions on HLJT performance may be more modest than previously suggested. Moreover, the

results presented here indicate that proprioceptive disruptions only significantly affect HLJT performance when the limb being simulated is out of sight.

Limitations

This study has limitations which should be considered when interpreting its results. First, the present experiment manipulated proprioceptive feedback by stimulating the median and ulnar nerves in the anterior forearm, producing paresthesia in the hand and wrist. Detection threshold and self-reported PNQ scores suggest that this method was effective for disrupting proprioceptive feedback from the hands; however, much of the information we use to determine the position of our hand in space comes from assessing the position of our shoulder and elbow joints, neither of which would be impacted by Digitimer stimulation in this study. Second, the number of HLJT trials presented to participants in this experiment was relatively high, which may have resulted in significant practice effects. Practice effects are not a major concern in this study, given that the order in which conditions were presented was counterbalanced. However, a post hoc analysis of RT and accuracy scores for each condition found that by the fourth experimental block, all differences had diminished, which may have artificially lowered the effect sizes observed in this study.

Directions For Future Research

Given that this experiment did not find evidence that participants compensated for disruptions to one sensory modality by increasing their reliance on the other, future research on sensory integration processes in motor imagery could help better understand the differences between motor imagery and execution. Experiments utilizing motor imagery tasks that require more precision than the HLJT (e.g. simulated pointing movements) may yield different results

than the present experiment in this regard. Second, future research could investigate whether online sensory feedback influences the effectiveness of motor imagery-based training protocols. This experiment found that disruptions to online sensory feedback impaired participants' ability to simulate actions effectively; however, it is unclear how these impairments might impact motor imagery training and its ability to enhance overt motor performance. Finally, neuroimaging research would help better understand how online feedback is used in motor imagery performance and which specific cognitive processes involved in action simulations are affected by sensory disruptions.

Conclusion

Overall, this study found that disrupting visual and proprioceptive feedback from participants' hands during HLJT performance significantly increased the time needed to identify a hand's laterality. Participants used motor imagery strategies to identify palm-view stimuli in each experimental condition, and the RT increases observed in the NV-DP condition were exclusive to palm-view stimuli. Together, these results indicate that online sensory feedback disruptions limited participants' ability to simulate actions, leading to higher RTs to palm stimuli in the NV-DP condition compared to the control condition. The results of the present experiment indicate that motor imagery uses both top-down and bottom-up sensory information to simulate actions, and that online feedback is needed to simulate movements, despite the inability of simulated movements to produce observable feedback. Lastly, this study found that both visual and proprioceptive feedback are used to simulate the actions involved in making laterality judgements. This finding indicates that HLJT performance elicits both visual and kinesthetic motor imagery, utilizing information from visual and proprioceptive sources, respectively.

Conflicts of Interest

No conflicts of interest related to this research exist.

References

- Alivisatos, B., & Petrides, M. (1997). Functional activation of the human brain during mental rotation. *Neuropsychologia*, 35(2), 111-118. [https://doi.org/10.1016/s0028-3932\(96\)00083-8](https://doi.org/10.1016/s0028-3932(96)00083-8)
- Ashraf, R., Abdoli, B., Khosrowabadi, R., Farsi, A., & Pineda, J. A. (2023). The effect of modeling methods on mirror neuron activity and a motor skill acquisition and retention. *Basic and Clinical Neuroscience*, 14(5), 631-646. <http://dx.doi.org/10.32598/bcn.2021.3245.1>
- Bastian, C. H. (1887). The “muscular sense”; its nature and cortical localization. *Brain*, 10(1), 1-89. <https://doi.org/10.1093/brain/10.1.1>
- Beck, E. N., Ehgoets, Martens, K. A., & Almeida, Q. J. (2015). Freezing of gait in Parkinson’s Disease: An overload problem? *PLOS One*, 10(12). <https://doi.org/10.1371/journal.pone.0144986>
- Bek, J., Humphries, S., Poliakoff, E., & Brady, N. (2022). Mental rotation of hands and objects in ageing and Parkinson’s disease: Differentiating motor imagery and visuospatial ability. *Experimental Brain Research*, 240, 1991–2004. <https://doi.org/10.1007/s00221-022-06389-5>
- Bhanpuri, N. H., Okamura, A. M., & Bstian, A. J. (2013). Predictive Modeling by the Cerebellum Improves Proprioception. *The Journal of Neuroscience*, 33(36), 14301-14306. <https://doi.org/10.1523/JNEUROSCI.0784-13.2013>
- Blank, A., Okamura, A. M., & Kuchenbecker, K. J. (2008). Identifying the role of proprioception in upper-limb prosthesis control: Studies on targeted motion. *ACM Transactions on Applied Perception*, 7(3), 1-23. <https://doi.org/10.1145/1773965.1773966>

- Brady, N., Miguinness, C., & Choidealbha, A. N. (2011). My hand or yours? Markedly different sensitivity to egocentric and allocentric views in the hand laterality task. *PLOS One*, 6(8).
<https://doi.org/10.1371/journal.pone.0023316>
- Callow, N., & Hardy, L. (2004). The relationship between the use of kinaesthetic imagery and different visual imagery perspectives. *Journal of Sport Sciences*, 22(2), 167-177.
<https://doi.org/10.1080/02640410310001641449>
- Cameron, B. D., De la Malla, C., & Lopez-Moliner, J. (2014). The role of differential delays in integrating transient visual and proprioceptive information. *Frontiers in Psychology*, 5.
<https://doi.org/10.3389/fpsyg.2014.00050>
- Chernikoff, R., & Taylor, F. V. (1952). Reaction time to kinesthetic stimulation resulting from sudden arm displacement. *Journal of Experimental Psychology*, 43(1), 1-8.
<https://doi.org/10.1037/h0056952>
- Choidealbha, A. N., Brady, N., & Maguinness, C. (2011). Differing roles for the dominant and non-dominant hands in the hand laterality task. *Experimental Brain Research*, 211, 73-85.
<https://doi.org/10.1007/s00221-011-2652-9>
- Confalonieri, L., Pagnoni, G., Barsalou, L. W., Rajendra, J., Eickhoff, S. B., & Butler, A. J. (2012). Brain activation in primary motor and somatosensory cortices during motor imagery correlated with motor imagery ability in stroke patients. *ISRN Neurology*, 2012, 613595. <https://doi.org/10.5402/2012/613595>
- Connel, L. A., Lincoln, N. B., & Radford, K. A. (2008). Somatosensory impairment after stroke: Frequency of different deficits and their recovery. *Clinical Rehabilitation*, 22(8).
<https://doi.org/10.1177/0269215508090674>

- Conson, M., Rosa, A. D., Polito, F., Zappullo, I., Baiano, C., & Trojano, L. (2021). “Mind the thumb”: Judging hand laterality is anchored on the thumb position. *Acta Psychologica*, 219, 103388. <https://doi.org/10.1016/j.actpsy.2021.103388>
- Coslett, H. B., Medina, J., Kliot, D., & Burkey, A. (2010). Mental motor imagery and chronic pain: The foot laterality task. *Journal of the International Neuropsychological Society*, 16(4), 603-612. <https://doi.org/10.1017/S1355617710000299>
- Dayan, E., & Cohen, L. G. (2011). Neuroplasticity subserving motor skill learning. *Neuron*, 72(3), 443-454. <https://doi.org/10.1016/j.neuron.2011.10.008>
- Decety, J. (1996). The neurophysiological basis of motor imagery. *Behavioural Brain Research*, 77(1-2), 45-52. [https://doi.org/10.1016/0166-4328\(95\)00225-1](https://doi.org/10.1016/0166-4328(95)00225-1)
- Decety, J., & Jeannerod, M. (1995). Mentally simulated movements in virtual reality: Does Fitt’s law hold in motor imagery? *Behavioural Brain Research*, 72(1-2), 127-134. [https://doi.org/10.1016/0166-4328\(96\)00141-6](https://doi.org/10.1016/0166-4328(96)00141-6)
- Decety, J., Jeannerod, M., Durozard, D., & Baverel, G. (1993). Central activation of autonomic effectors during mental simulation of motor actions in man. *The Journal of Physiology*, 461(1), 549-563. <https://doi.org/10.1113/jphysiol.1993.sp019528>
- Decety, J., Jeannerod, M., Germain, M., & Pastene, J. (1991). Vegetative response during imagined movement is proportional to mental effort. *Behavioural Brain Research*, 42(1), 1-5. [https://doi.org/10.1016/S0166-4328\(05\)80033-6](https://doi.org/10.1016/S0166-4328(05)80033-6)
- Decety, J., Jeannerod, M., & Prablanc, C. (1989). The timing of mentally represented actions. *Behavioural Brain Research*, 34(1-2), 35-42. [https://doi.org/10.1016/s0166-4328\(89\)80088-9](https://doi.org/10.1016/s0166-4328(89)80088-9)

- Decety, J., & Michel, F. (1989). Comparative analysis of actual and mental movement times in two graphic tasks. *Brain and Cognition*, 11(1), 87-97.
[https://psycnet.apa.org/doi/10.1016/0278-2626\(89\)90007-9](https://psycnet.apa.org/doi/10.1016/0278-2626(89)90007-9)
- DeLang, F. P., Helmich, R. C., & Toni, I. (2006). Posture influences motor imagery: An fMRI study. *NeuroImage*, 33(2), 609-617. <https://doi.org/10.1016/j.neuroimage.2006.07.017>
- Desmurget, M., & Grafton, S. (2000). Forward modeling allows feedback control for fast reaching movements. *Trends in Cognitive Sciences*, 4(11), 423-431.
[https://doi.org/10.1016/S1364-6613\(00\)01537-0](https://doi.org/10.1016/S1364-6613(00)01537-0)
- Dickstein, R., & Deutsch, J. E. (2007). Motor imagery in physical therapist practice. *Physical Therapy & Rehabilitation Journal*, 87(7), 942-953. <https://doi.org/10.2522/ptj.20060331>
- Dominey, P., Decety, J., Broussolle, E., Chazot, G., & Jeannerod, M. (1995). Motor imagery of a lateralized sequential task is asymmetrically slowed in hemi-Parkinson's patients. *Neuropsychologia*, 33(6), 727-741. [https://doi.org/10.1016/0028-3932\(95\)00008-q](https://doi.org/10.1016/0028-3932(95)00008-q)
- Erickson, R. G., & Thier, P. (1992). Responses of direction-selective neurons in monkey cortex to self-induced visual motion. *Annals of the New York Academy of Sciences*, 656, 766-774. <https://doi.org/10.1111/j.1749-6632.1992.tb25255.x>
- Ernst, M. O., & Banks, M. S. (2002). Humans integrate visual and haptic information on a statistically optimal fashion. *Nature*, 415, 429-433. <https://doi.org/10.1038/415429a>
- Faul, F., Erdfelder, E., Buchner, A., & Lang, A. G. (2009). Statistical power analyses using G*Power 3.1: Tests for correlation and regression analyses. *Behavior Research Methods*, 41(4), 1149-60. doi:10.3758/BRM.41.4.1149

- Fiorio, M., Tinazzi, M., & Aglioti, S. M. (2005). Selective impairment of hand mental rotation in patients with focal hand dystonia. *Brain*, 129(1), 47-54.
<https://doi.org/10.1093/brain/awh630>
- Fitts, P. M. (1954). The information capacity of the human motor system in controlling the amplitude of movement. *Journal of Experimental Psychology: General*, 47(6), 381-391.
<https://doi.org/10.1037/h0055392>
- Fleishman, E. A., & Rich, S. (1963) Role of kinesthetic and spatial-visual abilities in perceptual-motor learning. *Journal of Experimental Psychology*, 66, 6-11.
<https://doi.org/10.1037/h0046677>
- Funk, M., Brugger, P., & Wilkening, F. (2005). Motor processes in children's imagery: The case of mental rotation of hands. *Developmental Science*, 8(5), 402-408.
<https://doi.org/10.1111/j.1467-7687.2005.00428.x>
- Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Sciences*, 2(12), 493-501. [https://doi.org/10.1016/s1364-6613\(98\)01262-5](https://doi.org/10.1016/s1364-6613(98)01262-5)
- Gerardin, E., Sirigu, A., Lehericy, S., Poline, J. B., Gaymard, B., Marsault, C., Agid, Y., & Bihan, D. L. Partially overlapping neural networks for real and imagined hand movements. (2000). *Cerebral Cortex*, 10(11), 1093-1104. <https://doi.org/10.1093/cercor/10.11.1093>
- Gibson, J. J. (1958). Visually controlled locomotion and visual orientation in animals. *British Journal of Psychology*, 49(3), 182-194. <https://doi.org/10.1111/j.2044-8295.1958.tb00656.x>

- Glazebrook, C. M., Brown, K., Prime, S. L., Passmore, S. R., & Marotta, J. J. (2019). Both reaching and grasping are impacted by temporally induced paresthesia. *Somatosensory & Motor Research*, 37(2), 106-116. <https://doi.org/10.1080/08990220.2020.1750359>
- Gordon, J., Ghilardi, M. F., & Ghez, C. (1995). Impairments of reaching movements in patients without proprioception. I. Spatial errors. *Journal of Neurophysiology*, 73(1), 347-360. <https://doi.org/10.1152/jn.1995.73.1.347>
- Gorst, T., Marsden, J., & Freeman, J. (2019). Lower limb somatosensory discrimination is impaired in people with Parkinson's Disease: Novel assessment and associations with balance, gait, and falls. *Movement Disorders, Clinical Practice*, 6(7), 593-600. <https://doi.org/10.1002/mdc3.12831>
- Goudarzian, M., Ghavi, S., Shariat, A., Shirvani, H., & Rehim. (2017). Effects of whole body vibration training and mental training on mobility, neuromuscular performance, and strength in older men. *Journal of Exercise Rehabilitation*, 13(5), 573-580. <https://doi.org/10.12965/jer.1735024.512>
- Guthrie, B. L., Porter, J. D., & Sparks, D. L. (1983). Corollary discharge provides accurate eye position information to the oculomotor system. *Science*, 221(4616), 1193-1195. <https://doi.org/10.1126/science.6612334>
- Halleman, A., Ortibus, E., Meire, F., & Aerts, P. (2010). Low vision affects dynamic stability of gait. *Gait & Posture*, 32(4), 547-551. <http://dx.doi.org/10.1016/j.gaitpost.2010.07.018>
- Han, J., Waddington, G., Adams, R., Anson, J., & Liu, Y. (2016). Assessing proprioception: A critical review of methods. *Journal of Sport and Health Science*, 5(1), 80-90. <https://doi.org/10.1016/j.jshs.2014.10.004>

- Hardy, L., & Callow, N. (1999). Efficacy of external and internal visual imagery perspectives for the enhancement of performance on tasks in which form is important. *Journal of Sport and Exercise Psychology*, 21(2), 95-112. <https://doi.org/10.1123/jsep.21.2.95>
- Harris, I. M., & Miniussi, C. (2003). Parietal lobe contribution to mental rotation demonstrated with rTMS. *Journal of Cognitive Neuroscience*, 15(3), 315-323. <https://doi.org/10.1162/089892903321593054>
- Haslam, B. S., Butler, D. S., Timothy, S., Kim, A., & Carey, L. (2023). Body schema as assessed by upper limb left/right judgement tasks is altered in stroke: Implications for motor imagery training. *Journal of Neurologic Physical Therapy*, 47(1), 26-34. <https://doi.org/10.1097/NPT.0000000000000412>
- Hausheer, F. H., Schilsky, R. L., Bain, S., Berghorn, E. J., & Lieberman, F. (2006). Diagnosis management and evaluation of chemotherapy-induced peripheral neuropathy. *Seminars in Oncology*, 33(1), 15-49. <https://doi.org/10.1053/j.seminoncol.2005.12.010>
- Hebb, D. O. (2002). *The organization of behavior: A neuropsychological theory*. Psychological Press. <https://doi.org/10.4324/9781410612403>
- Helmich, R. C., Lange, F. P. D., Bloem, B. R., & Toni, I. (2007). Cerebral compensation during motor imagery in Parkinson's disease. *Neuropsychologia*, 45(10), 2201-2215. <https://doi.org/10.1016/j.neuropsychologia.2007.02.024>
- Herter, T. M., Scott, S. H., & Dukelow, S. P. (2019). Vision does not always help stroke survivors compensate for impaired limb position sense. *Journal of NeuroEngineering and Rehabilitation*, 16, 129. <https://doi.org/10.1186/s12984-019-0596-7>
- Hesslow, G. (2012). The current status of the simulation theory of cognition. *Brain Research*, 1428, 71-79. <https://doi.org/10.1016/j.brainres.2011.06.026>

Higgins, J. R., & Angel, R. W. (1970). Correction of tracking errors without sensory feedback.

Journal of Experimental Psychology, 84(3), 412-416.

<https://psycnet.apa.org/doi/10.1037/h0029275>

Hinshaw, K. E. (1991). The effect of mental practice on motor skill performance: Critical

evaluation and meta-analysis. *Imagination, Cognition and Personality*, 11(1).

<https://doi.org/10.2190/X9BA-KJ68-07AN-QMJ8>

Hoyek, N., Di Rienzo, F., Collet, C., Creveaux, T., & Guillot, A. (2013). Hand mental rotation is

not systematically altered by actual body position: Laterality judgement versus same-

different comparison tasks. *Attention, Perception, & Psychophysics*, 76, 519-526.

<https://doi.org/10.3758/s13414-013-0577-z>

Imbiriba, L. A., Rodrigues, E. C., Magalhaes, J., & Vargas, C. D. (2006). Motor imagery in blind

subjects: The influence of the previous visual experience. *Neuroscience Letters*, 400(1-2),

181-185. <https://doi.org/10.1016/j.neulet.2006.02.042>

Jeannerod, M. (1994). The representing brain: Neural correlates of motor intention and imagery.

Behavioral and Brain Sciences, 17(2).

<https://psycnet.apa.org/doi/10.1017/S0140525X00034026>

Jeannerod, M. (2001). Neural simulation of action: A unifying mechanism for motor cognition.

NeuroImage, 14(1), 103-109. <https://doi.org/10.1006/nimg.2001.0832>

Jeannerod, M., & Decety, J. (1995). Mental motor imagery: A window into the representational

stages of action. *Current Opinion in Neurobiology*, 5(6), 727-732. [https://doi-](https://doi-org.uml.idm.oclc.org/10.1016/0959-4388(95)80099-9)

[org.uml.idm.oclc.org/10.1016/0959-4388\(95\)80099-9](https://doi-org.uml.idm.oclc.org/10.1016/0959-4388(95)80099-9)

Jeannerod, M., & Frak, V. (1999). Mental imaging of motor activity in humans. *Current Opinion*

in Neurobiology, 9(6), 735-739. [https://doi.org/10.1016/S0959-4388\(99\)00038-0](https://doi.org/10.1016/S0959-4388(99)00038-0)

- Jeannerod, M., & Pacherie, E. (2004). Agency, simulation, and self-identification. *Mind & Language*, 19(2), 113-146. <https://doi.org/10.1111/j.1468-0017.2004.00251.x>
- Jones, H. G., Braithwaite, F. A., Edwards, L. M., Causby, R. S., Conson, M., & Stanton, T. R. (2021). The effect of handedness on mental rotation of hands: A systematic review and meta-analysis. *Psychological research*, 85, 2829-2881. <https://doi.org/10.1007/s00426-020-01444-8>
- Jongsma, M. L. A., Meulenbroek, R. G. J., Okely, J., Baas, C. M., Van Der Lube, R. J., & Steenbergen, B. (2013). Effects of hand orientation on motor imagery – event related potentials suggest kinesthetic motor imagery to solve the hand laterality judgement task. *PLOS ONE*, 8(9). <https://doi.org/10.1371/journal.pone.0076515>
- Kasess, C. H., Windischberger, C., Cunningham, R., Lanzenberger, R., Pezawas, L., & Moser, E. (2008). The suppressive influence of SMA on M1 in motor imagery revealed by fMRI and dynamic causal modeling. *NeuroImage*, 40(2), 828-837. <https://doi.org/10.1016/j.neuroimage.2007.11.040>
- Kasuga, S., Crevecoeur, F., Cross, K. P., Balalaie, P., & Scott, S. H. (2022). Integration of proprioceptive and visual feedback during online control of reaching. *Journal of Neurophysiology*, 127(2), 354-372. <https://doi.org/10.1152/jn.00639.2020>
- Keele, S. W. & Posner, M. I. (1968). Processing of visual feedback in rapid movements. *Journal of Experimental Psychology*, 77(1), 155-158. <https://doi.org/10.1037/h0025754>
- Kilteni, K., Andersson, B. J., Houborg, C., & Ehrsson, H. H. (2018). Motor imagery involved predicting the sensory consequences of the imagined movement. *Nature Communications*, 9, 1617. <https://doi.org/10.1038/s41467-018-03989-0>

- Klatzky, R. L. (2010). On the relation between motor imagery and visual imagery. *Behavioural and Brain Sciences*, 17(2). <https://doi.org/10.1017/S0140525X00034178>
- Klein, L. K., Maiello, G., Stubbs, K., Proklova, D., Chen, J., Paulun, V. C., Culham, J. C., & Fleming, R. (2023). Distinct neural components of visually guided grasping during planning and execution. *The Journal of Neuroscience*, 43(49), 8504-8514. <https://doi.org/10.1523/JNEUROSCI.0335-23.2023>
- Kosslyn, S. M., Digirolamo, G. J., Thompson, W. L., & Alpert, N. M. (2003). Mental rotation of objects versus hands: neural mechanisms revealed by positron emission tomography. *Psychophysiology*, 35(2), 151-161. <https://doi.org/10.1111/1469-8986.3520151>
- Kurukuti, N. M., Avrillon, S., & Pons, J. L. (2025). A session of transcutaneous electrical nerve stimulation changes the input-output function of motoneurons and alters the sense of force. *Journal of Neurophysiology*, 133(6). <https://doi.org/10.1152/jn.00140.2024>
- Ladda, A., M., Lebon, F., & Lotze, M. (2021). Using motor imagery practice for improving motor performance – A review. *Brain and Cognition*, 150, 105705. <https://doi.org/10.1016/j.bandc.2021.105705>
- Lotze, M., Montoya, P., Erb, M., Hülsmann, E., Flor, H., Klose, U., Birbaumer, N., & Grodd, W. (1999). Activation of cortical and cerebellar motor areas during executed and imagined hand movements: And fMRI study. *Journal of cognitive neuroscience*, 11(5), 491-501. <https://doi.org/10.1162/089892999563553>
- Lyu, Y., Guo, X., Bekrater-Bodmann, R., Flor, H., & Tong, S. (2016). Phantom limb perception interferes with motor imagery after unilateral upper-limb amputation. *Scientific Reports*, 6, 21100. <https://doi.org/10.1038/srep21100>

- Macefield, V. G. (2021). The roles of mechanoreceptors in muscle and skin in human proprioception. *Current Opinion in Physiology*, 21, 48-56.
<https://doi.org/10.1016/j.cophys.2021.03.003>
- Mahoney, M. J., & Avenier, M. (1977). Psychology of the elite athlete: An exploratory study. *Cognitive Therapy and Research*, 1, 135-141. <https://doi.org/10.1007/BF01173634>
- Marigold, D. S. (2008). Role of peripheral visual cues in online visual guidance of locomotion. *Exercise and Sport Sciences Reviews*, 36(3), 145-151.
<https://doi.org/10.1097/JES.0b013e31817bff72>
- Martens, K. A. E., Ellard, C. G., & Almeida, Q. J. (2013). Dopaminergic contributions to distance estimation in Parkinson's disease: A sensory-perceptual deficit? *Neuropsychologia*, 51(8), 1426-1434.
<https://doi.org/10.1016/j.neuropsychologia.2013.04.015>
- McCormick, K., Zaluchi, N., Hudson, M. L., & Moseley, G. L. (2007). Faulty proprioceptive information disrupts motor imagery: An experimental study. *Australian journal of Physiotherapy*, 53(1), 41-45. [https://doi.org/10.1016/S0004-9514\(07\)70060-0](https://doi.org/10.1016/S0004-9514(07)70060-0)
- Miall, R. C., & Woplert, D. M. (1996). Forward models for physiological motor control. *Neural Networks*, 9(8), 1265-1279. [https://doi.org/10.1016/s0893-6080\(96\)00035-4](https://doi.org/10.1016/s0893-6080(96)00035-4)
- Mibu, A., Kan, S., Nishigami, T., Fujino, Y., & Shibata, M. (2020). Performing the hand laterality judgement task does not necessarily require motor imagery. *Scientific Reports*, 10, 5155. <https://doi.org/10.1038/s41598-020-61937-9>
- Monaco, S., Malfatti, G., Culham, J. C., Cattaneo, L., & Turella, L. (2020). Decoding motor imagery and action planning in the early visual cortex: Overlapping but distinct neural

- mechanisms. *Neuroimage*, 218, 116981
<https://doi.org/10.1016/j.neuroimage.2020.116981>
- Mortaza, N., Passmore, S. R., & Glazebrook, C. M. (2023). Adapting to altered sensory input: Effects of induced paresthesia on goal-directed movement planning and execution. *Brain Science*, 13(9), 1341. <https://doi.org/10.3390/brainsci13091341>
- Nicholson, V., Watts, N., Chani, Y., & Keogh, J. W. L. (2019). Motor imagery training improves balance and mobility outcomes in older adults: A systematic review. *Journal of Physiotherapy*, 65(4), 200-207. <https://doi.org/10.1016/j.jphys.2019.08.007>
- Notterman, J. M., & Page, D. E. (1962). Evaluation of mathematically equivalent tracking systems. *Perceptual and Motor Skills*, 15(3), 683-716.
<https://doi.org/10.2466/pms.1962.15.3.683>
- Page, S. J. (2000). Imagery improves upper extremity motor function in chronic stroke patients: A pilot study. *The Occupational Therapy Journal of Research*, 20(3), 200-215.
<https://doi.org/10.1177/153944920002000304>
- Page, S. J., Levine, P., Sisto, S., & Johnston, M. V. (2001). A randomized efficacy and feasibility study of imagery in acute stroke. *Clinical Rehabilitation*, 15(3).
<https://doi.org/10.1191/026921501672063235>
- Parsons, L. M. (1987a). Imagined spatial transformations of one's hands and feet. *Cognitive Psychology*, 19(2), 178-241. [https://doi.org/10.1016/0010-0285\(87\)90011-9](https://doi.org/10.1016/0010-0285(87)90011-9)
- Parsons, L. M. (1987b). Imagined spatial transformation of one's body. *Journal of Experimental Psychology: General*, 116(2), 172-191. <https://doi.org/10.1037/0096-3445.116.2.172>

- Parsons, L. M. (1994). Temporal and kinematic properties of motor behavior reflected in mentally simulated action. *Journal of Experimental Psychology: Human Perception and Performance*, 20(4), 709-730. <https://psycnet.apa.org/doi/10.1037/0096-1523.20.4.709>
- Patla, A. E. (1997). Understanding the roles of vision in the control of human locomotion. *Gait & Posture*, 5(1), 54-69. [https://doi.org/10.1016/S0966-6362\(96\)01109-5](https://doi.org/10.1016/S0966-6362(96)01109-5)
- Pellegrino, G. D., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research*, 91(1), 176-180. <https://doi.org/10.1007/bf00230027>
- Pelisson, D., Goffart, L., & Guitton, D. (1995). On-line compensations of gaze shifts perturbed by micro-stimulation of the superior colliculus in the cat with unrestrained head. *Experimental Brain Research*, 106, 196-204. <https://doi.org/10.1007/BF00241115>
- Porro, C. A., Francescato, M. P., Cettolo, V., Diamond, M. E., Baraldi, P., Zulianai, C., Bazzocchi, M., & Di Prampero, P. E. (1996). Primary motor and sensory cortex activation during motor performance and motor imagery: A functional magnetic resonance imaging study. *Journal of Neuroscience*, 16(23), 7688-7698. <https://doi.org/10.1523/JNEUROSCI.16-23-07688.1996>
- Proske, U., & Gandevia, S. C. (2012). The proprioceptive senses: Their roles in signaling body shape, body position, and movement, and muscle force. *Psychological Reviews*. <https://doi.org/10.1152/physrev.00048.2011>
- Reiser, M. (2015). Strength gains by motor imagery of maximal muscle contractions. *Zeitschrift für Sportpsychologie*, 12(1), 11-21. <https://doi.org/10.1026/1612-5010.12.1.11>
- Richards, L. G., Stewart, K. C., Woodbury, M. L., Senesac, C., & Couraugh, J. H. (2008). Movement-disorder stroke recovery: A systematic review and meta-analysis of TMS and

fMRI evidence. *Neuropsychologia*, 46(1), 3-11.

<https://doi.org/10.1016/j.neuropsychologia.2007.08.013>

Rizzolatti, G., Camarda, R., Fogassi, L., Gentilucci, M., Luppino, G., & Matelli, M. (1988).

Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movements. *Experimental Brain Research*, 71(3), 491-507.

<https://doi.org/10.1007/bf00248742>

Saran, A., & Marotta, J. J. (2024). Implicit motor imagery: Examining motor vs visual strategies in laterality judgements among older adults. *Frontiers in Psychology*, 15.

<https://doi.org/10.3389/fpsyg.2024.1445152>

Saunders, J., & Knill, D. C. (2005). Humans use continuous visual feedback from the hand to control both the direction and distance of pointing movements. *Experimental Brain Research*, 162, 458-473.

<https://doi.org/10.1007/s00221-004-2064-1>

Saimpont, A., Malouin, F., Tousignant, B., & Jackson, P. L. (2011). The influence of body configuration on motor imagery of walking in younger and older adults. *Neuroscience*, 222, 49-57.

<https://doi.org/10.1016/j.neuroscience.2012.06.066>

Scalha, T. B., Miyasaki, E., Lima, N. M. F. V., & Borges, G. (2011). Correlations between motor and sensory functions in upper limb chronic hemiparetics after stroke. *Arq Neuropsiquiatr*, 69(4), 624-629.

<https://doi.org/10.1590/S0004-282X2011000500010>

Schmidt, R. A. (1975). A schema theory of discrete motor skill learning. *Psychological Review*, 82(4), 225-260.

<https://doi.org/10.1037/h0076770>

Schott, N., Hailbach-Beach, P., & Knopfle, V. N. (2021). The effects of visual impairment on motor imagery in children and adolescents. *Research in Developmental Disabilities*, 109, 103835.

<https://doi.org/10.1016/j.ridd.2020.103835>

- Schwartz, D. L., & Black, T. (1999). Inferences through imagined actions: Knowing by simulated doing. *Learning, Memory, and Cognition*, 25(1), 116-136.
<https://psycnet.apa.org/doi/10.1037/0278-7393.25.1.116>
- Schwoebel, J., Boronat, C. B., & Coslett, H. B. (2002). The man who executed “imagined” movements: evidence for dissociable components of the body schema. *Brain and Cognition*, 50(1), 1-16. [https://doi.org/10.1016/S0278-2626\(02\)00005-2](https://doi.org/10.1016/S0278-2626(02)00005-2)
- Sharma, N., & Baron, J. (2013). Does motor imagery share neural networks with executed movement: A multivariate fMRI analysis. *Frontiers in Human Neuroscience*, 7.
<https://doi.org/10.3389/fnhum.2013.00564>
- Sharma, N., Jones, P. S., Carpenter, T. A., & Bacon, J. C. (2008). Mapping the involvement of BA 4a and 4p during motor imagery. *Neuroimage*, 41(1), 92-99.
<https://doi.org/10.1016/j.neuroimage.2008.02.009>
- Sharma, N., Pomeroy, V. M., & Baron, J. (2006). Motor imagery: A backdoor to the motor system after stroke? *Stroke*, 37(7). <https://doi.org/10.1161/01.STR.0000226902.43357.fc>
- Silva, S., Loubinoux, I., Oliver, M., Bataille, B., Fourcade, O., Samii, K., Jeannerod, M., & Demonet, J. F. (2011). Impaired visual hand recognition in preoperative patients during brachial plexus anesthesia: Importance of peripheral neural input for mental representations of the hand. *Pain Medicine*, 114, 126-134.
<https://doi.org/10.1097/ALN.0b013e31820164f1>
- Simoneau, G. G., Ulbrecht, J. S., Derr, J. A., & Cavanagh, P. R. (1995). Role of somatosensory input in the control of human posture. *Gait and Posture*, 3(3), 115-122.
[https://doi.org/10.1016/0966-6362\(95\)99061-O](https://doi.org/10.1016/0966-6362(95)99061-O)

- Sirigu, A., Cohen, L., Duhamel, J. R., Pillon, B., Dubois, B., Agid, Y., & Pierrot-Deseilligny, C. (1995). Congruent unilateral impairments for real and imagined hand movements. *Cognitive Neuroscience and Neuropsychology*, 6(7), 997-1001.
<https://doi.org/10.1097/00001756-199505090-00012>
- Sober, S. J., & Sabes, P. N. (2005). Flexible strategies for sensory integration during motor planning. *Nature Neuroscience*, 8(4), 490-497. <https://doi.org/10.1038/nn1427>
- Suica, Z., Behrendt, F., Gaumann, S., Gerth, U., Schmidt-Trucksass, A., Ettlin, T., & Schuster-Amft, C. (2022). Imagery ability assessment: A cross-disciplinary systematic review and quality evaluation of psychometric properties. *BMC Medicine*, 20, 166.
<https://doi.org/10.1186/s12916-022-02295-3>
- Takeuchi, N., & Izumi, S. (2013). Rehabilitation with poststroke motor recovery: A review with a focus on neural plasticity. *Stroke Research and Treatment*, 2013(1).
<https://doi.org/10.1155/2013/128641>
- Taylor, N. F., Dodd, K. J., Shields, N., & Bruder, A. (2007). Therapeutic exercise in physiotherapy practice is beneficial: A summary of systematic reviews 2002-2005. *Australian Journal of Physiotherapy*, 53(1), 7-16. [https://doi.org/10.1016/S0004-9514\(07\)70057-0](https://doi.org/10.1016/S0004-9514(07)70057-0)
- Tessitore, A., Russo, A., Cirillo, M., Giordano, A., Marcuccio, L., & Tedeschi, G. (2010). Hemiparkinsonism and hemiatrophy syndrome: A rare observation. *Clinical Neurology and Neurosurgery*, 112(6), 524-526. <https://doi.org/10.1016/j.clineuro.2010.03.016>
- Todorov, E., & Jordan, M. I. (2002). Optimal feedback control as a theory of motor coordination. *Nature Neuroscience*, 5, 1226-1235. <https://doi.org/10.1038/nn963>

- Toussaint, L., Tahej, P. K., Thibaut, J. P., Possamai, C. A., & Badets, A. (2013). On the link between action planning and motor imagery: A developmental study. *Experimental Brain Research*, 231, 331-339. <https://doi.org/10.1007/s00221-013-3698-7>
- Turville, M., Carey, L. M., Matyas, T. A., & Bienerhassett, J. (2017). Change in functional arm use is associated with somatosensory skills after sensory retraining poststroke. *Americal Journal of Occupational Therapy*, 71(3). <https://doi.org/10.5014/ajot.2017.024950>
- Vries, D. S., Tepper, M., Feenstra, W., Oosterveld, H., Boonstra, A. M., & Otten, B. (2013). Motor imagery ability in stroke patients: The relationship between implicit and explicit motor imagery measures. *Fronteirs in Human Neuroscience*, 7. <https://doi.org/10.3389/fnhum.2013.00790>
- Wang, Y., & Morgan, W. P. (1992). The effect of imagery perspectives on the psychophysiological responses to imagined exercise. *Behavioural Brain Research*, 52(2), 167-174. [https://doi.org/10.1016/S0166-4328\(05\)80227-X](https://doi.org/10.1016/S0166-4328(05)80227-X)
- Wilcox, R. R. (1995). ANOVA: A paradigm for low power and misleading measures of effect size? *Review of Educational Research*, 65(1), 51-77. <https://psycnet.apa.org/doi/10.2307/1170478>
- Williams, S. E., Cumming, J., Ntoumanis, N., Nordin-Bates, S. M., Ramsey, R., & Hall, C. (2012). Further validation and development of the movement imagery questionnaire. *Journal of Sport and Exercise Psychology*, 34(5), 621-646. <https://doi.org/10.1123/jsep.34.5.621>
- Wolpert, D. M., & Flanagan, J. R. (2001). Motor prediction. *Current Biology*, 11(18), 729-732. [https://psycnet.apa.org/doi/10.1016/S0960-9822\(01\)00432-8](https://psycnet.apa.org/doi/10.1016/S0960-9822(01)00432-8)

Wraga, M., Thompson, W. L., Alpert, N. M., & Kosslyn, S. M. (2003). Implicit transfer of motor strategies in mental rotation. *Brain and Cognition*, 52(2), 135-143.

[https://doi.org/10.1016/S0278-2626\(03\)00033-2](https://doi.org/10.1016/S0278-2626(03)00033-2)

Wuehr, M., Schiepp, R., Pradhan, C., Imberger, J., Strupp, M., Brandt, T., & Jahn, K. (2012).

Differential effects of absent visual feedback control on gait variability during different locomotion speeds. *Experimental Brain Research*, 224, 287-294.

<https://doi.org/10.1007/s00221-012-3310-6>

Yue, G., & Cole, K. J. (1992). Strength increases from the motor program: Comparison of

training with maximal voluntary and imagined muscle contractions. *Journal of Neurophysiology*, 67(5), 1114-1123. <https://doi.org/10.1152/jn.1992.67.5.1114>

Zandvleit, S. B., Kwakkel, G., Nijland, R. H. M., Van Wegen, E. E. H., & Meskers, C. G. M.

(2020). Is recovery of somatosensory impairment conditional for upper-limb motor recovery early after stroke? *Neurorehabilitation and Neural Repair*, 34(5).

<https://doi.org/10.1177/1545968320907075>

Zapparoli, L., Invernizzi, P., Gandola, M., Berlingeri, M., Santis, A. D., Zerbi, A., Banfi, G., &

Paulesu, E. (2014). Like the back of the (right) hand? A new fMRI look on the hand laterality task. *Experimental Brain Research*, 232, 3873-3895.

<https://doi.org/10.1007/s00221-014-4065-z>

Appendix
Participant Exclusion Criteria

Exclusion Criteria:	# of participants excluded
> 20% error rate across the entire study	6
> 40% error rate for one orientation	7
> 40% error rate for one condition	2
No monofilament fibre detection threshold increases in Digitimer conditions compared to control conditions	1
Combination of minor thresholds increases (i.e. only 1 testing site threshold increase) with an average PNQ score < 3.0 in DP or NV-DP conditions	4

Note. Appendix provides a description of exclusion criteria and the number of participants who met exclusion criteria for each category. Participants who met or exceeded exclusion criteria for any of the above categories had their data removed from further analyses. Participants who met exclusion criteria for more than one category will be counted in each category where they met exclusion criteria. In total, 13 participants were removed from analyses for meeting one or more of the defined thresholds listed above.