An investigation of perceptual-motor processes in people with mild-moderate idiopathic Parkinson's disease: Perceptual-Motor Calibration, Motor imagery, and Body Perception

By

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Declaration

I declare that this thesis is entirely my own work completed under the supervision of Dr Sally A. Linkenauger, Professor Trevor J. Crawford and Dr Ellen Poliakoff. None of this thesis has been submitted elsewhere in support of application for the award of a higher degree.

Please note. The parts of this thesis that have been published, or submitted for publication, in academic journals during the course of this doctoral degree have been indicated in the statement of authorship chapter.

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Abstract

Safe, successful interaction within one's environment is contingent upon the perceivers' ability to rapidly decipher whether the performance of a given action over a visually specified range is permissible. That is, perceivers must be reliably in tune with the maximum extent to which they can perform an action, known as an action boundary. This mapping between the visually specified parameters of the environment and one's action capabilities is known as *perceptual-motor* calibration. Indeed, healthy young individuals are reliably calibrated to their action boundaries, and can flexibly adjust their perceptions to accommodate for alterations in their action capabilities. However, this accurate flexible updating occurs in response to somewhat stable variability. Previous studies have typically subjected the perceiver's morphology to one alteration that then remains stable. For example, hand size has been consistently increased by the addition of a padded prosthesis. However, there are conditions in which motor abilities are subject to continual unstable variability over time, such as in Parkinson's disease (PD). Many individuals with PD experience unilateral symptom presentation and fluctuations in their motor abilities. Presumably, this leads to variability in perceptual-motor experience relating to ones ability to perform actions. To date, the influence of PD on perceptual-motor calibration remains unknown. Therefore, in the first part of this thesis (Chapters 3-5), I investigated how PD influences ones perceptual-motor calibration capabilities. First, I found that when healthy younger individuals' grasping ability was artificially varied (in virtual reality), the perceptual system calibrates to the average of all action boundaries experienced (regardless of the frequency of experience with each action boundary). While this study does not directly relate to PD, it serves to inform how we may anticipate PD will influence individuals' perceptions of their action capabilities. Further experiments showed that individuals with PD perceive their action capabilities for reaching,

grasping and aperture passing, comparably to healthy older adult controls. Given the potential functional role of motor imagery when judging one's action capabilities, I then investigated how specific symptom severity influences individuals with PD's motor imagery capabilities. Overall symptom severity and tremor did not predict the vividness of motor imagery. However, greater severity of the slowness of movement (bradykinesia) in the left-side of the body was associated with more vivid overall and left-side specific kinesthetic motor imagery. Taken together, these findings imply that perceptual-motor calibration is largely preserved in individuals with mild-moderate idiopathic PD. The second part of this thesis (Chapter 6) then shifted gears and explored the influence of PD on the perceptions of the relative proportions of one's body. It was found that individuals with PD displayed the same large systematic distortions in the perception of one's body proportions commonly observed in healthy younger adults. By examining perceptual-motor calibration, and the perception of the relative proportions in individuals with PD, this thesis improve our understanding of the underlying deficits associated with PD. Specifically; I argue that PD is not associated with a deficit in the calibration between perceptual and motor systems.

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Chapter 1

1. Introduction

1.1. Overview

Rapidly deciphering whether one can successfully perform a given action over a visually specified range is ubiquitous in daily living, and safe and successful interaction within one's environment is contingent upon this ability. The maximum extent to which one can perform an action, known as an action boundary (Fajen, 2007), is dictated by one's morphology, physiology, and behavioural capabilities (Proffitt & Linkenauger, 2013). When determining whether an action can be successfully performed, perceivers are required to compare the visually specified parameters over which an action must be performed, to their phenotypically specified action boundary (Ramenzoni, 2017). For the performance of an action to be possible, the visually specified range, over which the action must be performed, must be within the perceivers' action boundary. For example, for a crevasse to be jumpable, the distance between the two banks of a stream must be within the perceiver's action boundary for jumping. This mapping between the visually specified parameters of the environment, or object within the environment, and one's action capabilities is known as *perceptual-motor* calibration (Bingham & Pagano, 1998; Warren, 1984).

An abundance of literature has demonstrated that healthy young individuals are reliably in tune with their action boundaries for reaching (Carello et al., 1989; Linkenauger et al., 2009), grasping (Linkenauger et al., 2009; Linkenauger et al., 2012), stair climbing (Warren, 1984), and aperture passing behaviours (Warren & Whang, 1987; Franchak &Adolph, 2012; Ishak et al., 2014). In addition, healthy young individuals are capable of flexibly adjusting their perceptions to accommodate

for alterations in action capabilities. For example, Mark (1987) found that when individuals' eye heights were elevated, by standing on a block, they retuned their action boundary for "sitting on" and "climbing on" behaviours to accommodate for this increase in elevation. Specifically, the maximum seat and riser height participants perceived to be sit-on-able and climbable increased when standing on the block. Similarly, the minimum doorway width individuals perceived to be passable increased when walking through a doorway donning a pregnancy pack (Franchak & Adolph, 2014a). Moreover, the minimum aperture individuals perceived they could pass their hand through increased when hand size was increased by a prosthesis (Ishak et al., 2008).

While it appears that the perceptual system can flexibly update to accommodate for variance in one's action capabilities, the variability analysed in the current body of literature is somewhat consistent by nature. Within these studies, the perceiver's morphology is subject to one alteration that then remains stable. However, in certain contexts, the perceptual-motor feedback specifying one's action boundary is subject to continuous unstable variability. A clear example of this is in Parkinson's disease (PD).

PD is a multifaceted movement disorder clinically characterised by slowed movement execution (bradykinesia), tremor, rigidity, and postural instability (Politis et al., 2010; Jankovic, 2008). The motor manifestations of PD are particularly eminent during the performance of voluntary actions (Brown & Marsden, 1988; Meara, 2010). Biochemically, PD arises due to the progressive degeneration of dopaminergic nigrostriatal neurons of the basal ganglia, coupled with intracellular alpha-synuclein lewy bodies (Obeso et al., 2000a; Triarhou, 2013). The motor manifestations of PD typically commence unilaterally (Sveinbjornsdottir, 2016). For example, while the left

side of the body may be profoundly affected, the right side may be seemingly unimpaired (Sveinbjornsdottir, 2016).

The current 'gold standard' treatment for PD is levodopa drug therapy (Troncoso-Escudero et al., 2020). Initially, levodopa therapy effectively controls individual's motor symptoms (Hälbig & Koller, 2007), and reduces the progression of disability (Poewe et al., 2010). However, following several years of levodopa drug therapy, individuals' with PD often experience motor complications, including fluctuations in their motor abilities (Dupont, et al., 1996). Specifically, with disease progression the benefit of levodopa "wears off" between doses. As a result, individuals cycle between times in which their motor symptoms are under good control ('On' times) and times in which their motor symptoms are not well controlled, and so are particularly debilitating ('Off' times; Lees, 1989). In some circumstances, these motor fluctuations are predictable and related to consumption of antiparkinsonian medication (Stacy et al., 2005). However, in other circumstances, these fluctuations are highly unpredictable both in onset and duration (Lang et al., 1982). This unstable variability, in motor capabilities, may mean that individuals with PD's perceptual-motor experience regarding their action capabilities will be unstable and variable. Subsequently, individuals with PD's ability to calibrate to their action boundaries ns may be altered.

When deciding whether the performance of an action is possible, perceivers must scale the visual information, specifying the environment, against their phenotypically dictated action capabilities (Proffitt & Linkenauger, 2013). Although the basal ganglia, a group of subcortical nuclei, are primarily responsible for motor control (Lanciego et al., 2012), they also provide extensive links between areas implicated in visual (Turcano et al., 2019; Middleton & Strick, 1996; Silkis 2007;

Seger, 2008; Seger, 2013) and somatosensory processing (Beudel et al., 2020). Subsequently, successful perception of one's action capabilities may be contingent upon effective basal ganglia functioning. Given that PD arises due to alterations in one's basal ganglia functioning, one may reasonably anticipate that PD will influence the perception of one's action capabilities.

Considering these factors as a whole, it is likely that PD will affect individuals' perceptual-motor calibration capabilities. As a result of the unstable variability in perceptual-motor experience and altered basal ganglia functioning, it is likely that individuals with PD will not be reliably in tune with their capabilities to perform actions.

Large systematic distortions in perceived body size, across different body parts, are a part of healthy cognition (Longo, 2017). For example, healthy younger adults estimate the length of the torso to be approximately 1.75 times, and the foot to be approximately 0.95 times the length these body parts actually are (Linkenauger et al. 2015). Interestingly, individuals' perceptions of their body proportions appear to relate the length of body parts, to the combination of visual and tactile information (Linkenauger et al., 2015; Longo 2017). Such that less sensitive body parts are perceived to be disproportionately larger than highly sensitive body parts (Linkenauger et al., 2015). Although PD is classically considered to be a movement disorder (Hughes, 1994), reductions in peripheral epidermal nerve fibres (Nolano et al., 2008), and alterations in tactile perception have been observed in PD (Schneider et al., 1987; Nolano et al., 2008; Artieda et al., 1992; Sathian et al., 1997). Therefore, we may anticipate that individuals with PD's perceptions of their body proportions may be altered.

1.2. Problem statement

PD currently affects approximately 137,000 people in the UK alone (NICE, 2021). Ageing is considered the main risk factor of PD (De Lau, & Breteler, 2006). Therefore, as we are an ageing society, the number of individuals impacted by Parkinson's is only ever going to increase. Unfortunately, PD is currently incurable (Pan et al., 2021). Subsequently, the management of PD is of particular clinical importance.

Successful interaction within one's environment is contingent upon one's ability to accurately perceive their action boundaries for a plethora of actions. Therefore, if an individual is not reliably in tune with their action boundaries, their ability to successfully, and safely, interact within the environment may be impaired. Despite there being sound theoretical reasoning to anticipate that perceptual-motor calibration may be altered in PD, the influence of PD on perceptual-motor calibration and the perceptions of ones action capabilities remains unknown.

The present thesis will address this fundamental gap in the literature by investigating individuals with mild-moderate idiopathic PD's perceptions of their action capabilities. Moreover, this thesis will investigate the influence of PD on an additional distinct, yet related to perception and action, phenomena; the perception of the relative proportions of the body.

In doing so the present thesis aims to improve our understanding of the underlying deficits associated with PD. Specifically; I will determine whether a deficit in the calibration between perceptual and motor systems occurs in PD.

1.3. Thesis construction

1.3.1 Thesis Structure

This thesis is organised in the following way. First, in Chapter 2, I review evidence that the visual perceptual system has evolved not to provide a veridical representation of the environment, but rather is tailored to specify the perceivers' possibilities for action within the environment. Subsequently, successful interaction within one's environment is contingent upon the ability to accurately perceive the extent over which one can successfully perform actions. Behavioural evidence for the accuracy of the perception of action capabilities in neurotypical younger adults is introduced. I then consider how variability in motor capabilities, altered basal ganglia functioning, and motor imagery, may influence perceptual-motor calibration in PD. Finally, I introduce an additional intrinsically related process, the perception of the relative proportions of one's body.

Following this, in Chapter 3, I present the first empirical study. In this study, the influence of artificially induced variability (in virtual reality) in grasping experience on perceived grasp ability is investigated. This chapter informs how we may anticipate PD to influence individual's perceptions of their action capabilities. In Chapter 4, I analyse individuals' with mild-moderate PD's perceptions of their action capabilities for reaching, grasping and aperture passing. The findings obtained in Chapter 4 suggest that the perception of action capabilities is preserved in PD. This may in part be due to the preservation of the generation of motor imagery in PD. Therefore, in Chapter 5 the influence of Parkinson's symptomology, specifically bradykinesia and tremor, on MI vividness is analysed.

Chapters 4 and 5 suggest that the perception of one's action capabilities is somewhat preserved in PD. Therefore, in the final empirical study, Chapter 6, I slightly shifted gears and investigated how PD is related to the perception of the relative proportions of the body. This thesis then concludes with Chapter 7, in which

the results and implications of Chapters 3-6 are collated and discussed, and future directions for research are proposed.

1.3.2 Rationale for Alternative Format

The studies in this thesis (Chapters 3-7) are written in publishable manuscript format, with three having already been published (Chapter 3; Psychonomic Bulletin and Review, Chapter 4; Attention, Perception and Psychophysics, and Chapter 6; Psychonomic Bulletin and Review). Chapter 5 has been submitted for peer review in Journal of Neuropsychology, and is therefore presented in 'submitted for publication' format.

Given the nature of these studies and the series of interesting findings obtained, I find it appropriate to implement the alternative format for this thesis. Moreover, whilst the chapters presented in this thesis are distinct papers, they follow one coherent story and provide interrelated findings. That is, all studies investigate the calibration between perceptual and motor systems in mild-moderate idiopathic PD.

1.3.3 My Contributions

I was responsible for theoretical conceptualisation, study design, data collection, data analysis, and manuscript development for all studies presented in this thesis. This occurred under the guidance of my supervisors, Dr Sally Linkenauger, Professor Trevor Crawford and Dr Ellen Poliakoff. The exception to this was the study in Chapter 5. Due to the changing COVID-19 pandemic restrictions, in Chapter 5 (Motor imagery vividness and symptom severity in Parkinson's disease), we elected to analyse retrospective data collected by Dr Judith Bek (University of Toronto), who

at the time of data analysis and manuscript development was a postdoctoral fellow within Dr Ellen Poliakoff's research group. Dr Bek also assisted in the analysis of this data. Furthermore, Dr Neil McLatchie provided Bayesian statistical analysis support for the papers in Chapters 4 and 7 (How far can I reach? The influence of Parkinson's Disease on perception of one's upper body action capabilities; The Distorted Body: The perception of the relative proportions of the body is preserved in Parkinson's Disease). Professor Matthew Longo (Birkbeck, University of London) supported theoretical conceptualization and study design for the paper in Chapter 7 (The perception of the relative proportions of the body is preserved in Parkinson's Disease).

Chapter 2

2. Background

2.1 The Ecologically Adapted Visual Perceptual System

It is easy to assume that humans' visual percepts of the environment in which they inhabit are grounded in physical reality, that is, we perceive a veridical representation of the environment, as it truly exists. However, whilst the human brain is an immensely powerful intricate processing system, it is also fundamentally limited in capacity (Broadbent, 1958; Kahneman, 1973). In terms of the energy required to process information, the brain is the most expensive organ in the human body; it consumes 20% of one's available energy, while only accounting for 2% of one's mass (Drubach, 2000). Subsequently, the energetic benefits obtained from the visual perceptual system must outweigh the metabolic costs associated with its functioning. This raises the question of whether we only perceive information which will enable us to effectively interact with the environment.

A frog will starve in a room full of dead flies, not because the frog cannot eat them; but because the frog cannot see them. The retinal ganglion cells of frog's eyes detect only four types of stimuli: overall dimming, stationary edges, moving edges and moving dark spots (Lettvin et al., 1959; Nishio et al., 2007). Thus, if a fly does not move and hence is a stationary dark spot, the frog will not see it. Presumably, the frog's retinal ganglion cells have evolved in this way because the frog is far more likely to encounter moving dark spots (moving flies) than stationary dark spots (dead flies) within its environment. Therefore, expending energy in perceiving stationary flies provides little energetic benefit to the frog. Similarly, a lobster, due to the structure of their photoreceptors, is blind in bright light, but can almost always see motion in dimly lit environments (Cobb & Phillips, 2012; Meyer-Rochow, 1994). As

lobsters inhabit a deep-sea ecosystem they are rarely, if ever, naturally exposed to bright light. Subsequently, the energetic costs associated with enabling lobsters to see motion in bright lights far outweigh the benefits.

Although these examples are based on non-human animals, the human visual perceptual system operates in a similar manner. Specifically, humans too only perceive visual information that is useful in their ecological niche. For example, whilst some animals, such as bees, can readily see ultraviolet light (light of a wavelength below 380 nanometres), the physiology of the lens of the human eye prevents humans from seeing ultraviolet light (Douglas & Jeffery, 2014). Presumably, this differentiation has evolved because seeing ultraviolet light provides great advantages to bees when seeking nectar. Whereas, seeing ultraviolet light provides very little benefit to humans in the environment in which they inhabit (Kevan et al., 2001). Similarly, due to the density of functional photoreceptors, rods and cones, in the retina, many birds have a much greater visual acuity than humans (Fite, 1973). For example, buzzards can see objects up to 3km away (RBPS, n.d). Given the ecological niche birds inhabit compared to humans, being able to see prey in the distance provides great benefit to birds. Whereas, humans would have little use for such refined visual acuity. As a result of having two centrally located eyes, humans have a great degree of binocular overlap, which facilitates exceptional depth perception in front of the body (where humans perform most actions) (Read, 2021). In contrast, other animals, typically prey animals such as songbirds, have two laterally located eyes. Although at the expense of refined depth perception, this causes the prey animals to have visual fields close to 360^{o}. Considering the ecological niche that songbirds inhabit compared to humans, for songbirds it is far more important to be able to see predators over a vast visual field than it is to have depth perception (given

the birds lack of ability to perform actions). Whereas for humans, it is far more important to take full advantage of depth perception than it is to have a vast field of view. These examples clearly illustrate that the human visual perceptual system does not function to provide a detailed veridical representation of the environment, as it truly exists; rather it provides humans with the minimum information necessary to enable survival and successful interaction within the environment in which they inhabit.

Congruent with these assumptions, Gibson's (1979) framework of direct visual perception postulates that one's perceptions of the environment are tailored by the affordances. Affordances signify the opportunities for action for a given organism within a particular environmental context (Heras-Escribano & Pinedo-García, 2018). For example, if a terrain is flat enough, sufficiently extended and of sufficient rigidity for a given organism that ambulates, then that terrain affords support and is a transverseable. However, if the terrain does not fulfil these requirements or the animal is incapable of ambulating, it will not be perceived as a transverseable surface (Gibson, 1979).

An infinite number of affordances are present for any organism within an environment at any one time. However, the extent to which an object affords a specific behaviour is determined by the relationship between the dimensions of the object and the abilities of the perceiver's body (Proffitt & Linkenauger, 2013). Consider, for example, the world perceived by Alice in Lewis Carroll's classical novel *Alice's Adventures in Wonderland* (1865). On drinking the contents of the "Drink me bottle", as Alice's body begins to shrink, seemingly the world around her begins to grow. The once small bottle, that Alice could easily grasp, is now far too large for her to grasp. Thus, the bottle is no longer a graspable object. When Alice

then eats the “eat me” cake, her body begins to grow until she is extremely tall, and seemingly the world around her begins to shrink. The table that once was waist height, prior to drinking the potion, is now ankle height. Under such circumstances, it is physically impossible for Alice to sit at and rest upon the table, therefore the table no longer affords sitting at and resting upon behaviours. While the physical form of the environment remains constant, the ability to interact with objects drastically changes as a consequence of the morphological changes in Alice’s body. Therefore, as a consequence of morphology one environmental feature can afford two entirely different behaviours.

2.2 Can I Successfully Perform this Action? The Perception of one’s Action Capabilities.

Successful interaction within the environment is contingent upon an individual’s ability to accurately calibrate to their action capabilities to allow for the distinction between possible and impossible opportunities for action (Ramenzoni, 2017). For example, when a perceiver decides whether they can successfully pick up a glass, they must compare the visually specified diameter of the glass to their morphologically dictated grip aperture. If the diameter of the glass fits within the maximal grip aperture of the hand, then this glass is perceived to be graspable. This calibration is known as *perceptual-motor calibration,* and the extent to which performance of an action is possible is known as an action boundary (Fajen, 2005).

Due to growing and ageing, the morphology of the human body changes throughout the lifespan. Subsequently, action boundaries must be learnt over time through perceptual-motor experience gained from exploration within ones environment (Gibson, 2000). Five-month-olds perform 100 - 250 exploratory hand

movements every 10 minutes (Wallace & Whishaw, 2003), and 12-month-olds walk approximately 297 meters per hour (Adolph et al., 2012). Presumably, this exploration allows infants to learn the visual specification of actions that are possible and impossible, enabling them to become finely attuned to their action boundary (Proffitt & Linkenauger, 2013).

By early adulthood, one's bodily morphology remains fairly consistent. Subsequently, the perceptual-motor experience specifying one's action capabilities will also be largely consistent. Therefore, perceivers will have a reliable reference of morphological capabilities to scale visual information against. Previous research has shown that healthy young individuals can reliably scale visual information to their morphological capabilities to accurately decipher whether the performance of an action, over a specified range, is possible. For example, Warren (1984) found that individual's perceptions of the climbability of steps varied as a function of leg length. Specifically, tall participants perceived taller steps to be more climbable than shorter participants. Thus, indicating that perceivers scaled the height of the stair to their leg length to accurately determine their action boundary for stair climbing.

Similarly, Carello et al. (1989) observed that individuals' perceptions of their maximal horizontal reach capabilities varied in line with physical arm length. This high degree of accuracy has also been observed when participants are asked to estimate the smallest door opening they can pass through (Warren & Whang, 1987), the smallest size opening they can fit their hand through (Ishak et al., 2014), and the largest object they can grasp (Linkenauger et al., 2009).

Importantly, our bodies and the world in which we inhabit are continually changing (Franchak & Adolph, 2014b). Consider the gestation period in women for example. During this period, women experience several extreme alterations to their

morphology (Branco et al., 2014), which subsequently alters the constraints placed on their action capabilities. As a result, successful interaction within ones environment is also contingent upon one's ability to update their perceptions of their action capabilities to accommodate for varying constraints.

Additional research has observed that perceivers flexibly adjust their perceptions of their action boundaries in conjunction with alterations in action capabilities. For example, individuals retuned their action boundary for aperture passing when their hand size was enlarged by a padded prosthesis (Ishak et al., 2008), and when their girth was increased by donning a pregnancy pack (Franchak & Adolph, 2014a). Similarly, individuals retuned their action boundary for climbing and sitting upon behaviours when their eye height was elevated by standing on blocks (Mark, 1987). Furthermore, perceived distances towards targets are compressed when participants are provided with a hand tool (Witt et al., 2005; Witt & Proffitt, 2008). Under these circumstances, the hand tool extends reaching capabilities. As participants perceived the distance to targets to be shorter, these results can be taken to indicate that participants retuned their action boundary for reaching, to accommodate for the extension of the tool (Proffitt & Linkenauger, 2013).

Although it appears that our perceptual system seemingly recalibrates following alterations in one's action capabilities, the alterations in action capabilities examined in the current body of literature are predominantly stable in nature. Consider Ishak et al. (2008), for example. When participants' hands were enlarged by a padded prosthesis, the participants hand morphology, and consequently action capability, was subjected to one stable change that then remained constant. Under these circumstances, the perceivers' perceptual-motor experience specifying their action capabilities, will also be consistently altered. As the perceiver's perceptual-motor

experience remains stable, presumably, they will gain sufficient experience with their altered action boundary to rapidly recalibrate to. Resultantly, individuals will hold reliable references of their altered action boundaries to scale the visually specified environment against. Therefore, it is likely that individuals will remain reliably in tune with their altered action boundaries.

While it is important to understand how the perceptual system accounts for stable alterations in one's action capabilities, there are certain conditions in which individuals' action capabilities are subject to unstable variability. Under these circumstances, the perceivers' perceptual-motor experience, specifying their action capabilities, will be subject to a large degree of unpredictable variability. Presumably, this high degree of variability will prevent individuals from gaining sufficient consistent perceptual-motor experience, specifying their action boundaries, to rapidly recalibrate to. Subsequently, individuals will not hold a reliable reference of their altered action capabilities to scale the visually specified environment against. Presumably, this will prevent the perciever from being reliably in tune with their action boundaries. A clear example of this occurs in people with Parkinson's disease.

2.3 Parkinson's Disease (PD)

PD, the second most pervasive neurodegenerative disorder after Alzheimer's Disease (De Lau, & Breteler, 2006), is a paradigmatic movement disorder that affects approximately 0.5-3% of the worldwide population over 65 years old (Tanner & Goldman, 1996). Pathologically, PD is thought to arise due to the progressive degeneration of dopaminergic nigrostriatal neurons originating in the substantia nigra pars compacta of the basal ganglia and projecting to the striatum, coupled with intracellular alpha-synuclein protein aggregates (Obeso et al., 2000a; Triarhou, 2013).

These alterations in dopaminergic neurons result in the reduction of striatal dopamine levels (Hornykiewicz, 2006; Salat, & Tolosa, 2013). Which, in turn clinically manifests as the slowing of movement execution (bradykinesia), tremor, rigidity, and postural instability (Politis et al., 2010; Jankovic, 2008). Moreover, particular difficulties with voluntary, internally generated actions are observed in PD (Brown & Marsden, 1988; Meara, 2010).

Parkinson's tremor, the involuntary rhythmic movement of one or more body parts (Helmich et al., 2013), is thought to arise as a consequence of aberrant neural oscillations within the cortico-basal ganglia-thalamic neural circuits (Singh, 2018). Parkinson's tremor can be further subdivided into resting, postural and action tremor. Resting tremor (frequency 4-6Hz; Jankovic, 2008) occurs when an individuals muscles are not voluntarily activated and are being maintained in a fully supported position (e.g. the hands are held in the lap). Postural tremor (frequency 5-9 Hz) occurs when an individual maintains a body position against gravity (e.g. holding the arms outstretched in front of the body), and action (kinetic) tremor (frequency (3-10Hz) occurs with voluntary movement (e.g. pouring and writing; Thenganatt & Louis, 2012). Tremor has a significant impact on individuals' ability to perform tasks of daily living, to the extent that tremor was cited as the most bothersome symptom in a survey of 75 individuals with mild PD (Uebelacker et al., 2014).

While tremor is perhaps the most well known and easily recognised symptom of PD, approximately 30% of people with PD do not experience tremor (Jankovic, 2008). In comparison, almost all people with PD experience the slowing of movement execution (bradykinesia), to a greater or lesser degree (Chaudhuri & Ondo, 2011). Bradykinesia is thought to occur as a result of the failure of basal ganglia output to reinforce cortical mechanisms associated with the preparation and execution of

actions (e.g., Berardelli et al., 2001). Supporting this assumption, neuroimaging studies, using PET (Jahanshahi et al., 1995), fMRI (Haslinger et al., 2001) and EEG (Dick et al., 1989) have found that the supplementary motor area (SMA) and dorsolateral prefrontal cortex, both which are implicated in motor preparation (Makoshi et al., 2011; Picard & Strick, 1996), are systematically under activated in PD. For example, Dick et al. (1989) observed that Bereitschaftspotential, a negative EEG potential that occurs before the onset of voluntary movement, in the SMA is reduced 1-2seconds before movement, and is larger than normal approx. 650ms before movement in individuals with PD who had been withdrawn from their medication 12 hours prior to their participation. In addition, the spatiotemporal pattern of movement related desynchronisation preceding voluntary movement in the premotor area is delayed in untreated PD patients (Defebvre et al., 1996). Taken as a whole, these alterations in cortical activation preceding motor execution support the notion that motor preparation is impaired in PD.

In addition to bradykinesia, the magnitude of movement execution is often abnormally diminished in PD (Simões & Litvan, 2010). This reduction in movement amplitude, is known as hypokinesia (Berardelli et al., 2001). Importantly, when hypokinesia occurs, the individuals' muscular strength is preserved (Simões, & Litvan, 2010). Therefore, while it is physically possible for the individual to perform an action over a certain range, in practicality, execution of the action in question over this range cannot occur. Furthermore, in certain circumstances, PD patients experience a total absence of voluntary movement, commonly referred to as akinesias (Spay et al., 2019).

Tremor, bradykinesia, and hypokinesia profoundly impact individuals' ability to perform activities of daily living (Heusinkveld et al., 2018). For example, action

tremor of the hand is likely to constrict an individual's ability to grasp objects, such as mugs, and postural tremor of the arm is likely to impede an individuals' ability to hold the mug steady. Moreover, upper body bradykinesia is likely to significantly reduce the speed at which an individual can extend their arm to catch a falling object, and the presence of hypokinesia may reduce the extent to which an individual can open their hand to their maximal grip aperture. Thus enhancing the likelihood of the object not being caught and the action failing to be performed effectively.

The motor manifestations of PD typically begin unilaterally, in one limb (Sveinbjornsdottir, 2016), when the dopamine concentrations of the contralateral striatum drop below 60-70% (Rodriguez-Oroz et al., 2009). For example, an individual may present with severe resting tremor in the right arm, whilst the left side of the body may be seemingly unaffected (Sveinbjornsdottir, 2016). Indeed, the prevalence of unilateral symptom presentation in PD is so great that several definitions of early-stage PD require unilateral symptom presentation for a diagnosis (Toth et al., 2004; Gelb et al., 1999; Hoehn & Yahr, 1998). Throughout the progression of PD, the asymmetry of motor manifestations persists in over 50% of individuals with PD (Lee et al., 1995; Yagi et al., 2010). For example, Barrett et al. (2011) found that 86.5% of 1173 individuals with PD presented motor symptoms asymmetrically. Moreover, some research has observed an association between dominant handedness and the side of initial unilateral symptom presentation. Specifically, the dominant hand side is affected first in the majority of individuals (Barrett et al., 2011).

Although PD is traditionally considered a movement disorder, recent clinical investigations have highlighted that PD encompasses a host of non-motor symptoms that can precede the motor manifestations by many years (Kumaresan & Kahn, 2021).

For example, declines in attention, executive functions, memory and visuospatial skills have frequently been observed in individuals with PD (Watson & Leverenz, 2010). More specifically, approximately 20-50% of people with PD have comorbid mild cognitive impairment and approximately 80% of people with PD eventually receive a diagnosis of dementia (Goldman et al., 2018). In terms of sensory abnormalities, olfactory impairments have been shown to predate the motor manifestations of PD by up to four years (Ross et al., 2008). Furthermore, significant increases in two-point tactile discrimination thresholds (Schneider et al., 1987; Nolano et al., 2008) and tactile temporal discrimination thresholds (Artieda et al., 1992) relative to age matched controls have been observed in PD.

Currently, the oral consumption of levodopa, a precursor to dopamine, is the 'gold standard' treatment for PD (Fahn, 2006; Dorszewska et al., 2014). When combined with a decarboxylase inhibitor (e.g. carbidopa), which prevents the peripheral metabolism of levodopa, levodopa can pass the blood-brain barrier. Once levodopa crosses the blood-brain barrier, it can be rapidly converted into dopamine (LeWitt, 2008). Therefore, levodopa treats the symptoms of PD by effectively replacing lost dopamine (Salat & Tolosa, 2013).

Initially levodopa drug therapy offers substantial reductions in symptom intensity and reduces disability progression (Poewe et al., 2010), with very few adverse effects (Marsden & Parkes, 1977). However, chronic levodopa therapy (e.g. 5+ years of leveodopa therapy) is associated with the development of a series of motor complications in the vast majority of individuals (Dupont, et al., 1996). Specifically, with disease progression the benefit of levodopa "wears off". This results in individuals fluctuating between times in which their motor symptoms are under good control ('On' times) and times in which their motor symptoms are particularly

debilitating ('Off' times). This fluctuation in motor capabilities in PD is often referred to as the On-Off phenomenon (Obeso et al., 2000b).

When in an 'On', time individuals are responding well to their levodopa medication, and so their motor symptoms are well controlled. Therefore, in 'On' times, individuals can often perform actions as normal. However, during 'Off' times, individuals' responses to their levodopa therapy do not sufficiently treat their motor symptoms. Subsequently, ability to perform motor actions during 'Off' times is severely compromised (Lees, 1989). 'Off' periods can be predictable and related to the time of medication administration (Stacy et al., 2005). Alternatively, 'Off' periods can be highly unpredictable in both onset and duration (Lang et al., 1982).

2.4 The Functional Role of the Basal Ganglia

The basal ganglia are a group of subcortical nuclei including the striatum, globus pallidus, subthalmic nucleus, and the substantia nigra (Albin et al., 1989). The nuclei of the basal ganglia can broadly be considered as either input nuclei, those that receive input from cortical regions (striatum and subthalmic nucleus), or output nuclei, those that send basal ganglia output to the thalamus (globus pallidus and substantia nigra) (Lanciego et al., 2012). As the basal ganglia receive input from virtually all cortical regions, the basal ganglia are thought to be involved in a variety of functions (Nagano- Saito et al., 2014).

As highlighted by the symptomology of PD, one of the main roles of the basal ganglia is motor control (Lanciego et al., 2012), notably, the selection of the most appropriate motor programs to be executed (Groenewegen, 2003; Lanciego et al., 2012). Given that PD is also associated with a host of non-motor symptoms, it is perhaps unsurprising that the role of the basal ganglia extends beyond motor control.

The basal ganglia are also thought to have a role in visual processing. For example, it has been proposed that the basal ganglia interact directly with the visual cortex through the visual corticostriatal loop (Middleton & Strick, 1996; Silkis 2007; Seger, 2008; Seger, 2013). Congruent with this, individuals with PD have impaired contrast detection (the ability to detect an object from its background) (Regan & Neima, 1984), colour discrimination (Price et al., 1992; Büttner et al., 1995), and saccadic eye movements (Turcano et al., 2019) compared to healthy age matched controls. Furthermore, visuoperceptual abilities are considerably altered in PD (See Cronin- Golomb & Amick, 2001 for review). For example, Harris and colleagues (2003) found that individuals with PD perceived a rectangle in left space to be narrower than an identical rectangle in right space. Comparatively, healthy controls perceived the rectangle in right space to be narrower. Corroborating these empirical measures, individuals with PD frequently report that they bump into objects often and struggle navigating around their everyday environment (Lee & Harris, 1999).

The basal ganglia are also known to receive input from cortical somatosensory areas (Beudel et al., 2020). Neuroimaging techniques have shown that preferential activation of the dorsal putamen (a key structure of the basal ganglia) occurs during somatosensory, particularly pain, processing (Arsalidou et al., 2013). In addition, significant increases in two-point tactile discrimination thresholds (Schneider et al., 1987; Nolano et al., 2008), and tactile temporal discrimination thresholds (Artieda et al., 1992), as well as increased error rates during somatosensory tasks (Schneider et al., 1986) have been observed in individuals with PD compared to healthy controls.

2.5 Motor Imagery

Motor imagery (MI), also referred to as “mental practice”, is a dynamic state during which an individual mentally simulates an action in the complete absence of overt motor output (Jeannerod 1994; 1995). Some research suggests that when perceiving an environment, with the intention to perform an action, individuals mentally simulate the performance of said action and the outcome of this simulation influences perception (Witt & Proffitt, 2008). For example when perceiving a ball with the intention to kick it, individuals will mentally simulate kicking the ball, and the outcome of this simulation will influence their perceptions. Supporting this assumption, when individuals are asked to judge whether an image of a rotated hand is the left or right hand, (mental rotation task) the time taken to make the judgment is proportional to the time taken to physically move ones hand into the position of the stimuli (Parsons 1987a, 1987b, 1994).

Relating this to the perception of ones action capabilities, it appears reasonable to assume that, when deciding whether performance of a given action over a visually specified range is possible, the perceiver will mentally simulate the action to be performed. The perceivers ability to perform the action, as determined by the mental simulation, will then be scaled against the visually specified range over which the action must be performed to successfully decipher whether successful performance of the action is permissible. Subsequently, one may reasonably assume that individual’s perceptions of whether the performance of an action is possible or not may be influenced by the perciever’s ability to generate vivid MI.

It is widely accepted that MI shares neural mechanisms with processes employed in overt motor control (Decety, 1996). Neuroimaging studies, using functional magnetic resonance imaging (fMRI), have found that both MI and overt motor output recruit regions including the primary motor cortex, premotor cortex,

SMA, and the basal ganglia (see Hardwick et al., 2018 for review). For example, Kühn et al. (2008) observed that suppression in the beta band of the subthalmic nucleus (a key node in the cortico-basal ganglia-thalamo- cortical circuit; Bevan, 2016) occurred during both physical and imagined wrist flexion in individuals with PD.

While nigrostriatial dopaminergic deficiencies are the principal biochemical characteristic of PD (Obeso et al., 2000a; Triarhou, 2013), abnormal reductions in SMA excitability have also been consistently observed in PD (Cunnington et al., 1997; Dick et al, 1989). Given that both the basal ganglia and SMA are functionally involved in the imagination of movements, one may reasonably anticipate that MI performance will be affected in individuals with PD.

Despite the alterations in basal ganglia and SMA functioning associated with PD, some research has observed that MI is considerably preserved in PD. For example, ratings of MI vividness, measured by the Kinesthetic Visual Imagery Questionnaire (KVIQ) in individuals with PD are comparable to healthy controls (e.g. Bek et al., 2019; Heremans, 2011). Similarly, individuals with PD's judgements of the laterality of hands presented at various angular rotations are similar to older controls (van Nuenen et al., 2012; Scarpina et al., 2019).

However, the consensus of the influence of PD on MI is far from unanimous. Rather, additional research has observed that individuals with PD take longer to judge the laterality of hands and their subsequent judgements are less accurate than controls (e.g. Helmich et al., 2007; Dominey et al., 1995). Although, additional research suggests that these alterations in MI are reflective of impairments in motor capabilities caused by PD (Poliakoff, 2013; Caligiore et al., 2017; Conson et al., 2014) rather than an inability to perform MI. For example, MI and physical motor

execution are slowed to the same extent (Heremans et al., 2011). Further supporting this postulation, MI is reflective of motor fluctuations (the on-off phenomenon) in individuals with PD. For example, Dominey (1995) observed that a patient, who was physically incapable of performing a motor sequence with her right hand in an 'Off' time, was also unable to imagine performing the action in this time.

2.6 Parkinson's Disease and the Perception of Action Capabilities

In PD, motor complications which occur following chronic levodopa therapy, cause individuals' action capabilities to continually and often unpredictably fluctuate (Obeso et al., 2000b). Subsequently, individuals with PD's perceptual- motor experience specifying ones action capabilities will be subject to a large degree of unpredictable variability. Presumably, this high degree of perceptual-motor variability will prevent individuals recalibrating to their altered action capabilities. As a result, individuals will not have a reliable reference of action boundary to scale visual information against when deciphering whether the performance of an action is possible or impossible (Ramenzoni, 2017; Proffitt & Linkenauger, 2013). Resultantly, we may anticipate that individuals with PD's perception of their action capabilities may differ from both younger and healthy older adults.

Presumably, the occurrence of unilateral symptom presentation in PD (Toth et al., 2004; Gelb et al., 1999; Hoehn & Yahr, 1998; Barrett et al., 2011) will also give rise to inconsistent perceptual-motor experience regarding one's action capabilities. Consider an individual with left-side lateralised tremor and bradykinesia for example. The presence of lateralised tremor and bradykinesia in the left-upper body is likely to largely impede the individual's ability to reach towards and open their hand to grasp a glass with their left arm and hand. In comparison, the absence of motor symptoms in

the right-upper body will enable the individual to easily reach toward and grasp the same glass with the right hand to the maximum extent their morphology permits. Subsequently, individuals with PD will gain inconsistent perceptual-motor experience relating to their ability to perform an array of actions dependent upon the body side the action is performed with. Akin to the influence of motor complications, this instability in the ability to perform actions, dependent upon body side, will ultimately prevent individuals with PD from holding a reliable reference of their action boundaries to scale visually specified information against. Subsequently this unstable variance, due to unilateral symptom presentation, may affect a person with PD's ability to accurately perceive their action boundaries for a range of actions.

When deciding whether the successful performance of an action is possible or not, and hence one's action boundary, visual information specifying the environment is scaled by the perceivers' phenotypically dictated capabilities (Proffitt & Linkenauger, 2013). As visual information is scaled by motor and proprioceptive information, presumably, successful perception of one's action capabilities is contingent upon effective intermodal processing between these domains. As the basal ganglia provide links between areas implicated in visual, somatosensory and motor processing (Nagano- Saito et al., 2014), it may be that successful perception of one's action capabilities is somewhat reliant upon effective basal ganglia functioning. Given that basal ganglia functioning is affected in PD, we may anticipate that PD will influence the perception of one's action capabilities.

When perceiving an environment, with the intention to perform an action, individuals mentally simulate the performance of said action and the outcome of this simulation influences perception (Witt & Proffitt, 2008). Therefore, it may be that, when perceiving one's action boundaries, the perceiver will mentally simulate

themselves performing the action in question (Witt & Proffitt, 2008). The perceiver's ability to perform the action, as determined by the mental simulation, will then be scaled against the visually specified environment to determine the extent at which the performance of an action ceases to be possible. Subsequently, individuals' perceptions of their action boundaries may be influenced by their ability to generate vivid MI. Given that individuals with PD's motor imagery abilities appear to be largely preserved, we may anticipate that individuals with PD's perceptions of their action capabilities will too be preserved.

2.7 Body perception

Humans' relationship with their bodies is uniquely intimate. We continuously receive an abundance of visual information, specifying the relative dimensions of our bodies, and so experience our bodies from the outside in the same way as we experience any other object. But, we also experience our bodies from the inside, as an object of immediate experience (Longo, 2017). Given that we continuously receive a wealth of information regarding our bodies, its morphology and capabilities, from multiple sources it appears reasonable to assume that we will be reliably in tune with the relative proportions of our bodies. However, in practicality this does not appear to be the case. For example, amputees often continue to perceive an amputated limb to exist (Ramachandran & Hirstein, 1998), individuals with anorexia insist they are fat even when emaciated (Treasure et al., 2010) and individuals with body dysmorphia insist one part of their body is hideously ugly, though it appears normal to everyone else (Phillips et al., 2008. One facet all individuals with these clinical conditions share in common is that they have an altered representation of their body.

A developing body of research has begun to show that distortions in body representations are not limited to distinct clinical circumstances, and rather they are a part of 'normal' cognition (Longo, 2017). Specifically, large systematic distortions in the perceived proportions of body parts are observed in healthy younger adults (Longo 2017; Linkenauger et al 2015).

The neural information underlying the perception of ones body proportions appears to relate the length of one's body parts to the combination of visual and tactile information (Linkenauger et al., 2015; Longo 2017). Such that (a) less sensitive body parts are perceived to be disproportionately larger than highly sensitive body parts, and (b) given equal sensitivity, larger body parts are distorted less than smaller body parts (Linkenauger et al., 2015). For example, when estimating the length of their body parts using their hand as a metric, healthy younger adults overestimate the length of the torso, a body part of low tactile sensitivity the most and the foot, a body part of high tactile sensitivity, the least (Linkenauger et al. 2015; Sadibolova et al., 2019; Linkenauger et al., 2017).

Although PD is traditionally considered a movement disorder (Hughes, 1994), recent research has shown that significant reductions in peripheral epidermal nerve fibres, meissner corpuscles, and free encapsulated nerves occur in PD (Nolano et al., 2008). Moreover, significant increases in two-point tactile discrimination thresholds (Schneider et al., 1987; Nolano et al., 2008), temporal discrimination thresholds (Artieda et al., 1992), and groove width required to distinguish grating orientation (Sathian et al., 1997), have been observed in PD. Given that the perception of ones body proportions appears to be inextricably related to the body parts tactile sensitivity, we may anticipate that individuals with PD's perceptions of their body proportions may be altered.

2.8 Summary

In this chapter, I have reviewed the relevant literature concerning the perception of one's action capabilities, motor imagery abilities and body perception. When determining the boundary at which the successful performance of an action ceases (action boundary), individuals must relate the visually specified environment to their morphologically dictated action capabilities (Proffitt & Linkenauger, 2013). Healthy controls are reliably in tune with their action boundaries, and can flexibly update these boundaries to accommodate for alterations in one's action capabilities (e.g. Carello et al., 1989; Ishak et al., 2008). However, the alterations analysed within the present body of literature are somewhat stable in nature. There are certain conditions in which alterations in motor capabilities, and unstable variability in perceptual-motor experience occurs. A clear example of this is PD. However, the influence of PD on perceptual-motor calibration, and the perception of one's action capabilities, currently remains unknown. Considering the unstable nature of motor fluctuations, unilateral motor symptoms and alterations in basal ganglia functioning that occur in PD, we may anticipate that PD will influence individuals' perceptions of their action capabilities. In contrast, given the potential role of motor imagery in the perception of one's action capabilities, and the fact that motor imagery appears to be persevered in PD. We may anticipate that the perception of ones action capabilities will be preserved in PD.

Individuals' perceptions of the relative proportions of their body are far from accurate. Rather, large systematic distortions in the perceived proportions of body parts are observed in healthy individuals (Longo 2017; Linkenauger et al 2015). Characteristically, individuals perceive less sensitive body parts to be disproportionately larger than highly sensitive body parts (Linkenauger et al. 2015;

Sadibolova et al., 2019; Linkenauger et al., 2017). Importantly, the neural information underlying the perception of ones body proportions appears to relate the length of body parts to the combination of visual and tactile information (Linkenauger et al., 2015; Longo 2017). The influence of several clinical conditions, including amputation, anorexia and body dysmorphia, on the perception of the relative proportions of one's body has been a focus of research interest. However, the specific influence of PD on ones perceptions of their body proportions remains unanalysed. Given that the tactile sensitivity is altered in PD, we may anticipate that individuals with PD's perceptions of their body proportions may be altered.

The studies presented in the subsequent chapters sought to address these fundamental gaps in the literature by analysing the influence of PD on ones perceptions of their action capabilities, motor imagery, and the perception of the relative proportions of their body.

In the first study, Chapter 3, I found that when healthy individuals' action capabilities for grasping are subjected to artificial variability the perceptual system calibrates to the average action boundary experienced (regardless of the frequency of experience with each action boundary).

In the second study, Chapter 4, I found that individuals with PD's perceptions of their action capabilities were not significantly less accurate than healthy older controls. However, overall individuals with PD and healthy older adults were more conservative in their estimations of their ability to perform actions than healthy younger controls. In the third study, Chapter 5, I found that greater severity of the slowness of movement (bradykinesia) in the left-side of the body was associated with more vivid overall and left-side specific kinesthetic motor imagery.

In the final study, Chapter 6, I found that individuals with PD experience

distortions in body size comparable to the patterns observed in healthy older and younger adults. Taken as a whole, these findings suggest that the perception of one's action capabilities, motor imagery and overall body perception are preserved in PD. Therefore, indicating that PD is not associated with a deficit in the calibration between perceptual and motor systems.

Chapter 3

Paper One; It's in Your

Hands: How variable perception affects grasping estimates in virtual reality.

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BRIEF REPORT

It's in your hands: How variable perception affects grasping estimates in virtual reality

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Abstract

Successful interaction within one's environment is contingent upon one's ability to accurately perceive the extent over which actions can be performed, referred to as action boundaries. As our possibilities for action are subject to variability, it is necessary for individuals to be able to update their perceived action boundaries to accommodate for variance. While research has shown that individuals can update their action boundaries to accommodate for variability, it is unclear how the perceptual system calibrates to this variance to inform our action boundaries. This study investigated the influence of perceptual motor variability by analysing the effect of random and systematic variability on perceived grasp ability in virtual reality. Participants estimated grasp ability following perceptual-motor experience with a constricted, normal, extended, or variable grasp. In Experiment 1, participants experienced all three grasping abilities (constricted, normal, extended) 33% of the time. In Experiment 2 participants experienced the constricted and normal grasps 25% of the time, and the extended grasp 50% of the time. The results indicated that when perceptual-motor feedback is inconsistent, the perceptual system disregards the frequency of perceptual-motor experience with the different action capabilities and considers each action capability experienced as a type, and subsequently calibrates to the average action boundary experienced by type.

Keywords Embodied perception · Grasp ability · Affordance perception · Virtual reality

Introduction

In ecological terms, successful interaction within the environment is contingent upon one's ability to accurately perceive the affordances such an environment provides (Gibson, 1979). Affordances are the opportunities for action for a given organism within a particular environmental context (Gibson, 1979; Heras-Escribano & Pinedo-García, 2018). The extent to which an object affords behaviour is determined by the relationship between the specifications of the object and limitations of our bodies (Proffitt & Linkenauger, 2013). For example, the human hand morphology enables grasping, yet constrains the sizes of objects over which grasping can be performed. This maximum extent of one's action capability is known as an *action boundary* (Fajen, 2005).

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Presumably, the development of knowledge concerning ones action boundaries occurs during infancy (Proffitt & Linkenauger, 2013). For example, 5-month-olds perform 100–250 exploratory hand movements every 10 min (Wallace & Whishaw, 2003). Presumably, this exploration allows infants to learn the visual specification of actions that are possible and impossible, enabling them to become finely attuned to their action boundary (Proffitt & Linkenauger, 2013). By adulthood, individuals are highly accurate at perceiving the largest block that affords grasping (Graydon et al., 2012; Linkenauger et al., 2012), the smallest aperture that is passable (Warren & Whang, 1987), and the furthest distance that is reachable (Carello et al., 1989; Linkenauger et al., 2009).

Additionally, individuals can flexibly adjust their affordance estimations to account for alterations in action capabilities (Taylor-Covill & Eves, 2016). For example, the minimum aperture participants attempt to pass their hands through increases accordingly when their hand sizes are enlarged by a prosthesis (Ishak et al., 2008) and the minimum doorways perceived to be passable alters in accordance with changes in girth that occur when participants don a pregnancy pack (Franchak & Adolph, 2014b). While our perceptual

system seemingly recalibrates following changes in constraints, previous research has focussed on stable changes that allow us to gain experience with the visual specification of the altered action boundary. However, there are circumstances in which continuous unstable variance in individuals' abilities occurs. In these cases, an individual's experience provides them with inconsistent information as to the actions they can and cannot perform. Consider recovery from a broken thumb. While ability to grasp is initially compromised, one's ability to perform grasping actions will recover in accordance with the rate of healing. Unfortunately, how our perceptual system determines the action boundary following this inconsistency remains unclear.

Successful action can be conceptualised as a binary function, categorised by the ability to succeed or fail in action performance. Accordingly, one might assume that the perception of action capability is also a binary function; whether we perceive an affordance for the action (success) or not (failure) – often measured through terms of an affordance threshold (Franchak et al., 2012). However, as one's action capabilities across the same task can vary (Fetters, 2010), affordances should not be presumed as categorical. Rather we should measure affordances in terms of a probabilistic function, whereby the likelihood of success is compared to the cost of failure (Franchak & Adolph, 2014a). Although evidence points towards a system of affordances designed to address this variability, how individuals determine their action boundaries after experiencing this variability remains unclear.

It may be that our perceptual system applies a weighted average approach (Loeb & Fishel, 2014) in which the average of all action boundaries experienced weighted by the degree of their occurrence is considered (Körding & Wolpert, 2006). Consider a perceiver who can perform grasps that are 100% of their ability half of the time, and 50% of their ability the remaining time. In assessing the grasp-ability of an object, the perceptual system will calibrate to the average of the perceptual motor feedback, 75% of their maximum ability (see Fig. 1A). While this postulation is in line with the growing application of Bayesian theorem to visual perception (Fiser et al., 2010), the data processing necessary is computationally costly. Therefore, rather than expending vast amounts of resources in calculating the weighted average, the perceptual system may rely on heuristics in this decision-making process (Tversky & Kahneman, 1974).

Two potential heuristic mechanisms are conservative or liberal action boundary placement. When applying a conservative heuristic, individuals may calibrate to the most conservative grasp experienced (see Fig. 1B; Merikle et al., 2001). Because this heuristic would lead to the minimization of failed attempts it would be useful when harmful consequences are associated with failure. Alternatively, individuals may calibrate the most liberal grasp experienced (see Fig. 1C; Buzsaki et al., 2014). Employment of the liberal action boundary would result in most successfully performed actions, but also most failed attempts. Hence, this heuristic would be most useful if a failed attempt had no negative consequence.

Lin et al. (2020) recently analysed the influence of variable perceptual motor experience on action boundary determination for reaching in virtual reality (VR). The authors demonstrated that when perceptual-motor experience for reaching was randomly varied (participants experienced a constricted reach (50% of their maximal ability) 50% of the time and an extended reach (150% of their maximal ability) 50% of the time), perceptions of their action boundary for reaching were biased towards liberal estimations. Notably, this bias also occurred when variability systematically favoured both the constricted reach (participants experienced a constricted reach 50%, normal reach 25%, and extended reach 25% of the time), and the extended reach (participants experienced an extended reach 50%, normal reach 25%, and extended reach 25% of the time).

Whilst Lin et al. (2020) provide insight into the mechanism employed in the face of variability in reaching, reaching is a unsophisticated behaviour that acts to support more intricate actions. Due to this, if failure occurs, an individual can simply re-attempt a reach before completing the more intricate action. Thereby causing reaching to be a low cost-benefit action. Comparatively, grasping is a specialized, complex behaviour (Jeannerod, 1996). In this sense, grasping is a high cost-benefit action as failure may result in breakage or the requirement of the re-performance of several actions. Accounting Franchak and Adolph's (2014a) view of affordances as probabilistic functions, people will be more likely to have an incautious estimate of their action capabilities for reaching compared to grasping. Therefore, one can question whether the same mechanism would be employed in the face of variability in both reaching and grasping behaviours.

In a series of studies we analysed the influence of both random and systematic variability, favouring a liberal action capability, on individuals' perceptions of their action boundary for grasping. As it is near impossible to create controlled changes in grasping ability in the real world, perceptual-motor feedback was manipulated in VR. Previous research has shown that participants interact with self-representing, self-animated avatars in virtual environments in a manner comparable to their bodies in the real world (Kilteni et al., 2012; Normand et al., 2011). For example, Funkhouser (2020) observed that individuals overestimate their reaching ability by approximately 15% in VR, which closely corresponds to the 10–20% degree of overestimation observed out of VR (Linkenauger et al., 2009). On these grounds, we expected that participants would interact with the virtual hand in a way comparable to how they would behave in the natural world.

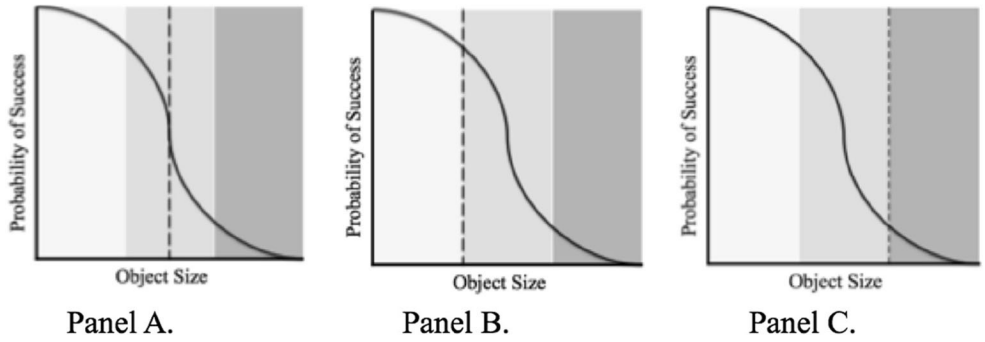

Fig. 1 Possible action boundaries that the perceptual system could calibrate to in the face of variability in one's grasping ability. The dotted perpendicular line in **panel A** represents the action boundary an individual would calibrate to if they were to employ a weighted average approach in which the average of all experience weighted by the degree of occurrence is considered. The dotted perpendicular line in **panel B** represents the action boundary an individual would calibrate to if they were to employ a conservative heuristic in which an individual would calibrate to the most conservative action capability regardless of experience. The dotted perpendicular line in **panel C** represents the action boundary an individual would calibrate to if they were to employ a liberal heuristic in which an individual would calibrate to the most liberal action boundary experienced

Experiment 1

In this experiment, we investigated the influence of random variability on the perception of action boundaries for grasping. Participants calibrated to a constricted grasp, a normal grasp, or an extended grasp, or a variable grasp – in which participants experienced all three grasping capabilities 33% of the time, and then provided estimates of their grasp ability for each condition.

Method

Participants

G*Power software (Faul et al., 2007) was used to perform an a priori power analysis to ascertain the required sample size to achieve adequate power. The required power (1- β) was set at .80 and the significance level (α) was set to .05. Based on Lin et al. (2020) Experiment 1, where a similar VR paradigm was used to analyse the influence of random variability in reaching ability, we anticipated a large effect size of 0.8. This was deduced as this study obtained a ηp^2 of .38 with a sample of N =21. For the frequentist parameters defined, a sample size of N = 3 is required to achieve a power of .80 at an alpha of .05.

Thirty Lancaster University students (eight males) aged between 18 and 30 years (M_{age} = 21.00, SD_{age} = 2.24), participated. All participants received course credit for their participation. All participants were right-handed, had normal or corrected-to-normal vision, and had no known medical history of motoric or rheumatic difficulties.

Stimuli and apparatus

Participants completed this study sittin at a chair positioned an arm's length away from the front of a standardised table. A virtual environment was developed in Unity 3D© Gaming Engine with the Leap Motion plugin. The 3D VR colour display comprised a model of a room in which a table was located in the middle (see Fig. 2), and the 3D avatar and camera were placed in front of this table. Upon this table were either two yellow dots (Calibration trials; see Fig. 2A) or a grey block (Test phase trials; see Fig. 2B). The participants viewed the virtual enviornment from a first-person perspective calibrated to their natural eye height. The environment was presented to participants through an Oculus Rift CV1 HMD, which displayed the stereoscopic reality at 2,160 × 1,200 at 90 Hz split over both displays (Binstock, 2015).

The movement of the head was tracked by the head mounted display (HMD) and the perspective of the participant was updated in real time as the participant looked around the environment. The location and position of the participant's hand was tracked in real time using the Leap Motion hand-tracking sensor mounted on to the Oculus Rift CV1 HMD, and was mapped onto the virtual hand thereby causing the virtual hand to move in correspondence with the natural hand. The avatar hands utilised were taken from the rigged human hand assets provided by Leap Motion for Unity.

Procedure

Participants were informed that, when estimating graspable objects over the duration of the study, they were to visualise employing a power grasp in which their thumb was placed on one edge of the block and their hand was extended over the surface of the block so that one of their fingers was placed on the parallel edge of the block. Thereafter participants donned the oculus rift HMD with attached Leap Motion Sensor and completed the four experimental conditions (constricted grasp, normal grasp, extended grasp, and variable grasp); the order of completion was counterbalanced across participants.

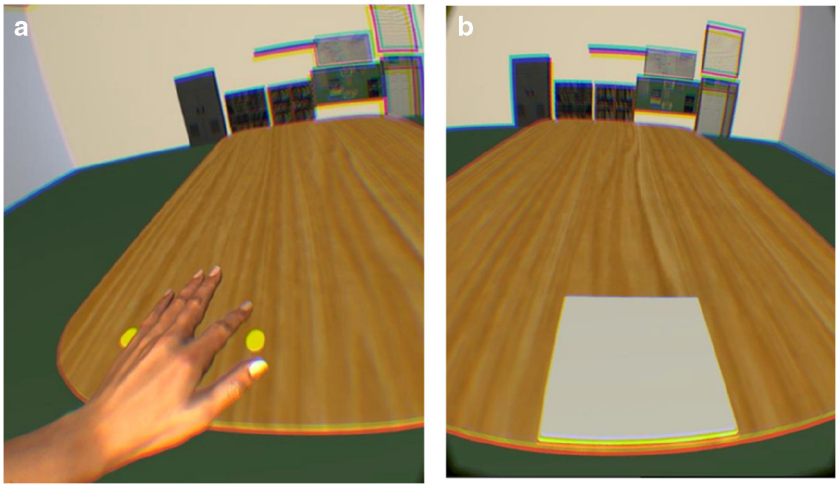

Fig. 2 Virtual reality (VR) display presented to participants. **Panel A** depicts the VR set up of the VR display within the calibration phase. **Panel B** depicts the VR set up during the test phase

In the constricted grasp condition, the virtual hand was 50% of the size of their actual hand, therefore constricting the grasp to 50% of the normal grasp ability. In the normal grasp condition, the virtual hand reflected the true size of their actual hand; therefore, grasp ability was 100% of their normal grasp ability. In the extended grasp condition, the virtual hand was 150% of the size of their actual hand thereby extending their grasp ability 50% beyond normal grasp ability. In the variable grasp condition the participants experienced the constricted hand size 33.3% of the time, the normal hand size 33.3% of the time and the extended hand size 33.3% of the time.

Each experiential condition consisted of two phases: the calibration phase and the test phase. The calibration phase consisted of 30 trials in which two parallel dots were presented in front of the participant (see Fig. 2A). Participants were instructed to touch, using their dominant hand, the rightmost dot with their rightmost digit and the leftmost dot with their leftmost digit. Participants were informed that if they could not reach the dot, to position the virtual hand as close to the dots as possible and perform the action as normal. After the participants had performed the action touching both dots, the two dots disappeared and reappeared in a different location on the table. This calibration phase served to provide the participants with the necessary synchronous visual motor information to embody the virtual hand (Kilteni et al., 2012), and provide participants with visual and motor experience regarding the action boundary associated with the virtual hand.

On completion of the calibration phase, participants were instructed to move their hands behind their back out of range of the Leap Motion sensor, which caused the virtual hands to not be visible in the VR. At this time the VR display was altered so that there was a white block on the table (see Fig. 2B). Participants were then instructed to imagine that they were going to grasp the block with one hand from above with a precision grasp. The experimenter then altered the size of the block using the right and left arrow keys of a keyboard until the participant stated the size of the block to reflect the maximum size they believe they would be able to grasp with their dominant hand. Each button press altered the size of the block by 1 cm. Once the participant was satisfied that the size of the block reflected the maximum size they could grasp with their dominant hand, the researcher saved the final size and presented another block. Eight trials were presented; in four of trials the block started at 3 cm and in the remaining four trials the block started at 20 cm. This occurred in order to control for the potential influence previous perception has on later judgements, a phenomenon commonly known as hysteresis (Poltoratski & Tong, 2014).

Results

One participant was excluded prior to analysis as the results obtained were ±2 SD away from the mean. To analyse the influence of random variability in perceptual motor experience on perceptions of grasping ability, a 4 × 2 repeated-measures ANOVA: 4 (Action capability: Constricted, Normal, Extended, Variable) × 2 (Block Size: Small, Large) was conducted.

A Greenhouse-Geisser correction was applied to correct for violations of sphericity. Analysis revealed a significant main effect of action capability on estimate of grasp ability, F (1.957, 54.807) = 27.24, $p < .001$, $\eta p^2 =$. 49. Grasping ability estimates were larger in the extended grasp condition (M = 16 cm, SE = .6 cm) than in the normal (M = 14 cm, SE = .5 cm, $p < .001$), and constricted grasp (M = 11 cm, SE = .7 cm, $p < .001$) conditions. Grasp-ability estimates in the variable grasp condition (M = 13 cm, SE = .6 cm) were larger than the

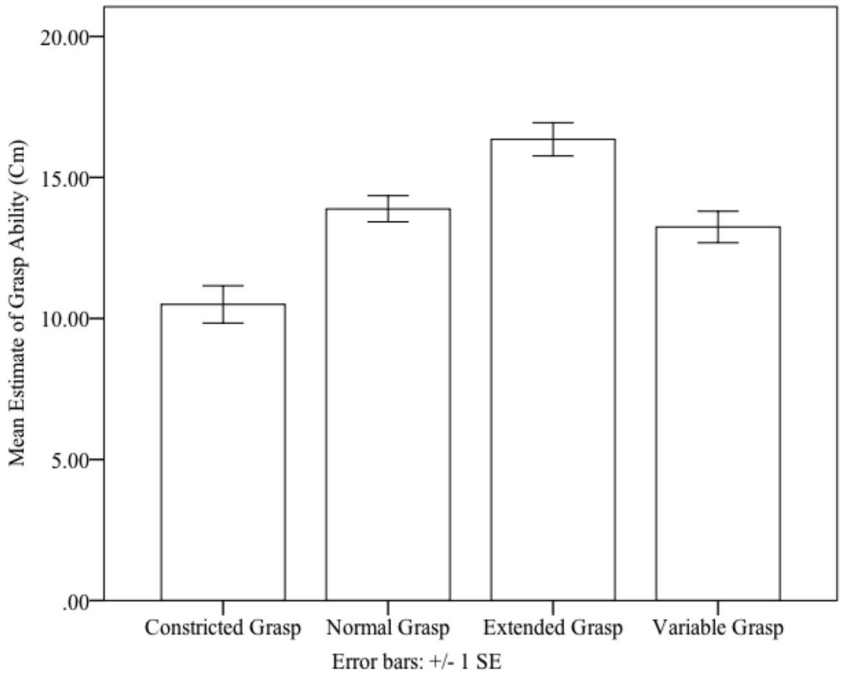

Fig. 3 Means (and standard errors) of grasp-ability estimates for Constricted, Normal, Extended, and Variable grasp conditions. Error bars represent 1 ± 1 SEM, calculated within subjects for each condition

constricted grasp condition (p = .006) and smaller than the extended grasp condition (p < .001). However, they were not significantly different from the normal grasp condition (p = .900; see Fig. 3).

A significant main effect of Hysteresis, $F(1, 28) = 28.07$, p < .001, ηp^2 = .50, was observed. Participants estimated grasping ability to be larger when the starting block began the large (M = 14 cm, SE =.4 cm), than when the starting block began small (M = 13 cm, SE = .4 cm). No significant interaction between hand size and hysteresis was found, F (3, 84) = 2.07, p = .110.

Experiment 2

The findings from Experiment 1 can be taken to indicate that when participants experience all action capabilities with equal probability, the perceptual system employs a mechanism based on weighted averages. If this is correct, then systematically varying experience to favour the extended grasp should shift participants perceptions to more closely reflect the extended grasp condition. Therefore, in Experiment 2 participants gained experience with the constricted and normal grasps 25% of the time and the extended grasp 50% of the

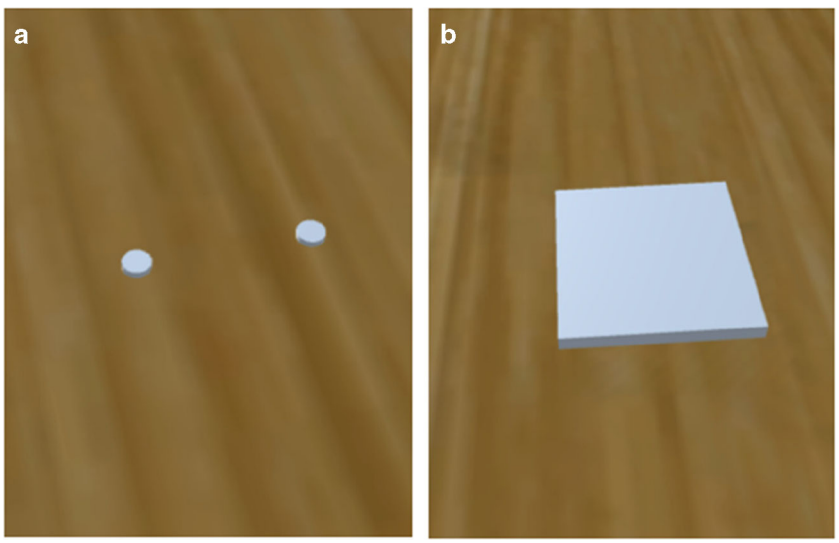

Fig. 4 An example of the environment presented to participants in the calibration trials (**A**) and the block size manipulation trials (**B**)

time in the variable grasp condition prior to estimating their grasping ability.

Method

Participants

G*Power software (Faul et al., 2007) was used to perform an a priori power analysis to ascertain the required sample size to achieve adequate power. The required power (1- β) was set at .80 and the significance level (α) was set to .05. Based on Lin et al. (2020) Experiment 2, where a similar VR paradigm was used to analyse the influence of systematic variability in reaching ability, we anticipated a large effect size of 0.7. This was deduced as this study obtained a ηp^2 of .34 with a sample of N =21. For the frequentist parameters defined, a sample size of N = 3 is required to achieve a power of .80 at an alpha of .05.

Thirty Lancaster University students (eight males) aged between 18 and 35 years (M_{age} = 19.72, SD_{age} = 3.16), participated. All participants received course credit for their participation. Twenty-six participants were right-handed, three participants were left-handed, and one participant was mixed-handed. The one mixed-handed participant elected to complete the study with their right hand. All participants had normal or corrected-to-normal vision and had no known medical history of motoric or rheumatic difficulties. All participants provided informed consent.

Stimuli and apparatus

The stimuli and apparatus used in Experiment 2 were consistent with those used in Experiment 1. Only minor aesthetic differences in the virtual environment (Fig. 4A) and colour of the dots in calibration trials (Fig. 4B) occurred.

Procedure

The procedure followed in Experiment 2 was consistent with the procedure followed in Experiment 1, with the only difference being the proportion of experience participants gained with each hand size in the variable grasp condition. In Experiment 2, the participants' experience with each of the three grasps was systematically weighted so that participants experienced the constricted hand size 25% of the time, the normal hand size 25% of the time, and the extended hand size 50% of the time.

As in Experiment 1, each condition required participants to complete the calibration and test phases, whereby the test phase in each condition included eight trials. Therefore, eight estimates of grasp ability for each experimental condition were obtained from each participant.

Results

One participant was excluded prior to analysis as the results obtained were ±2 SD away from the mean. To analyse the influence of random variability in perceptual motor experience on perceptions of grasping ability, a 4 × 2 repeated-measures ANOVA: 4 (Grasp ability: Constricted, Normal, Extended, Variable) × 2 (Block Size: Small, Large) was conducted.

A Greenhouse-Geisser correction was applied to correct for violations of sphericity. Analysis revealed a significant main effect of hand size on estimate of grasp ability, F (2.155, 60.33) = 34.317, p < .001, ηp^2=. 551. Grasp ability estimates were larger in the extended grasp condition (M = 18 cm, SE = 1 cm) than in the normal (M = 14 cm, SE = .5 cm, p = .002) and constricted grasp (M = 9 cm, SE = .6 cm, p < .001) conditions. Grasp-ability estimates in the variable grasp condiiton (M = 13 cm, SE = .7 cm) were larger than the constricted grasp condition (p = .001), and smaller than the extended grasp condition (p = .001). However, estimates of grasp ability were not significantly different from the normal grasp condition (p = .346; see Fig. 5).

A significant main effect of hysteresis was observed, F (1, 28) = 34.853, p <.001, ηp^2 = .555. Estimates of grasp ability were larger when the block initially started large (M = 14 cm, SE = .4 cm) than when the block initially started small (M = 13 cm, SE = .4 cm). No significant interactions were found, F (3, 84) = 3.682, p = 0.15.

Discussion

The effect of random and systematic variability in perceptual-motor experience for grasping ability on individuals' perceptions of their action boundaries was examined in two experiments. Consistent with existing literature, the results showed that when perceptual motor experience was altered consistently (e.g. the constricted, normal, and extended grasp conditions), participants' perceptions of their action boundaries altered to reflect the motor experience gained.

Regarding variable perceptual motor experience for grasping, the results obtained here indicate that when variability is random, participants appear to consider all experience and calibrate to the weighted average, resulting in similar estimates to normal experience. Conversely, when variability is systematic, favoring an extended grasp, participants' perceptions of grasp ability appeared to disregard the amount of perceptual-motor experience gained with each action boundary and calibrate to the middle action boundary. Although participants had more perceptual-motor experience with the extended-grasp, participants' subsequent perceptions of their action boundary for grasping did not significantly differ from normal grasp condition and were significantly smaller than the

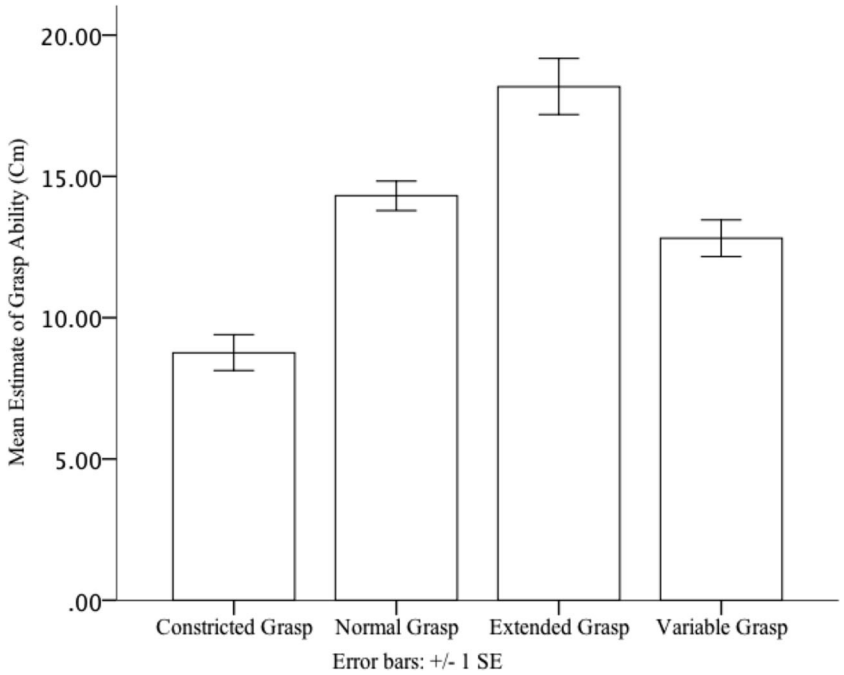

Fig. 5 Means (and standard error) of grasp-ability estimates for Constricted, Normal, Extended, and Variable Grasp Conditions. Error bars represent 1 ± 1 SEM, calculated within subjects for each condition

extended grasp condition. Therefore, in circumstances in which one's action capability is systematically varied to favour extended grasping capabilities, the perceptual system appears to calibrate to the average action boundary by type.

These findings may indicate that participants were unable to effectively calibrate to the variable hand condition and estimated their capability for future action inconsistently. Through this, the average of randomly selected estimates would align with the middle hand size condition. In this case, we would expect more variance in the variable condition than in the other conditions. However, the variances obtained across all conditions ($SE_{\text{VariableCondition}}$ = .007 m; $SE_{\text{ExtendedCondition}}$ = 1 cm; $SE_{\text{NormalCondition}}$ = .5 cm; $SE_{\text{Constricted}}$ = .6 cm) are largely similar. Thus, we find it unlikely that our results are due to individual differences in uncertainty.

Instead, it seems that when perceptual-motor experience is systematically varied, favouring an extended grasping capability, perceptual-motor experience is considered by type, rather than by frequency. Participants may disregard the amount of perceptual-motor experience with each action boundary and focus on variance by type, and subsequently calibrate to the average action boundary experienced by type. Here participants may disregard that they gained more experience with the extended grasp, and calibrate to the action boundary that is the average of the three types of grasp experienced, the normal grasp. This approach falls in line with a Bayesian stance, whereby information is prioritised in relation to intended actions as well as the frequency of experience (Weiss et al., 2002). Specifically, the type of perceptual-motor experience is of higher priority than the frequency of each type of perceptual-motor experience.

Alternatively, the perceptual system may employ a heuristic that allows for the selection of the middle action capability in terms of type. As in both experiments participants experienced three sets of action capabilities, 50%, 100% or 150%, a "take the middle" approach would lead participants to estimate future actions in accordance with the normal hand size. This heuristic would enable individuals to achieve some of the error minimization of applying a Bayesian inferencing approach while sacrificing accuracy for a reduction in computational cost.

Notably, the sample recruited here was restricted to young adults ($\text{Range}_{\text{age}}$ = 18–35 years). As action capabilities develop from infancy into early adulthood and then relapse into late adulthood (Leversen et al., 2012), presumably the participants sampled here are in the most stable developmental phase of their action capabilities. Previous research has shown that adults are more accurate than children at perceiving their maximal vertical and horizontal reaching ability (Plumert, 1995) and aperture passing abilities (Franchak, 2019). Additionally, the ability to effectively use experience to recalibrate one's perceptions of one's action capabilities has been observed to increase as a function of age (Franchak, 2019). Furthermore, of particular relevance to the methodologies employed here, Creem-Regehr et al. (2019) observed that when placed in a virtual environment, children underestimated the width of their maximum crossable gap compared to adults. Interestingly, when participants completed the same task in the real world there was no difference between adults and

children's perceptions, thereby indicating that virtual environments may have a unique influence on individual's perceptions. These trends support an age-modulated mechanism for determining the probability of future action. Therefore, future research utilising a wider age range to investigate any potential age-modulated effects on individuals' perceptions of their action capabilities following variability in perceptual-motor ability is necessary.

As this series of studies considers only the effect of random and systematic variance favouring an extended grasp, it would be unreasonable to assume that the results obtained here can be generalized to the selection of one's action boundary following all types of variability, for example, systematic variability favouring constricted grasping capabilities. Corroborating this, Lin et al. (2020) observed that individuals' general bias towards liberal estimations of one's action boundary following variability in reaching ability can be somewhat reduced by systematically biasing variability to favour a constricted action capability. Therefore, analyses of the influence of systematic variability, favouring a constricted grasping capability, are required.

As the results obtained here regarding grasping ability are incongruent with the results obtained regarding reaching ability (Lin et al., 2020), one may assume that the mechanism employed by the perceptual system in the face of variable perceptual motor experience may be contingent on the action in question. Specifically, we observed that when perceptual motor experience for grasping is randomly or systematically varied to favour an extended grasp, participants appear to disregard the frequency of experience and calibrate to the middle action boundary by type. Conversely, Lin et al. (2020) observed that regardless of the nature of variance, be it completely random or systematically varied to favour either a constricted or an extended grasp, individuals have a bias towards liberal estimations. As different actions have differential demands upon the body (Jeannerod, 1996) and carry with them differential cost-benefit ratios (Franchak & Adolph, 2014a), employing one blanket mechanism would not be flexible enough to accommodate a range of actions in various contexts. Rather, selection of the most appropriate action-specific mechanism to employ, considering associated risks of actions, appears more intuitive.

In summary, these studies demonstrate that manipulation of perceptual-motor feedback from virtual bodies influence one's subsequent perceptions of one's action boundaries. When perceptual-motor feedback is inconsistent, favoring greater experience with an extended grasping capability, the perceptual system appears to disregard the frequency of perceptual-motor experience and rather focuses on variance by type, and subsequently calibrates to the average action boundary experienced by type. Regardless of the amount of experience with different action capabilities, the perceptual system considers all possible action boundaries with equal weight when specifying the capacity for future action. However, it may be that additional factors such as age may be influencing the mechanism employed in the face of variability. Finally, differences between these results in the findings concerning reaching ability suggest that the perceptual system employs an action-specific mechanism to deal with variability in action capabilities.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.3758/s13423-021-01916-x.

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Data Availability The data and materials for all experiments are available as Online Supplementary Material. Neither Experiment 1 nor Experiment 2 was preregistered.

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3.1. Statement of thesis continuous commentary

In this series of experiments, I investigated the influence of random and systematic variability (favouring a liberal action capability) in grasping experience on healthy younger individuals' perceptions of their action boundaries for grasping. Experiment 1 showed that when individuals' action capabilities for grasping were subject to random variability, that is participants experienced a constricted, normal and extended grasping capability with equal probability, the perceptual system calibrates to the average of all experience (the normal action capability). Experiment 2 showed that when individuals' action capabilities for grasping were subject to systematic variability, favouring a liberal action capability, the perceptual system calibrates to the average action capability experienced by type. Specifically, the perceptual system disregards the frequency of perceptual-motor experience gained with each action capability and considers each action capability as a type.

The present paper induced variability in healthy younger individuals perceptual-motor experience artificially. However, the nature of this variability (in particular the random variability induced in experiment 1) may be somewhat comparable to the natural variability in perceptual-motor experience individuals with PD may experience. Subsequently, we can draw insights from the results of this paper to inform (a) whether we would anticipate individuals with PD's perceptions of their action capabilities to be altered, and (b) if so how they may be altered.

Based upon these findings, we may anticipate that individuals with PD will calibrate to the average of all perceptual-motor experience they have gained by type. Specifically, individuals with PD's perceptual systems will consider one's action capabilities, both during 'On' and 'Off' times, and calibrate to the average of this experience. Antiparkinsonian medication reduces swings in motor performance

(MacMahon et al., 1990), ensuring that individuals with PD experience 'On' times more frequently than 'Off' times. As a result, the average of all perceptual-motor experience gained by type will presumably be one's action capability in the 'On' time. Individuals are able to move and function well, and so perform actions normally, when in an 'On' phase. Therefore, we may anticipate that individuals with PD will calibrate to their true morphologically-derived action boundary. Subsequently, individuals with PD's perceptions of their action boundaries may not differ from healthy age matched controls that do not experience such variability.

It is, however, important to reflect on the incongruence of the results obtained in Chapter 3 compared to previous literature. For example, Lin et al (2020) found that when individuals reaching experience was artificially varied, their subsequent perceptions of reachability tended towards more liberal estimates. Due to the inconsistency in the results obtained between these two studies, we may anticipate that the influence of perceptual-motor variability as a result of PD will depend upon the action one is judging their action boundary for.

Therefore, to investigate the influence of PD on one's perception of their action boundaries, in the following paper (Chapter 4; Paper Two; How far can I reach? The perception of upper body action capabilities in Parkinson's Disease. Readman, M. R., McLatchie, N. M., Poliakoff, E., Crawford, T. J., & Linkenauger, S. A.) individuals with mild-moderate idiopathic PD estimated their maximal abilities for reaching, grasping and aperture passing behaviours. Individual's perceived action boundaries were then compared to their physical action boundaries to decipher the accuracy of their perceptions. This accuracy value was then compared to healthy older adult controls to investigate the influence of PD on the perception of ones action capabilities.

Chapter 4

Paper Two; How far can I reach? The perception of upper body action capabilities in Parkinson's Disease. Readman, M. R., McLatchie, N. M., Poliakoff, E., Crawford, T. J., & Linkenauger, S. A.

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How far can I reach? The perception of upper body action capabilities in Parkinson's disease

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Abstract

Successful interaction within the environment is contingent upon one's ability to accurately perceive the extent over which they can successfully perform actions, known as action boundaries. Healthy young adults are accurate in estimating their action boundaries and can flexibly update them to accommodate stable changes in their action capabilities. However, there are conditions in which motor abilities are subject to variability over time such as in Parkinson's disease (PD). PD impairs the ability to perform actions and can lead to variability in perceptual-motor experience, but the effect on the perceptions of their action boundaries remains unknown. This study investigated the influence of altered perceptual-motor experience during PD, on the perceptions of action boundaries for reaching, grasping, and aperture passing. Thirty participants with mild-to-moderate idiopathic PD and 26 healthy older adults provided estimates of their reaching, grasping, and aperture-passing ability. Participants' estimates were compared with their actual capabilities. There was no evidence that individuals with PD's perceptions were less accurate than those of healthy controls. Furthermore, there was some evidence for more conservative estimates than seen in young healthy adults in reaching (both groups) and aperture passing (PD group). This suggests that the ability to judge action capabilities is preserved in mild to moderate PD.

Keywords Parkinson's disease · Movement disorder · Affordance perception · Perceptual-motor integration

According to the ecological approach to visual perception (Gibson, 1979), successful interaction within the environment is contingent upon one's ability to detect and select the affordances available within such an environment (Gibson, 1979). Affordances signify the reciprocal relationship between a given organism and its environment. That is, affordances are the opportunities for action for a given organism within a particular environment (Gibson, 1979; Heras-Escribano & Pinedo-García, 2018). Whilst an infinite number of affordances are present for any organism within an environment at any one time, the extent to which an object affords a specific behaviour is determined by the relationship between the specifications of the object and the morphological limitation of the perceiver's body (Proffitt & Linkenauger, 2013). For example, the morphology of the human hand enables the performance of a grasping motion, yet constrains the range of object sizes over which this action can be performed. Therefore, as a consequence of morphology, one environmental feature can afford two entirely different behaviours to two different individuals.

The limits at which the successful performance of an action can no longer occur are known as action boundaries (Fajen, 2005). Successful interaction within the environment relies upon an individual's ability to perceive such action boundaries accurately. Intuitively, this knowledge is acquired throughout childhood (Proffitt & Linkenauger, 2013). Specifically, 5-month-old infants perform hundreds of exploratory hand movements every 10 minutes (Wallace & Whishaw, 2003), transverse vast distances, and fall approximately 15 times per hour (Adolph et al., 2012). These exploratory movements provide infants with extensive visual feedback regarding what actions are possible and impossible. Which, in turn, facilitates the development of precise, fine-tuned knowledge regarding ones' action boundaries (Proffitt & Linkenauger, 2013). Following development, adults are reliably in tune with their action boundaries, such that individuals are highly accurate at estimating the maximum step

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height that affords stepping (Warren, 1984), the farthest distance they can reach (Carello et al., 1989), the largest object they can grasp (Linkenauger et al., 2009), the smallest door opening they can pass through (Warren & Whang, 1987), and the smallest size opening they can fit their hand through (Ishak et al., 2014).

Whilst this research points towards individuals being reliably in tune with their maximal action boundaries present in stable environments, our bodies and the world in which we inhabit are continually changing, resulting in variations in one's action boundaries (Franchak & Adolph, 2014a). Consider the rehabilitation period following an injury to the elbow that precludes arm extension. Immediately following the injury, the individuals' ability to perform a reaching action will be severely compromised. However, during rehabilitation, the individuals' ability to perform a reaching action will slowly recover in accordance with the healing of the injury. Therefore, in order for successful interaction within the environment to occur, it is imperative for individuals to detect varying constraints and update their action boundaries to account for such constraints.

Indeed, research has shown that healthy individuals can flexibly update their action boundaries to account for varying constraints (Proffitt & Linkenauger, 2013). For example, when hand size is enlarged by a prosthesis, the minimum size aperture participants attempt to fit their hand through increases in accordance with the increase in hand size (Ishak et al., 2008). Similarly, when the size of the hand is increased by magnification, participants subsequently perceived graspable objects to be smaller in size than when the hand was not magnified (Linkenauger et al., 2011). Additionally, the minimum doorway aperture perceived as passable increases in accordance with the increase in girth that occurs when individuals don a pregnancy pack (Franchak & Adolph, 2014b).

This evidence corroborates the notion that the perceptual system is in tune with one's action boundaries and can flexibly update to accommodate for variance. But, this literature focuses on stable changes that allow individuals to gain relevant information regarding the visual specification of the altered action boundary. There are circumstances in which individuals action boundaries are not only permanently altered, but are also subject to fluctuations that are rapid and unpredictable in nature, thereby preventing learning of the visual specification of one's altered action from occurring. A clear example of this occurs in people with Parkinson's disease.

Parkinson's disease (PD) is characterized by motoric atypicalities including tremor, rigidity (Berardelli et al., 1983; Politis et al., 2010), bradykinesia, hypokinesia, akinesia, and postural instability (Guttman et al., 2003). These motoric atypicalities characteristically impair the performance of many actions. For example, tremor of the hand is likely to constrict the individuals' ability to grasp objects. Similarly, rigidity, both in the form of "lead pipe" rigidity, where a continuous resistance to movement throughout the range of motion is present (Guttman et al., 2003), and "cogwheel" rigidity, where patients' ability to perform an action fluidly is replaced by small jerky movements (Ghiglione et al., 2005; Guttman et al., 2003), will restrict the individuals' ability to perform various actions and reduce the range over which these actions can be performed. Importantly, when hypokinesia, the dismissed magnitude of the performance of movements (Berardelli et al., 2001; Simões & Litvan, 2010), occurs the patient's muscular strength is preserved, and although access to motor programs can be delayed, access is still possible (Simões & Litvan, 2010). Therefore, whilst it is physiologically possible for the individual to perform an action over a certain range, in practice, execution of the action over this range cannot occur. These physiological reductions in the ability to perform actions and the range over which such actions can be performed will be accompanied by a reduction in the action boundary associated with the affected actions.

In addition to the reduction in the ability to perform actions, individuals with PD may receive inconsistent perceptual motor experience regarding what actions are possible and impossible. Characteristically, prior to diagnosis and during the earliest stages of PD, patients may experience unilateral symptom presentation; for example, whilst the left side of the body may be affected, the right side of the body may remain unaffected (Sveinbjornsdottir, 2016). When this arises, the individual will receive inconsistent perceptual-motor experience regarding the extent to which and the range over which they can perform actions based on which the side of the body they are using. Consider, for example, a patient with left-side lateralized rigidity performing a reaching action. The patient's ability to perform a reach with the left arm will be severely compromised, whilst they will be able to perform a reaching action with the right arm to the maximum extent their morphology permits.

Dopaminergic medications, particularly Levodopa, are currently the "gold standard" treatment for PD (Dorszewska et al., 2014; Fahn, 2006). Levodopa treats the symptoms of PD by effectively replacing the loss of dopamine (Gandhi & Saadabadi, 2019) that occurs due to the degeneration of dopaminergic nigrostriatal neurons originating in the substantia nigra pas compacta of the basal ganglia and projecting to the striatum of the basal ganglia (Agid et al., 1987). Initially, dopaminergic medications offer substantial reductions in symptom intensity with very few adverse effects (Marsden & Parkes, 1977). However, following several years of levodopa therapy (Marsden & Parkes, 1977), according to Dupont et al. (1996), at least 50% of patients experience fluctuations in response to their dopaminergic medication throughout the course of a day. These fluctuations, in turn, may also produce fluctuations in the intensity of the motor symptoms displayed at different times even within a single day; this phenomenon is known as the on–off phenomenon (Bhidayasiri & Tarsy, 2012).

Notably, patients report that when they are in an "on" phase they can perform actions as normal; however, during "off" phase, their ability to perform motor actions is severely compromised (Lees, 1989). Some "off" periods may be predictable and related to the time of medication administration. For example, a patient may always have an "off" time at 3 p.m. (Stacy et al., 2005). Alternatively, some "off" periods may be highly unpredictable in both onset and duration (Lang et al., 1982). This means that individuals with PD will gain inconsistent perceptual-motor experience relating to their ability to perform an array of actions. Taken together this unstable variance, resulting from on–off symptom fluctuation and unilateral symptom presentation may affect a person with PD's ability to accurately perceive their action boundaries for a range of actions.

Another reason that the perception of action capabilities may be affected in PD is due to changes in sensory and perceptual functions that occur as a consequence of changes in the basal ganglia in PD. Although the functional role of the basal ganglia has primarily been hypothesized to be motor (Schwarz et al., 1984), additional research highlights that the basal ganglia exert much wider functions in sensory and cognitive domains as well as motor (Haber & Gdowski, 2005; Marsden, 1982). For example, substantial deficits in basic visual processes such as light/dark adaptation, visual acuity, peripheral vision, and visual processing speed, have been observed in individuals with nontremor PD (Seichepine et al., 2011). Furthermore, deficits in visuospatial functions including distance perception (Davidsdottir et al., 2005), size perception (Lee et al., 2001), spatial navigation (Davidsdottir et al., 2008), spatial working memory (Kemps et al., 2005; Possin et al., 2008; Siegert et al., 2008), and spatial planning (Altgassen et al., 2007), have largely been observed in individuals with PD (Boller et al., 1984; Seichepine, 2012). Furthermore, Schneider, Diamond, and Markham (1986) showed that PD patients made significantly more errors in somatosensory tasks compared with age-matched healthy controls. As the perception of one's action boundaries relies primarily on the integration of these sources of information, deficits in these processes could also lead to deficits in the ability to anticipate the range over which one can perform an action in PD.

Additionally, recent research points towards the notion that individuals with PD are not reliably in tune with the severity of the symptoms they present. That is, when both PD patients and clinicians are asked to rate the severity of the symptoms an individual is presenting, 30%–50% of nondemented, nondepressed PD patients indicate their symptoms to be less severe than clinicians' ratings of them (Maier et al., 2012). Due to this partial lack of subjective awareness of motor deficits (Maier et al., 2012), it could be that some patients are not reliably in tune with their action capabilities as they fail to perceive the motor deficits they present.

The influence of natural variability on the subsequent perception of one's action boundaries has yet to be investigated. However, we can draw on insights obtained from analyses of the effect of artificial variability to inform how we may anticipate individuals' perceptions of their action capabilities to be influenced by natural variability that may occur in PD. For example, Lin et al. (2020) observed that when participants' reaching ability varied from 50% to 150%, from reach to reach, individuals displayed a bias towards liberal estimations of their action boundary. Notably, this effect was observed regardless of whether the variability was completely random or systematic. Furthermore, Readman et al. (2021) observed that when grasping ability varied from 50% to 100% to 150% from grasp to grasp, so that participants gained equal experience with all grasping capabilities, participants estimated their action boundary to be similar to the normal condition. Similarly, when variability was systematic, so that participants gained more perceptual-motor experience with the extended grasp (150%), participants also estimated their action boundary to be the normal grasp.

Based upon these findings we may anticipate that individuals with PD's perceptions of their action boundary for reaching would be more liberal, and thereby less accurate, than typically ageing individuals. However, regarding the perception of one's grasping ability, we may anticipate that PD patients will calibrate to the middle of all experience they have gained—that is, both during "on" and "off" times, which presumably would be their true morphologically derived action boundary. Consequently, PD patients' subsequent perceptions of their action boundary for grasping may not significantly differ from healthy age-matched controls who do not experience this variability.

The incongruence of the results obtained concerning the influence of artificial variability may be taken to indicate that the perceptual system does not inevitably employ the same mechanism in the face of variability irrespective of the action in question. Therefore, we may anticipate that natural variability in one's perceptual-motor experience as a consequence of PD, may differentially influence PD patients' perceptions of their action boundaries based on the action in question. Therefore, in addition to the primary research aim, this study will also address a further question: Is the effect of PD on the perception of one's action boundaries the same regardless of the action in question?

To address these questions individuals with mild-to-moderate idiopathic PD and healthy ageing controls estimated the maximum extent to which they can perform reaching, grasping, and aperture-passing actions. Participants' estimations of their action capabilities were then compared with their actual ability.

Method

Participants

G*Power software (Faul et al., 2007) was used to perform an a priori power analysis to ascertain the required sample size in

order to achieve adequate power. Three individual power analyses, for each of the three tasks employed, were performed. The required power ($1 - \beta$) was set at .80 and the significance level (α) was set to .05. The individual effect sizes for each task were based on Graydon et al. (2012), who employed the same methodology as employed here. For the reaching ability task, we anticipated a medium effect size of 0.37. Therefore, for the frequentist parameters defined, a sample size of $N = 8$ (four per condition) is required to achieve a power of .80 at an alpha of .05. For the grasping ability task, we anticipated a large effect size of 0.60. Therefore, for the frequentist parameters defined, a total sample size of $N = 70$, $N = 35$ per condition, is required to achieve a power of .80 at an alpha of .05. For the aperture passing task, we anticipated a small effect size of 0.18. Therefore, for the frequentist parameters defined, a total sample size of $N = 36$ (18 per condition) is required to achieve a power of .80 at an alpha of .05.

Unfortunately, due to the COVID-19 global pandemic, the sample size recruited, and subsequent data analyzed, was smaller than necessary in order to achieve adequate power for the grasping task ($N_{PD} = 19$, $N_{\text{Healthy older adult controls}} = 21$; *but* only the grasping task). However, the sample size recruited was greater than that of the previously validated Graydon et al. (2012) study.

Thirty patients with idiopathic PD (10 females), and 26 healthy older adult controls (15 females) participated. The mean age between the two groups did not significantly differ, $t(54) = -1.198$, $p = .236$. Fifty-one (27 PD patients) participants were right-handed, four (two PD patients) were left-handed, and one PD patient was mixed-handed (Oldfield, 1971). The one mixed-handed participant elected to complete the task with their left hand. All participants had normal or corrected-to-normal vision with a visual acuity between 20/20– 20/30 in both the left and the right eye, as classified by the Snellen chart.

Participants were screened for the presence of cognitive impairment using the Montreal Cognitive Assessment (MOCA; Nasreddine et al., 2005). The MOCA was used because previous research has shown that it is perhaps the most sensitive cognitive examination for screening for mild cognitive impairment in the presence of PD (Dalrymple-Alford et al., 2010; Hoops et al., 2009; Kandiah et al., 2014). Participants' data were included in analysis only if they scored within the normal range (≥26 out of 30). Following this exclusion criterion 13 (10 PD patients) participants' data were removed prior to analysis. Average MOCA scores did not significantly differ between patients and controls, $t(41) = -.836$, $p = .408$. One control participant indicated a history of a neurological illness; therefore, their data were removed prior to analysis. Subsequently following exclusion on these grounds, 42 (20 PD) participants' data were included in the following analyses.

Of the 42 participants whose data were included in analysis, 11 participants (five PD patients) indicated they had a current or history of a diagnosis of rheumatic illnesses, 10 participants (four PD patients) disclosed that they had a history of a diagnosis of a psychiatric illness, including depression (three PD patients, four controls), and anxiety (one PD patient, two controls). All participants were screened for the presence of depression and anxiety using the Hospital Anxiety and Depression Score (HADS; Zigmond & Snaith, 1983; see Table 1, for HADS data).

PD patients were selected who were at a Hoehn and Yahr Stage 3 or less. The Hoehn and Yahr stage provides an overall summary of the severity and laterality of symptoms presented by the individual with Parkinson's. Ten patients presented unilateral symptoms only (Stage 1), seven patients presented symptoms bilaterally but with no impairment of balance (Stage 2), and three patients displayed bilateral symptoms with some postural instability but were physically independent (Stage 3). Parkinsonian symptoms were assessed using the motor examination and the motor complication subscales of the Movement Disorder Society–Unified Parkinson's Disease Rating Scale (MDS-UPDRS; Goetz et al., 2008). All but one PD patients were receiving parkinsonian medication and were tested under their usual medication regime. Twelve patients indicated that they experienced motor fluctuations. All of these patients were in a typical functioning "ON" phase at the time of testing. Eighteen patients were

Table 1 The mean (*SD*) background characteristics for the Parkinson's disease (PD) and control groups

Group	PD	Control
Age	65.85 (7.21) Range: 54–76	67.86 (6.84) Range: 54–77
MOCA	27.60 (1.27) Range: 26–30	27.91 (1.51) Range: 26–30
HADS–Anxiety	6.50 (4.523) Range: 0 -15	6.27 (4.05) Range: 1–15
HADS–Depression	4.13 (2.50) Range: 1–9	1.77 (1.60) Range: 0–6
Years since diagnosis	4.26 (4.41) Range: 0.833–17	
MDS-UPDRS Motor examination	36.20 (7.81) Range: 24–50	
MDS-UPDRS Motor complications	3.20 (3.12) Range: 0–9	
Hoehn and Yahr stage	1.65 (.75) Range: 1–3	
Years on medication	4.09 (4.13) Range: 0.833–15	
Time since last dosage of medication (minutes)	146.94 (83.96) Range: 0–300	
L-Dopa dosage (mg)	477.88 (255.04) Range: 0–1290	

taking combination drugs (containing levodopa and a peripheral dopa-decarboxylase inhibitor; e.g., Madopar), five patients were taking a dopamine agonist (e.g., Ropinirole), five patients were taking a monoamine oxidase inhibitor (e.g., Rasagiline) and one patient was taking a Catechol-O-Methyl Transferase (e.g., Entacapone; see Table 1 for patient characteristics).

PD patients were recruited through the Royal Preston Hospital, and through advertisement with Parkinson's UK. The healthy controls were either the partners or relatives of the PD patients or were recruited through the ageing research database at Lancaster University. Testing occurred at either the clinical research facility at Royal Preston Hospital or in the adult testing facilities at Lancaster University. This study was approved by the local National Health Service (NHS) ethics committee.

Stimuli and apparatus

Participants completed all three tasks sat at a chair positioned an arm's length away from a standardized table (140 cm × 80 cm).

Task 1: Perception of reaching ability Five axis stickers placed at 30° and 15° to the left, at the centre, and 15° and 30° to the right, were placed on the far side of the table. A sixth origin sticker was located directly in front of the participants' torso (see Fig. 1). Reaching judgements were made using a green chip that was moved towards and away from the participant along a diagonal specified by an axis sticker and the origin sticker.

Task 2: Perception of grasping ability A set of 16 1cm thick foam board square blocks, were used as the graspable stimuli. The width of these square blocks ranged from 4- 25cm and increased in 1.4cm increments. Each block had two parallel black lines (3cm) long drawn in the centre of opposing sides, this occurred to indicate where the participant was to imagine placing their finger and thumb when grasping the object (See Figure 1).

Task 3: Perception of aperture passing A portable apparatus with an easily manipulated aperture was created. This apparatus was made up of 3D printed black triangles that open and close alike to a camera lenses aperture. All 3D printed components were attached to a grey wooden frame. The size of the aperture was manipulated by moving a handle towards the right to create a larger aperture and towards the left to create a smaller aperture (see Fig. 1).

Procedure

To commence the testing session participants were screened for mild cognitive impairment and depression and/or anxiety, and background cognitive and health measures were obtained.

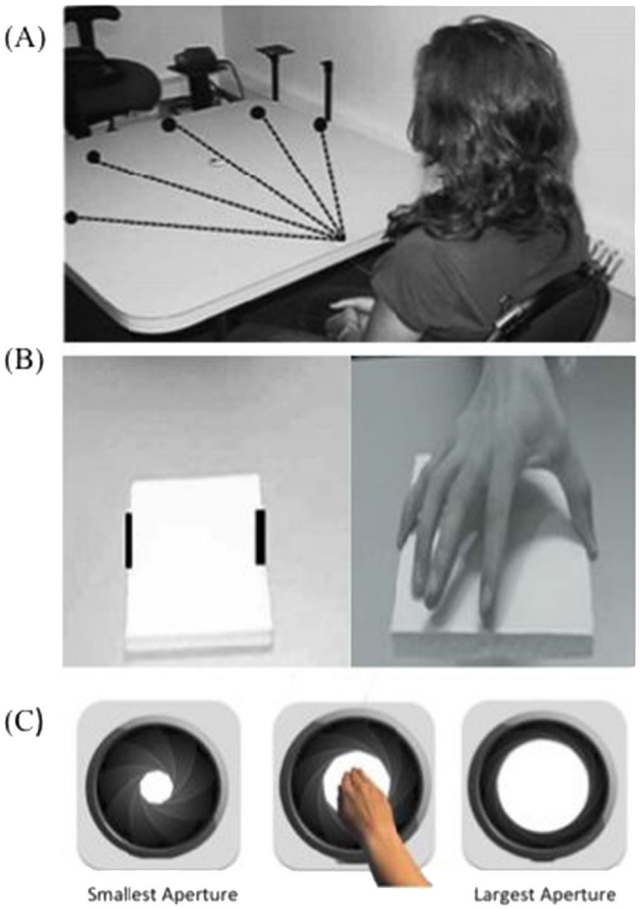

Fig. 1 Visual illustrations of the (**a**) reaching ability task, (**b**) grasping ability task, (**c**) aperture passing task. **a** The solid dots represent the 30°, 15° unilateral/ipsilateral and centre axis stickers. The dotted black line represents the axis along which the chip was moved either towards or away from the participant. **b** The black lines on the parallel edges of the block were where the participant was asked to imagine extending their hand from and to when estimating grasping ability and were where participants were told to place their fingers when deducing actual grasping ability

PD patients' Parkinsonian symptoms were assessed using the motor examination and motor complications subscales of the MDS-UPDRS. The order in which the participants completed the three tasks was counterbalanced.

Task 1: Perception of reaching ability Participants sat an arm's length away from the table, with the back of their clothing clipped to the chair so that their shoulders were held against the back of the chair, and their hands on their lap (see Fig. 1). This occurred to serve as a constant reminder of the range of motion that they were to use when making their estimates of anticipated reach and to ensure that all participants estimated reachability in the same way. Participants were informed that they would be required to estimate their maximum reaching ability for all diagonals. At no point before providing their estimations were participants allowed to overtly perform a reaching movement over the table. This precaution prevented

participants from receiving confirmatory information about their actual abilities prior to their estimates. The researcher then moved a 1-inch green chip either towards or away from the participant, along one of the diagonals specified by an axis sticker and the origin (see Fig. 1a). Participants were asked to indicate when the chip was just in reach of their dominant hand, whilst maintaining the specified posture. Participants were encouraged to ask the researcher to adjust to the chip's location to ensure the estimate of reaching ability was as accurate as possible.

To control for hysteresis, the starting position of the green chip was either directly in front of the participant, at the origin sticker, or at the end of the movement axes, and moved both towards and away from the participant for each of the five diagonals. Therefore, participants made 10 reachability estimations. The order of trials was counterbalanced across participants. When the chip was moved away from the participant, the chip started at the origin sticker and was moved towards one of the axis stickers. When the chip was moved towards the participant, the chip started at one of the axis stickers and was moved towards the origin sticker.

Once participants were satisfied that the chip was located in the correct position, participants were instructed to close their eyes, and the distance from the origin to the centre of the chip was measured and recorded. Participants were required to close their eyes in order to prevent feedback regarding the distance of reachability being obtained and used in later trials.

On completion of all perceived reachability trials, a measure of actual reachability for each diagonal was obtained. To do so, participants were instructed to move the chip as far away as they could along one diagonal whilst maintaining the specified posture.

Task 2: Perception of grasping ability Participants were seated at the standard table and instructed that they would be required to estimate whether they could grasp a series of blocks with their dominant hand. Grasping was defined as the ability to place their thumb on the black line on one edge of the block and extend their hand over the surface of the block so that one of their fingers was placed on the black line on the parallel edge of the block. Participants were asked to close their eyes whilst the researcher placed one of the 16 blocks on the table perpendicular to the participant. Participants were asked to close their eyes at this time in order to prevent them from gaining visual information regarding the researcher's ability to grasp the blocks and subsequently use this information to guide their grasping-ability estimations. Once the block had been placed, participants were instructed to open their eyes and use visual inspection only to indicate whether they would be able to grasp the block with their dominant hand. This procedure occurred for all 16 blocks, and the order of completion was counterbalanced across participants. On completion of all estimation trials, a measure of actual grasping ability was obtained. This was obtained by asking participants to overtly grasp the largest block they could with their dominant hand. Participants were encouraged to try the next size up to ensure that a true measure of maximal grasping ability was obtained.

Task 3: Perception of aperture passing Participants were seated at a standard table, upon which the aperture passing apparatus was located in the centre of the table (see Fig. 1c). Participants were instructed to estimate the point at which they could just fit their dominant hand through the aperture without coming into contact with the black inner triangles, whilst keeping their hands on their lap. Participants were asked to imagine performing the aperture-passing movement with their hand with their fingers closed. Participants completed four trials; in two trials, participants were presented with the largest size aperture, and the researcher gradually made the aperture smaller. In the remaining two trials, the participant was presented with the smallest aperture, and the researcher gradually increased the aperture size. At the point at which the participant indicated to the researcher they could just fit their hand through the hole, the participant was instructed to close their eyes and the researcher measured the aperture. Participants were instructed to close their eyes to prevent them from gaining visual feedback on the aperture size and using this information in later trials. Following the perceived aperture-passing trials, a measure of smallest aperture size that the participant could actually fit their hand through was obtained. To obtain this, participants were asked to place their hand in the hole, and the researcher gradually reduced the size of the aperture to the point at which the hand just fitted in the aperture without coming into contact with the black triangles.

Data analysis

For each of the three tasks, we report independent-samples *t*-test analyses of differences in the actual abilities of PD patients compared with healthy older adult controls. The accuracy of the perceived action boundary was measured by calculating the ratio of the estimated ability, to the actual ability. A value of more than 1 indicates that the participant overestimated their ability, whilst a value of less than 1 indicates the participant underestimated their ability. For reaching ability, this ratio was calculated for each of the five diagonals independently. The accuracy ratios were then compared between the PD and healthy controls (reaching: mixed ANOVA; grasping: independent-samples *t*-test; aperture passing: mixed ANOVA).

As a single nonsignificant *p*-value cannot be used to infer evidence for the null hypothesis (for a further discussion, see Lakens et al., 2020), we also report Bayes factors for all 1-*df* analyses. Bayes factors provide a continuous measure of evidence regarding how well the data were predicted by one

hypothesis (e.g., the null; H0), relative to another hypothesis (e.g., the alternative; H1). We calculate Bayes factors using the Dienes and McLatchie (2018) R script calculator and follow Jarosz and Wiley's (2014) thresholds, and interpret Bayes factors between 0.33 and 3 as weak and inconclusive, Bayes factors between 0.05 and 0.33 and 3 and 20 as moderate evidence for the null and experimental hypotheses, respectively, and Bayes factors <0.05 and >20 as strong evidence for the null and experimental hypotheses, respectively. Bayes factors require one to specify an approximate scale-of-effect predicted by one's theory, and we specify in the footnotes throughout each Results section the prior research we use to specify our scale-of-effect. Lastly, we report robustness regions to indicate the sensitivity of the categorical conclusions drawn from the Bayes factors to the approximate scale-of-effect used. Robustness regions are reported as $RR(S, L)$, where S corresponds to the smallest scale-of-effect and L to the largest scale-of-effect that would still yield the same conclusion.

Previous studies have shown that anxiety significantly influences participants' perceptions of their action boundaries for reaching behaviours (Graydon et al., 2012). Given that anxiety disturbances are recognized as one of the most common nonmotor comorbidities of PD (Chen & Marsh, 2014), a mixed analysis of covariance (ANCOVA) was completed in order to ascertain the potential influence of anxiety, as measured by the HADS, on participants perceptions of their action boundaries. Across all three tasks, anxiety did not significantly influence individuals' perceptions of their action capabilities (see Appendix 1 for the full statistical analysis).

Furthermore, arthritis can affect both overt movement and motor imagery (the ability to mentally rehearse actions; Gandola et al., 2017; Sacheli et al., 2018). Therefore, a mixed ANCOVA was completed to ascertain the potential influence of the presence of rheumatic illnesses on participants' perceptions of their action boundaries. Across all three tasks, the presence of arthritis did not significantly influence individuals' perceptions of their action capabilities (see Appendix 2 for full statistical analysis). Therefore, both anxiety and the presence of rheumatic illnesses should not be considered confounding factors in this analysis.

Results

Task 1: Perception of reaching ability Forty participants (18 PD patients) were included in this analysis. One PD patient's data were removed for providing estimations that were ±2 standard deviations away from the mean, and one PD patient failed to fully complete the reaching ability task

There was no significant difference between the average actual reaching ability (across the five diagonals) of PD patients (M = 46.16, SD = 5.49) compared with the reaching abilities of healthy older adult controls (M = 43.48, SD= 5.37), although the evidence for the null hypothesis was only weak, $t(38) = 1.55$, $p = .129$, $B_{N(0,8.35)}$[1] = 0.64, RR[0, 16.59].

The perception of the action boundary for reaching was analyzed by a mixed ANOVA [Diagonal direction (30° contralateral, 15° contralateral, directly in front, 15° ipsilateral, 30° ipsilateral) × Group (PD or typically ageing older adult)]. A Greenhouse—Geisser correction was applied to correct for violations of sphericity. A significant main effect of diagonal direction on perceived action boundary for reaching was observed, $F(2.039, 77.497) = 19.087$, $p < .001$, η_p^2=. 33). Participants overestimated contralateral estimates (M_{D1} = 1.16, SE_{D1} = .033; M_{D2} = 1.11, SE_{D2} = .023) more than ipsilateral estimates (M_{D4} = 1.02, SE_{D4} = .017; M_{D5} = 1.01, SE_{D5} = .019; see Fig. 2).

There was no significant difference in the accuracy of the perceived action boundaries for reaching between the PD (M_{acc}= 1.050, SE_{acc} = .028) and healthy older adult groups (M_{acc}= 1.093, SE_{acc} = .025), $F(1, 38) = 1.309$, $p = .260$ (see Fig. 3), although the Bayes factor indicated that the evidence only weakly favoured the null, $B_{H(0,0.09)} = 0.70$, RR[0, 0.21].[2]

Task 2: Perception of grasping ability Forty participants' (19 PD patients) data were included in the final analysis. Two (one PD patient) participants' data were removed prior to analysis because they provided estimations that were ±2 standard deviations away from the mean.

There was no significant difference and moderate evidence for the null when comparing the physical actual grasping ability of PD patients (M = 16.16, SD = 1.81) compared with the physical actual grasping ability of healthy older adult controls (M = 15.93, SD= 1.57), $t(38) = .42$, $p = .677$, $B_{N(0,4)}$[3] = 0.15, RR[1.69, ∞].

An independent-samples t test revealed no significant difference between the accuracy of the perceived action boundary for grasping between the PD (M_{acc} = 1.017, SD_{acc} = .114) and healthy older adult groups (M_{acc}= 1.011, SD_{acc} = .125), $t(38) = .76$, $p = .882$ (see Fig. 3). Bayes factor indicated that the evidence provided moderate support for the null, $B_{H(0,0.08)}$ = 0.13, RR[0.03, ∞].[4]

Task 3: Perception of aperture passing All 42 participants' (20 PD) data were included in the analysis. An independent-samples t test revealed that there was no significant difference

[1] The model of H1 was specified using differences in arm length between 10-year-olds and 18-year-olds reported by Živičnjak et al. (2003; M_{diff} = 16.70) as an upper limit of the extent arm reach may have differed between conditions.
[2] Model of H1 specified using the results of Graydon et al. (2012, Experiment 1) who interpreted a difference in reaching accuracy ratios of 0.09 as evidence for the alternative hypothesis.
[3] Model of H1 specified using the range of pinch grip aperture (13 cm to 21 cm, range: 8) reported by Holt et al. (2013) as a maximum upper limit of differences expected in reach aperture across conditions.
[4] Model of H1 specified using the results of Graydon et al. (2012, Experiment 2).

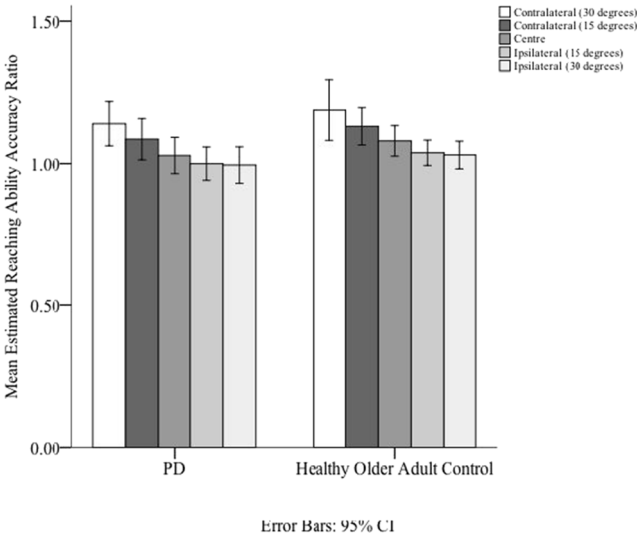

Fig. 2 Means (and standard deviations) of estimated/actual reaching ability ratios for each diagonal. Error bars represent 95% confidence intervals, calculated within subjects for each condition

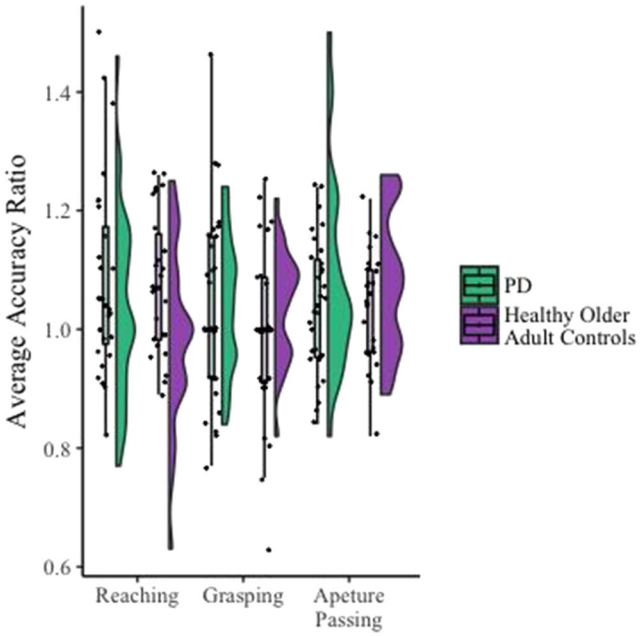

Fig. 3 Group means (and standard deviations), data distribution, and jittered raw data (raincloud; each dot represents an individual participant) of estimated/actual reaching, grasping, and aperture-passing ability ratios for the PD and healthy older adult control groups. Error bars represent ±2 *SEM*, calculated within each condition. There was no significant difference in accuracy ratio between people with Parkinson's and those without (reaching ability; $p = .260$, grasping ability $p = .882$; aperture passing ability $p = .760$; see text for details)

and moderate evidence for the null hypothesis when comparing the actual aperture-passing ability of PD patients (M = 8.84, SD = .90) compared with the aperture-passing abilities of healthy older adult controls (M = 8.56, SD= .77), $t(40)$ = 1.05, p = .298, $B_{N(0,4.28)}$[5] = 0.11, RR[1.32, ∞].

A repeated-measures ANOVA [Initial aperture size (Small or Large) × Group (PD or typically ageing older adult)] indicated that there were no significant differences in the perceived action boundary for aperture passing between the PD patients (M_{acc} = 1.043, SE_{acc} = .022) and the healthy older adult controls (M_{acc} = 1.053, SE_{acc} = .021), $F(1, 40)$ = .094, p =.760 (see Fig. 3). Bayes factor indicated that the data provided only weak evidence for the null hypothesis that patient accuracy for aperture did not differ from the control accuracy, $B_{H(0,0.08)}$ = 0.39, RR[0, 0.09].

A significant main effect of hysteresis was observed, $F(1, 40)$ = 33.377, $p < .001$, whereby participants overestimated the minimum size opening they could successfully pass their hand through to be larger when the aperture started at the largest size and moved inwards (M_{acc} = 1.074, SE_{acc} = .017), than when the aperture started at the smallest size and moved outwards (M_{acc} = 1.022, SE_{acc} = .015).

Across all three tasks Across all three tasks we found no significant difference in the accuracy of individuals with PD's perceptions of their action boundaries compared with healthy older adult controls (see Fig. 3). Additionally, in Tasks 1 and 3, Bayes factors indicated that the evidence only weakly favoured the null hypothesis, whereas in Task 2 the Bayes factor indicated that the evidence moderately favoured the null hypothesis.

[5] Model of H1 specified using the room-to-move heuristic outlined by Dienes (2019).

Visual analysis of the accuracy ratios obtained within these tasks compared with the accuracy ratios obtained in previous studies, recruiting young adult samples (such as Graydon et al., 2012), indicate that overall, both PD patients' and healthy older adults' perceptions of their action boundaries are more conservative than younger controls. Analysis of variance on the summary data (means and standard errors) obtained in this study compared with Graydon et al. (2012) show that healthy older adults ($M_{Control}$ = 1.093 , $SE_{Control}$ = .025) and individuals with PD (M_{PD} = 1.050, SE_{PD} = .028) overestimated their reaching ability significantly less often than did younger adults (M = 1.21, SE = 0.03; p = .014 and $p < .001$, respectively). Similarly, individuals with PD (M_{PD} = 1.043, SE_{PD} = .022) overestimated their aperture passing ability significantly less than younger adults (M = 1.14, SE = 0.04; p = .045). However, healthy older adults ($M_{Control}$ = 1.053 , $SE_{Control}$=.021) did not differ significantly from younger adults (p = .073) in their aperture passing ability . Furthermore, both healthy older adults ($M_{Control}$ = 1.011 , $SE_{Control}$ = .125) and individuals with PD (M_{PD} = 1.017, SE_{PD} = .114) did not differ from younger adults (M = 1.10, SE = 0.03; p = .838 and p = .863, respectively) in their estimation of their grasping ability.

Exploratory correlational analyses, with a Bonferroni correction for multiple comparisons, were conducted to analyze the influence of specific disease characteristics on individuals'

perceptions. No clinical disease related characteristics significantly correlated with perceived reaching ability, grasping ability and aperture passing ability accuracy (see Appendix 3), although the Bayes factor robustness regions indicated the correlational data were inconclusive for all models of H1 specified with scale-of-effects ranging from zero to large correlations (e.g., *r*s > .60). The only exception was that the correlation between years on medication and aperture accuracy estimate ratio provided strong evidence for the alternative hypothesis, $B_{N(0,0.2)} = 95.07$, *RR*[.09, .63].

Discussion

The influence of altered perceptual-motor experience associated with PD on perceptions of their action boundaries was examined for upper body actions across three tasks. The findings obtained indicate that both PD patients and healthy older adult controls perceptions of their action capabilities for reaching are more conservative than healthy younger adult controls. Similarly, individuals with PD's perceptions of their aperture-passing capabilities were more conservative than those of healthy younger adult controls. However, both individuals with PD and healthy older adult controls perceive their grasping capabilities comparably to healthy younger controls. Importantly, relating to our key interest, we observed that despite the reduced ability to perform actions and the natural variability in perceptual-motor experience relating to one's ability to perform actions that may occur in PD, no significant differences from the control group in terms of the accuracy of one's perceptions were observed. We will first consider why both PD patients and healthy older adult controls' perceptions of their action capabilities are more conservative than younger adults before considering overall why individuals with PD's ability to accurately perceive their action capabilities are preserved.

Consistent with the vast body of literature, which has shown that individuals overestimate their reaching (Fischer, 2000; Linkenauger et al., 2009), grasping (Linkenauger et al., 2009; Linkenauger et al., 2011), and aperture passing abilities (Graydon et al., 2012), both PD and healthy older adult controls overestimated their action boundaries for these actions. However, the magnitude of overestimation obtained here regarding reaching compared with previous studies, which typically recruit young adults, suggests that both people with PD and healthy older adults are more conservative in their estimations of their action boundaries for reaching than healthy younger controls. Similarly, individuals with PD, but not healthy older adult controls, are more conservative in their estimations of their action boundaries for aperture passing. Intuitively, it would be advantageous for older adults to be more conservative when estimating the maximum extent to which they can perform an action. Ageing is associated with a decline in muscular strength (Hunter et al., 2016), the speed at which motor actions are performed (Voelcker-Rehage, 2008), and the accuracy of motor control (Rodrigue et al., 2005). Consequently, older adults may be more risk averse than younger adults and tend towards more conservative estimations of their action boundaries.

However, importantly, the healthy older adult group were not more conservative in their estimations of their action boundaries for aperture passing and both individuals with PD and healthy older adults estimate their action boundaries for grasping in a comparable way to healthy young adult controls. This may in part be due to the nature of the action in question. Specifically, reaching and aperture passing are ballistic movements that act to support more intricate actions, such as grasping (Jeannerod, 1996). Due to these differential mechanical demands on the body, reaching, grasping, and aperture-passing behaviours will carry differential cost-benefit ratios (Franchak & Adolph, 2014a). Specifically, as reaching and aperture passing support more intricate actions such as grasping, if failure to perform a reach or aperture-passing movement occurs, the individual will also be prevented from performing the more intricate movement the reach or aperture passing movement supports. As a result, failure to perform reaching and aperture passing movements may be more consequential than grasping movements. Previous research has indicated that individuals' perceptions of their action capabilities take into consideration the likelihood of success compared with the cost of failure (Franchak & Adolph, 2014a). Therefore, it may be that older adults and individuals with PD are more cautious in their estimations of their action capabilities for reaching and aperture passing but not grasping due to the costs associated with the failure of performance of these actions.

However, as this study did not directly analyze the influence of ageing on perceptions of action boundaries, these conclusions are somewhat speculative and should be approached with caution. Further research that recruits a sample spanning from younger adults (or perhaps children) to older adults and analyzes the influence of ageing on individuals' perceptions of their action boundaries is required.

Due to lack of difference between the accuracy ratios for PD patients and healthy older adult controls across all three experiments, our findings indicate that people with mild-to-moderate PD perceive their action boundaries in a comparable way with healthy age-matched controls, despite their altered motor experience. Additionally, the correspondence of the results obtained across all three tasks can be taken to indicate that the effect of PD is the same across the three upper body tasks analyzed. However, Bayes factors for reaching ability and aperture-passing ability indicated that the evidence was only weakly in favour of the null hypothesis that PD does not influence perceptions of individual's action boundary for reaching and aperture passing. Comparatively, regarding grasping, Bayes factors provided moderate support for the null hypothesis. Furthermore, correlational analyses revealed no significant correlations between specific disease characteristics and average estimated/actual ability accuracy ratio. Although it is worth noting that the current experiment was somewhat underpowered to detect anything but large correlations, and Bayes factors confirmed that all correlations were inconclusive. Furthermore, as no significant differences between the accuracy of PD and healthy older adults' perceptions of their action capabilities when anxiety was controlled for as a covariate were observed, we can reasonably conclude that anxiety did not significantly influence the pattern of results.

It is important to note that the grasping task was slightly underpowered due to the sample size recruited being smaller (N = 40) than suggested by priori power analyses (N = 54). This is problematic because not only do analyses of the results obtained in underpowered studies often result in biased conclusions being drawn (Crutzen & Peters, 2017), the parameters computed from the limited samples may differ from the overall population (Crutzen & Peters, 2017). This could mean that it is not appropriate to draw conclusions based on the grasping task employed here. However, the Bayes factor on the results obtained in the grasping task provides moderate support for the null. Consequently, there is support for the conclusion that PD does not significantly influence perceptions of action boundaries for grasping.

Although some evidence shows that certain individuals with PD show impaired awareness of their motor symptoms (Maier et al., 2012), it is also possible that other PD patients are more consciously aware of, and pay more attention to, their action capabilities and thus may be more reliably in tune with their action boundaries. Consistent with this, Proffitt and Linkenauger (2013) argue that it is the exposure to the visual specification of actions that are possible and impossible that enables individuals to be reliably in tune with their action boundaries. Presumably, if individuals with PD are more consciously aware of, and pay more attention to their action capabilities, they will have enhanced exposure to the visual specifications of actions that are possible and impossible, causing them to be reliably in tune with their action boundaries. Corroborating this, Ramenzoni et al. (2010) observed that healthy young participant's estimates of their action boundaries became more accurate over trials in which they were provided with optical information regarding their action boundary.

Previous research has also shown that individuals with PD simulate imagined movements (motor imagery; MI) comparably to their current motor capabilities (Abbruzzese, Avanzino, Marchese, & Pelosin, 2015). For example, Heremans et al. (2011) observed that whilst MI for individuals with PD is slower, MI was slowed to the same extent that physical execution was slowed (see also Avanzino et al., 2013; Dominey, et al., 1995). As MI is slowed to the same extent as physical motor performance is slowed, the slowness in MI appears reflective of the symptoms of PD rather than impairment in MI (Caligiore et al., 2017; Poliakoff, 2013). Furthermore, normal performance has been observed in tasks such as the hand rotation task, in which external stimuli implicitly demand the use of MI (Scarpina et al., 2019). In the current task, external objects provide a stimulus towards which an action can be imagined, and therefore motor imagery may be preserved.

Furthermore, MI in PD also reflects whether the individual is in the "on" or "off" phase. That is, if the participant was physically incapable of performing the action whilst in an "off" phase, they were also unable to imagine performing the action in this time (Dominey et al., 1995). Concerning the current study, all participants reported that they were currently in an "on" phase at the time of participation. Therefore, one would anticipate that their estimates would have been in keeping with their action boundary whilst in an "on" phase. Future research could explore whether their estimates change when tested off medication and/or directly compare limbs in people with asymmetrical PD.

Furthermore, whilst individuals can seemingly fluctuate from an "on" to an "off" time throughout the course of the day (Lang et al., 1982; Stacy et al., 2005), the stable maintenance of blood plasma levodopa concentration provided by medication reduces swings in motor performance (MacMahon et al., 1990), ensuring that patients spend more time in an "on" time throughout the course of a day. Within the sample tested here, 40% of patients reported they had no on/off time, 45% spent ≤25% of their waking hours in an "off" state, and the remaining 15% spent 26%–50% of their waking hours in an "off" state. Consequently, the individual will gain

a greater array of visual information regarding their action capabilities when they are in an "on" time than when they are in an "off" time. As the majority of the learning required in order for one to be reliably in tune with their action boundaries occurs in an "on" phase, when individuals are asked to estimate their action boundaries, patients may disregard the limited amount of visual information obtained regarding their action boundaries in an "off" state in favour of the more fruitful information regarding their action boundaries in an "on" phase. If this is the case, then it would be logical for their estimations to reflect their abilities during an "on" phase. As individuals can typically perform all actions as normal to their maximal boundary when functioning in an "on" phase (Lees, 1989), their subsequent perceptions of their action boundaries should not differ from that of healthy older adults who do not have this source of variability present.

Alternatively, the perceptual system may apply a mechanism based on weighted averages when determining the action boundary for the action in question. According to this mechanism, the perceptual system will take into consideration all prior experience weighted by their occurrence and calibrate to the average (Körding & Wolpert, 2006). For example, if a patient can perform a grasp that is 100% of their ability 75% of the time, whilst the remaining 25% of the time they can only perform a grasp 50% of their maximal ability. When the patient is then asked to estimate their action boundary, they will calibrate to the average of all perceptual motor experience, 87.5% of their maximal ability, to inform their estimation. Regarding the sample tested within this series of studies, as the majority/all patients experience a greater proportion of "on" time than "off" time, the calculated weighted average for all participants will fall substantially closer to the participants maximal morphologically dictated action boundary. Subsequently, one would not anticipate that PD patients' perceptions of their action boundaries would substantially differ from healthy older adult controls.

Another important factor to consider is that when patients are in an "off" phase, their ability to perform motor actions can be severely compromised to the extent that patients often report that they withdraw from society (Calne et al., 1996) and often simply do not perform motor actions. Subsequently, the patient may only obtain perceptual-motor experience regarding the maximal extent to which they can perform these actions whilst they are in an "on" phase, rather than obtaining variable perceptual motor experience in both "on" and "off" phases. Consequently, the patients' perceptual motor experience regarding their ability to perform these actions will not be subject to random variability. Therefore, when asked to estimate the maximal extent to which they can perform these actions, the patient will calibrate to the consistent perceptual-motor experience obtained during "on" phases.

With regard to the underlying brain mechanisms, in PD, the degeneration of dopaminergic cells in the substantia nigra pars compacta initiates a cascade of functional changes affecting all basal ganglia structures (Blandini et al., 2000). Therefore, the findings obtained here may be taken to suggest that the basal ganglia do not affect the ability to judge one's action capabilities and generate MI. However, it is possible that individuals with PD may use an alternative compensatory mechanism to ensure this ability remains intact. For example, it may be that individuals with PD rely more heavily on visual processing. Such that, rather than instinctively rapidly estimating their action capabilities, they may draw on conscious motor imagery processes, and take their time in making estimations as to whether the performance of an action would be successful or not. To the authors' best knowledge, this is the first analysis of the influence of neurological conditions and altered neural processing on individual's perceptions of their action capabilities. Therefore, to further inform our understanding of the underlying mechanism of anticipating one's action capabilities, further work using this task with alternative patient groups (e.g., Huntington's disease and focal brain injury patients) is required.

These findings have important implications for individuals suffering with mild-to-moderate PD. Despite the reduction in their ability to perform actions and variability in perceptual-motor experience that occurs in PD, individuals' ability to accurately perceive their action boundaries for their upper limbs is preserved. Therefore, one can reasonably assume that they can use this knowledge to move safely within their environment. Physiotherapists and occupational therapists working with people with PD, may also draw upon this observation. It is important to highlight that individuals with PD may have developed a compensatory mechanism to preserve this function. Therefore, future research should investigate the method employed by people with PD when they perceive their action boundaries. Additionally, all tasks employed within this study focus solely on the perception of one's action capabilities for upper body actions. As the execution of different motor actions is different mechanically and will have a differential demand upon the body (Jeannerod, 1996), it would be unreasonable to assume that the results obtained in this study can be generalized to the perception of action capabilities relating to both upper and lower body actions. Therefore, future research should analyze the perception of lower body

action capabilities in PD. Finally, as all individuals with PD analyzed here display mild-to-moderate PD, it would be particularly interesting to analyze whether action boundary perception is less accurate in those with more severe motor symptoms.

In summary, these studies demonstrate that natural variability in one's perceptual-motor feedback, as a consequence of PD, does not influence one's subsequent perceptions of their action boundaries for reaching, grasping, and aperture passing. This implication is principally supported in the lack of significant difference (and support for the null using BF) between PD patients' perceptions of their action capabilities and healthy older adult controls' perceptions of their action capabilities. This finding may in part be due to the notion that typically PD patients spend a greater proportion of their waking hours in an "on" phase as opposed to an "off" phase. This result may also be explained by the notion that when PD patients are in an "off" phase, they characteristically do not perform actions and rather withdraw themselves from daily activities. Hence, they have little conflicting perceptual motor information specifying their action boundaries from when they are in their "on" phase.

These findings have important implications for people with PD. Specifically, as the results obtained indicate that individuals with PD's ability to accurately perceive their action boundaries is preserved. One can reasonably assume that individuals with PD's ability to use this information to ensure safe interaction with their environment remains intact. However, as all tasks employed here exclusively consider upper body actions these conclusions may be exclusive to the perception of upper body action capabilities.

Appendix 1

Analysis of covariance—The influence of anxiety on the perception of action capabilities

Task 1: Perception of reaching ability

Analyses revealed that there was no significant difference in the accuracy of the perceived action boundaries for reaching between the PD (M_{acc} = 1.050, SE_{acc} = .028) and healthy older adult groups (M_{acc} = 1.093, SE_{acc} = .025) after controlling for the effect of anxiety, although the evidence still only weakly supported the null, $F(1, 37) = 1.278$, $p = .266$, $B_{H(0,0.09)} = 0.67$, $RR[0, 0.20]$).

Task 2: Perception of grasping ability

Analysis revealed that there was no significant difference in the accuracy of the perceived action boundaries for grasping between the PD (M_{acc} = 1.017, SE_{acc} = .028) and healthy older adult groups (M_{acc} = 1.011, SE_{acc} = .026) after controlling for the effect of anxiety, although the Bayes factor now indicated that the evidence was now only weakly favoured the null, $F(1, 37) = .030$, $p = .864$, $B_{H(0,0.08)} = 0.40$, $RR[0, 0.09]$).

Task 3: Perception of aperture passing

Analysis revealed that there was no significant difference in the accuracy of the perceived action boundaries for aperture passing between the PD (M_{acc} = 1.043, SE_{acc} = .022) and healthy older adult groups (M_{acc} = 1.053, SE_{acc} = .021) after controlling for the effect of anxiety, although the Bayes factor still indicated that the data only weakly favoured the null hypothesis, $F(1, 39) = .093$, $p = .762$, $B_{H(0,0.08)} = 0.39$, $RR[0, 0.09]$).

Appendix 2

Analysis of covariance—The influence of the presence of rheumatic illnesses on the perception of action capabilities

Task 1: Perception of reaching ability

Analyses revealed that there was no significant difference in the accuracy of the perceived action boundaries for reaching between the PD (M_{acc} = 1.050, SE_{acc} = .028) and healthy older adult groups (M_{acc} = 1.093, SE_{acc} = .025) after controlling for the effect of the presence of rheumatic illness, $F(1, 37) = 1.278$, $p = .266$.

Task 2: Perception of grasping ability

Analysis revealed that there was no significant difference in the accuracy of the perceived action boundaries for grasping between the PD (M_{acc} = 1.017, SE_{acc} = .028) and healthy older adult groups (M_{acc} = 1.011, SE_{acc} = .026) after controlling for the effect of anxiety, although the Bayes factor now indicated that the evidence was now only weakly favoured the null, $F(1, 37) = .030$, $p = .884$.

Task 3: Perception of aperture passing

Analysis revealed that there was no significant difference in the accuracy of the perceived action boundaries for aperture passing between the PD (M_{acc} = 1.043, SE_{acc} = .022) and healthy older adult groups (M_{acc} = 1.053, SE_{acc} = .021) after controlling for the effect of anxiety, although the Bayes factor still indicated that the data only weakly favoured the null hypothesis, $F(1, 39) = .093$, $p = .787$.

Appendix 3

	Actual reaching ability	Perceived reaching ability	Actual Grasping ability	Perceived grasping ability	Actual aperture passing ability	Perceived aperture passing ability
Years since diagnosis	−.288	−.370	−.274	−.173	.038	−.050
Years on medication	−.328	−.374	−.256	−.183	.059	−.042
Time since last dosage of medication (minutes)	−.134	.364	.063	.315	.127	−.051
LEDD	.308	−.461	−.266	−.244	−.005	−.189
UPDRS motor examination	.200	−.167	.087	.014	.213	−.157
UPDRS motor complications	.297	−.208	−.082	.107	−.031	.021
HADS–Anxiety Score	−.138	−.165	−.287	−.217	−1.44	.091
HADS– Depression Score	.097	−.001	−.041	−.063	−.061	.118
Rheumatic	−.196	−.004	−.361*	−.002	.025	.239

Pearson correlations between saverage estimated/actual reaching ability ratio and Parkinson's disease characteristics

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Availability of data and materials All data generated or analyzed during this study are included in this published article [and its supplementary information files].

Code availability Not applicable.

Declarations

Conflicts of interest The authors have no conflicts of interest to declare that are relevant to the content of this manuscript.

Ethics approval All procedures performed in this study were in accordance with the ethical standards of the UK National Health Service (NHS) and with the 1964 Helsinki Declaration and its later amendments or comparable ethical standards. The study was approved by the NHS North West-Greater Manchester Research Ethics Committee (19/NW/0007).

Consent to participate Informed consent was obtained for all individual participants included within the study.

Consent for publication The authors affirm that all participants provided informed consent to have their data included in publication.

Open practices statement All data generated or analyzed during this study are included in this published article [and its supplementary information files]; this study was not preregistered.

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4.1 Statement of thesis continuous commentary

This series of experiments investigated the influence of variable perceptual-motor experience and altered basal ganglia functioning, on individuals with mild-moderate idiopathic PD perceptions of their action boundaries for reaching, grasping, and aperture passing behaviours. Across all three actions individuals with PD's perceptions of their action boundaries did not significantly differ from the control group (and support for the null was provided using Bayes Factors). However, both individuals with PD and healthy older adult controls were more conservative in their estimations of reachability than younger controls. Similarly, individuals with PD were more conservative in their estimations graspability than younger controls. Overall these findings can be taken to indicate that the perception of one's action boundaries is preserved in mild to moderate PD.

Previous research suggests that when individuals perceive an environment, with the intention to perform an action, individuals mentally simulate the performance of said action and the outcome of this simulation influences perception (Witt & Proffitt, 2008). Subsequently when judging the maximum extent to which one can reach for example, individuals may mentally simulate reaching, and the outcome of this simulation will inform their perceived action boundaries. Therefore, arguably the perception of action capabilities is to some degree influenced by an individual's motor imagery capabilities.

Previous research has observed that motor imagery capabilities in PD are substantially preserved (e.g. Bek et al., 2019; Heremans, 2011;van Nuenen et al., 2012; Scarpina et al., 2019) and are reflective of the perciever's current action capabilities (E.g. Dominey, 1995; Abbruzzese et al., 2015). Subsequently, in Chapter

4, I reasoned that the preservation of individuals' with PD's perceptions of their action capabilities might in part be due to the preservation of motor imagery capabilities in PD.

However, symptom presentation and severity is largely heterogeneous in PD (Greenland et al., 2019). For example, while some individuals with PD present with tremor as the most dominant motor feature, others never experience tremor (Greenland et al., 2019). Moreover, symptom presentation is often unilateral (Sveinbjornsdottir, 2016). Subsequently, it is important to consider how individual differences in symptom presentation and severity may influence motor imagery.

Importantly, few investigations have considered the influence of specific symptoms on motor imagery independently. Therefore, in the following chapter (Chapter 5; Paper Three; Motor imagery vividness and symptom severity in Parkinson's disease Megan Rose Readman, Trevor J. Crawford, Sally A. Linkenauger, Judith Bek, Ellen Poliakoff) I investigate the relationship between specific symptom (tremor and bradykinesia) severity and presentation on individuals with mild-moderate PD's overall motor imagery vividness.

Note. I find it particularly important to note here that the conception of the following paper was largely influenced by one participant's observations when participating in the present study. Specifically, one individual with PD stated *"I find it particularly hard to guess how big an object I can pick up when my tremor makes it so hard for me to pick things up"*. This lead me to question, does symptom presentation and severity influence ones motor imagery capabilities.

Chapter 5

Paper Three; Motor imagery vividness and symptom severity in Parkinson's disease

Megan Rose Readman, Trevor J. Crawford, Sally A. Linkenauger, Judith Bek, Ellen Poliakoff

Author note; This paper has been submitted and received peer reviews from the Journal of Neuropsychology.

Abstract

Motor imagery (MI), the mental simulation of movement in the absence of overt motor output, has demonstrated potential as a technique to support rehabilitation of motor disorder in neurological conditions such as Parkinson's disease (PD). The therapeutic utility of this technique is contingent upon the ability to perform MI, which existing evidence suggests is largely preserved in PD. However, previous studies typically examined global measures of MI and have not considered the potential impact of individual differences in symptom presentation on MI. The present study investigated the influence of severity of overall motor symptoms, bradykinesia, and tremor on MI vividness scores in 44 individuals with mild to moderate idiopathic PD. Linear mixed effects modelling revealed that imagery modality and the severity of left-side bradykinesia significantly influenced MI vividness ratings. Consistent with previous findings, participants rated visual imagery (VMI) to be more vivid than kinesthetic imagery (KMI). Greater severity of left-side bradykinesia (but not right-side bradykineisa) predicted increased vividness of KMI, while tremor severity and overall motor symptom severity did not predict vividness of MI. These findings may reflect the differential neurophysiology of tremor and bradykinesia. Furthermore, the specificity of the effect to the left side may reflect enhanced baseline vividness of KMI for the dominant (right) side, or increased attention to more effortful movements on the left side of the body resulting in more vivid kinesthetic imagery.

Keywords: Motor imagery, Visual Imagery, Kinesthetic Imagery, Parkinson's Disease, Bradykinesia

Motor imagery vividness and symptom severity in Parkinson's disease

Motor imagery (MI) is the mental rehearsal of an action in the absence of overt motor output (Jeannerod 1994; 1995), which may be differentiated into visual motor imagery (VMI) and kinesthetic motor imagery (KMI) (Abbruzzese et al., 2015). VMI relates to the generation of visual representations of oneself performing an action, while KMI relates to the sensations associated with simulating an action (McAvinue & Robertson 2008). Importantly, functional neuroimaging and lesion studies have observed that MI and motor execution share similar cortical activations. Specifically, the primary motor cortex (Sirigu et al., 1996; Schnitzler et al., 1997), and pre-motor areas including the supplementary motor area (SMA) (Grafton et al., 1996; Dechent et al., 2004) are activated during both overt motor output and MI (see Hardwick et al., 2018 for review). Through activating such motor areas even in the absence of overt motor output, MI can facilitate the learning of new actions (Driskell et al., 1994).

MI may also enable individuals to mentally practice actions that they are unable to perform due to physical impairments (Zimmermann-Schlatter et al., 2008) and can facilitate safe self-paced training in those with motor deficits (Agostini, et al., 2021). Thus, MI has been identified as a potential technique for promoting the recovery of motor functioning in neurological conditions (Malouin & Richards, 2013; Caligiore et al., 2017; Cuomo et al., 2022.). However, MI ability may be compromised in conditions that limit movement. Supporting this assumption alterations in MI have been observed in non-neurological conditions that limit movement such as chronic pain (e.g. Breckenridge et al, 2019) and fibromyalgia (e.g. Scandola et al., 2021).

In Parkinson's disease (PD), the progressive degeneration of dopaminergic nigrostriatal neurons originating in the substantia nigra pars compacta of the basal ganglia and projecting to the striatum (Agid et al., 1987) results in profound motor symptoms including tremor, rigidity, slowed movement execution (bradykinesia), and reduced movement amplitude (Politis et al., 2010; Crawford III & Zimmerman, 2011). Moreover, particular difficulties with voluntary, internally generated actions are observed in PD (Brown & Marsden, 1988). MI, in addition to traditional physical therapy and functional rehabilitiation (Carrasco & Cantalapiedra, 2016), may be advantageous in PD neurorehabilitation by supporting the maintenance of motor capabilities (Caligiore, et al., 2017), but a critical question is whether motor impairments in PD also impacts on MI abilities (e.g., Poliakoff, 2013).

MI has been investigated through various paradigms (McAvinue & Robertson, 2008), which can be broadly categorised as implicit or explicit measures. Implicit MI occurs when motor representations are employed without direct instruction (Jeannerod, 1994). Hand laterality judgement tasks are widely used to assess implicit MI, whereby participants are asked to judge the laterality of images of hands presented at various angular rotations (e.g., Ter Horst et al., 2010; Parsons, 1987a; Parsons, 1987b). The time required to make a laterality judgement in this task is proportional to the time required to physically rotate the hand into the corresponding angle (e.g., Parsons, 1987a; 1995). A small number of studies employing this task with people with PD have found evidence of slowing and reduced accuracy (Dominey et al., 1995; Helmich et al., 2012). However, these alterations in MI appear to parallel alterations in motor capabilities, and so may be reflective of PD motor symptomatology rather than an inability to perform MI (Dominey et al., 1995). Moreover, additional studies have found similar performance in PD and control

groups when judging hand laterality (van Nuenen et al., 2012; Scarpina et al., 2019; Bek et al., preprint).

In contrast to implicit tasks, explicit MI measures involve instructing participants to deliberately engage in MI (Jeannerod, 1994). For example, in a mental motor chronometry task, the reported time taken to imagine an action closely parallels the measured time taken to physically perform the same action (Decety et al., 1989; Milner, 1986). Some research suggests that mental chronometry may be less accurate and/or slower in individuals with PD (Scarpina et al., 2019). Moreover, Heremans et al. (2011) found that while response times were significantly longer in individuals with PD, the degree of slowing was significantly correlated with duration of physical execution, suggesting parallel slowing of MI and motor execution.

Self-rating scales such as the Kinesthetic and Visual Imagery Questionnaire (KVIQ; Malouin et al., 2007) are also used as explicit measures of MI, in which participants imagine themselves performing an action, and then rate the vividness of the visual image or the intensity of the kinesthetic sensations of the imagined action. Typically, healthy individuals rate VMI to be more vivid than KMI (e.g. Malouin et al., 2007; Lorant & Nicolas, 2004 ; Randhawa et al., 2010), Moreover, ratings of MI vividness in people with PD have been found to be comparable to healthy older adults (Bek et al., 2019; Abbruzzese et al., 2015; Peterson et al., 2012; Heremans, 2011; Pickett et al., 2012).

Given the heterogeneity of symptom presentation and severity in PD (Lang & Lozano, 1998), it is important to consider how individual differences in symptoms may influence MI. For example, some patients present with tremor as the most dominant motor feature, whereas others never experience tremor (Greenland et al., 2019). Moreover, during the earliest stages of PD, and often throughout disease

progression, patients may exhibit unilateral symptom presentation (Sveinbjornsdottir, 2016). Previous studies have observed no significant effect of symptom severity, measured by overall motor scores on the Unified Parkinson's Disease Rating Scale (UPDRS; Fahn et al., 1987), on MI vividness (Heremans, 2011; Pickett et al., 2012), although this observation may have been affected by the exclusion of participants with severe tremor (Heremans, 2011). Importantly, few investigations of MI in PD have considered the influence of specific symptoms on MI. However, one study (Helmich et al., 2012) observed that individuals with tremor made fewer errors on a hand laterality task than individuals without tremor, and this enhanced performance was coupled with increased somatosensory activation. Additionally, individuals with strongly lateralised symptoms were markedly slower in laterality judgments for images corresponding to the more affected hand (Dominey et al., 1995; Helmich et al., 2007; Helmich et al., 2009). These findings suggest that alterations in MI may reflect alterations in motor capabilities or sensorimotor experience.

While the above findings provide important insights regarding the relative preservation of MI in PD, further investigation is needed into the influence of individual differences in symptom presentation and severity on MI. For example, it is possible that particular symptoms such as tremor and bradykinesia may affect global MI measures, or that symptoms affect MI in a lateralised manner. To address this, the present study analysed the influence of overall symptom severity, tremor and bradykinesia, on MI vividness in individuals with mild to moderate PD. Moreover, potential lateralised effects on the relationship between symptom severity and MI vividness were investigated by analysing the influence of side-specific bradykinesia and tremor on side-specific (i.e., left and right) VMI and KMI vividness scores. To

investigate the temporal stability of MI vividness in individuals with PD, the test-retest reliability of VMI and KMI was also examined in a subset of participants.

Methods

Participants

Participants were recruited through local neurology clinics and Parkinson's UK. Forty-four participants (30 males) aged 47 to 79 years (M = 64.5, SD = 6.8) with mild to moderate idiopathic PD were included in this analysis. Based on the Edinburgh Handedness Inventory (Oldfield, 1971), forty participants were right-handed, three were left-handed and the remaining participant was mixed handed. All participants had normal or corrected-to-normal vision and had no history of other neurological or psychiatric conditions. Participants were screened for cognitive impairment (Addenbrookes Cognitive Examination III; Hsieh et al., 2013).

All participants except one were taking dopaminergic medication at the time of participation, including levodopa combination drugs (e.g., Madopar), dopamine agonists (e.g., Ropinirole), monoamine oxidase inhibitors (e.g., Rasagiline) and Catechol-O-Methyl Transferase (e.g., Entacapone)

The research was approved by a UK National Health Service (NHS) research ethics committee and participants provided written informed consent. Participants were compensated for their travel and participation.

Procedure

The data analysed here was collected as part of two previous studies (Bek et al., 2019, 2021), in which participants completed either the full (20-item) or short (10-

item) version of the KVIQ (Malouin et al., 2007). A subset of participants (N= 19) completed the KVIQ on two separate occasions at least 8 months apart.

The KVIQ requires participants to physically perform and then imagine performing, from a first-person perspective, a series of simple actions (e.g., thumb-to-finger taps and foot tapping) involving different body parts (Malouin et al., 2007). Measures of VMI and KMI are obtained by asking participants to rate the vividness of their imagery on five-point scales for the clarity of the visual image (1 = no image, 2= blurred image, 3= moderately clear image, 4= clear image, 5 = as clear as seeing yourself executing the action), and the intensity of the imagined sensations (1= no sensation, 2 = mildly intense, 3 = moderately intense, 4 = intense, 5 = as intense as executing the action).

The motor examination of the MDS-UPDRS (Goetz et al., 2008) was used to assess the severity of a range of symptoms, including tremor and bradykinesia. Each item is rated on a scale of 0-4, where 0 indicates a complete absence of the symptom, and 4 indicates severe disability. Severity is assessed independently for each limb and side where applicable (e.g., for resting tremor).

Data analysis

As participants completed either the full KVIQ or the short-form KVIQ-10, only items from the KVIQ-10 (Malouin et al., 2007) were included in the present analysis for all participants. The KVIQ-10 includes several limb-specific movements and one trunk movement. For the purpose of the present study, each of the limb-specific actions was repeated for both sides of the body, providing a measure of VMI and KMI vividness for each body side.

To analyse the influence of motor symptoms on MI at a body side-specific level, the following KVIQ items were analysed separately for right and left limbs: forward shoulder flexion, thumb to finger tips, hip abduction, and foot tapping. For the overall analysis, items from both sides as well as forward trunk flexion were included.

From the MDS-UPDRS (hereafter, "UPDRS"), overall motor scores as well as measures of overall bradykinesia and tremor severity, and side-specific severity of tremor and bradykinesia were calculated. For bradykinesia at a side-specific level, the following MDS-UPDRS items were analysed separately for right and left limbs: finger tapping, hand movements, pronation-supination of hands, toe tapping, leg agility. For the overall analysis, items from both sides were included, as well as global spontaneity of movement (bradykinesia). For side-specific tremor, the following MDS-UPDRS items were analysed separately for right and left limbs: postural tremor of the hands, kinetic tremor of the hands, rest tremor amplitude (upper and lower limbs). For the overall analysis, items from both sides were included, as well as rest tremor amplitude for the lip/jaw, and constancy of rest tremor.

Linear mixed effects modelling (LMM) was used to analyse the association of symptom severity with KVIQ-10 scores (i) overall and (ii) at a side-specific level. Given that healthy adults commonly rate VMI to be more vivid than KMI (e.g. Malouin et al., 2007; Randhawa et al., 2010), imagery modality (VMI, KMI) was also included as a predictor when analysing the effects of symptoms. LMM allows the influence of fixed effects of independent variables to be analysed, while accounting for random effects corresponding to unexplained differences such as variation between participants (Baayen et al., 2008). Models were fitted using the maximum likelihood procedure with the Satterthwaite adjustment method in the lme4 package

(Bates et al., 2016) in R (R Core Team, 2021). Models were compared using likelihood ratio tests. A further analysis that included only right-handed participants produced the same pattern of results, so all participants were included in the final analyses.

The KVIQ (KVIQ-10 and KVIQ-20; Malouin et al., 2007) has established test-retest reliability over duration of 5-12 days (Randhawa et al., 2010 (N= 11). Given that a subset of participants (N= 19) completed the KVIQ on two separate occasions at least 8 months apart, a paired samples t-test was conducted to analyse the change in KVIQ scores between the two time-points and an intraclass correlational analysis was conducted to analyse the temporal stability of VMI and KMI scores from the KVIQ-10 from a subset of 19 participants (15 males). Overall vividness scores did not differ between the two time points (p = 0 .99). Moreover, intraclass correlation coefficients (one-way random effect model, with the 95% lower confidence limit) revealed good test-retest reliability for overall KVIQ (0.70), and moderate test-retest reliability for both VMI (0.55) and KMI (0.67) between timepoints (interpretation of test-retest reliability statistics follows Portney et al., 2009) (See Appendix 1 for full statistical analysis).

Results

MI and motor symptoms

UPDRS motor scores and KVIQ-10 scores are presented in Table 1. All participants had mild to moderate symptoms as indicated by the Hoehn and Yahr scale (M =2.01, SD = 0.76), with a mean UPDRS score of 37.20 (SD = 9.71).

Table 1. Participant descriptives, mean (SD), for overall and symptom specific MDS-UPDRS scores, and overall and modality specific KVIQ-10 scores.

	All participants (N = 44)	Test-retest Subset (N = 19)		Analysis of difference between T1 and T2
Overall MDS-UPDRS Subscale III	37.20(9.71)	Test 1: 39.06 (10.55)	Test 2: 44.61 (12.42)	$t(17) = -2.98$, $p = .008$
Overall Bradykinesia	14.78(5.44)	Test 1: 15.00(5.99)	Test 2: 19.83(6.51)	$t(17) = -4.13$, $p = .001$
Right Bradykinesia	5.56(3.20)	Test 1: 5.83(3.72)	Test 2: 8.28(3.34)	$t(17) = -3.40$, $p = .003$
Left Bradykinesia	7.88(3.20)	Test 1: 7.78(3.17)	Test 2:9.56(3.54)	$t(17) = -3.29$, $p = .004$
Overall Tremor	5.34(4.35)	Test 1: 6.72(4.79)	Test 2: 6.28(6.07)	$t(17) = .55$, $p = .592$
Right Tremor	1.80(1.44)	Test 1: 2.39(1.42)	Test 2: 2.22(2.24)	$t(17) = .363$, $p = .721$
Left Tremor	2.20(2.82)	Test 1: 2.78(2.80)	Test 2:2.44(2.31)	$t(17) = .842$, $p = .412$
Hoehn and Yahr	2.01(0.76).	Test 1:	Test 2:	$t(14) = -$

2.01(0.76).		1.97(0.80)	2.06(0.68)	1.10, p = .290
Overall KVIQ	78.07 (24.11)	Test 1: 77.61(23.78)	Test 2: 61.11(19.75)	$t(17)$ = 3.58, p = .002
Overall VMI	34.17(9.18)	Test 1: 33.78 (9.38)	Test 2: 33.06 (9.83)	$t(17)$ = .329, p = .746
Overall KMI	45.00(17.94)	Test 1: 27.72 (9.60)	Test 2: 27.56 (11.31)	$t(17)$ = .081, p = .937
Right VMI	15.34(4.05)	Test 1: 15.00(4.16)	Test 2: 15.06(4.36)	$t(17)$ = -.058, p = .954
Left VMI	14.85(4.33)	Test 1: 14.72(4.56)	Test 2: 14.22 (4.49)	$t(17)$ = .489, p = .631
Right KMI	13.00(4.04)	Test 1: 12.39(4.27)	Test 2: 12.06 (5.03)	$t(17)$ = .381, p = .708
Left KMI	12.61(4.16)	Test 1: 12.22(4.48)	Test 2: 12.72 (5.05)	$t(17)$ = -.505, p = .620

Effects of modality and symptoms on overall MI. To examine the influence of overall symptom severity, tremor, bradykinesia, and MI modality on overall MI vividness, LMM analysis was conducted with total KVIQ-10 score (MI) as the dependent measure, modality (KMI or VMI), UPDRS total motor score, overall bradykinesia and overall tremor scores as fixed effects and individual participants as random effects on the intercepts.

MI was only significantly influenced by modality, reflecting higher vividness ratings for VMI compared to KMI *(b* = 5.66, *SE* = 1.21, t(44) = 4.67; *p* <.001*)*.

In a subsequent model, overall tremor and bradykinesia scores were replaced with side-specific tremor and bradykinesia scores. KVIQ scores were predicted by modality, again reflecting higher vividness ratings for VMI compared to KMI (*b* = 5.66, *SE* = 1.21, t(44) = 4.67; *p* <.001), and by left-side bradykinesia (*b* = 1.54, *SE* = .59, t(44) = 2.64; *p* =.011), such that higher bradykinesia scores in the left side of the body were associated with higher MI vividness ratings.

Comparison of the two models revealed no significant difference ($\chi^2(2)$ = 5.15; *p*=.076), Moreover, removing all non-significant predictors from the original model did not significantly affect the fit of the model ($\chi^2(3)$ = 4.65; *p*=.20; such that the best-fitting model included only the random intercept for participants and the fixed effect of Modality (see Table 2).

Effects of modality and symptoms on side-specific MI. KVIQ scores for left and right sided movements were analysed in separate models, with modality (VMI or KMI), UPDRS total motor score, side-specific bradykinesia, and side-specific tremor as fixed effects, and random intercept effects of participants. For left-side MI, modality (b = 2.45, SE = .61, t(44) = 4.03; p <.001) and left-side bradykinesia (b =

.42, SE = .21, t(44) = 2.00; p = .045) were significant. Removing all non-significant predictors did not affect the model fit ($\chi^2(2) = .53$; p=.77), and the model including both modality and left-side bradykinesia was superior to models with modality alone ($\chi^2(1) = 5.21$; p=.022), or bradykinesia alone ($\chi^2(1) = 13.84$; p <.001) (Table 2). As illustrated in Figure 1, VMI (vs. KMI) and higher left-side bradykinesia scores were associated with higher vividness scores. For right-side MI, modality (b = 2.50, SE = .52, t(44) = 4.77; p <.001) and UPDRS total motor score (b = .15, SE = .068, t(44) = 2.17; p = .035) were significant. Excluding all non-significant predictors did not significantly affect the model fit ($\chi^2(3) = 4.56$; p=.21); moreover, removing UPDRS score did not significantly reduce the model fit ($\chi^2(1) = 2.34$; p=.13), indicating that the model including modality only provided the best fit (Table 2). Again, vividness scores were higher for VMI than KMI (see Figure 1).

Table 2. Summary of best-fitting linear mixed-effect models analysing the effects of modality (visual vs. kinesthetic) and symptoms (MDS-UPDRS III) on motor imagery (KVIQ-10) scores overall and for left and right sides of the body.

Model	Predictors (b, SE, df, t, p)	Model df	BIC	AIC	LogLik	Deviance	Marginal/ Conditional R2
Overall KVIQ		84	623.7	633.6	-307.9	615.7	.09/.63
(Intercept)	25.21, 5.35, 45.14, 4.71, <.001						
Modality: Visual	5.66, 1.21, 44, 4.67, <.001						
Left-side KVIQ		83	491.5	503.9	-240.8	481.5	.16/.57
(Intercept)	9.26, 1.46, 47.98,6.34, <.001						
Modality: Visual	2.45, .61, 44, 4.03, <.001						
Bradykinesia_ Left	.40, .17, 44, 2.35, .023						
Right-side KVIQ		84	479.7	489.6	-235.8	471.7	.09/.65
(Intercept)	12.84, .60, 63.70, 21.40, <.001						
Modality: Visual	2.50, .52, 44, 4.77, <.001						

The relationship between left-side bradykinesia and VMI and KMI scores for the left side were further explored using Spearman correlation coefficients (see Figure 2). There was a significant positive association between left side KMI and left side bradykinesia ($rs(40) = .31$; $p = .042$) but no significant association between left side VMI and left side bradykinesia ($rs(40) = .20$; $p = .20$)..

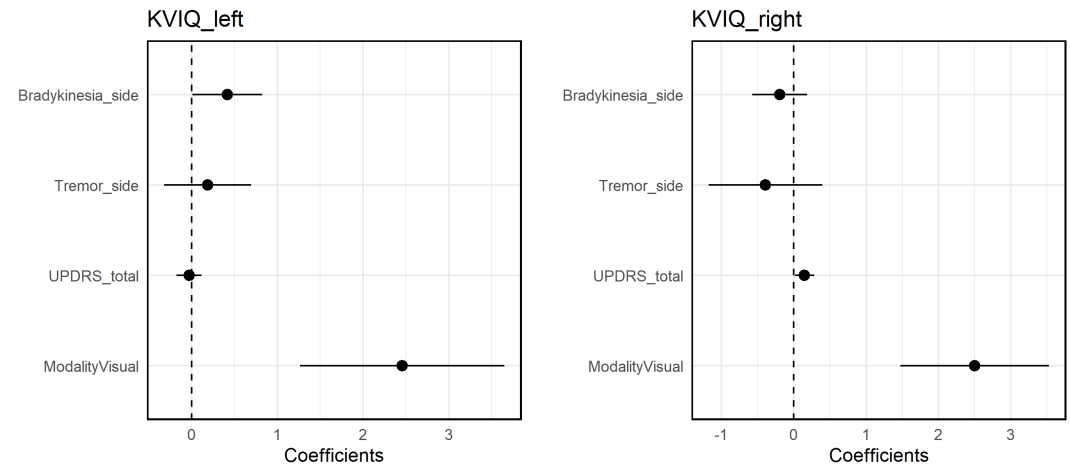


Figure 1. Dot-and-whisker plots (coefficients and 95% CIs) showing prediction of left and right side KVIQ scores by imagery modality (visual vs. kinesthetic), UPDRS total motor score, and side-specific bradykinesia and tremor. For the left side, MI score was best predicted by modality and bradykinesia, while right side MI was best predicted by modality alone.

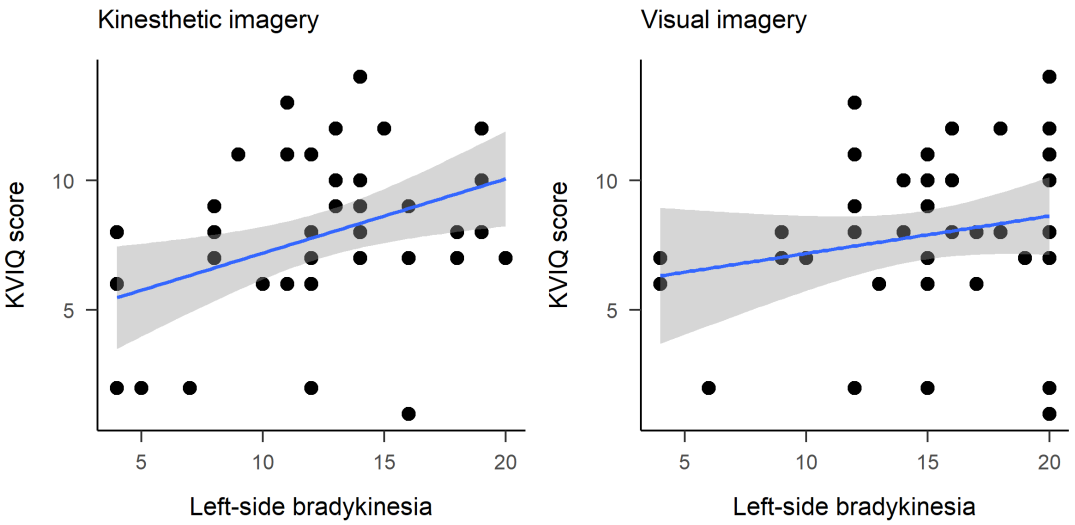


Figure 2. Scatterplots showing the correlation between left-side bradykinesia and left-side KVIQ scores, which was significant for KMI (left) but not VMI (right).

Discussion

The present study examined the influence of motor symptom type and lateralisation on MI vividness in individuals with mild to moderate PD. While MI vividness was not associated with overall motor symptom severity or tremor, greater severity of left-side bradykinesia was associated with increased vividness of kinesthetic MI for the left side of the body.

Although tremor is a common symptom of PD, approximately 30% of individuals with PD do not experience tremor (Crawford III & Zimmerman, 2011). In comparison, almost all individuals with PD experience some degree of bradykinesia (Chaudhuri & Ondo, 2011). It has been proposed that bradykinesia occurs as a result of the failure of basal ganglia output to stimulate cortical mechanisms associated with the preparation and execution of actions (e.g., Berardelli et al., 2001). This is supported by electrophysiological evidence showing that the spatiotemporal pattern of movement related desynchronisation preceding voluntary movement is delayed in untreated PD patients, indicating that motor preparation is impaired (Defebvr et al., 1996).

Several studies have observed that the cortical activity of MI substantially overlaps with the cortical activity during motor planning (Monaco et al., 2020; Jeannerod, 2001; Lotze & Halsband, 2006). For example, the dorsolateral prefrontal cortex and corresponding regions of the frontal thalamus are recruited in both motor preparation and MI but not motor execution (Hardwick et al., 2018). This has subsequently led to the proposal that MI is more closely related to motor planning than to motor execution (Toovey et al., 2020; Toussaint et al., 2013)

Parkinsonian tremor is thought to arise as a consequence of aberrant neural oscillations within the cortico-basal ganglia-thalamic neural circuits (Singh, 2018).

While some studies have observed relationships between low frequency oscillatory activity in the SMA and the onset of voluntary action in healthy individuals (Schmidt et al., 2016; Armstrong et al., 2018), these studies have not determined whether such oscillatory activities have a causal role in motor planning and initiation or are a by-product of in motor planning and initiation (Armstrong et al., 2018). Furthermore, the relationship between the oscillatory activity associated with tremor and motor planning and initiation in PD is still largely unknown. As a result, the different neurophysiology of tremor and bradykinesia and their relationship to motor planning could potentially explain why bradykinesia and tremor may differentially influence MI.

Although the present study did not find a significant influence of tremor on vividness of MI, Helmich and colleagues (2012) found that increased tremor was associated with reduced error in a hand laterality task. Therefore, the influence of specific symptoms on MI may differ according to how MI is assessed. That is, an accumulation of research suggests that MI is multidimensional (Kraeutner et al., 2020). Specifically, the generation, maintenance, and manipulation of MI represent distinct dimensions of MI, and thus may involve different processes (Kraeutner et al., 2020). Relating to this assumption the hand laterality task is thought to involve the maintenance and manipulation of MI, whereas the KVIQ is thought to involve the generation of MI. Moreover, Saimpont et al. (2015) found that MI vividness, measured through the KVIQ-10, did not significantly correlate with measures of MI manipulability (finger-thumb opposition task) or motor chronometry. Therefore, further analyses directly comparing the influence of specific symptoms on multiple measures of MI, are required to confirm this postulation.

However, this is not to say that the KVIQ-10 is not a valid method of assessing MI vividness. Specifically, although relying upon self-report measures, the KVIQ (KVIQ-10 and KVIQ-20; Malouin et al., 2007) has established test-retest reliability (e.g. Randhawa et al., 2010; Malouin et al., 2007), and good concurrent validity with alternative analyses of MI vividness (e.g. MIQ-R; Randhawa et al., 2010). As such, the KVIQ is frequently employed in analyses of MI vividness in individuals with PD (Bek et al., 2019; Abbruzzese et al., 2015; Peterson et al., 2012; Heremans, 2011; Pickett et al., 2012). Therefore, there is substantial reason to assume that the KVIQ is an appropriate analysis to employ when considering the influence of symptomology on MI vividness in PD.

Additional research suggests that MI may be assessed in both a first and a third person perspective (i.e., as if looking at someone else) (Isaac et al., 1986; Roberts et al., 2008). Investigations of gesture (Humphries et al., 2016) and body representation (Conson et al., 2014) in PD, point towards people with PD having an increased tendency to represent actions from the third-person perspective (i.e., as if looking at someone else), which may be due to a difficult in adopting a first person perspective ((De Bellis et al., 2017; Saxe et al., 2006). Thus, it may be that symptomology influences first and third person MI differently. The KVIQ does not specify the person perspective the individual is to take whilst imagining the performance of actions. Therefore additional studies that compare first and third person MI in relation to symptoms are required to confirm this assumption.

The present study is the first to demonstrate a specific influence of left-side bradykinesia on KMI, but the mechanisms underlying this relationship are yet to be determined. One possible explanation for this finding focuses on the cortical lateralisation of MI. In PD, lateralised symptoms are reflective of dopaminergic

degeneration and uptake in the contralateral substantia nigra and putamen (Choe et al., 1998; Lin et al., 2014; Wang et al., 2015), such that left-side bradykinesia reflects disruption in the right lateralised basal ganglia.

While the lateralisation of MI is not yet fully understood, some research suggests that KMI may be more lateralised to the right hemisphere (Ehrlichman & Barrett, 1983). For example, Lebon et al (2018) found that when healthy participants imagine performing a finger tapping sequence especially high KMI was associated with strong activation of the right inferior parietal lobe. Similarly, Zabicki (2019) found a significant correlation between KMI vividness and both the right inferior and superior parietal lobe activation. Therefore, if KMI is a right parietal function (Lebon et al., 2018; Zabicki, 2019), then we may anticipate that left-body bradykinesia may influence MI to a greater extent than right-side bradykinesia. It is, however, important to note that alternative analyses yield conflicting results. For example, Evans et al (2016) observed that when left inferior parietal lobe activity was inhibited using tDCS participants made significantly slower responses when identifying whether a hand was in the correct posture to perform a pre-specified action. Thus implicating the left inferior parietal lobe in kinaesthetic motor imagery. In light of such contradictory findings, the laterality of MI may not fully explain the results obtained in the present study.

The present study observed that despite changes in symptom severity as indicated by UPDRS motor scores, VMI and KMI vividness scores, were temporally stable in the long term (8+ months). Specifically, although the severity of overall motor symptoms, overall bradykinesia and side specific bradykinesia increased across the two time points both overall and side specific VMI and KMI vividness did not significantly alter. This finding, together with the absence of a relationship between

KVIQ scores and overall symptom severity in the above analysis, suggests that MI vividness may be relatively robust to general motor decline in PD, but rather is influenced more specifically by particular symptoms and lateralisation (see also Dominey et al., 1995; Helmich et al., 2007; Helmich et al., 2009).

The laterality of initial symptom onset and subsequent symptomatology in PD has been associated with different profiles. For example left-side rigidity/bradykinesia lateralised symptoms are associated with more rapid disease progression (Gasparoli et al., 2002; Shinotoh et al., 2000; Riederer & Sian-Hülsmann, 2012). Further, while right-lateralised symptoms are associated with language and verbal memory deficits, left-lateralised symptoms are associated with spatial attention, visuospatial orienting, visuospatial memory, and mental rotation deficits (Verreyt et al., 2011). For example, visual imagery scores, assessed by the Vividness of Visual Imagery Questionnaire and Test of Visual Imagery Control, and VMI scores, assessed through mental rotation tasks, are poorer in the presence of predominantly left-side lateralised symptoms in PD (Monaco et al., 2018; Verreyt et al., 2011). Conversely, KMI as measured by the Vividness of Motor Imagery Questionnaire was not found to be influenced by left-side lateralised symptoms. These findings indicate that different profiles of cognitive impairment may contribute to the differential association of left and right lateralised symptoms with MI.

It is, however, important to note that these findings relate to lateralised symptomology rather than unilateral symptomology. Specifically, whilst the participants recruited in this study may have displayed more dominant symptomology in one side of the body than the other (lateralised symptoms), no participants displayed symptoms exclusively in one side of the body (unilateral symptom

presentation). Thus, future research should consider analysing the influence of purely unilateral symptomology on MI vividness.

Another possibility is that the specific influence of left-side bradykinesia on KMI relates to hand dominance. Most of the participants in the present study (93%) were right-hand dominant. In healthy right-handed individuals, KMI is found to be more vivid for the dominant hand than the non-dominant hand (Matsuo et al., 2020). The absence of an effect of right-side bradykinesia in the present study may therefore reflect the tendency for more vivid imagery for the dominant side of the body, such that it is more resistant to symptomatic effects.

Moreover, as the physical performance of left-sided movement is more difficult for right-dominant individuals (Judge & Sterling, 2003; Incel et al., 2002), it may be that bradykinesia in the left side increases attention to movements on that side as they become slower and more effortful than usual. This account would be consistent with previous research that found MI to be slowed in accordance with motor execution in PD (Dominey et al., 1995; Conson et al., 2014; Heremans et al., 2011) and that MI can show lateralised effects in PD (Helmich et al., 2007; Dominey et al., 1995; Conson et al., 2014).

The present study focused on the association of motor symptom severity, specifically bradykinesia and tremor, with measures of MI vividness. Thus, the findings may be limited to explicit measures of MI. Future research should analyse the influence of symptom profiles across a range of MI indices including implicit measures such as hand laterality judgement.

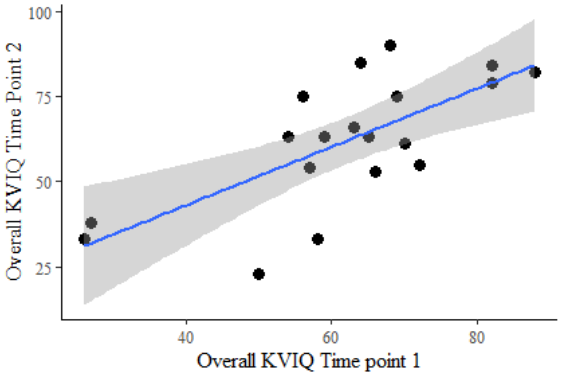
The present study demonstrated that in people with mild to moderate PD, similar to healthy participants, vividness is higher for VMI than for KMI. Furthermore, the severity of left-body side bradykinesia significantly predicted the

vividness of KMI. Finally, overall KVIQ, VMI and KMI vividness scores were temporally stable over 8+ months. The difference in influence of bradykinesia and tremor on KMI may be due to the different neurophysiology underlying these symptoms. Moreover, enhanced baseline vividness of KMI in the dominant body-side, and increased effort and slowing of movements in the non-dominant side may explain the observed enhanced vividness of KMI. These findings indicate that MI, in particular KMI, may differ between body sides in accordance with differences in symptomatology. While further research is needed to replicate and extend these findings, such differences should be taken into consideration when designing MI-based interventions for people with PD.

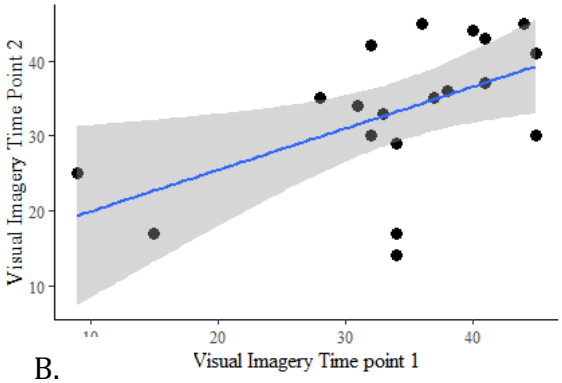
Appendix 1

Test-retest reliability analysis

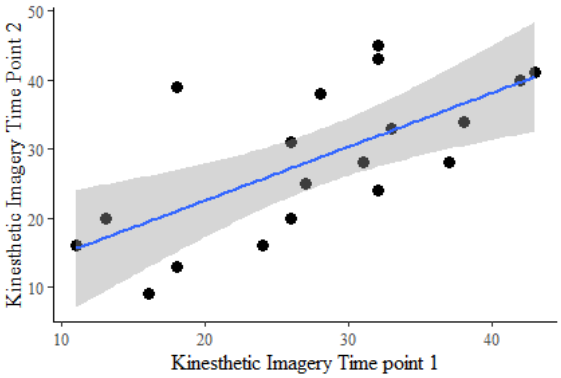
Paired-samples t-test analysis of data from the subset of participants for whom the KVIQ-10 was completed at two time points revealed that overall vividness scores did not differ between the two time points (p = 0 .99). Moreover, intraclass correlation coefficients (one-way random effect model, with the 95% lower confidence limit) revealed good test-retest reliability for overall KVIQ (0.70), and moderate test-retest reliability for both VMI (0.55) and KMI (0.67) between timepoints (interpretation of test-retest reliability statistics follows Portney et al., 2009).



A.



B.



C.

Figure 3. Scatterplots showing the interclass correlation between timepoints one and two for A. overall KVIQ score, B. VMI score and C. KMI score.

Discussion of test-retest reliability analysis

The present study observed that despite changes in symptom severity as indicated by UPDRS motor scores, overall KVIQ, as well as VMI and KMI vividness scores, were temporally stable in the long term (8+ months) in a larger sample than previous research in PD (Randhawa et al., 2010). This finding, together with the absence of a relationship between KVIQ scores and overall symptom severity in the above analysis, suggests that MI vividness may be relatively robust to general motor decline in PD, but rather is influenced more specifically by particular symptoms and lateralisation (see alsoDominey et al., 1995; Helmich et al., 2007; Helmich et al., 2009).

It is, however, important to note that a sensitivity power analysis (alpha=.05 power=.8 N=19) of this analysis yields a sensitivity =.56. Thus effects smaller than .56 are undetectable in this analysis. Subsequently, the conclusions drawn from this analysis should be treated with a degree of caution and further validated by additional larger scale test-retest reliability analyses.

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5.1. Statement of thesis continuous commentary

In Chapter 5, I investigated the relationship between overall and specific symptom (tremor and bradykinesia) severity, and the vividness of motor imagery in individuals with mild-moderate PD. In addition, I also investigated the influence of body side-specific bradykinesia and tremor on body side-specific motor imagery vividness. The present study found that overall symptom severity, overall bradykinesia, and overall tremor did not predict overall motor imagery vividness. However, the extent of left-side specific bradykinesia was associated with the vividness of both overall and left-side specific kinestheic motor imagery. Specifically, greater severity of bradykinesia in the left-side of the body was associated with higher ratings of kinestheic motor imagery vividness.

Reflective exploratory analysis revealed that the individual's with PD who participated in the experiments, within Chapter 4, presented with more severe bradykinesia (M = 16.8 (5.47), out of a possible 44) than tremor (M = 6.17 (5.10), out of a possible 40). More specifically, the extent of left-body bradykinesia was more severe (M = 8.47 (3.95)) than right body bradykinesia (M = 6.8 (3.56)). Therefore, it may have been that the severity of left-body bradykinesia present in those individuals with PD, caused the individuals to have more vivid motor imagery when imagining themselves performing the actions being judged. Which in turn, enabled these individual's to be reliably in tune with their action boundaries.

Chapter 6

Paper Four; The Distorted Body: The perception of the relative proportions of the body is preserved in Parkinson's Disease. Readman, M. R., Longo, M. R., McLatchie, N. M., Crawford, T. J., & Linkenauger, S. A.

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BRIEF REPORT

The distorted body: The perception of the relative proportions of the body is preserved in Parkinson's disease

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Abstract

Given humans' ubiquitous visual experience of their own body, one reasonable assumption is that one's perceptions of the lengths of their body parts should be accurate. However, recent research has shown that large systematic distortions of the length of body parts are present in healthy younger adults. These distortions appear to be linked to tactile sensitivity such that individuals overestimate the length of body parts of low tactile sensitivity to a greater extent than body parts of high tactile sensitivity. There are certain conditions featuring reduced tactile sensitivity, such as Parkinson's disease (PD) and healthy older ageing. However, the effect of these circumstances on individuals' perceptions of the lengths of their body parts remains unknown. In this study, participants visually estimated the length of their body parts using their hand as a metric. We show that despite the reductions in tactile sensitivity, and potential alterations in the cortical presentation of body parts that may occur in PD and healthy older ageing, individuals with mild-moderate PD and older adults of comparable age experience body size distortions comparable to healthy younger controls. These findings demonstrate that the ability to perceive the length of one's body parts is well preserved in mild-moderate PD.

Keywords Parkinson's disease · Motor disorder · Body perception · Somatosensory

Introduction

Humans receive constant visual information specifying the relative proportions of their body. For example, when looking into a mirror the length of the arm relative to the torso is apparent. Consequently, one may assume that individuals will be reliably in tune with the relative proportions of their body parts. However, this does not appear to be the case; for example, although arm span and height are approximately equal, many deem height to be longer (Dreyfuss & Tilley, 1993)

The neural information underlying the perception of body proportions appears to relate the length of body parts to their tactile sensitivity (Linkenauger et al., 2015; Longo 2017). Furthermore, as body part tactile sensitivity is related to the respective cortical representation within the somatosensory cortex (Ackerley et al., 2014; Penfield & Boldrey, 1937), the perception of our body proportions appears to be related to the cortical representation of the body part in the somatosensory cortex (Linkenauger et al., 2015).

The cortical representation of body parts in the somatosensory cortex is heterogeneous (Mancini et al., 2014; Weinstein, 1968). Specifically, there is a relative magnification of cortical area devoted to body parts recruited in complex actions (e.g. the hands; Reed, & Ziat, 2018). Furthermore, as body parts with larger cortical representation display a higher tactile acuity (Reed & Ziat, 2018), tactile sensitivity is not homogenous across the body (Weinstein, 1968).

Heterogeneous tactile sensitivity influences perceptions of tactile size in that the distance between two points is

Public Significance Statement

We assessed how reductions in tactile sensitivity and potential alterations in cortical representation of body parts associated with Parkinson's disease may influence individuals' perceptions of their body proportions. We found that despite these alterations, individuals with Parkinson's perceive their body proportions in a comparable way to both healthy older and younger adults, therefore, the perception of ones body proportions appears to be preserved in Parkinson's.

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perceived to be greater when the points span a region of high tactile sensitivity, for example the palm, than when they span a region of low tactile sensitivity, for example the forearm (Weber's Illusion; Weber, 1834). Furthermore, objects of the same size are perceived to be larger when placed on a region of higher tactile sensitivity (Anema et al., 2008; Weber, 1834). However, the magnitude of Weber's illusion experienced is substantially less (approximately 10%) than would be anticipated if perceived tactile distance was solely derived from tactile sensitivity (Taylor-Clarke et al., 2004). Consequently, the perceptual system must be employing a mechanism that preserves tactile constancy.

One potential account proposes that distorted cortical representations are rescaled according to the visually specified size of the body parts (Taylor-Clarke et al., 2004). Corroborating this, merely seeing the hand significantly reduces the perceived size of tactile stimuli (Longo & Sadibolova, 2013). Alternatively, the 'reverse distortion' hypothesis (Linkenauger et al., 2015), asserts that individuals perceive less sensitive body parts to be disproportionately larger than more sensitive body parts to a magnitude that offsets most of Weber's Illusion. Based on this account (a) less sensitive body parts will be overestimated more, and (b) given equal sensitivity, larger body parts will be distorted less (Linkenauger et al., 2015). Supporting this hypothesis, when estimating the length of their body parts using their hand as a metric, participants overestimate the length of the torso, a body part of low tactile sensitivity (Mancini et al., 2014; Weinstein, 1968), the most, and the foot, a highly sensitive body part (Mancini et al., 2014; Weinstein, 1968), the least (Linkenauger et al. 2015; Linkenauger et al., 2017; Sadibolova et al., 2019).

While it is important to ascertain how healthy individuals perceive their body size, we must also consider clinical conditions that include altered tactile sensitivity such as Parkinson's disease (PD). Although PD is considered to be a paradigmatic movement disorder (Politis et al., 2010), alterations in tactile sensitivity have been observed in PD. For example, increases in two-point tactile discrimination thresholds (Nolano et al., 2008; Schneider et al., 1987), tactile temporal discrimination thresholds (Artieda et al., 1992) and groove width required to distinguish grating orientation (Sathian et al., 1997), relative to age-matched controls have been observed in PD. If perceived body size is distorted as a function of tactile sensitivity, then we may anticipate that the perceived lengths of one's body parts may be altered when tactile sensitivity is altered. Therefore, we may anticipate that people with PD's perceptions of the relative lengths of their body parts may be different from healthy younger and older adults.

These reductions in tactile sensitivity may arise from the significant loss of peripheral epidermal nerve fibres, Meissner corpuscles, and free encapsulated nerves observed in PD (Nolano et al., 2008). Prior research has shown that reducing inflow from peripheral nerves in the hand to the somatosensory cortex results in increases in perceived finger size (Gandevia & Phegan, 1999). Therefore, it may be that reductions in peripheral nerve fibres lead to altered perception of body proportions in PD.

Furthermore, alterations in motor ability have been shown to influence the somatosensory cortical representation of body parts. For example, hand immobilisation results in impaired tactile perception and reduced cortical activation of the corresponding hand representation in the somatosensory cortex (Lissek et al., 2009; Weibull et al., 2011). Furthermore, expansion of cortical representations have been observed following long-term learning in the left hand of string players (Elbert et al., 1995) and in the reading finger of Braille readers (Pascual-Leone et al., 1993; Pascual-Leone & Torres, 1993). As the perception of our body proportions are related to the respective somatosensory cortical representation (Linkenauger et al., 2015; Longo 2017), altered motor ability may influence body perception in PD. Corroborating this, Bassolino et al. (2015) observed that, following 10 h of overuse, individuals perceived the arm to be longer.

Individuals' with PD often display a greater reliance on visual information relative to other (e.g., somatosensory) information (Halperin et al., 2021; Yakubovich et al., 2020). Given that visual information alters the perceived size of tactile stimuli (e.g., Longo & Sadibolova, 2013), an increased reliance on visual information specifying the relative proportions of one's body may mitigate the influence of altered tactile information on the perception of one's body proportions. Under these circumstances we may anticipate that individuals with PD will display the same systematic distortions as young healthy controls.

Throughout healthy ageing reductions in tactile sensitivity (Kenshalo, 1986; Thornbury & Mistretta, 1981; McIntyre et al., 2021), and an increase in spatial thresholds (Sathian et al., 1997), coupled with a decrease in the density and distribution of touch receptors in the skin (Stevens & Patterson, 1995; Wickremaratchi & Llewelyn, 2006) have been observed. Therefore, healthy ageing may also influence perceived body proportions.

To explore the potential influence of PD and healthy ageing on individuals' perceptions of the relative proportions of the body, individuals with mild-moderate PD, healthy older and younger adult controls estimated the length of various body parts using their hand as a metric.

Method

Participants

G*Power software (Faul et al., 2007) was used to perform an a priori power analysis to ascertain the sample size required to achieve adequate power. The required power (1- β) was set at .80 and the significance level (α) was set to .05. Linkenauger et al. (2015) used the same methodology as employed here to analyse the influence of tactile sensitivity (using the hand as a metric vs. a piece of dowel) on perceived body proportions; as we too are comparing groups whose tactile sensitivity may differ, we modeled anticipated effect size on the results obtained by Linkenauger et al. (2015, Experiment 1). Due to this, we anticipated a medium effect size of f = 0.6. For the frequentist parameters defined, a sample size of N = 9 is required to achieve a power of .80 at an alpha of .05.

Thirty healthy young controls (21 females), 30 healthy older adult controls (17 females), and 30 individuals (11 females) with mild-moderate PD participated. Here the exclusion criteria applied to both individuals with PD and healthy controls were those who had a diagnosis of any cognitive or additional neurological conditions beyond PD. Furthermore, as physical disability may itself alter body perception, individuals who presented with a physical disability were ineligible for the study. The mean age between the healthy older adult controls and PD patients did not differ ($t(58) = -1.131$, $p = .263$; Bayes factors provided evidence for the null for all scale-of-effects greater than 14.2 years). Eighty-four participants were right-handed (29 healthy young controls, 27 healthy older adult controls, 28 PD), and six were left-handed (one healthy young control, three healthy older adult controls, two PD patients). All participants had normal or corrected-to-normal vision. Nine participants (five PD, three older adult controls, one younger control) reported a current or a history of a diagnosis of visual impairment, including glaucoma, red/green colour blindness, macular degeneration and convergence inefficiencies.

All participants were screened for the presence of cognitive impairment through the Montreal Cognitive Assessment (MOCA; Nasreddine et al., 2005). As this study was completed virtually, due to the COVID-19 pandemic, a condensed version of the MOCA was completed. Although an abbreviated telephone version of the MOCA, excluding only visual elements, is available, completion of this version of the MOCA requires the participants to state the location of the research group. As the research group conducting this study function out of multiple locations, the research team deemed it appropriate to also remove the orientation questions relating to the location of the research lab. The normal range cut-off point for the entire MOCA is ≥ 26 out of 30 (86.66%) and the telephone-abbreviated MOCA is ≥ 19 out of 22 (86.3%). Transposing this to the subset used within this study (20 questions), the cut-off was set at ≥ 17 (85%). Following this exclusion criterion, two PD patients' data were excluded prior to analysis. Average MOCA scores did not significantly differ between groups ($F(2,84) = .902$, $p = .41$; Bayes factors confirmed evidence for the null when comparing each condition for all scale-of-effects greater than 1.56). One younger control's data were removed prior to analysis as their estimations were ±2 SD away from the means. Subsequently, data from 87 participants (28 PD, 30 healthy older adult controls, 29 young controls) were included in final analysis.

Of the 87 participants included in analysis, 16 (eight PD, four healthy older adult controls, two younger controls) reported a current or history of a diagnosis of psychiatric illnesses, including depression, anxiety and bipolar disorder. Furthermore, 14 participants reported a current or history of a diagnosis of rheumatic illnesses (ten PD patients, four older adult controls).

Parkinsonian symptoms were assessed using the motor aspects of daily living, the motor examination and the motor complications subscales of the Movement Disorder Society Unified Parkinson's Disease Rating Scale (MDS-UPDRS; Goetz et al., 2008). Due to the virtual nature of this study, only the items pertaining to bradykinesia and tremor of the motor examination subscale were assessed. Therefore, bradykinesia and tremor severity scores are reported separately. Furthermore, as not all aspects of the motor examination were completed, a Hoehn and Yahr stage was not calculated. Twenty-seven participants were receiving Parkinsonian medication and were tested under their normal medication regime. Eighteen participants indicated that they experience motor fluctuations, 16 of these participants stated that they were in a typical functioning 'ON' phase at the time of testing. Twenty patients were taking combination drugs (containing levodopa and a peripheral dopa-decarboxylase inhibitor, e.g., Madopar), 17 patients were taking a dopamine agonist (e.g., ropinirole), nine patients were taking a monoamine oxidase inhibitor (e.g., rasagiline) and three patients were taking a catechol-O-methyl transferase inhibitor (e.g., entacapone). Please refer to Table 1 for patient characteristics.

This study was ethically approved both by Lancaster University and the local National Health Service research ethics committee.

Procedure

The study procedure used here replicated the methodology used by Linkenauger et al. (2015), with the only difference

Table 1 Mean (SD) background and medical characteristics for the Parkinson's disease (PD) healthy older adult control and younger control groups

Group	PD	Healthy older adult controls	Younger control
Age, y	65.07 (8.72) Range 51–85	68.00 (8.70) Range 54–86	24.14 (3.85) Range 18–34
Condensed MOCA (20 items included)*	18.54 (1.23) Range 17–20	18.50 (1.22) Range 17–20	18.86 (.915) Range 17–20
Years since diagnosis	5.65 (3.59) Range 1.5–16		
MDS-UPDRS motor aspects of daily living	12.24 (5.37) Range 1–22		
Condensed MDS-UPDRS motor examination-bradkykinesia **	16.54 (4.86) Range 8–29		
Condensed MDS-UPDRS motor examination – tremor ***	7.75 (6.57) Range 0–18		
MDS-UPDRS motor complications	3.82 (4.19) Range 0–15		
Years on medication	5.23 (4.20) Range .08–15		
Time since last dosage of medication (min)	157.86 (139.71) Range 5–540		
Levodopa daily dosage (mg)	625.19 (651.78) Range 100–3240		

* A condensed version of the MOCA comprising 20 questions relating to memory, attention, language, abstraction, delayed recall and four out of six items relating to orientation were administered (normal cut-off point ≥ 17 (85%)

** Average overall bradykinesia score across both sides of the upper and lower body (MDS-UPRDS items included 3.4, 3.5, 3.6, 3.7, 3.8)

*** Average overall tremor score obtained from items relating to postural and kinetic tremor of hands, and overall resting tremor amplitude and frequency (MDS-UPRDS items included 3.15, 3.16, 3.17, 3.18)

being that this study was completed via video call. Participants' video camera facilities were turned on for the duration of the study, enabling the researcher to observe their behaviour and ensure they performed the tasks correctly. To commence this session participants were screened for the presence of mild cognitive impairment, and background health measures were obtained. At this time PD patients' parkinsonian symptoms were assessed.

Participants were asked to make a series of estimates regarding the vertical length of parts of their bodies using their dominant hand as a metric (see Table 2; e.g., how many of your hand lengths would fit into the length of your leg). Hand length was defined as the palm-wrist intersection to the longest fingertip. Participants were encouraged to be as accurate as possible and use fractions where appropriate. Participants provided one estimation for each body part. The order of estimation was counterbalanced. All body parts were defined to the participant prior to their estimation. Following estimation, participants measured the actual length of the body parts estimated. Additionally, hand length was measured. To obtain these measures, participants were asked to call upon the assistance of another individual who placed a soft tape measure over the body region. This occurred whilst the participant was engaged in the video call. Participants were provided with a detailed instruction manual, with additional pictorial representations, detailing the body landmarks that define the lengths of the body parts in question to ensure these measures were accurate.

Table 2 Body parts (and associated definitions) estimated by participants

Body part	Definition
Full body	From the top of head to the bottom of the heel whilst standing
Torso	From the top of the shoulder to the hip bone
Leg	From the hip bone to the bottom of the heel whilst standing
Arm	From the protrusion of the shoulder to the tip of the longest finger when the arm is outstretched
Head	From the tip of the head to the lowest point of the jawline
Foot	From the back of the heel to the tip of the longest toe

Data analysis

Participants' estimates of the length of their body parts with respect to the hand were initially transformed into centimetres by multiplying the body part estimate by the hand length. Following this, accuracy ratios were computed for each body part by dividing the estimated length by the actual length. Consequently, a value over 1 indicates that the participant overestimated the length of that body part, and a value under 1 indicates that the participant underestimated the length of that body part. A Greenhouse-Geisser correction was applied when analyses indicated a violation of sphericity.

To ascertain whether the same overall pattern of body proportion distortion displayed here is congruent to that in the current body of literature (Linkenauger et al. 2015; Linkenauger et al., 2017; Sadibolova et al., 2019), a repeated-measures ANOVA detailing the overall pattern of distortions was completed for each group.

To analyse the influence of altered tactile perception and motoric capabilities, observed in PD, on individual's perceptions of their body proportions; we report a mixed analysis of variance in which group (PD, healthy older adult control, young control) formed the between-subjects measure, body part (full body, torso, leg, arm, head, and foot) formed the within-subjects measure and accuracy ratio formed the dependent measure.

As a single non-significant p-value cannot be used to infer evidence for the null hypothesis (see Lakens et al., 2020), we also report Bayes factors for all 1-df analyses. Bayes factors provide a continuous measure of evidence regarding how well the data were predicted by one hypothesis (e.g., the null; H0), relative to another hypothesis (e.g., the alternative; H1). Bayes factors were calculated using the Dienes and McLatchie (2018) R script calculator and follow Jarosz and Wiley's (2014) thresholds in which Bayes factors between 0.33 and 3 are interpreted as weak and inconclusive, Bayes factors between 0.05 and 0.33 and between 3 and 20 as moderate evidence for the null and experimental hypotheses respectively, and Bayes factors < 0.05 and > 20 as strong evidence for the null and experimental hypotheses, respectively. The model of H1 was specified using the results of Linkenauger et al. (2015, Experiment 1), who interpreted a difference in accuracy ratios of 0.31 as evidence for the alternative hypothesis. Lastly, we report robustness regions to indicate the sensitivity of the categorical conclusions drawn from the Bayes factors to the approximate scale-of-effect used. Robustness regions are reported as $RR(S, L)$, where S corresponds to the smallest scale-of-effect and L to the largest scale-of-effect that would still yield the same conclusion.

Furthermore, to examine the influence of specific disease characteristics, such as years since diagnosis, time since last dose of medication, levodopa equivalent daily dose (LEDD), tremor and bradykinesia, on participants' estimations of the length of their body parts, we report bivariate correlational analyses with a bootstrapping correction applied.

Anxiety significantly influences individuals' perceptions of the maximum extent to which they can perform actions (Graydon et al., 2012). Perceiving the maximum extent to which one can perform an action requires individuals to scale visual information specifying the environment to one's morphologically dictated action capabilities (Proffitt & Linkenuager, 2013), and, therefore, is somewhat contingent upon the individual's representation of the morphology of their body part. Therefore, it may be that anxiety and related psychiatric conditions influence individuals' perceptions of their body proportions. Subsequently a mixed analysis of covariance (ANCOVA) was conducted to ascertain whether psychiatric conditions influenced individuals' perceptions of their body proportions in this sample. Psychiatric conditions did not influence healthy younger controls or individuals with PD's perceptions of their body proportions, nor did controlling for anxiety influence the differences between groups (see 14 for the full statistical analysis). However, the presence of psychiatric conditions significantly influenced the pattern of body size overestimation in healthy older adults.

Results

Overall body proportion distortions

Healthy younger controls

There was a significant main effect of body part ($F(2.649, 74.172) = 12.707$, $p < .001$, $\eta p^2 = .312$). Bayes factors provided moderate to strong evidence that the torso was overestimated the most ($8.14 <$ all $Bs < 1.82 \times 10^5$), and the foot the least ($29.10 <$ all $Bs < 1.82 \times 10^5$; see Table 3). The full body was overestimated more than the arm ($B_{N(0,0.31)} = 7.89$), but the data were inconclusive when comparing the full body with the leg ($B_{N(0,0.31)} = 1.98$) or the head ($B_{N(0,0.31)} = 1.83$). The leg was overestimated to the same extent as the head ($B_{N(0,0.31)} = 0.31$), but the data were inconclusive when comparing the leg with the arm ($B_{N(0,0.31)} = 0.38$). Participants overestimated the length of the arm and head to the same extent ($B_{N(0,0.31)} = 0.23$).

This pattern of distortions reflects that observed by Sadibolova et al. (2019), with the only exception being that we observed that participants overestimated the leg to the same extent as the arm, while Sadibolova et al. (2019) observed the reverse.

Healthy older adult controls

There was a significant main effect of body part $F(2.37, 68.822) = 6.601$, $p < .001$, $\eta p^2 = .185$). Bayes factors provided strong evidence that all body parts were overestimated

Table 3 Group means (and standard deviations) of estimated/actual body length accuracy ratio for each body estimates across the Parkinson's disease (PD), healthy older adult controls and young control groups

	Healthy younger adults	Healthy older adults	PD
Body part			
Full body	1.417 (.082)	1.612 (.169)	1.302 (.344)
Torso	1.625 (.104)	1.671 (.099)	1.604 (.468)
Leg	1.292 (.070)	1.433 (.118)	1.219 (.431)
Arm	1.220 (.058)	1.320 (.082)	1.189 (.287)
Head	1.242 (.049)	1.319 (.065)	1.194 (.329)
Foot	1.031 (.032)	1.096 (.058)	1.094 (.238)

more than the foot (11.78 < all $Bs < 2.70 \times 10^7$; see Table 3). There was moderate to strong evidence that participants overestimated the torso more than the arm ($B_{N(0,0.31)} = 14.90$) and head ($B_{N(0,0.31)} = 638.12$), but the evidence was inconclusive when comparing the torso to the full body ($B_{N(0,0.31)} = 0.48$) or leg ($B_{N(0,0.31)} = 1.95$). The data were inconclusive for all other comparisons (0.53 < all Bs < 1.79) with the exception of the comparison between the arm and head, for which there was moderate evidence for the null hypothesis ($B_{N(0,0.31)} = 0.29$).

This pattern of distortions is comparable to that observed by Sadibolova et al., (2019), with the only deviation being that here participants overestimated the arm and leg to the same extent, whereas Sadibolova et al. (2019) observed that participants overestimated the arm more than the leg.

Individuals with Parkinson's disease (PD)

There was a significant main effect of body part ($F(3.64, 98.30) = 10.27$, $p < .001$, $\eta p^2 = .276$). Bayes factors provided extremely strong evidence that participants overestimated the torso the most (138.77 < all $Bs < 1.44 \times 10^6$; see Table 3). There was strong evidence that participants overestimated the full body relative to the foot ($B_{N(0,0.31)} = 21.10$). There was moderate evidence that estimates for the leg, arm and head did not differ from one another (0.17 < all Bs < 0.31). The data were inconclusive for all other comparisons (0.41 < all Bs < 1.12).

This pattern of distortions parallels previous literature; however, individuals with PD overestimated the size of the head more and the arm less than previously observed (Linkenauger et al., 2015; Sadibolova et al., 2019).

The influence of PD on the perception of body proportions of self

There were no significant differences in the accuracy of the perceived length of body parts between the PD (M_{acc}= 1.267, SE_{acc} = 0.058), healthy older adult (M_{acc}= 1.408, SE_{acc} = 0057), and younger control groups (M_{acc}= 1.304, SE_{acc} = 0.057; $F(2, 84) = 1.637$, $p = .201$, $\eta_p^2 = .038$; see Fig. 1). Bayes factors provided strong evidence that PD patients and healthy older adults overestimated to the same extent ($B_{H(0,0.31)} = 0.09$), moderate evidence that PD patients and healthy younger adults overestimated to the same extent ($B_{H(0,0.31)} = 0.28$), and inconclusive evidence for the null when comparing healthy older adults and healthy younger adults ($B_{H(0,0.31)} = 0.55$).

The influence of PD characteristics on self perceptions of their body proportions

Years since diagnosis, years on medication, time since last dosage of medication, the presence of tremor and motor complications were not related to the accuracy of perceived body proportions. LEDD correlated with head ($r = .561$, $p = .004$) accuracy. Overall motor aspects of daily living correlated with head ($r = .527$, $p = .008$) and arm ($r = .413$, $p = .045$) accuracy. Bradykinesia correlated with head ($r = .514$, $p = .010$), arm ($r = .516$, $p = .010$) and torso ($r = .513$, $p = .010$) accuracy (see 14).

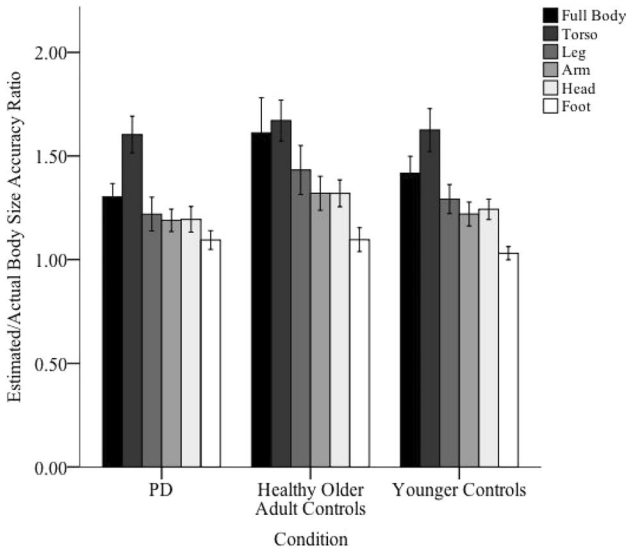

Fig. 1 Group means of estimated/actual body length accuracy ratio for each body estimate across the Parkinson's disease (PD), healthy older adult controls and young control groups. Error bars represent ±1 SE calculated within each condition

Discussion

Systematic distortions in the perception of the relative proportions of body parts have been observed in healthy younger adults (Longo, 2017; Linkenauger et al., 2015; Linkenauger et al., 2017; Sadibolova et al., 2019). However, the influence of altered tactile perception and motor capabilities in ageing and PD on the perception of the relative proportions of the body remains unknown.

Across all groups, the pattern of relative body size distortions paralleled previous findings (Linkenauger et al., 2015; Linkenauger et al., 2017; Sadibolova et al., 2019). This may indicate that impaired tactile sensitivity and motor function do not alter the distortion in the perception of one's body proportions. Alternatively, it may be that alterations in tactile sensitivity and motor abilities induce variability in individuals' perceptions. In this sense, while some may overestimate the length of their body parts, others underestimate the length of their body parts. Through this, although the average may not differ from younger controls, we would expect greater variability. Inspection of group variances indicated

that the variance across all groups differed only for full body ($p < .001$) and leg ($p = .012$) estimates. Consequently, it is unlikely that the results are an artefact of variability, and rather reflect the preservation of body distortions in PD and healthy older adults.

Reduced bradykinesia was associated with more accurate perceptions of the relative lengths of the head, arm and torso in individuals with PD. However, as all individuals with PD recruited here had mild-moderate PD, additional studies recruiting individuals with more advanced PD are required to fully decipher the influence of clinical characteristics.

As we analysed the influence of altered tactile perception and motor capabilities on the perception of the *relative* length of ones' body parts, the data analysed are reflective of the ratio of hand length to the length of each body part. Subsequently, the conclusions only follow if hand size perception is the same across all participants. It is, however, possible that individuals with PD and healthy older adults perceive their hand size or entire body as smaller or larger than controls, and this was not captured. Subsequently, additional studies analysing absolute body size perception (e.g., Longo & Haggard's (2010) implicit hand map methodology or comparison of body lengths to a visual standard, e.g., Slade & Russell (1973)) are required to ascertain whether absolute hand and body size perception is also preserved. Moreover, whilst this work relates body size perception to tactile sensitivity, no direct assessment of tactile sensitivity occurred. Therefore, studies that directly relate measured tactile sensitivity to the perception of the relative lengths of body parts are required to confirm this link.

The observed preservation of the perceptual abilities is based on visual judgements. Therefore, whilst visually guided perceptions may remain unaffected, analysing body perception via alternative channels may reveal a different picture. In this sense although we did not observe an effect of age, previous studies have found significant alterations of body representation in ageing through the landmark localization task (Sorrentino et al., 2021). Similarly, neurotypicals embody tools and alien limbs within their body representations (e.g., Garbarini et al., 2015); however, this ability appears impaired in PD (Scarpina, et al., 2019).

It may be that the observed reductions in tactile sensitivity are not paralleled with alterations in the somatosensory cortex. Specifically, as alternations in tactile perception have been observed in the fingers (Nolano et al., 2008; Schneider et al., 1987), forearm (Sathian et al., 1997), thigh (Nolano et al., 2008), leg (Nolano et al., 2008) and foot (Prätorius et al., 2003), it appears that tactile sensitivity is globally reduced in PD. Consequently, the somatosensory cortical representation of all body parts may be altered uniformly, and so preserving the topographical representation of the body. If body size perception reflects the inverse of the representation of body parts within the somatosensory cortex (Linkenauger et al., 2015), under these circumstances alterations in body perceptions will not occur. However, future research analysing clinical circumstances in which localised alterations in tactile sensitivity is required to confirm this postulation.

Dopaminergic medications are the first-line treatment for PD (Dorszewska et al., 2014; Rogers et al., 2017). Whilst initially these medications offer vast reductions in symptoms (Marsden & Parkes, 1977), following several years of levodopa therapy around 50% of patients experience fluctuations in their motor capabilities (Dupont et al., 1996), known as the *on-off phenomenon* (Bhidayasiri, & Tarsy, 2012). During 'on' times individuals can perform motoric actions as normal; however, during 'off' times the individual's ability to perform motor actions is severely compromised (Calne et al., 1996; Lees, 1989).

Although some research indicates that altered motor ability influences cortical representations within the somatosensory cortex (Lissek et al., 2009; Weibull et al., 2011), these effects occur following prolonged alterations in motoric abilities. For example, reduced cortical activation of the hand representation has been observed following 4–10 weeks (Lissek et al., 2009), 3 days (Weibull et al., 2011) and 10 h of hand immobilisation (Avanzino et al., 2011; Avanzino et al., 2014; Bassolino et al., 2014). Moreover, the area of cortical alteration correlates with the duration of motor disruption (Liepert et al., 1995). Antiparkinsonian medication reduces motor fluctuations (DeMaagd & Philip, 2015; MacMahon et al., 1990), therefore most individuals with PD typically do not experience severely reduced motoric abilities for prolonged periods (Nutt et al., 1984). Specifically, here 50% of participants reported they had no on/off time, 30% spent ≤ 25% of their waking hours in an 'off' state, 14% spent 26–50% of their waking hours in an 'off' state, and 6% spent 51–75% of waking hours in an 'off' state. As individuals with PD motor capabilities are typically not severely reduced for prolonged periods, the cortical representation of the respective affected body part may not be altered.

Alternatively, individuals with PD may employ compensatory mechanisms to preserve their perceptions of their body proportions. For example, dopaminergic medication somewhat normalises tactile perception in PD (Conte et al., 2010; Lee et al., 2005; Lyoo et al., 2012; Shin et al., 2005). Thus dopaminergic medication may normalise individuals' body proportion perceptions.

Moreover, we found that the presence of psychiatric conditions significantly influenced the pattern of body size overestimation in healthy older adults but not in individuals with PD or younger adults. Some evidence suggests that dopamine receptor deficiencies are associated with depression and anxiety (e.g., Leggio et al., 2013; Moraga-Amaro et al., 2014). Dopaminergic medications used to treat PD mitigate dopamine receptor deficiencies by effectively replacing lost dopamine (Gandhi & Saadabadi, 2021). Therefore, it may be that dopaminergic

medication also protects the individual's perceptions from the influence of the presence of psychiatric conditions.

Individuals with PD place greater reliance on visually specified information compared to other information (Halperin et al., 2021; Yakubovich et al., 2020). This reliance upon the visually specified lengths of their body parts may somewhat mitigate the influence of altered tactile sensitivity when judging the relative proportions of one's body parts. However, future research analysing eye-movement fixation patterns, whilst estimating the relative proportions of their body parts, are required to support this assumption.

In summary, this study demonstrated that despite the reductions in tactile sensitivity and motoric capabilities, the perceptions of individuals with mild-moderate PD of the relative lengths of their body parts are similar to that of healthy older and younger adults. Appendix Table 4

Appendix A

Analysis of covariance – The influence of anxiety on the perception of body proportions

Healthy younger adults

Analysis revealed that there was no significant interaction between body part estimate and the presence of psychiatric conditions (($F(2.64, 71.53) = .813$ $p = .477$).

Healthy older adults

Analysis revealed that the presence of psychiatric conditions in healthy older adults significantly influences body size perception (($F(2.50, 70.10) = 5.88$ $p = .002$).

Parkinson's disease

Analysis revealed that there was no significant interaction between body size perception and the presence of psychiatric conditions (($F(3.57, 92.80) = .503$ $p = .713$).

Across all conditions

Analysis revealed that the presence of psychiatric conditions did not significantly influence body perception between the three participant groups (($F(2, 83) = 1.032$ $p = .173$).

C. Bootstrap results are based on 1000 bootstrap samples

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Data availability All data generated or analysed during this study are included in this published article and its supplementary files.

Code availability No substantial code was used in this analysis

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Declarations

Conflicts of interest/Competing interests The authors have no conflicts of interest to declare that are relevant to the content of this article.

Ethics approval All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki Declaration and its later amendments or comparable ethical standards. The study was approved by the National Health Service Research Ethics Committee (IRAS number: 237405; protocol number: 0.2.)

Consent to participate Informed consent was obtained from all individual participants included in the study.

Consent for publication All participants provided informed consent for their data to be included in publication.

Table 4 Pearson correlations between average estimated/actual body part accuracy ratio and Parkinson's Disease characteristics

	Full Body Accuracy	Torso Accuracy	Leg Accuracy	Arm Accuracy	Head Accuracy	Foot Accuracy
Years since diagnosis	-.080	.009	-.111	.195	.165	.092
Years on medication	-.158	-.045	-.228	.086	.037	-.058
Time since last dosage of medication (minutes)	.113	-.133	-.187	-.163	-.168	-.309
LEDD	.042	.004	-.060	.066	.561**	.361
UPDRS motor aspects of daily living	-.084	.263	-.122	.413*	.527**	.260
UPDRS Tremor	-.326	.035	.009	.114	.110	-.189
UPDRS Bradykinesia	-.011	.513*	-.190	.516**	.514*	.306
UPDRS motor complications	-.010	.075	-1.84	.207	.371	.301

** Correlation is significant at the 0.01 level (2-tailed)

* Correlation is significant at the 0.05 level (2- tailed)

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6.1. Statement of thesis continuous commentary

In Chapters 3-5, I investigated how mild-moderate idiopathic PD influences perceptual-motor calibration and the perception of ones action capabilities. In Chapter 6, I then shifted focus and explored how PD is related to the perception of the relative proportions of the body.

Healthy younger adult's perceptions of the length of their body parts appear to relate body part length to the combination of visual and tactile information for the given body (Linkenauger et al., 2015; Longo 2017). This results in large systematic distortions in the relative proportions of the body. Specifically, less sensitive body parts are perceived to be disproportionately larger than highly sensitive body parts (Linkenauger et al., 2015). Although PD is typically conceptualised as a motor disorder (Hughes, 1994), alterations in tactile perception have been observed in PD (Schneider et al., 1987; Nolano et al., 2008; Artieda et al., 1992; Sathian et al., 1997). Subsequently, in the present paper, I investigated the influence of alterations in tactile sensitivity, and potential alterations in the cortical presentation of body parts, that may occur in PD and healthy older ageing on individuals' perceptions of the relative proportions of their body. I showed individuals with mild-moderate PD and older adults of comparable age, experience body size distortions comparable to healthy younger controls. Thus demonstrating that the perceptions of the relative lengths of one's body parts are preserved in mild-moderate PD.

Chapter 7

7. General discussion and Conclusions

7.1 Summary of Studies

Successful interaction within one's environment is contingent upon *perceptual-motor calibration;* accurate calibration to one's action capabilities allows for the distinction between possible and impossible opportunities for action (Ramenzoni, 2017). A wealth of research has investigated perceptual-motor calibration in healthy younger adult controls, whose action capabilities are largely stable or are subjected to stable changes (e.g. Carello et al., 1989; Linkenauger et al., 2009; Linkenauger et al., 2012; Warren, 1984 Warren & Whang, 1987; Franchak &Adolph, 2012; Ishak et al., 2014)). However, the influence of clinical conditions characterised by unstable variability in one's action capabilities, such as PD remains unknown. Therefore, in this thesis, I explored how perceptual-motor calibration, specifically the perception of action capabilities, may be influenced by PD. I then investigated how specific PD symptomology may influence individuals with PD's motor imagery capabilities, and how the ability to generate vivid motor imagery may be related to the perception of one's action capabilities. Finally, I shifted gears and investigated how PD may influence ones' representations of their body proportions. Through these investigations, I aimed to determine whether a deficit in the calibration between perceptual and motor systems occurs in PD.

In Chapter 3, I showed that when one's action capabilities for grasping are artificially made more variable, the perceptual system, calibrates to the average action capability experienced by type (regardless of the frequency of experience gained with each action capability). In Chapter 4, I found that individuals' with PD's perceptions

of their action boundaries for reaching, grasping and aperture passing did not differ significantly from the control group, in terms of the accuracy. In Chapter 5, I found that overall symptom severity, overall bradykinesia, and overall tremor did not predict overall motor imagery vividness. However, the extent of left-side specific bradykinesia was associated with the vividness of both overall and left-side specific kinesthetic motor imagery. Specifically, greater severity of bradykinesia in the left-side of the body was associated with higher ratings of kinesthetic motor imagery vividness. Finally, in Chapter 6, I found individuals with mild-moderate PD experience distortions in body size across different body parts analogous to the pattern of distortions observed in healthy older and younger adult controls. Taken as a whole, these findings suggest that the perception of one's action capabilities, motor imagery and overall body perception are preserved in PD. Thereby, based on these findings I make an argument that PD is not associated with a deficit in the calibration between perceptual and motor systems.

I will now discuss the potential roles of action capabilities prior to the onset of PD, medication, and an increased reliance on visual information in the preservation of these abilities. However, ultimately I will argue that PD is not associated with a deficit in the calibration between perceptual and motor systems. Following this, I will discuss how these findings fit within the current body of literature. Finally, this thesis will conclude by highlighting the importance of understanding how PD may influence perceptual-motor calibration, motor imagery and body perception.

7.2 Potential compensatory mechanisms that may lead to the preservation of perceptual-motor calibration, and body perception in Parkinson's disease

7.2.1 Prior Experiences

Logically, one's action boundaries are learnt over time through perceptual-motor experience gained from motor exploration of one's environment (Gibson, 2000). That is, healthy younger individuals are reliably in tune with their action boundaries as a result of a lifetime of pairing visual information with motor commands (Proffitt & Linkenauger, 2013). Since the onset of PD typically occurs between 60-69 years of age (Pagano et al., 2016), the onset of variability in ones action capabilities occurs late in said individual's life. Therefore, it may be that individuals with PD simply disregard their limited variable perceptual-motor experience, obtained during the course of PD progression, and rather calibrate to their stable action capabilities prior to the onset of PD.

Consider an individual, who develops PD symptomology at 65, starts to experience motor fluctuations at 70, and is estimating their action capabilities at 80, for example. This individual will have had approximately 52 years (from early adulthood, (say 18) to the point at which their motor capabilities become variable) of perceptual-motor experience with presumably, relatively stable, or gradually declining, action capabilities. Given that we become in tune with our action capabilities due to a wealth of learning (Gibson, 2000; Proffitt & Linkenauger, 2013), it may be that this individual will disregard their limited (10 years) variable perceptual-motor experience, and rather calibrate to their wealth (52 years) of presumably largely stable perceptual-motor experience, prior to the onset of PD.

Somewhat in line with this postulation, previous research suggests that individuals with PD are not reliably in tune with the severity of the symptoms they present. For example, 30-50% of individuals with PD indicate their symptoms are less severe than clinicians rate them to be (Maier, et al., 2012). Thus, suggesting that individuals' with

PD may not update to their altered capabilities and rather remain calibrated to their capabilities prior to the onset of PD.

If this assumption is correct, then one would anticipate that individuals with PD would be unable to flexibly adjust their perceptions to account for alterations in their action capabilities. That is, if individuals with PD disregard altered perceptual-motor experience, we would anticipate that they would not update their perceptions to account for alterations in their action capabilities. For example, individuals with PD would not update their perceptions for reaching when reaching with a tool, or when arm length is extended in VR. Indeed, investigating whether individuals with PD flexibly update their perceptions, to account for alterations in their action capabilities, was one of the original aims of this thesis. However, due to COVID-19 testing restrictions, such investigations were prohibited (See COVID-19 Impact Statement). Therefore, future research should expand upon the theoretical basis presented in this thesis, and investigate whether PD is associated with deficits in updating ones perceptions following alterations in their action capabilities.

The postulation that individuals with PD will disregard variable perceptual-motor experience rests upon the assumption that when judging one's action capabilities individuals, individuals with PD will retrieve memories regarding their prior motor capabilities, and calibrate to the remembered capabilities (Baddeley & Hitch, 2001). This stipulation seems somewhat unlikely on a number of levels. First, the energetic benefits obtained from the visual perceptual system must outweigh the metabolic costs associated with its functioning. Here, the computational costs associated with retrieving and holding memories of one's prior motor capabilities, for the individual then to scale the visually specified environment to (Proffitt & Linkenauger, 2013), are high. Conversely, within the parameters of the tasks in Chapter 3, successfully

perceiving the extent to which an individual can perform an action is of very little benefit. Therefore, the costs associated with this computationally costly mechanism seem to far outweigh the benefits. Subsequently, in line with the theory of evolutionary psychology (Buller & Hardcastle, 2000), this mechanism seems highly unlikely.

Reflecting upon previous literature considering motor imagery further casts doubt on the application of this mechanism. Specifically, individuals' with PD's motor imagery is reflective of their current action capabilities. For example, individual's with PD's motor imagery is slowed in accordance with slowing motor execution (Dominey et al., 1995; Conson et al., 2014; Heremans et al., 2011) can show lateralised effects (Helmich et al., 2007; Dominey et al., 1995; Conson et al., 2014) and is reflective of motor fluctuations (Dominey, 1995).

Some evidence suggests that when deciding whether performance of a given action over a visually specified range is possible, the perceiver mentally simulates the action to be performed (Witt & Proffitt, 2008). Given that individuals with PD's motor imagery is reflective of their current motor capabilities, it would stand to reason that when perceiving one's action capabilities, individuals will mentally simulate the action in line with their current, variable, action capabilities. Under these circumstances, individuals with PD would not be disregarding their variable perceptual-motor experience obtained during the course of PD progression. Thus, further buttressing the assumption that the application of this mechanism is unlikely.

The doubt of the application of this mechanism is further supported within the empirical data obtained within this thesis. In Chapter 4 I found that years since diagnosis, was not significantly related to the accuracy of perceived reaching, grasping or aperture passing abilities. Years since diagnosis can serve as a measure of

the ratio of perceptual-motor experience prior to PD onset compared to during the progression of PD. Specifically fewer years since diagnosis would represent a ratio in which perceptual-motor experience prior to PD onset outweighs perceptual-motor experience during the progression. Given that years since onset did not influence the accuracy of perceived action boundaries, it seems somewhat unlikely, within the parameters of the population sampled here, that this postulation accurately explains the observed results.

7.2.2 State Dependent Calibration

Individuals learn their action boundaries over time as a result of perceptual-motor experience gained from motor exploration of one's environment (Gibson, 2000; Proffitt & Linkenauger, 2013). Given that individuals with PD experience both 'On' and 'Off' times daily for many years, presumably they will gain sufficient perceptual motor experience during both 'On' and 'Off' times to reliably calibrate to multiple *state dependent* action capabilities. Specifically, it may be that instead of simply disregarding their limited variable perceptual-motor experience and rather calibrating to their stable action capabilities prior to the onset of PD, individuals with PD may acquire a state-dependent adaptation to their on/off variability. By such an account, individuals with PD will have different perceptual-motor calibrations specific to their 'On' or 'Off' state.

Corroborating the assumption of state dependent adaptation, Brennan et al. (2012) observed that with experience individuals could maintain two separate context dependent perceptual-motor calibrations for standard walking and walking on a treadmill. Specifically, Brennan et al. (2012) had participants engage in 20 minutes of standard walking, in which participants followed a 1.61 km walking route on the

University of Virginia grounds, or treadmill walking, in which participants walked on a treadmill at a pace of 4.83 km/h, for a course of 15 sessions (7 normal walking and 8 treadmill walking). On completion of the walking condition perceptual motor calibration was assessed through forward drift. Forward drift is the notion that walking in the absence of perceptual flow (on a treadmill) disrupts the perceptual motor calibration between the flow of the perceptual world and locomotion. Subsequently, when individuals attempting to walk in-place without vision they inadvertently drift forward (Proffitt et al. 2003; Durgin et al., 2005). Through this, Brennan et al (2012) demonstrated that the magnitude of forward drift following treadmill walking decreased as a function of increased experience of walking on treadmills. Importantly, no alterations in forward drift were observed in the standard walking condition. Thus, these results suggest that alterations in the perceptual-motor aftereffect following treadmill experience are not attributable to general changes in forward drift, and rather are indicative of participants maintaining two separate context dependent perceptual-motor calibrations. Specifically, as experience walking on a treadmill was acquired, the context of walking on a treadmill (walking in the absence of perceptual flow) became sufficiently distinguished from the standard walking context (walking in the presence of perceptual flow). Which, in turn allowed facilitated the maintenance of two separate context dependent perceptual-motor calibrations. If individuals have the capability to develop context dependent perceptual-motor calibrations following the limited perceptual motor experience gained in this circumstance, it is likely that individuals with PD, who have experienced years of context ('On' or 'Off' time) dependent motor abilities, will too have developed context (state) dependent perceptual-motor calibrations.

Relating these assumptions to the context of Chapter 4, all participants reported that they were in an 'On' time at the point of participation. Therefore, one would anticipate that individual's perceptions would have been a reflection of their state dependent, 'On' time, action boundary. Individuals' symptoms are under good control, and so they can perform actions largely 'normally', in 'On' times. Therefore, we would anticipate that individuals with PD's state dependent 'On' time action boundary would reflect their true morphologically derived capabilities, and so not differ from healthy older adult controls.

Furthermore, state dependent calibration may too effectively explain the differences in the results obtained regarding artificial variability (Chapter 3) and natural variability (Chapter 4). Specifically, during the test trials of the artificially induced variable grasp condition (Chapter 3) participants were asked to place their hands out of sight. Therefore, the participants did not know which action boundary (hand size) was applicable to the task they were completing. Thus preventing them from a context (state) dependent calibration. Comparatively, individuals with PD (Chapter 4) were all well aware of the context (whether they were in an 'On' or 'Off' time) of their estimations, thus enabling them to employ a context (state) dependent calibration.

If individuals with PD are indeed employing state dependent calibration, then one would anticipate that individuals with PD's perceptions of their action capabilities would differ dependent upon the context of their estimation. Specifically, whether they are in an 'On' or 'Off' time at the point if estimation. Given that this study was the first to consider the influence of the PD on perceptual-motor calibration and the perceptions of one's action, whether individuals with PD have different state dependent calibrations remains unknown. Therefore, future research could explore

this by assessing individuals with PD's perceptions of their action capabilities both whilst in an 'On' time and 'Off' time and analysing whether the two differ.

7.2.3 Medication

Following several years of chronic levodopa drug therapy, many individuals with PD develop 'motor complications', including fluctuations in one's motor capabilities (Dupont, et al., 1996; Marsden & Parkes, 1977). That is, with disease progression and prolonged drug therapy the benefit of levodopa "wears off" between doses such that individuals fluctuate between 'On' and 'Off' responses to their dopaminergic medication (Obeso et al., 2000b). Ultimately, these fluctuations give rise to a high degree of variability in individuals' ability to perform actions. Which, presumably, gives rise to a high degree of variability in perceptual-motor experience used to specify one's action capabilities. This high degree of variability in perceptual-motor experience may then prevent individuals' with PD from being reliably in tune with their action boundaries.

The occurrence of motor fluctuations is largely associated with the consumption of levodopa (Stocchi et al., 2010). However, the prevalence of 'Off' times can be reduced by adjunctive therapies, such as dopamine agonists, monoamine oxidase inhibitors, and catechol-O-methyl transferase inhibitors (Ondo, 2011). Motor fluctuations are a substantial clinical burden, and reduce individuals with PD's quality-of-life (Tanner, 2020). Thereforem it is common practice within the clinical treatment of PD to prescribe adjunctive medications with levodopa medication. Within the studies presented in this thesis, 40% of participants in Chapter 4, and 63% of participants in Chapter 6 were taking an adjunctive medication in combination with their levodopa medication.

It may be that antiparkinsonian medications, specifically adjunctive medications, provide some form of protection when judging one's action capabilities within Chapter 4. That is, as the degree of variability in perceptual-motor experience of paring visual information with their altered action capabilities is reduced, individuals may be able to gain sufficient consistent perceptual-motor experience to rapidly recalibrate their altered action capability. Thereby, enabling them to be reliably in tune with their altered action boundaries.

Moreover, previous research has observed that dopaminergic medication somewhat regulates tactile abnormalities in PD. For example, the temporal interval required for two tactile stimuli to be perceived as distinct is significantly higher when individuals have not taken medication for 12 hours compared to when under their normal medication regime (Lee et al., 2018; Conte et al., 2010; Lee et al., 2010). Similarly, grating orientation thresholds, a test of tactile spatial resolution (Van Boven & Johnson, 1994), are significantly reduced following 3- 10 months of antiparkinsonian medication therapy (Shin et al., 2005). Thus indicating that tactile spatial resolution is enhanced following antiparkinsonian therapy. The perception of one's body proportions appears to relate the length of one's body parts to the combination of visual and tactile information (Linkenauger et al., 2015). As antiparkinsonian medication somewhat regulates tactile perception, it may be that antiparkinsonian medication leads to the preservation of distortions in the relative proportions of one's body, in PD.

However, in Chapter 4, I found that levodopa equivalent daily dosage (LEDD; an artificial summary of the total levodopa a patient receives daily (Julien et al., 2021), was not significantly related the accuracy of perceived reaching, grasping or aperture passing abilities. Similarly, LEDD only correlated with the accuracy of perceived

head size (See appendix of Chapter 6). Therefore, it seems somewhat unlikely, given the parameters of the population sampled here, that medication leads to the perseveration of perceptual-motor calibration and body perception in PD.

Supporting this assumption, previous studies have found that medication does not significantly influence individuals motor imagery abilities. Specifically, no significant differences in motor imagery vividness were observed when individuals had not taken medication for 12 hours prior to analysis compared to when under their normal medication regime (Peterson et al., 2012). However, to fully rule out medication as an influencing factor, future research could explore whether individuals with PD's perceptions of their action capabilities and body are different prior to commencing drug therapy or when medication has been withdrawn for a sufficient period (per the prior literature 12 hours).

7.2.4 Reliance upon visual information (with specific regard to the perception of the relative proportions of one's body)

Vision, a dominant sense in humans, is highly relied upon by all individuals everyday. Such that, a recent survey found that that vision is the sense that individuals are most afraid to lose (Hutmacher, 2019). Importantly, it is frequently observed that people with PD display greater reliance upon visual information than healthy controls (Halperine et al., 2021). For example, individuals with PD overweigh visual cues when integrating them with vestibular cues (Yakubovich et al., 2020). Moreover, individuals with PD are less accurate than healthy controls when pointing (Adamovich et al., 2001), reaching or grasping (Schettino et al., 2006) an object in the dark.

This increased dependence on visual information may serve as a compensatory mechanism when estimating the relative proportions of one's body. Specifically, the perception of one's body proportions appears to relate the length of one's body parts to the combination of both visual and tactile information (Linkenauger et al., 2015). Some evidence suggests that looking at a body part can enhance tactile acuity in that body part (e.g. Kennett et al., 2001; Serino et al., 2007). Moreover, merely seeing the hand significantly reduces the perceived size of tactile stimuli (Longo & Sadibolova, 2013). Subsequently, placing greater reliance on visual information when integrating visual and tactile may somewhat mitigate the influence of altered tactile sensitivity judging the relative proportions of ones body parts.

Importantly, alterations in tactile acuity and the perceived size of tactile stimuli occur following direct vision of the body part (Kennett et al., 2001; Serino et al., 2007;Longo & Sadibolova, 2013). However, when making estimations of the relative proportions of ones body, in Chapter 6, participants were not directly viewing the body part at the time of estimation. Subsequently, it seems unlikely that increased reliance upon visually specified information would mitigate the influence of altered tactile sensitivity when judging the relative proportions of ones body, given the parameter's of the methodology employed (Chapter 6).

However, to rule out increased reliance upon visual information as a compensatory mechanism, leading to the preservation of distortions in perceived body size across different body parts, future research should consider employing eye-tracking methodologies during estimation of the relative lengths of their body. Patterns of eye movement fixation, while individuals estimate the relative proportions of their body, have not previously been analysed. However, alternative research has revealed systematic eye-movement fixation patterns, when estimating the size of their

overall body (Gardner et al.,1990; Gardner & Morrell, 1991). Therefore, investigating whether individuals with PD display different gaze fixation patterns would provide strong evidence to support or refute the existence of a visual compensatory mechanism.

7.2.5 The preservation of calibration between perceptual and motor systems, or different sensory systems in PD.

Importantly, all results obtained within this thesis converge in one fundamental respect. That is, all experiments did not observe significant differences in perceptual-motor capabilities between individuals with mild-moderate PD and healthy older controls, of comparable age. Given this high degree of convergence, it appears reasonable to assume that the preservation of perceptual-motor capabilities in PD is the most likely explanation for the obtained results.

Occam's razor is the principle than an explanation of observed results should be no more complicated than is necessary (Berger & Jefferys, 1992). When applied to theoretical development, Occam's razor principle asserts that when all is equal, the theory that rests upon the fewest assumptions is most likely true.

Theorising that individuals with PD simply disregard their limited variable perceptual-motor experience obtained during the course of PD progression, and rather calibrate to their stable action capabilities prior to the onset of PD, rests upon a number of assumptions. Specifically, (1) the perceptual system will favor a computationally costly process and (2) that individuals with PD possess the memory capabilities to carry out this process. Similarly, theorising that medication leads to the preservation of perceptual-motor processes rests on the assumptions (1) that the medication, consumed by those who participated in this series of studies, effectively reduces motor fluctuations and (2) somewhat normalises tactile perception.

Theorising that enhanced reliance on visual information mitigates the influence of altered tactile perception rests on the assumptions (1) individuals who participated in this array of studies do display the enhanced reliance visual information observed in the literature, and (2) the perceptual system favours visual information when integrating visual and tactile information during judging the relative proportions of ones body parts.

However, theorising that PD is not associated with a deficit in the calibration between perceptual and motor systems rests on one assumption, the postulation itself. In line with the logic of Occam's razor this final theory rests upon the fewest assumptions. Therefore, we have reason to believe this theory is most likely to be true.

7.3 Implications of these findings

Many hypotheses concerning the functional role of the basal ganglia have been strongly influenced by clinical behavioural studies on patients with disorders presumed to be due to atypical basal ganglia functioning, notably PD (Schwarz et al., 1984). Therefore, the results of this thesis may inform our understanding of the functional role of the basal ganglia. Specifically, given that the perception of one's action capabilities, motor imagery and body perception appear to be preserved in PD, it may be that the basal ganglia do not affect the calibration between perceptual and motor systems. However, as neuroimaging techniques were not employed in this thesis these postulations should be treated with caution. Therefore, future studies could substantiate these claims through empirical analysis of cortical activation during the perception of ones action capabilities, generation of MI and body perception in individuals with PD compared to healthy controls.

Some previous research points to possible deficits in perceptual motor calibration in individuals with PD. For example, individuals with PD respond in a similar manner to both action relevant and action-irrelevant stimuli (Poliakoff et al., 2007), and show deficits in using their perceptual-motor systems to anticipate the actions of others (Kloeters, et al., 2017). While these deficits could be explained by a deficit in perceptual motor calibration, to this point, motor calibration in individuals with PD had not been directly investigated. Subsequently, this thesis fills a gap in the literature and may potentially explain or refute previously unexplained observed results.

While this thesis is the first to investigate the influence of naturally occurring variability in perceptual motor experience on the perception of one's action capabilities, the influence of variability as a whole on this process has not been completely unacknowledged in the current body of literature. Specifically, a growing body of literature (including Chapter 3) has begun to investigate the influence of artificially induced variability in perceptual motor experience on the perception of ones action capabilities. For example, Lin and colleagues (2020) observed that when individuals' perceptual-motor experience concerning their reaching capabilities is subject to artificial variability (in virtual reality) individuals' subsequent perceptions of their action boundary for reaching were biased towards liberal estimations. In contrast when variability was artificially induced in a real world setting Lin and colleagues (2021) found that participants were subsequently more conservative when estimating their reaching capabilities.

Taken as a whole, the prior observations of Lin and colleagues (2020; 2021), and the observations outlined within this thesis may imply that the perceptual system accounts for variability in perceptual-motor experience differently dependent upon the

nature of the variability. That is, whether the variability (a) occurs over the short term or long term, (b) whether it is artificial or natural by nature, and (c) whether it occurs in natural or artificial settings. Further analysis of the influence of the nature of variability would be an interesting line of future research.

A wealth of research has investigated the generation of motor imagery in individuals with PD (See Caligiore et al., 2017 for review). While some studies have considered the influence of the overall severity of PD (e.g. Heremans, 2011; Pickett et al., 2012), Chapter 5 is the first study to start to unpack the specific effects of symptom type on motor imagery vividness. This study observed that greater severity of bradykinesia in the left-side of the body was associated with higher ratings of kinestheic motor imagery vividness. Thereby suggesting that analysing the influence of specific symptomology on facets of motor imagery is an important area of investigation.

The foundation of the occurrence of distortions in body size across different body parts remains a hotly debated topic. Given the interrelatedness of sensory and motor systems (Creem & Proffitt, 1998; Witt et al., 2005; Creem, & Proffitt, 2001) it may be that body distortions are influenced by visual, tactile and motor information. Therefore, investigating how distortions in body size are influenced by clinical conditions that are inherently motor, but are also associated with tactile atypicalities, may inform the extent to which visual, tactile and motor information influence the occurrence of these distortions.

7.4 The Clinical Importance of Perceptual-Motor Calibration in PD

Safe and successful interaction within one's environment is contingent upon one's ability to accurately perceive the extent over which they can successfully perform a

plethora of actions (action boundaries). Therefore, ascertaining circumstances in which individuals are not reliably in tune with their action boundaries is of clinical importance, particularly to physiotherapists and occupational therapists working with people with PD.

Motor capabilities can be improved through perceptual -motor training, such as video simulation training (Dicks et al., 2008). Furthermore, it is also possible to use the eye tracking data to redirect how patients sample visual information to improve motor behaviour. For example, Van Kampen (2010) improved penalty kick anticipatory behaviours in inexperienced goalkeepers through instructions to redirect gaze during visual search training. It appears that that PD is not associated with a deficit in the calibration between perceptual and motor systems. Therefore, it may be that individuals with PD's motor capabilities could be improved through rehabilitation employing perceptual-motor training.

Motor imagery can also enable the rehearsal and self-paced training of actions that individuals are unable to perform due to physical impairments (Zimmermann-Schlatter et al., 2008; Agostini, et al., 2021). Subsequently, motor imagery has undeniable potential as a rehabilitation technique for promoting the recovery of motor functioning in neurological conditions (Malouin & Richards, 2013). Chapter 5 found that motor imagery vividness is not influenced by overall symptom severity and tremor severity. However, greater severity of bradykinesia in the left-side of the body was associated with higher ratings of kinestheic motor imagery vividness. Thus highlighting that motor imagery vividness may be relatively robust to general motor decline in PD. Therefore, these findings further support the application of motor imagery training in neurorehabilitation for those with PD. Moreover, the differential influence of PD symptomology should be taken into consideration when designing

motor imagery-based interventions for people with PD. For example, interventions that rely upon particularly vivid motor imagery, would perhaps be most suitable for individuals who present with left-side dominant bradykinesia.

It is particularly important to note here that all participants with PD who participated in present studies within this thesis were physically independent (Hohen and Yahr Stage III or less). Therefore, arguably these individuals presented with mild-moderate PD. Subsequently, the findings obtained within this thesis may only apply to those with mild-moderate PD. PD is a neurodegenerative disorder, and the effect of levodopa therapy diminishes over time, such that as PD progresses individuals experience more and more frequent fluctuations between 'On' and 'Off' times (Thanvi & Lo, 2004). Therefore, those with more advanced PD will (a) experience more variability in perceptual motor experience and (b) experience more severe tactile abnormalities, than those with mild-moderate PD. Therefore, perception of one's action capabilities, motor imagery and body perception may be differently affected in advanced stage PD compared to mild-moderate PD. Subsequently, future research should also consider investigating the perception of one's action capabilities, motor imagery and body perception in those with advanced stage PD.

7.5 Conclusions

To conclude, in this thesis I addressed a fundamental, theoretically and clinically interesting, gap in the literature by investigating the influence of variable perceptual-motor experience on individuals with mild-moderate idiopathic PD's perceptions of their action capabilities. Moreover, I investigated the influence of symptom presentation and severity on motor imagery and how the generation of motor imagery may be related to the perception of action capabilities in PD. Finally; I

investigated the influence of PD on the perception of the relative proportions of the body. As a whole the results obtained indicate that perceptual-motor calibration, generation of motor imagery, and the perception of the relative proportions of the body are preserved in individuals with mild-moderate PD. Thus, I argue that PD is not associated with PD a deficit in the calibration between perceptual and motor systems

This thesis addresses this fundamental gap in the literature. However, our understanding of how PD influences perceptual-motor calibration, generation of motor imagery, and the perception of the relative proportions of the body story is far from complete. Rather, additional investigations of individuals with PD's ability to update their perceptions to account for alterations in their action capabilities, potential compensatory mechanisms, and the influence of more advanced PD are required to complete this story.

Chapter 8

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