Experimental Brain Research (2019) 237:1325–1337
https://doi.org/10.1007/s00221-019-05512-3

RESEARCH ARTICLE

Differential influence of habitual third-person vision of a body part on mental rotation of images of hands and feet

Louisa M. Edwards[1] · Ryan S. Causby[1] · Halton Stewart[2] · Tasha R. Stanton[1,3]

Received: 30 July 2018 / Accepted: 8 March 2019 / Published online: 14 March 2019

Abstract

Left/right judgement (LRJ) tasks involve determining the laterality of presented hand or feet images. Allocentric images (third-person perspective; 3PP) take longer to identify than egocentric images (first-person perspective; 1PP), supporting that implicit motor imagery (IMI)—mentally manoeuvring one's body to match the shown posture—is used. While numerous cognitive processes are involved during LRJs, it remains unclear whether features of the individual (e.g., visual exposure, experience, task-dependent use) influence the type of recognition strategy used during LRJs (IMI versus non-IMI). To investigate whether an individual's routine visual exposure to hands/feet in 3PP disrupts the typical perspective–reaction time (RT) relationship in LRJs, hand therapists, podiatrists, and healthy controls completed online LRJ tasks of hand and feet images. A group-specific reduction in RT for only allocentric images would represent a switch to non-IMI strategies. The results show that routine visual exposure to feet in 3PP (podiatrists) results in quicker RTs only for allocentric images of feet, suggesting a switch from IMI to non-IMI (e.g., visual object-based recognition) strategies. In contrast, routine visual exposure to hands in 3PP (hand therapists) does not alter RT for allocentric images, suggesting maintenance of IMI. However, hand therapists have quicker RTs (vs other groups) for egocentric hand images, supporting enhanced sensorimotor processing for the hand, consistent with task-dependent use (precise hand use). Higher accuracy in health professionals (vs control) on both tasks supports enhanced body schema. Combined, this suggests that 3PP visual exposure to body parts and task-dependent use contribute to LRJ performance/recognition strategy.

Keywords Left/right judgement task · Implicit motor imagery · Visual object-based recognition · Frame of reference · Egocentric · Allocentric

Introduction

Mental imagery refers to the process of generating and transforming mental images by accessing the internal representation of one's own body. Implicit motor imagery (IMI) is a form of mental imagery that occurs outside of conscious awareness, activating brain areas involved in movement planning and coordination (Kawamichi et al. 1998). IMI is commonly evaluated using a left/right judgement (LRJ) task, typically providing images of hands and feet, and participants are asked to identify the laterality (left–right orientation) of the shown image. LRJs are thought to involve two stages—an initial rapid visual recognition of laterality followed by IMI (i.e., accessing internal limb representations to mentally manoeuvre one's own limb to match the posturing of the limb shown in the picture) to confirm or refute the initial judgement (Cooper and Shepard 1975; Gentilucci et al. 1998; Ni Choisdealbha et al. 2011; Parsons and Fox 1998). What is presently unclear, however, is whether IMI is the predominant process used during LRJs, or whether, in certain situations and/or in certain people, other processes such as visual object recognition (i.e., recognition based on known attributes of stimuli) might dominate.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00221-019-05512-3) contains supplementary material, which is available to authorized users.

✉ Tasha R. Stanton
tasha.stanton@unisa.edu.au

1 School of Health Sciences, University of South Australia, G.P.O. Box 2471, Adelaide, SA 5001, Australia

2 Neuro Orthopaedic Institute (NOI), 19 North Street, Adelaide, SA 5000, Australia

3 Neuroscience Research Australia, Barker Street, Randwick, NSW 2031, Australia

Evidence suggests that there are numerous and varying cognitive processes that occur during LRJ tasks. First, that sensorimotor processes (e.g., IMI) contribute to LRJs is supported by findings that task reaction times (RTs) show a clear relationship with the orientation of the image. Generally, the further the image's orientation is away from zero (see Fig. 1), the longer it takes to make a judgement (Ionta et al. 2012), and the time it takes to make a judgement mirrors the time it takes to physically attain the pictured hand position (Parsons 1987; Parsons and Fox 1998; Shepard and Cooper 1986; Shepard and Metzler 1971). Neuroimaging during LRJ tasks shows increased brain activation in the same areas that are activated during genuine physical movement, e.g., the premotor cortex (Parsons and Fox 1998) thus supporting the use of underlying internal movement representations for the body part (i.e., IMI strategies). The contribution of sensorimotor processes to LRJs is further supported by research showing proprioceptive influence (i.e., biomechanical posture) on task performance. Placing one's hand behind the back results in increased RTs for images corresponding to that hand (Ionta and Blanke 2009; Ionta et al. 2007; Ni Choisdealbha et al. 2011; Qu et al. 2018).

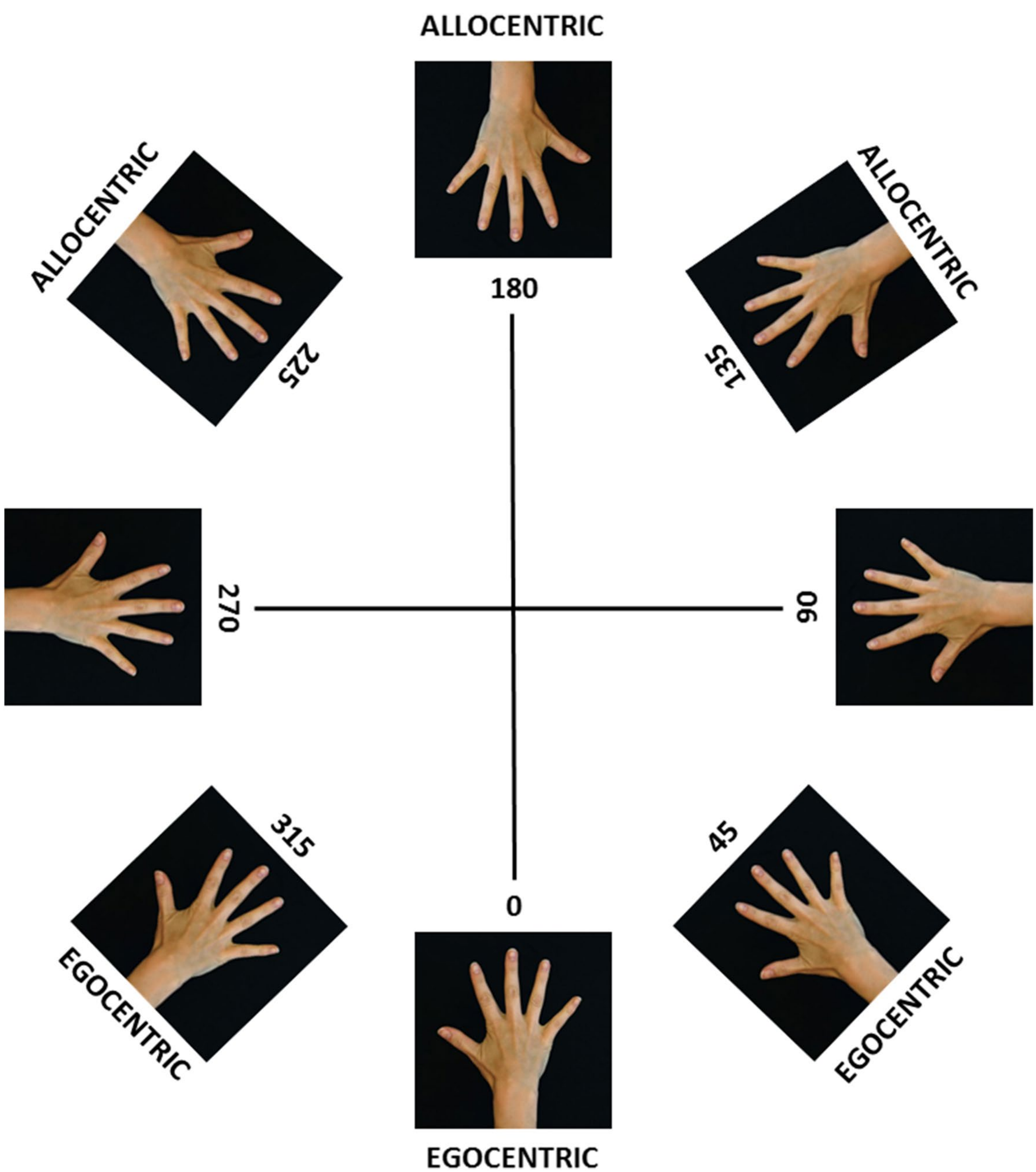

Fig. 1 Allocentric and egocentric frame of reference (FoR). Pictorial display of right-hand images in egocentric and allocentric orientations

In contrast, LRJs are faster when the viewed hand position (i.e., hand image shown) and actual hand position are congruent (Qu et al. 2018). Additionally, when viewed and actual hand position are congruent there is stronger activation of the motor and parietal cortices seen on functional magnetic resonance imaging (fMRI) than during conditions of incongruency (Qu et al. 2018). Such findings support the contribution of sensorimotor processing and IMI strategies to improved performance for congruent images.

Second, evidence supports that visual processing contributes to LRJ performance. Hand LRJs are quicker when hands are rotated towards the body's midsagittal plane (i.e., medial orientation) versus away from it (i.e., lateral orientation), despite being at similar relative departures from 0 degree orientation (Parsons 1987). Such findings support the use of a proprioceptive–visual matching strategy—i.e., matching the felt hand with the visually seen hand—and less reliance on sensorimotor processing (i.e., IMI) (De Simone et al. 2013). Indeed, that RTs for right- and left-hand images are inverted when displayed in the opposite (left versus right) visual fields provides further evidence for visual processing contribution to LRJ performance (De Simone et al. 2013).

Last, there is evidence that other cognitive strategies are used during mental rotation and that the use of these strategies might be individually specific (Hegarty 2018; Khooshabeh et al. 2013; Xue et al. 2017). For example, some individuals use analytical strategies during mental rotation whereby focus is placed on identifying features of the image rather than mentally transforming the image in space (Hegarty 2018). In addition, "good imagers" are shown to use holistic mental rotation strategies, but with the ability to update strategies based on task demand/complexity, while "bad imagers" are less flexible (Khooshabeh et al. 2013). However, such work has focussed on traditional object mental rotation tasks, so the influence of an individual's characteristics on body-relevant (i.e., images of hands and feet) LRJ task performance is less clear.

During body-relevant LRJs, the type of recognition strategy used may depend upon features of the task itself. Prior work has shown that tasks that promote taking another's perspective of the body ("other" versus "self") reduce the use of IMI. Specifically, when participants are asked to judge the laterality of a hand when it is attached to another person's body (i.e., picture of a person facing the participant), the interdependence between image orientation and RT (i.e., used a marker of IMI) is absent, but is present for traditionally presented hand image stimuli (Ionta et al. 2012). Similar findings are seen when participants judge the location of a red dot on a hand (left versus right side), but not the laterality of the viewed hand (De Simone et al. 2013). Together, these findings suggest the use of a visual recognition strategy, whereby individuals reference the image's intrinsic coordinate frames and perform an object recognition process. Neuroimaging studies show distinct neural underpinnings for mental transformation of one's own body versus another's body (Ganesh et al. 2015) or an object (Kosslyn et al. 1998; Wraga et al. 2005). However, what these findings do not elucidate is whether the recognition strategy used is consistent within the LRJ task.

A within-task feature that may be a key influence on the type of recognition strategy used is the frame of reference (FoR) of an image (see Fig. 1), namely whether an image is in an egocentric (first-person perspective; 1PP) or an allocentric (third-person perspective; 3PP) FoR. Distinct neural activations are seen for visual stimuli of body parts shown in an egocentric versus allocentric FoR (Saxe et al. 2006). Specifically, the extrastriate body area (EBA) in the lateral occipitotemporal cortex responds preferentially to body stimuli and exhibits differential activation based on image FoR. The right EBA shows stronger activation with allocentric images (Saxe et al. 2006) and with partial (upper limb) versus full body stimuli (Blanke et al. 2010). Behavioural findings also support the possibility of FoR-specific LRJ recognition strategies. Judgements for egocentric images of hands maintain the expected image orientation-related RT profile, implying the use of IMI (Brady et al. 2011). However, this orientation–RT profile is not maintained for allocentric images of hands: a larger-than-expected increase in RT occurs, suggesting a "switch" from an IMI strategy to another recognition strategy, such as reframing allocentric stimuli to an egocentric FoR (Brady et al. 2011). While such findings support the idea that image FoR influences the LRJ strategy used, it is presently unknown whether features of the individual (e.g., motor and visual experiences) might also influence the type of strategy used for egocentric versus allocentric body images.

Given the involvement of visual processes in LRJs of body stimuli, an individual's specific visual exposure to bodily stimuli might play a role in LRJ task performance. Indeed, quicker RTs for egocentric images (seen in some participants) have been partially attributed to visual recognition of an image as coming from one's own body (versus another's) whereby perception of an image's properties is attributed to logical, familiar attributes (DiCarlo and Cox 2007). Relevant to such findings is that healthy adults have different habitual visual exposure to bodies (e.g., hands and feet). For example, professionals such as hand therapists and podiatrists consistently view patients' hands and feet, respectively, in an allocentric FoR. This raises the possibility that increased exposure to body parts in a 3PP could promote visual recognition processes during LRJs by increasing familiarity of allocentric images.

Thus, the primary aim of this study was to determine whether habitual visual exposure to hands (hand therapists) or feet (podiatrists) in 3PP results in selectively reduced RTs for hand and feet allocentric images, respectively, compared with a healthy control sample. We specifically hypothesised that RTs for allocentric images would be decreased in health professionals, consistent with use of visual object-based recognition strategies, but that RTs for egocentric images would not differ between groups. Such an effect would be predicted by findings from skilled populations: gymnasts (i.e., expert in real-body rotations) have significantly reduced RTs for whole body stimuli (versus handball players), that are most enhanced for typically unfamiliar (allocentric) stimuli (Habacha et al. 2017). Critically, such an effect would be in the opposite direction than that shown by previous work, i.e., allocentric images result in a larger than expected increase in RT (Brady et al. 2011), showing that distinct processes underlie LRJ performance changes.

Secondarily, we evaluated the influence of motor expertise and habitual visual exposure to these body parts on the accuracy of LRJ performance and whether greater periods of habitual exposure (i.e., clinical experience) correlated with better LRJ performance (RT). We expected the clinical groups to be more accurate than healthy controls at their respective LRJ tasks. Further, given that both hand therapists and podiatrists also regularly perform precise, fine-grained, and controlled movements of the hands (task-dependent use), we predicted that both clinical groups would be more accurate than healthy controls for LRJs of hand images. Such effects would be predicted given skill- and experience-based differences seen in mental rotation performance in athletes that participate in sports that require spatial awareness (i.e., orienteers and gymnasts) compared with non-athletes (Schmidt et al. 2016). Last, we hypothesised that greater clinical experience would relate to improved RT on the LRJ task. That LRJ task training improves performance and increases cortical efficiency in the motor regions [as demonstrated with fMRI (Berneiser et al. 2018)] would predict effects of clinical experience on LRJ performance.

Materials and methods

Participants

Three groups of participants were recruited: hand therapists (occupational therapists or physiotherapists who work specifically in hand rehabilitation or therapy), podiatrists, and healthy volunteers. Health professionals were considered those holding valid licensing within their listed country and were required to have practical clinical experience in their respective fields. Healthy volunteers were considered eligible if they were adults who did not work as hand therapists, physiotherapists or podiatrists. All participants were required to be aged between 18 and 65 years, free of self-reported cognitive impairment, free of current pain (or past history of chronic pain), and have internet access via a desktop computer, laptop, or tablet during testing. This study received ethical approval from the University of South Australia's Human Research Ethics Committee. All methods were carried out in compliance with the Declaration of Helsinki (1964) and all participants provided digital informed consent prior to participation in the study.

Potential participants were invited to the study via email, through professional networks of the University of South Australia and organisations such as the Hand Therapy Association and the Australian Podiatry Associations. A link to the study's online tests was provided within the email. In addition, the study link was also posted on numerous social media platforms [Facebook, Body in Mind (BiM) blog] for interested volunteers to directly access.

A total of 178 healthy individuals (140 females, mean age 36.2 years, SD 11.8) volunteered for and completed the hand image task; of these, 71 participants identified as licensed podiatrists, 52 as licensed hand therapists and the remaining 55 as neither, forming the healthy control group. A total of 158 were right handed, as assessed using the Edinburgh Handedness Inventory (Oldfield 1971). A total of 172 individuals (136 females, mean age 36.7 years, SD 11.9) volunteered for and completed the feet image task; of these, 66 participants identified as licensed podiatrists, 56 as licensed hand therapists and the remaining 50 as neither, forming the healthy control group. Similarly, 154 of 172 were right handed.

A sample size calculation was performed prior to subject recruitment. Given an anticipated small effect size ($f = 0.10$) for our primary hypothesis of a group-specific change in RT only for allocentric images (i.e., significant Group × FoR interaction) (Brady et al. 2011), and based on three groups, six reaction time measures (three allocentric and three egocentric), a within-measure correlation of 0.50, power of 0.80 and alpha of 0.05 a total sample of 138 (46 participants per group) was required.

Stimuli

Experimental hand and feet LRJ tasks consisted of four individual photos of hands and four of feet (see Online Resource 1), each presented in eight different orientations: 0°, 45°, 90°, 135°, 180°, 225°, 270° and 315°. Each FoR was comprised of three image orientations: 0, 45°, and 315° for the egocentric FoR and 135°, 180°, and 225° for the allocentric FoR. Images in each orientation were repeated twice, resulting in a total of 128 images comprising the hand LRJ task, and 128 images comprising the feet LRJ task. Images were obtained from the Neuro Orthopaedic Institute (NOI) archives for the Recognise™ software platform. Left-lateralised images were mirror images of the right-lateralised images. Images were rated from easy to hard (See Supplementary Material 1) depending on ease of posture replication

(Ionta and Blanke 2009; Parsons 1987). Hands and feet were presented in both plantar/palmar and dorsal views. Note that for the present study, images in an orientation of 90° and 270° were not used for analysis as these images are neither allocentric nor egocentric, but rather, they were collected to allow comparison with other work in this area that typically uses these orientations (i.e., future use of the data).

Procedure

The experiment used online testing hosted on the NOI Recognise™ platform (http://www.research.noigroup.com). Participants were asked to use a desktop computer, laptop or tablet to access the online platform. Participants were encouraged to complete the test in a quiet space and to limit interruptions. Demographic information was collected prior to LRJ testing, which included questions regarding participant age, gender, occupation (licensed hand therapists or podiatrist), clinical experience (years of practice; if applicable), current pain state, and history of chronic pain. Handedness was assessed using an online version of the Edinburgh Handedness Inventory (EHI) (Oldfield 1971).

Participants were randomly assigned to complete testing for hand images first or feet images first. For both image sets, participants first completed a practice trial of 20 images (randomly chosen from a pool of 40 images) before completing two 128 test-image sets. Participants were instructed to identify the left/right nature of the image as quickly but as accurately as possible and were encouraged to take breaks in between image sets (via online written instructions provided prior to testing). Participants were explicitly instructed to avoid moving their own hands or feet (i.e., into the displayed image posture) during testing. This process was then repeated for images of the remaining body part (hands or feet).

A customised LRJ task was created such that each image (four of hands, four of feet) in each of eight orientations was randomly presented twice during each test-image set. Thus, all participants performed LRJs on identical image sets, but in different image orders. For each image, participants were given 5 s to respond after which the program automatically advanced, providing the next image. Responses were made using the right index finger to press the "N" key for right images and the left index finger to press the "V" key for left images (if performing LRJs on tablets, either "Left" or "Right" was pressed using respective index fingers). RTs and key responses (N/Left or V/Right) were recorded by the Recognise™ software and exported into Microsoft Excel.

Data handling

Participants who reported current pain in the hands or feet, chronic pain syndromes, neurological disorders, or an age less than 18 years/more than 65 years were excluded from analysis, given that these features can influence LRJ performance (Ionta et al. 2016; Schmid and Coppieters 2012; Stanton et al. 2012).

The performance data (accuracy, RT) for each test image ($4 \times$ hands, $4 \times$ feet) at each orientation were summarised (mean and standard deviation). Accuracy was calculated as the percentage of correct responses for each participant for images of hands and for images of feet. In accordance with previous work using the LRJ task (Ionta and Blanke 2009; Stanton et al. 2012; Wallwork et al. 2013), RTs were calculated for images that had correct responses. Due to very low accuracy rates for image 4 (most difficult posturing) for both the hand and feet image task, performance results from these images were excluded from the analysis (insufficient data to calculate RT values for each orientation). Thus, the LRJ performance data used in analyses represented the average of performance over Images 1–3 for both hands and feet. Further, given previous findings of a speed-accuracy tradeoff, (i.e., responses < 500 ms are not indicative of true task performance but rather represent either mistakenly hitting a key or a guess) (Ionta et al. 2012), RT responses < 500 ms were excluded.

In addition to the average RT data for each image and orientation, we also computed the overall ratio between performance on allocentric versus egocentric images (FoR RT ratio) for each type of image (hands/feet) and for each group. Specifically, the FoR RT ratio was computed as the average allocentric RT divided by the average egocentric RT. Ratios approaching 1.0 represent equal RT for egocentric and allocentric images, ratios > 1.0 represent the degree to which RT increases with allocentric images (compared with egocentric) or decreases with egocentric images (compared with allocentric), and vice versa with ratios < 1.0.

SPSS software (IBM SPSS version 22.0, USA) was used for all analyses. Data were first checked for normality using visual inspection of probability plots and the Shapiro–Wilk statistic. If normally distributed, parametric analyses were used. If not, data were transformed. A significance limit of $p < 0.05$ was used in all analyses.

Statistical analysis

In all analyses, age, gender, and handedness were considered as potential covariates given that these factors can influence LRJ performance (De Simone et al. 2013; Wallwork et al. 2013). A one-way ANOVA was used to evaluate if mean age differed between groups, and the chi-squared statistic evaluated differences in gender or handedness proportions between groups. If group differences approached statistical significance ($p < 0.10$), these variables were included as covariates in the analysis.

To determine if there were RT differences between groups, specific to the image FoR (allocentric versus egocentric), linear mixed model analyses were completed. RT was the dependent variable and independent variables included the image FoR (within: egocentric or allocentric) with image orientation as a nested factor [within: 0° and 180° (midline), 45°, 135° (easy orientation), 315°, 225° (difficult orientation)] and their interactions with the main factor of group (between: podiatrists, hand therapists, and healthy controls). Participants were considered to contribute to the model as random effects with any relevant covariates (e.g. age and gender) as fixed effects. Between-group significant interaction effects were further explored using post hoc independent t-tests considering both the FoR RT ratio and the analysis means. Residuals from predicted and actual results were plotted to ensure a linear mixed model was appropriate.

To determine if accuracy of LRJ task performance differed between groups, one-way ANOVAs were completed for hand and for feet images. Any significant differences were explored using post hoc independent *t* tests using a Holm–Bonferroni correction. Last, Spearman's ρ was used to determine if clinical experience related to overall RT (clinical experience was non-normally distributed). We further explored whether clinical experience was associated with RT based on image FoR (egocentric versus allocentric) in a final analysis.

Results

Of 385 total participants that initiated the online task, 122 completed the entire task of both hand and feet images. 172 participants completed at least one set of foot images and 178 completed one set of hand images. For RT data, removal of incorrect responses and RT responses < 500 ms accounted for a loss of 6.8% of data. Finally, 47 hand-image participants and 44 feet-image participants reported being in pain at the time of testing, resulting in exclusion of their data. This totalled 178 and 172 participants for hands and feet image-sets, respectively. See Table 1 for participant characteristics.

Group differences in the effect of Image FoR on RT (Fig. 2a)

Hand image

When controlling for age and gender, there was a main effect of Image FoR ($F_{1,175} = 331.9$, $p < 0.0001$) with all groups faster at recognising egocentric than allocentric images. There was a main effect of Image Orientation ($F_{2,180} = 9.13$, $p < 0.0001$; "easy" < "midline" < "difficult") but no main effect of Group ($F_{2,171} = 0.93$, $p = 0.40$) and no significant interaction between Group and Image FoR ($F_{2,175} = 1.190$, $p = 0.15$) or Group and Image Orientation ($F_{4,180} = 0.90$, $p = 0.47$).

Due to the small number of male podiatrists (and given that large inequities in categorical covariates can exert an undue influence on linear mixed model analyses), a sensitivity analysis was run for hand images using a female-only sample. See Fig. 2a for full RT data. Similarly, when controlling for age, there was a main effect of Image FoR (egocentric quicker than allocentric; $F_{1,25} = 348.39$, $p < 0.0001$) and Image Orientation ($F_{2,65} = 6.12$, $p = 0.004$; as above), but no effect of Group ($F_{2,141} = 0.10$, $p = 0.91$) and no Group × Image Orientation interaction ($F_{4,65} = 1.12$, $p = 0.35$). However, there was a significant Image FoR × Group interaction ($F_{2,25} = 3.70$, $p = 0.039$; see Fig. 2b). Post hoc analysis of the raw RT data revealed a significant difference between hand therapists and healthy

Table 1 Participant characteristics

	Healthy controls	Podiatrists	Hand therapists	Total	*p* value
Hand images					
N	55	71	52	178	–
Age (years)	33.6 ± 12.7	38.4 ± 11.9	35.8 ± 10.1	36.2 ± 11.8	0.015*
Gender	13M, 42F	8M, 63F	17M, 35F	38M, 140F	0.076
Handedness	4L, 51R	8L, 63R	8L, 44R	20L, 158R	0.415
Clinical experience (months)	–	166 ± 131.2	116.6 ± 94.6	145.3 ± 119.7	0.024*
Feet images					
N	50	66	56	172	–
Age (years)	34.8 ± 13.6	38.3 ± 11.6	36.6 ± 10.4	36.7 ± 11.9	0.28
Gender	12M, 38F	5M, 61F	19M, 37F	36M, 136F	0.001*
Handedness	3L, 47R	8L, 58R	7L, 49R	18L, 154R	0.476
Clinical experience (months)	–	163.8 ± 131.9	117.2 ± 95.0	141.8 ± 108.3	0.029*

M Male, *F* female, *L* left, *R* right

*$p < 0.05$

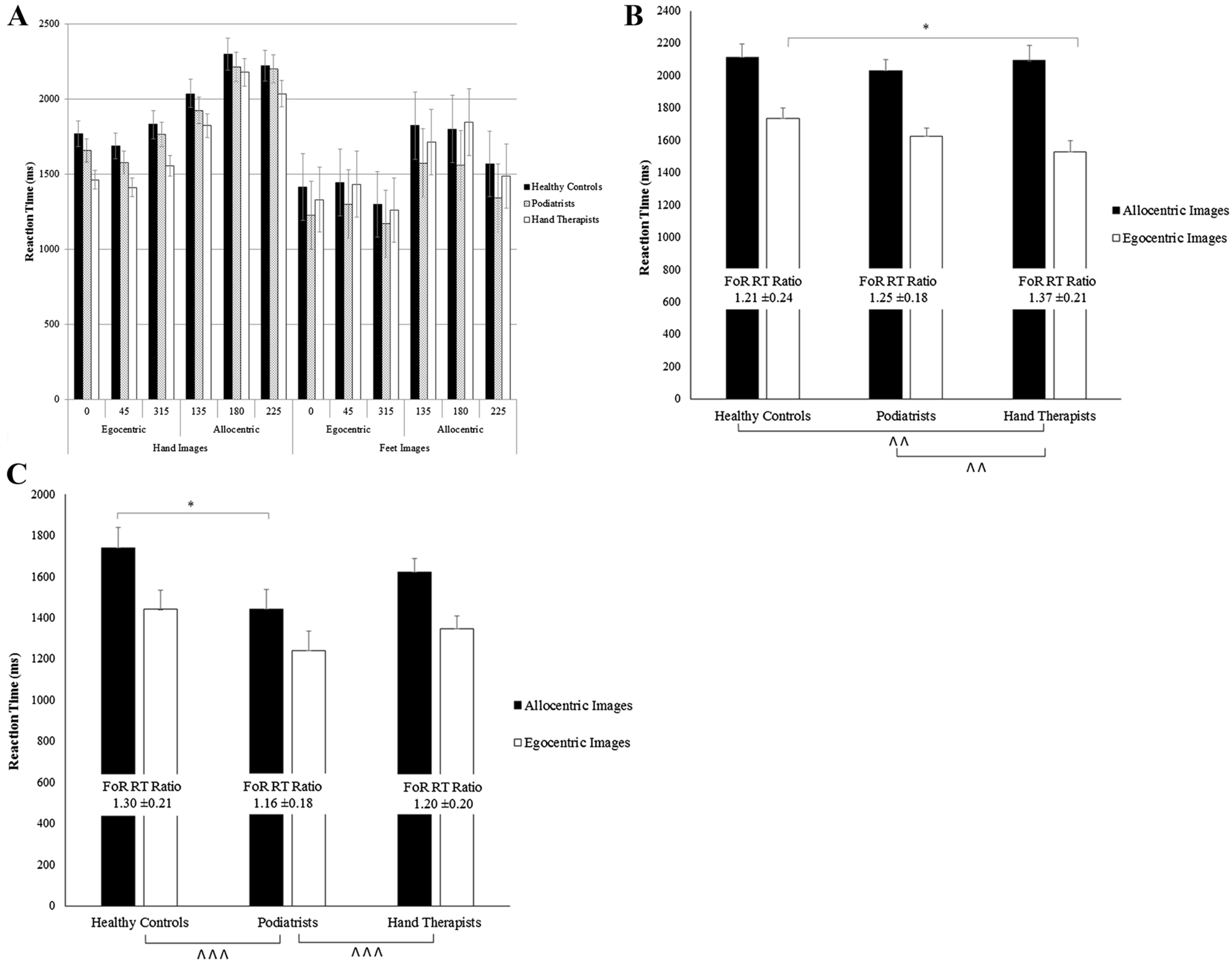

Fig. 2 Hand and feet image RT results based on Group and Frame of Reference (FoR). **a** Overall mean (standard error) RT results as a function of Task (hand/feet images), Group, Image FoR (egocentric/allocentric), and orientation (0°, 45°, 135°, 180°, 225°, 315°). **b** Mean (standard error) RT and FoR RT ratio for hand images as a function of Group and Image FoR (egocentric/allocentric) when controlling for age; *Post hoc RT results, $p<0.05$; ΛΛΛ Post hoc FoR RT ratio results, $p<0.001$. **c** Mean (standard error) FT and FoR RT ratio for feet images as a function of Group and Image FoR (egocentric/allocentric); *Post hoc RT results, $p<0.05$; ΛΛΛ Post hoc FoR RT ratio results, $p<0.0001$

controls for egocentric images of hands, wherein hand therapists were 207.9 ms faster than healthy controls ($p=0.029$; See Table 2), but hand therapists did not differ from healthy controls for allocentric images (19.9 ms difference, $p=0.87$). There was also no significant difference between hand therapists and podiatrists, or podiatrists and healthy controls for either egocentric or allocentric images, respectively (see Table 2). Post hoc tests of the FoR RT ratio revealed a significant difference between hand therapists (mean ± SD: 1.37 ± 0.21) and healthy controls (1.21 ± 0.24, $p=0.0004$, $d=0.71$), and podiatrists (1.25 ± 0.18, $p=0.0009$, $d=0.61$), but no difference between podiatrists and healthy controls ($p=0.29$, $d=0.19$). Thus, hand therapists take 37% longer to identify an allocentric image than an egocentric image, whereas podiatrists and healthy controls take ~20% longer; however, given post hoc results of RT data this increased FoR RT ratio for hand therapists is driven by a reduction in RT for egocentric images rather than an increase in RT for allocentric images.

Feet images

When controlling for age and gender, there was a significant effect of Image Orientation ($F_{2,169}=49.945$, $p<0.0001$; "easy" < "midline" < "difficult") and Image FoR (allocentric/egocentric; $F_{1,169}=230.36$, $p<0.0001$) whereby participants were faster for egocentric images than allocentric images. There was no main effect of Group ($F_{2,65}=1.08$, $p=0.43$),

Table 2 Mean differences with 95% confidence intervals for post hoc tests of group RT differences for hand and feet images

	Egocentric				Allocentric			
	Mean diff (ms)	95% CI	*p* value	*d*	Mean diff (ms)	95% CI	*p* value	*d*
Hand images								
Pod versus HC	−110.79	−270.32, 48.75	0.17	0.25	−82.76	−296.03, 130.52	0.44	0.14
HT versus HC	−207.84	−392.53, −23.15	0.028*	0.43	−19.93	−267.06, 227.20	0.87	0.031
HT versus Pod	97.06	−263.84, 69.73	0.25	0.21	62.83	−160.05, 285.70	0.58	0.11
Feet images								
Pod versus HC	−99.84	−366.50, 166.83	0.46	0.14	−297.28	−573.18, −21.39	0.035*	0.40
HT versus HC	6.67	−211.30, 224.64	0.95	0.012	−116.16	−346.19, 113.88	0.32	0.19
HT versus Pod	106.50	−122.64, 335.65	0.36	0.17	181.13	−58.14, 420.39	0.14	0.28

Mean diff Mean differences, *CI* confidence intervals, *ms* milliseconds, *d* Cohen's d value, *Pod* podiatrist, *HC* healthy control, *HT* hand therapist
*$p < 0.05$

but there was a significant Group × Image FoR interaction ($F_{2,169} = 3.136$, $p = 0.046$; see Fig. 2). Post hoc tests of the raw RT data revealed that podiatrists were significantly faster at identifying allocentric images of feet than healthy controls (297.3 ms, $p = 0.034$; see Table 2), but performance between the groups was not different for egocentric feet images. There was no significant difference between any of the other groups for egocentric or allocentric orientations (see Table 2). Post hoc tests of FoR RT ratios revealed a significant difference between healthy controls (1.30 ± 0.21), and both podiatrists (1.16 ± 0.18, $p < 0.0005$, $d = 0.72$) and hand therapists (1.20 ± 0.20, $p = 0.026$, $d = 0.49$) but podiatrists and hand therapists did not differ ($p = 0.25$, $d = 0.21$). Taken together, this suggests that podiatrists took only ~ 16% longer to identify allocentric feet images than egocentric feet images (vs ~ 30% longer in healthy controls), and that this ratio difference is driven by a reduction in RT for allocentric images in podiatrists. Hand therapists took ~ 20% longer to identify allocentric versus egocentric feet images, similarly driven by relatively improved performance for allocentric images, although raw RT values did not significantly differ from healthy controls. Sensitivity analyses evaluating gender influences found largely consistent results (see Supplementary Material 2).

Group differences in LRJ accuracy

For images of hands, there was a significant between-group difference for accuracy when controlling for age and gender ($F_{2,173} = 11.773$, $p < 0.0001$). Hand therapists were more accurate at identifying images of hands with a mean (SD) of 90.9% (6.3%) than both podiatrists [86.4% (9.0%), $p = 0.003$, $d = 0.58$] and healthy controls [81.6% (10.3%), $p < 0.0001$, $d = 1.09$). Podiatrists were also more accurate at identifying images of hands than healthy controls ($p = 0.006$, $d = 0.50$).

There was a significant between-group effect for images of feet ($F_{2,167} = 5.475$, $p = 0.005$), controlling for age and gender. Both hand therapists and podiatrists performed more accurately than healthy controls ($p = 0.0003$, $d = 0.72$; $p = 0.001$, $d = 0.62$), with mean (SD) accuracy values of 93.6% (7.5%), 93.1% (8.9%), and 87.0% (10.6%), respectively. There were no differences in accuracy between hand therapists and podiatrists ($p = 0.74$, $d = 0.06$).

Relationship between clinical experience and LRJ task performance

There was no relationship between clinical experience (total months of practice) and average RT for any of the health professional groups (see Table 3). There was a trend for correlation between overall experience and image RT for hands, suggesting that greater clinical experience resulted in shorter RTs, but this did not reach significance (Table 3). Further, when considering RTs for allocentric and egocentric images separately, there was no significant correlation between practicing months in podiatrists/hand therapists and RT performance for egocentric or allocentric images of hands or feet.

Table 3 Correlation (Spearman's ρ) between clinical experience and RT performance for hand therapists and podiatrists

	Hand therapists		Podiatrists	
	Spearman's ρ	*p* value	Spearman's ρ	*p* value
Hand images				
Overall	0.24	0.09	0.17	0.16
Egocentric	0.15	0.30	0.14	0.25
Allocentric	0.22	0.14	0.18	0.15
Feet images				
Overall	0.050	0.69	0.044	0.82
Egocentric	0.067	0.60	0.072	0.57
Allocentric	0.026	0.84	0.062	0.63

Discussion

We hypothesised that daily visual exposure to hands and feet in 3PP (by hand therapists and podiatrists, respectively) would result in a shift to visual object-based recognition strategies in the LRJ task, as evidenced by selective decreases in RTs for allocentric images. This hypothesis was partially supported. Podiatrists showed a selective decrease in RT for allocentric images of feet compared with healthy controls, consistent with a facilitation of visually experienced 3PP of feet and a potential switch from IMI to a visual object-based recognition strategy. In contrast, hand therapists showed a selective decrease in RT for egocentric images of hands compared with healthy controls, consistent with a facilitation of 1PP of hands. Such results suggest differential effects of habitual 3PP vision of the body on the recognition strategies used during LRJ task performance. Our secondary hypothesis that repeated clinical exposure to the mental rotation of hands/feet and increased hand task-dependent use in health professionals would result in increased accuracy during the respective LRJ task was supported. Health professionals were consistently more accurate at identifying images of hands and feet than were healthy controls. Finally, our hypothesis that the amount of clinical experience would negatively relate to task RTs was not supported. Together these findings have important theoretical and clinical implications.

Individual features that influence performance and recognition strategy during LRJs

Our results suggest that features inherent to the individual, namely visual exposure to hands/feet in 3PP and task-dependent use, influence the performance and type of recognition strategy used during LRJs.

Effect of habitual vision of the body in 3PP

Differential effects of habitual 3PP visual exposure of hands versus feet suggest that the relationship between LRJ performance, recognition strategy, and visual exposure is likely multifaceted. Regardless, our findings are generally supported by previous work showing that visual processes contribute to LRJ performance. For example, RTs are faster when hand images are provided in the congruent visual field (e.g., right hand, right visual field; left hand, left visual field) (Parsons and Fox 1998) and slower when provided in the incongruent visual field (right hand, left visual field; left hand, right visual field) (De Simone et al. 2013).

We found that habitual visual exposure to feet in a 3PP in podiatrists reduces RTs only for allocentric (3PP) foot images. Previous work using the hand LRJ task has shown that the FoR of the images impacts performance and recognition strategy: RTs for allocentric images increase more than would be expected (based on performance for egocentric images) and are not highly correlated with each other as occurs for egocentric images (Brady et al. 2011). Such results have been interpreted as moving from an IMI recognition strategy to a strategy that involves reframing allocentric stimuli to an egocentric FoR (Brady et al. 2011). Our results extend the previous work by showing an opposite effect of habitual 3PP vision of feet on RTs for allocentric images: RTs are decreased. This suggests that an individual's unique visual 3PP exposure to feet has a distinct effect on performance of the LRJ task. Our findings are supported by research in body rotation experts: gymnasts that have high level skill in body rotation and also commonly watch/view other gymnasts' body rotation have significantly faster RTs for body LRJs (versus handball players) and their RTs are most reduced for typically unfamiliar (allocentric) stimuli (Habacha et al. 2017).

In contrast, habitual 3PP vision of hands experienced by hand therapists did not influence their performance on allocentric images of hands, suggesting that the recognition strategy used during LRJs was not affected. Why might the effect of habitual 3PP vision of hands versus feet on LRJ performance differ? One clear difference is that general visual exposure to hands in 3PP in everyday life is much greater than that of feet. For example, research into human gesture recognition has shown that the identification of posture and orientation is important in understanding meaning behind hand movements (Vatavu et al. 2006). Observing another's movements or gestures engages the mirror neuron system allowing one to mentally simulate the perceived movement without actually executing the movement (Jeannerod 2001; Rizzolatti et al. 1996). Such repeated mental simulation of hands in 3PP during gesture recognition is likely to influence performance for allocentric images in all groups. Thus, any additional 3PP visual exposure of hands by hand therapists is potentially insufficient to add to the effects of general visual exposure to hands in 3PP during daily life. In contrast, only podiatrists repeatedly view others' feet in an allocentric (3PP) frame of reference. Repeated visual exposure to feet in 3PP may support a stronger visual representation, enhancing body identification (Hodzic et al. 2009); such findings would be predicted by animal studies showing that visual exposure enhances stimulus encoding in the primary visual cortex (Lazar et al. 2018), which can then be used for advanced processing. Future work exploring the patterns of brain activation during LRJ of allocentric images in podiatrists is warranted to determine if activation is consistent with IMI [i.e., in motor relevant areas, Parsons and Fox (1998)] or if activation occurs in areas subserving object-based recognition such as the ventral visual stream (DiCarlo et al. 2012).

Effect of individual experience and task-dependent use

Our findings that health professionals are generally more accurate and quicker (for specific comparisons) than healthy controls at hand/feet LRJ is consistent with past work that has shown that individuals' experience and use of a body part can influence their mental rotation ability. For example, athletes whose sports require high levels of spatial bodily awareness and motor expertise, such as gymnasts and orienteers, have enhanced performance on body LRJ tasks (Habacha et al. 2017; Schmidt et al. 2016).

We found that both hand therapists and podiatrists were more accurate than healthy controls on both the hand and the foot LRJ task. The ability to accurately perform mental rotation of bodily images is thought to depend upon one's "body schema" (Fiorio et al. 2007), that is, a complex representation of the body built on multimodal sensory inputs (Schwoebel and Coslett 2005), and which is formed by memories and perceptions of one's own and others' perceived anatomy (Berlucchi and Aglioti 1997). Our findings, therefore, support the presence of an overall enhancement of body schema in health professionals. Whether this enhancement develops due to intensive practice as a part of training/occupational demands or is inherent to the individual is unclear.

The contribution of task-dependent use to LRJ performance is also supported by our finding that hand therapists had significantly quicker RTs for egocentric images of hands (1PP) than healthy controls. First, our findings are generally consistent with previous work showing that experts in hand use (i.e., table tennis players) are faster at mentally rotating hand images than non-experts, and quicker for images of their dominant versus non-dominant hand (Habacha et al. 2014). Second, past work has shown that when the LRJ task is specific to the skilled spatial movement, as occurred in the present study, skilled populations (i.e., elite divers) have uniquely enhanced performance for the rotational stage (i.e., IMI) of the LRJ task that does not occur during object-based mental rotation (Feng et al. 2017). Such findings suggest that enhanced sensorimotor processing (IMI) in hand therapists drives the egocentric RT decrease rather than a switch to visual object-based recognition. Enhanced sensorimotor processing in hand therapists is likely due to precise motor use (Habacha et al. 2014), repeated habitual IMI simulation (Rizzolatti et al. 1996), with the resultant refining of internal representation of the hand. Last, that podiatrists' RTs did not differ from healthy controls for egocentric foot images would be predicted by an influence of task-dependent use on LRJ performance given that podiatrists do not use their own feet more than healthy controls (or hand therapists).

We also hypothesised that the duration of task-dependent use (i.e., amount of clinical experience) would correlate with enhanced performance given previous findings that training improves hand LRJ task performance (Berneiser et al. 2018) and that skilled populations have enhanced mental rotation performance (Feng et al. 2017; Habacha et al. 2014; Schmidt et al. 2016). While the present study provides evidence for enhanced movement representations (quicker RTs) in health professionals, the amount of clinical experience was not correlated with enhanced performance as hypothesised. This raises two possibilities: first, the lack of correlation may reflect that consistent task-dependent use maintains, rather than increases, enhanced motor representations that occurred due to initial professional training. Second, it may also reflect that people who are intrinsically more body aware (Craig 2009) self-select into professions that require good motor and spatial skills. While there is some evidence to suggest that body awareness and movement representations share similar cortical anatomy (Berti et al. 2005), heightened awareness of the body may also relate to more general mechanisms, such as those subserved by interoceptive processes supported in the anterior insular cortex (Craig 2009), which can promote motor skill acquisition (Toner and Moran 2015). Longitudinal testing that purposefully recruits populations that are about to undergo intensive training in precise hand movements would be fruitful.

Features that influence the shift from IMI to other recognition strategies

Our findings show FoR-specific differences in LRJ performance for feet images that likely represent changes to recognition strategies used in the LRJ task. Specifically, large differences in FoR RT ratios between podiatrists and healthy controls for the foot LRJ task, driven by a reduction in RT to 3PP images in podiatrists, strongly suggest that a different recognition strategy is being used.

A change in LRJ recognition strategy is consistent with past work demonstrating that individual differences in mental rotation ability are likely due to the use of varying recognition strategies (Khooshabeh et al. 2013; Mumaw et al. 1984). For example, in an object-based mental rotation task, people with high spatial ability have been shown to be faster in encoding the stimuli (i.e., stable visual representation) and in manipulating their visual representation (Mumaw et al. 1984), and are generally more accurate than people with low spatial ability (Khooshabeh et al. 2013). In addition, high-spatial ability imagers update their recognition strategy based on the familiarity of the image, whereas low-spatial ability imagers do not (Khooshabeh et al. 2013). That podiatrists show generally enhanced spatial ability compared with healthy controls (i.e., are more accurate for both hand and feet LRJs) would support their ability to update the recognition strategy used based on image familiarity (i.e., 3PP visual exposure to feet provides increased familiarity for allocentric images).

Past work has shown that features of a mental rotation task that promote embodiment ('self' versus 'other') can influence a shift from IMI to other recognition strategies, as evidenced by distinct neural underpinnings (Sirigu and Duhamel 2001). That is, when 1PP is used during a hand spatial position task (imagine your own hand), motor imagery processes are engaged, while if 3PP (imagine the experimenter's hand) is used, visual imagery processes are engaged (Sirigu and Duhamel 2001). As mentioned, image FoR provides perspectives that are consistent with a view of one's own hand/foot ('self': egocentric/1PP) or another's hand/foot ('other': allocentric/3PP), with distinct neural correlates (Saxe et al. 2006). The right EBA is selectively activated during mental rotation of body parts (Blanke et al. 2010), and has shown to be involved in identification of one's own versus another's body (Saxe et al. 2006), with distinct neural subpopulations that are selectively active during recognition of body 'self' and 'other' images (Myers and Sowden 2008). That is, research suggests that the right EBA uses perspective, i.e. allocentric or egocentric, to help identify body ownership (Saxe et al. 2006). Taken together, a switch from sensorimotor strategies (i.e., IMI) to visual strategies and vice versa would be predicted in association with perspective (1PP versus 3PP).

Our findings extend such a prediction by showing that an individual's habitual vision of feet in 3PP (others' feet) results in selectively improved performance for allocentric images of feet which would support enhancement of visual imagery strategies. Past work has hypothesised that unexpectedly large increases in RT for allocentric images represent reframing of allocentric images to an egocentric FoR. An alternate possibility is that IMI is still utilised to confirm or refute the initial judgement of laterality, but with allocentric images, the initial judgement is more likely to be wrong (i.e., more difficult), requiring re-confirmation of laterality via IMI and thus larger than expected increases in RT for allocentric images. It is accepted that visual exposure can contribute to representation and identification of the body (Hodzic et al. 2009). Thus, our findings of reduced RTs suggest that enhanced visual imagery processes may: (i) allow mental reframing of allocentric images to egocentric FoR to be avoided; (ii) increase the likelihood that the initial choice is correct (i.e., IMI is still used); (iii) avoid both processes via visual object-based recognition strategies, whereby one merely recognises an image based on past exposure. Visual inspection of Fig. 2a shows that podiatrists' recognition of foot images was facilitated most for images of 'other' (i.e., lateral orientation) versus 'self' (i.e., medial orientation) in both the allocentric (225° vs 135° orientation) and egocentric (315° vs 45°) FoR. Such findings are the opposite of what is normally seen (facilitation of medial versus lateral) (De Simone et al. 2013), and thus would more strongly support the use of visual object recognition based on past 3PP exposure (versus IMI or visual-proprioceptive matching).

Last, our work also extends past findings by showing that the relative weighting of both sensorimotor internal representation and visual exposure may be important to the recognition strategy used. Specifically, the effects of habitual 3PP vision of the body on LRJ performance seen here differed between body parts that had relatively strong/precise (hands) versus weak/imprecise (feet) sensorimotor representations. It has been shown that both sensorimotor and visual frames of reference are used to represent the body, and when sensorimotor input is removed (i.e., spinal cord injury), the relative weighting of visual contribution to bodily representation is increased, with visual imagery processes primarily used to make LRJs (Ionta et al. 2016). Our work suggests that the strength of internal sensorimotor representations may influence the degree to which visual contribution can overcome sensorimotor contribution during LRJs. Given consistent use of highly precise movements, hands typically have a strong internal representation. That we saw no congruent facilitation of habitual 3PP visual exposure to hands on RTs for allocentric hand images suggests a maintenance of IMI strategies. In contrast, such an effect would not be predicted for feet, given their relatively smaller (vs hands) internal representation. That is, the increased relative weighting afforded by visual exposure of feet in 3PP (versus less strong sensorimotor representation) would allow a switch to visual processing during LRJs of allocentric images.

Study strengths and limitations

This study is one of the first to recruit a large sample (worldwide) of clinical professionals and healthy controls. Our results showing generally slower RTs for allocentric versus egocentric images are consistent with past work (Parsons 1987; Wallwork et al. 2013), supporting the validity of our online protocol. However, there are limitations associated with the online data collection that may have resulted in increased variance in the data. Posture and biomechanical position affects LRJ performance (Ionta and Blanke 2009; Parsons and Fox 1998); thus during the task, participants are required to keep their hands and feet stationary. While provided with explicit instructions to stay stationary, due to our online data collection, it cannot be confirmed that this occurred.

Additionally, some healthy volunteers of this study had a medical/allied health background (other than podiatry/hand therapy). However, that between group differences are present suggests that any exposure/practice in the healthy controls was insufficient to impact LRJ performance. In addition, while we collected hand dominance data due to its known impact on LRJ task performance

(Wallwork et al. 2013), we did not collect foot dominance (Oldfield 1971). Given that past cohorts have predominantly found that foot dominance mirrors that of hand dominance (Stanton et al. 2012), it is unlikely to have had an effect. Last, gender balance differed between groups (i.e., a very low number of male podiatrists). Because low participant numbers for categorical covariates subdivides the sample allowing for undue influence of covariates in linear mixed model analyses, we performed sensitivity analyses. The LRJ performance results for hand images differed based on whether gender was included as a covariate or a female only sample was used. The present study is unable to determine whether this is a true gender effect or whether this is a sample/statistical model limitation; further work is needed to specifically answer this question.

Conclusion

This research found that regular visual exposure to the body in 3PP had differential effects on mental rotation of images of hands and feet. Regular visual exposure to the feet in 3PP (i.e., podiatrists) appears to promote a shift from IMI to non-IMI strategies (e.g., visual object-based recognition), as evidenced by selectively reduced RTs for allocentric feet images. However, regular visual exposure to the hands in 3PP (i.e., hand therapists) did not influence RT for allocentric hand images, rather, performance for egocentric (first person) hand images was enhanced, which is likely a function of enhanced internal representations of the hand. Indeed, task-dependent use (i.e., via a health professional background) resulted in general enhanced LRJ task performance, whereby the health professionals were more accurate at both hand and feet tasks than healthy controls, but not more accurate than each other. Together, the findings support the idea that both sensorimotor and visual processes contribute to LRJ performance and recognition strategy. Further work to delineate the conditions under which these (and other) processes interact and/or dominate during LRJs of body parts is warranted.

Acknowledgements TRS supported by a National Health & Medical Research Council Early Career Fellowship (ID1054041). We would also like to thank Dr David Butler and Mr Tim Cocks from NOIgroup Ltd for their assistance in setting up the left/right judgement task and for use of their NOIgroup research platform to host our online study.

Compliance with ethical standards

Conflict of interest TRS received travel and accommodation support from Eli Lilly Ltd for speaking engagements (September 2014, unrelated to the present topic). All other authors have no conflicts to declare.

References

Berlucchi G, Aglioti S (1997) The body in the brain: neural bases of corporeal awareness. Trends Neurosci 20:560–564

Berneiser J, Jahn G, Grothe M, Lotze M (2018) From visual to motor strategies: training in mental rotation of hands. NeuroImage 167:247–255

Berti A et al (2005) Shared cortical anatomy for motor awareness and motor control. Science 309:488–491

Blanke O, Ionta S, Fornari E, Mohr C, Maeder P (2010) Mental imagery for full and upper human bodies: common right hemisphere activations and distinct extrastriate activations. Brain Topogr 23:321–332

Brady N, Maguinness C, Ni Choisdealbha A (2011) My hand or yours? Markedly different sensitivity to egocentric and allocentric views in the hand laterality task. PloS One 6:e23316 https://doi.org/10.1371/journal.pone.0023316

Cooper LA, Shepard RN (1975) Mental transformations in the identification of left and right hands. J Exp Psychol Human Percept Perform 104:48–56

Craig AD (2009) How do you feel—now? The anterior insula and human awareness. Nat Rev Neurosci 10:59–70. https://doi.org/10.1038/nrn2555

De Simone L, Tomasino B, Marusic N, Eleopra R, Rumiati RI (2013) The effects of healthy aging on mental imagery as revealed by egocentric and allocentric mental spatial transformations. Acta Psychol 143:146–156. https://doi.org/10.1016/j.actpsy.2013.02.014

DiCarlo JJ, Cox DD (2007) Untangling invariant object recognition. Trends Cognit Sci 11:333–341. https://doi.org/10.1016/j.tics.2007.06.010

DiCarlo JJ, Zoccolan D, Rust NC (2012) How does the brain solve visual object recognition? Neuron 73:415–434. https://doi.org/10.1016/j.neuron.2012.01.010

Feng T, Zhang Z, Ji Z, Jia B, Li Y (2017) Selective effects of sport expertise on the stages of mental rotation tasks with object-based and egocentric transformations. Adv Cognit Psychol 13:248–256

Fiorio M et al (2007) Mental rotation of body parts and non-corporeal objects in patients with idiopathic cervical dystonia. Neuropsychologia 45:2346–2354. https://doi.org/10.1016/j.neuropsychologia.2007.02.005

Ganesh S, van Schie HT, Cross ES, de Lange FP, Wigboldus DHJ (2015) Disentangling neural processes of egocentric and allocentric mental spatial transformations using whole-body photos of self and other. NeuroImage 116:30–39

Gentilucci M, Daprati E, Gangitano M (1998) Right-handers and left-handers have different representations of their own hand. Cogn Brain Res 6:185–192

Habacha H, Molinaro C, Tabben M, Lejeune-Poutrain L (2014) Implementation of specific motor expertise during a mental rotation task of hands. Exp Brain Res 232:3454–3473

Habacha H, Lejeune-Poutrain L, Molinaro C (2017) Realistic stimuli reveal selective effects of motor expertise during a mental body rotation task. Am J Pscyhol 130:47–62

Hegarty M (2018) Ability and sex differences in spatial thinking: What does the mental rotation test really measure? Psychon Bull Rev 25:1212–1219

Hodzic A, Kaas A, Muckli L, Stirn A, Singer W (2009) Distinct cortical networks for the detection and identification of human body NeuroImage 45:1264–1271 https://doi.org/10.1016/j.neuroimage.2009.01.027

Ionta S, Blanke O (2009) Differential influence of hands posture on mental rotation of hands and feet in left and right handers. Exp Brain Res 195:207–217. https://doi.org/10.1007/s00221-009-1770-0

Ionta S, Fourkas AD, Fiorio M, Aglioti S (2007) The influence of hands posture on mental rotation of hands and feet. Exp Brain Res 183:1–7

Ionta S, Perruchoud D, Draganski B, Blanke O (2012) Body context and posture affect mental imagery of hands. PloS One 7:e34382 https://doi.org/10.1371/journal.pone.0034382

Ionta S, Villiger M, Jutzeler CR, Freund P, Curt A, Gassert R (2016) Spinal cord injury affects the interplay between visual and sensorimotor representations of the body. Sci Rep 6:20144. https://doi.org/10.1038/srep20144

Jeannerod M (2001) Neural simulation of action: a unifying mechanism for motor cognition. NeuroImage 14:103–109

Kawamichi H, Kikuchi Y, Endo H, Takeda T, Yoshizawa S (1998) Temporal structure of implicit motor imagery in visual hand-shape discrimination as revealed by MEG. Neuro Rep 9:1127–1132

Khooshabeh P, Hegarty M, Shipley TR (2013) Individual differences in mental rotation: piecemeal versus holistic processing. Exp Psychol 60:164–171

Kosslyn SM, DiGirolamo GJ, Thompson WL, Alpert NM (1998) Mental rotation of objects versus hands: neural mechanisms revealed by positron emission tomography. Psychophysiology 35:151–161

Lazar A, Lewis C, Fries P, Singer W, Nikolic D (2018) Visual exposure optimizes stimulus encoding in primary visual cortex. bioRxiv https://doi.org/10.1101/502328

Mumaw RJ, Pellegrino J, Kail R, Carter P (1984) Different slopes for different folks process analysis of spatial aptitude. Memory Cognition 12:515–521

Myers A, Sowden PT (2008) Your hand or mine? The extrastriate body area NeuroImage 42:1669–1677 https://doi.org/10.1016/j.neuroimage.2008.05.045

Ni Choisdealbha A, Brady N, Maguinness C (2011) Differing roles for the dominant and non-dominant hands in the hand laterality task. Exp Brain Res 211:73–85

Oldfield R (1971) The assessment and analysis of handedness: The Edinburgh Inventory. Neuropsychologia 9(1):91–113

Parsons LM (1987) Visual discrimination of abstract mirror-reflected three-dimensional objects at many orientations. Percept Psychophys 42:49–59. https://doi.org/10.3758/BF03211513

Parsons LM, Fox PT (1998) The neural basis of implicit movements used in recognising hand shape. Cognit Neuropsychol 15:22

Qu F, Wang J, Zhong Y, Ye H (2018) Postural effects on the mental rotation of body-related pictures: an fMRI study. Front Psychol. https://doi.org/10.3389/fpsyg.2018.00720

Rizzolatti G, Fadigo I, Fogassi L, Gallese V (1996) Premotor cortex and the recognition of motor actions. Cogn Brain Res 3:131–141

Saxe R, Jamal N, Powell L (2006) My body or yours? The effect of visual perspective on cortical body representations. Cereb Cortex 16:178–182

Schmid AB, Coppieters MW (2012) Left/right judgment of body parts is selectively impaired in patients with unilateral carpal tunnel syndrome. Clin J Pain 28:615–622. https://doi.org/10.1097/AJP.0b013e31823e16b9

Schmidt M, Egger F, Kieliger M, Rubeli B, Schuler J (2016) Gymnasts and orienteers display better mental rotation performance than nonathletes. J Individ Differ 37:1–7

Schwoebel J, Coslett HB (2005) Evidence for multiple, distinct representations of the human body. J Cognit Neurosci 17:543–553. https://doi.org/10.1162/0898929053467587

Shepard RN, Cooper LA (1986) Mental images and their transformations. Mental images and their transformations. The MIT Press, Cambridge

Shepard RN, Metzler J (1971) Mental rotation of three-dimensional objects. Science 171:701–703

Sirigu A, Duhamel JR (2001) Motor and visual imagery as two complementary but neurally dissociable mental processes. J cognit Neurosci 13:910–919

Stanton TR, Lin CW, Smeets RJ, Taylor D, Law R, Lorimer Moseley G (2012) Spatially defined disruption of motor imagery performance in people with osteoarthritis. Rheumatology 51:1455–1464. https://doi.org/10.1093/rheumatology/kes048

Toner J, Moran A (2015) Enhancing performance proficiency at the expert level: Considering the role of 'somaesthetic awareness'. Psychol Sport Exerc 16:110–117. https://doi.org/10.1016/j.psychsport.2014.07.006

Vatavu R, Pentiuc S, Chaillou C, Grisoni L, DeGrande S (2006) Visual recognition of hand postures for interacting with virtual environment. Paper presented at the 8th international conference on development and application systems, Suceava, Romania

Wallwork SB, Butler DS, Fulton I, Stewart H, Darmawan I, Moseley GL (2013) Left/right neck rotation judgments are affected by age, gender, handedness and image rotation. Man Ther 18:225–230. https://doi.org/10.1016/j.math.2012.10.006

Wraga M, Shepard JM, Church JA, Inati S, Kosslyn SM (2005) Imagined rotations of self versus objects: an fMRI study. Neuropsychologia 43:1351–1361

Xue J, Li C, Quan C, Lu Y, Yue J, Zhang C (2017) Uncovering the cognitive processes underlying mental rotation: an eye-movement study. Sci Rep 7:10076