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Probing links between action perception and action production in Parkinson's disease using Fitts' law

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ABSTRACT

Information on how the subcortical brain encodes information required to execute actions or to evaluate others' actions remains scanty. To clarify this link, Fitts'-law tasks for perception and execution were tested in patients with Parkinson's disease (PD). For the perception task, participants were shown apparent motion displays of a person moving their arm between two identical targets and reported whether they judged that the person could realistically move at the perceived speed without missing the targets. For the motor task, participants were required to touch the two targets as quickly and accurately as possible, similarly to the person observed in the perception task. In both tasks, the PD group exhibited, or imputed to others, significantly slower performances than those of the control group. However, in both groups, the relationships of perception and execution with task difficulty were exactly those predicted by Fitts' law. This suggests that despite dysfunction of the subcortical region, motor simulation abilities reflected mechanisms of compensation in the PD group. Moreover, we found that patients with PD had difficulty in switching their strategy for estimating others' actions when asked to do so.

1. Introduction

Previous theorizing has postulated a tight link between action perception and execution of movement (Prinz, 1997). In support of this theory, many behavioural and neuroimaging studies have shown that these two processes are tightly coupled. For example, observers were impaired in judging the walking speed of simulated walking persons while they were themselves walking (Jacobs and Shiffrar, 2005). Moreover, the judgment of the weight of a box lifted by another person depends on the weight of a box lifted by the observers (Hamilton et al., 2004). In addition to the behavioural evidence, electrophysiological studies have found evidence of a 'mirror neuron' system, where neurons in the premotor areas are active both when a monkey observes the experimenter performing an action and when the monkey produces the same action itself (Pellegrino et al., 1992). A similar 'mirror neuron system' was found in human cortical regions such as parts of the premotor and inferior parietal cortices, as revealed by several neuroimaging techniques (Iacoboni and Dapretto, 2006). For example, in expert dancers, observing one's own motor repertoire can activate the premotor areas (Calvo-Merino et al., 2005). This system can also be found in the early stages of development (Southgate et al., 2010) and in human single neurons (Mukamel et al., 2010). These studies suggest that perceiving another's action and producing the same action oneself recruit the same specific cortical regions. However, motor control is processed not only in the cortical regions but also in subcortical regions (Middleton and Strick, 2000). It remains unclear whether subcortical regions display the same overlap between action perception and action production as do cortical areas. To address this question, we aimed to determine whether a person's degree of subcortical action production ability would affect their degree of action perception ability.

Parkinson disease (PD) is a progressive neurological disorder characterized by preferential loss of dopaminergic neurons in the region of the substantia nigra. The disease leads to resting tremor, rigidity, bradykinesia, and postural instability. Previous neuroimaging studies in patients with PD have shown that subcortical regions such as the globus pallidus (GP) and the subthalamic nucleus (STN) can be involved in both action-related and perceptual processing. For example, sufficiently serious loss of dopamine in both internal and external (GPi and GPe)

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regions can contribute to the motor manifestations of PD (Rajput et al., 2008). Moreover, direct electrophysiological recording from the STN of patients with PD indicate that both action execution and observation can reduce power in the beta band (Alegre et al., 2010). The involvement of the subcortical regions in both perception and action processing has also been revealed in several neuroimaging studies in healthy controls. For example, the right basal ganglia are activated with increasing levels of motor difficulty (Eskenazi et al., 2012) and the GP, a locus encompassing both GPi and GPe regions, plays an important role in regulating the force of produced actions (Aparicio et al., 2005; Prodoehl et al., 2009). Therefore, there is a possibility that both the execution of movement and perception of others' actions in patients with PD are impaired in parallel.

Although it is obvious that patients with PD have difficulty in executing actions, findings are inconsistent regarding the link between the patients' action execution abilities and their perception of others' actions. Several studies have shown that motor impairment in patients with PD does not necessarily lead to impaired understanding of the actions of others. Poliakoff et al. (2010) reported that patients with PD were able to judge the weight that they observed an actor lifting, despite their own motor impairments). However, other studies (Castiello et al., 2009; Conson et al., 2014) have shown that patients' own motor abilities can modulate their ability to understand the performance of others' actions. For example, Castiello et al. (2009) reported that when patients with PD were required to reach to an object, the reaching movements were facilitated by observation of another person modelling the action only when the model was an individual with PD, not a healthy control. Moreover, Conson et al. (2014) reported that patients with PD were selectively impaired in mental transformation of back-facing human figures on the side corresponding to their own most severely impaired side; however, they performed adequately, like the healthy controls, on mental transformation of front-facing bodies and on letter rotation. These findings appear consistent with previous studies on healthy controls showing that one's own motor repertoire can modulate the judgment and understanding of others' actions (Calvo-Merino et al., 2005).

However, these studies have not directly assessed the relationship between patients' abilities to execute actions and their perception of the actions of other patients with PD. Therefore, it has yet to be determined whether the degree of impairment in executing actions in the patient correlates with the degree of patient impairment in the perception of others' actions. To resolve the inconsistent findings of the previous studies on action-perception coupling in patients with PD (Castiello et al., 2009; Poliakoff et al., 2010), we introduced an observational Fitts'-law task devised by Grosjean and colleagues (Grosjean et al., 2007) to test for the presence of a direct link between participants' action production abilities and their perception of the actions of other participants with PD (Aparicio et al., 2005; Prodoehl et al., 2009).

Fitts (1954) law is a well formulated law of human movement, which describes the time required to point as quickly and accurately as possible between two targets as a function of the width of the targets and the distance between them (for review, see (Plamondon and Alimi, 1997)). Fitts' law is formulated as follows:

$$\mathrm{MT} = a + b \times \mathrm{ID},$$

where the MT is the average movement time to reach a target, and is defined as a linear function of the index of difficulty (ID) of the movement. The ID, in turn, is a function of the distance to be covered, commonly referred to as the amplitude (A), and the width (W) of the target to be approached. The ID is expressed as follows.

$$\mathrm{ID} = \log_2(2\mathrm{A}/W)$$

The formula is based on participant performance in touching two bars. Grosjean and colleagues have shown that this law is applicable not only to action execution but also to action perception. Participants were shown apparent-motion displays of a person moving his/her arm between two identical targets. Target width, the separation between targets, and movement speed were systematically varied. The task was to decide whether the observed person could possibly move at the perceived speed without missing the targets. The movement times reported in the perception task as being just possible were exactly those predicted by Fitts' law for the action domain.

The Fitts'-law task should also be beneficial in evaluating the function of the action observation system in subcortical regions in patients with PD. A previous neuroimaging study on the Fitts' law observation paradigm, similar to that by Grosjean et al. (2007), has shown that with an increase in ID, increased activity is seen not only in the motor areas such as the primary motor cortex and right supplementary motor area, but also in the right basal ganglia such as the GP, where the increase is linear (Eskenazi et al., 2012). These findings indicate that the observational Fitts' law paradigm can describe the neural activities involved in action production in the basal ganglia, which is commonly impaired in patients with PD (Aparicio et al., 2005; Prodoehl et al., 2009).

In the present study, we adopted the previously described Fitts'-law task (Grosjean et al., 2007) and applied it to patients with PD to clarify whether both action execution and perception of others' actions share common processing pathways in subcortical regions. Adding to previously established information (Grosjean et al., 2007), we here explored the strategy patients with PD use for understanding others' actions. Thus, we provided participants explicit task instructions designed to reveal whether they adopted the strategy of judging others by the standard of their own motor abilities. In the first experiment (Experiment 1), we explicitly instructed participants to imagine themselves as the person in the display, 'as if you were executing the action' (simulating 'self' condition). In the second experiment (Experiment 2), to exclude the influence of their own motor abilities, we explicitly instructed participants to imagine that the person onscreen was someone else. In both experiments, we examined the ability of the patients with PD to make accurate judgements based on their action perception by conducting the observational Fitts' law task and subsequently the conventional, active Fitts' law task where participants are instructed to move their arm between two targets as quickly as possible.

Furthermore, we hypothesized that if the patients with PD adopted a motor simulation strategy when observing others and judging the actions seen, then the same slope should be observed in both tasks of the first experiment. However, if their perception and action processing can be dissociated and they are only impaired during action production, the same law should not be observed in both tasks. We further hypothesized that if patients with PD are unavoidably affected by their own motor abilities when they judge the actions of another, then their performances should be constrained by their own motor abilities even in Experiment 2, where participants are explicitly instructed to imagine the viewpoint of 'another' person. Moreover, if we observe similar slopes across experiments in patients with PD, then it is possible that they have difficulty in switching strategies in a top-down manner, in this case, based on the experimenter's instructions. This would point to additional dysfunction due to specific cortical regions, for example, the prefrontal cortex (Eskenazi et al., 2009).

2. Experiment 1

In the first experiment, we tested whether the movement times in both perception and action tasks are predicted by Fitts' law in the PD group. If patients' abilities in simulating others' actions are preserved, the perceived movement times should increase according to the index of difficulty, as predicted by Fitts' law.

2.1. Methods

2.1.1. Participants

All participants provided written, informed consent prior to the experiment, which was conducted in conformity with the tenets of the Declaration of Helsinki and approved by the Institutional Review Board at Jichi Medical University. Twenty-three patients with PD were recruited from the Division of Neurology at Jichi Medical University. The participants reported their hand dominance (left-handed or right-handed) before testing. Their Hoehn and Yahr (H&Y) stages, evaluated during the on-state of their medication cycle, ranged from 1 to 4. Motor status was also assessed when their medication status was on, using the Unified Parkinson Disease Rating Scale (UPDRS) part III (Fahn and Elton, 1987) or the Movement Disorder Society-sponsored revision of the Unified Parkinson Disease Rating Scale (MDS-UPDRS) part III (Goetz et al., 2008). The MDS-UPDRS scores were converted to UPDRS scores (Hentz et al., 2015). Excluded were participants with low scores on the Mini-Mental State Examination (MMSE) (less than 24), with severe tremor, or receiving deep brain stimulation treatment. One of the authors (SM) strictly screened the patients based on their clinical records, to exclude any who had been diagnosed with depression, mild cognitive impairment (MCI), or other neurological conditions. Moreover, SM confirmed that none of the participants had brain atrophy, based on MRI screening, and administered the Geriatric Depression Scale (GDS) and Montreal Cognitive Assessment (MoCA) during the medical examination if necessary.

Twenty-three healthy participants with no neurological or skeletomotor dysfunction served as the control group. Each control participant was matched to a patient for age (within 3 years), gender, and hand dominance. Detailed participant information is shown in Table 1. Neither the PD patients nor controls were taking any benzodiazepines, antidepressants, antipsychotics, or medication with anticholinergic properties that could affect motor performance.

2.1.2. *Apparatus*

Each participant was seated in a chair facing a 38 × 30-cm (‘19-in.’) touch panel display (Touch Panel Systems K.K., Kanagawa, Japan; 1280 × 1024 pixels; 60 Hz). The distance between the participant's eyes and the monitor was approximately 50 cm. All visual stimuli on the monitor were programmed in MATLAB© (MathWorks, Natick, MA) using the Cogent Toolbox software (University College London, London, UK, http://www.vislab.ucl.ac.uk/cogent.php). The position of the participant's touch on the display was recorded using a function of the Cogent Toolbox with sampling at 60 Hz.

2.1.3. *Procedure*

We conducted the perception task (i.e. apparent motion paradigm) first, followed by the action task. We chose this order to reduce the influence of recent motor action on judgments of observed movement.

2.1.3.1. *Task 1-1: perception task (apparent motion paradigm)*

2.1.3.1.1. Stimuli, responses, and design. The design of the stimuli used in Task 1–1 was based on that of previous studies (Eskenazi et al., 2012; Grosjean et al., 2007). The pictures were presented at the centre of the monitor at a size of 27.5 × 18.0 cm (width × height). As with previous studies (Eskenazi et al., 2012; Grosjean et al., 2007), we adopted an apparent motion paradigm by displaying alternating pictures instead of videos, to exclude any influence of movement trajectory cues. Each pair of pictures showed a right index finger touching one of two targets. Targets in each frame were of identical width (W) and were separated by a given movement amplitude (A). Three ID levels (2, 3, and 4) were constructed from different target widths (W) and movement amplitudes (A), see Table 2. Moreover, stimuli could have identical IDs but different W and A values. Fig. 1 shows two pairs of sample pictures that illustrate the latter situation.

Table 1
Participant information.

Variable mean ± SD	PD group	Control group (Experiment 1)	Control group (Experiment 2)
n	23	23	23
Age (y)	67.6 ± 7.2	68.3 ± 6.0 ($p = 0.69$)	68.6 ± 6.3 ($p = 0.60$)
Sex	16F/7M	16F/7M	16F/7M
Handedness	23R/0L	23R/0L	23R/0L
MMSE (/30)	27.1 ± 1.9	28.1 ± 1.6 ($p = 0.051$)	28.1 ± 1.6 ($p = 0.051$)
Disease duration (y)	5.9 ± 4.3	N/A	N/A
Most affected side	14R/9L	N/A	N/A
H&Y stage	2.6 ± 0.8	N/A	N/A
UPDRS score (/108)	26.0 ± 11.2	N/A	N/A

Table 2
Movement amplitude (cm) in Experiment 1.

Target width (cm)	Index of difficulty		
	2	3	4
2	4	8	16
4	8	16	32

The rate at which the picture alternated was controlled by 1 of 10 stimulus-onset asynchronies (SOAs). SOAs ranged from 67 to 517 ms in 50-ms increments. Participants were explicitly instructed to imagine themselves as the person in the display and ‘as if you were executing the action’ and then to judge whether the observed apparent motion was possible to perform with no failures to touch the target (simulating ‘self’ condition). Responses were made by touching either a left area labelled ‘possible’ or a right area labelled ‘impossible’ on the monitor. The participants performed two experimental blocks. Each block ran through all the 60 trial types (2 widths × 3 IDs × 10 SOAs), once each, in a pseudorandom order that varied from block to block. In each trial, the picture was altered eight times (i.e. four reciprocal apparent motions).

2.1.3.1.2. Analysis. For each participant, the proportion of ‘possible’ judgments was calculated for each of the 60 combinations of experimental conditions. For each of the six spatial combinations (2 widths × 3 IDs), the proportion of ‘possible’ judgments increased in a sigmoidal fashion with SOA (Grosjean et al., 2007). To estimate the perceived movement time (MT) in each of the six combinations, the proportions of ‘possible’ judgments were fitted with the cumulative density function of a Gaussian distribution. We used the optimization toolbox in MATLAB to apply a fitting procedure that depended on minimizing Pearson's chi-square statistic. We defined the perceived MT as the SOA at which the participants gave an equal proportion of ‘possible’ and ‘impossible’ judgments. To test whether the data followed Fitts’ law, we applied linear regression analysis to the perceived MTs and calculated the slopes of the regression lines in each participant.

2.1.3.2. *Task 1-2: action task (reciprocal tapping)*

2.1.3.2.1. Stimuli, responses, and design. Two rectangular targets were displayed. Both the width (W) and amplitude (A) of the targets were identical to those of the perception task (Table 2). The participants were asked to touch these two targets alternately as quickly as possible without touching outside the targets. The participants performed ten experimental blocks. Each block consisted of the six possible trial types (2 widths × 3 IDs) in a pseudorandom order that varied from block to block. In each trial, the participants were required to touch the targets alternately nine times (i.e. four reciprocal motions).

2.1.3.2.2. Analysis. In each trial type, we analysed actual MTs from the inter-touch intervals recorded by the touch panel display. For each condition, we computed the mean inter-touch interval of the eight intervals between the first touch and ninth touch. Using the same

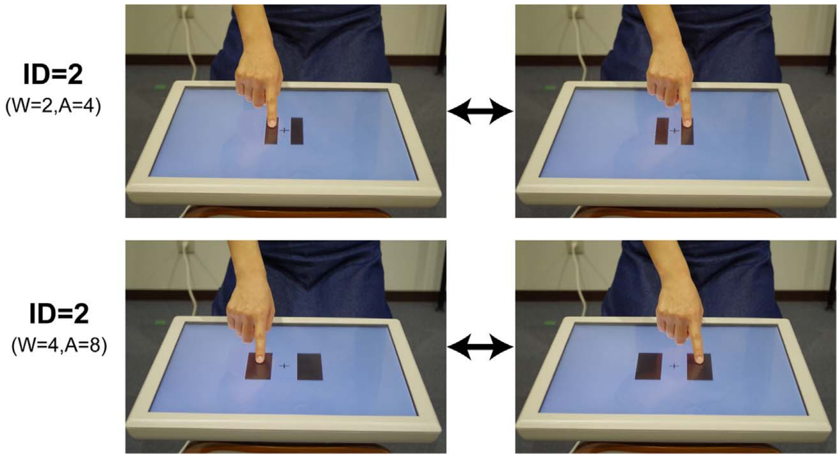

Fig. 1. Sample pictures used in perception tasks. Movement is simulated by flashing back and forth between the left picture and right picture. The index of difficulty (ID) levels are altered by altering the size of the rectangles (i.e. width) and the distance between targets (i.e. movement amplitude). Upper and lower pairs of pictures show identical IDs realised in alternative ways.

method as in the apparent motion paradigm, we conducted linear regression analysis on actual MTs and calculated the slopes of the regression lines.

2.1.4. Statistical analysis

We compared the perceived and actual MTs using a mixed-design repeated measures analysis of variance (ANOVA) with Greenhouse-Geisser epsilon correction for nonsphericity. A two-way ANOVA was applied to the slopes of the regression lines with participant group (PD vs. Control) as a between-subjects factor and task (perception vs. action) as a within-subject factor. Levene test (the standard test for inhomogeneity of variances) were conducted to test whether the variances in slopes across the two different groups were heterogeneous. We used a significance threshold of $p < 0.05$.

2.2. Results

Fig. 2 shows the proportion of 'possible' judgments as a function of SOA. Solid, dotted, and dashed lines indicate the different IDs. In both PD (Fig. 2**A** and **C**) and control (Fig. 2**B** and **D**) groups, the perceived MT (i.e. the SOA having an equal proportion of 'possible' and 'impossible' judgments) increased in proportion to the ID.

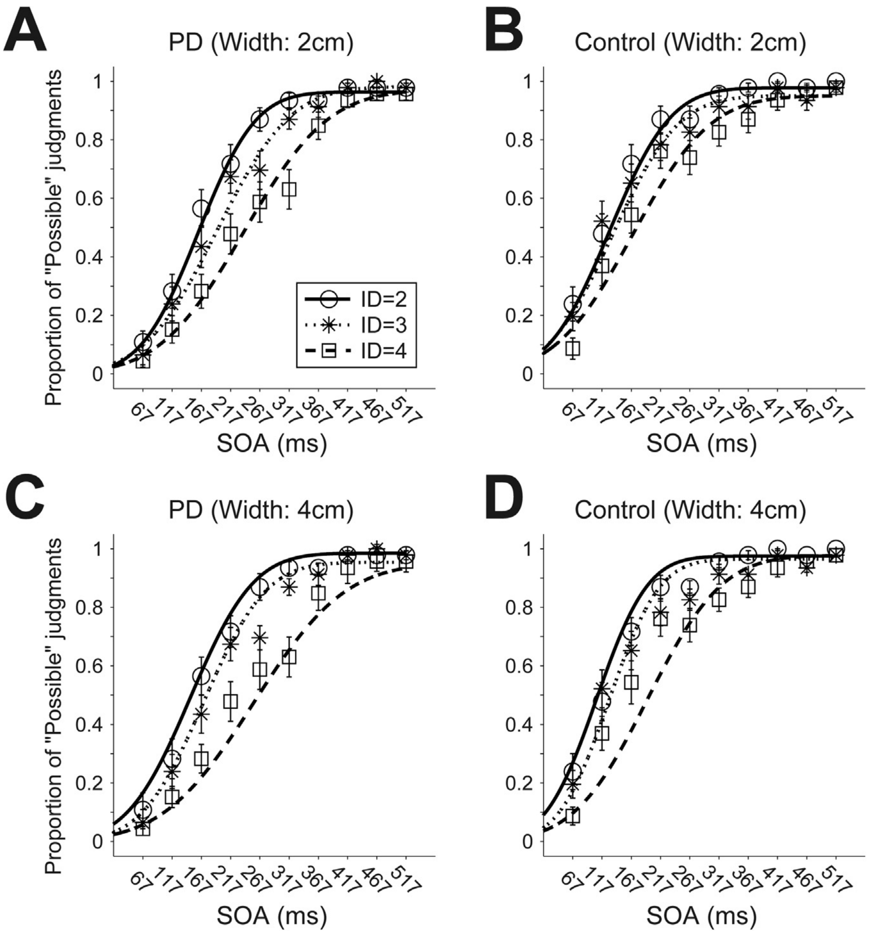

Fig. 2. Perception task results, Experiment 1. Proportion of 'possible' judgments in Parkinson's disease (PD) (A and C) and control (B and D) groups. In Experiment 1, participants are asked to imagine that they are the person shown performing the actions. Circles, asterisks, and squares show the mean proportions under different IDs. Error bars indicate standard error.

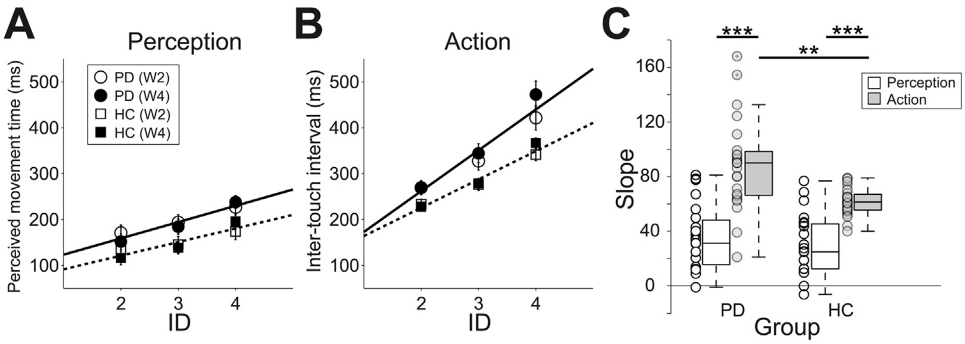

Fig. 3. Comparison of results of perception task and action task, Experiment 1. (A) Mean perceived movement time to reach the target (MT) and (B) mean actual MT as a function of ID and target width (W). (C) Mean Fitts'-law slopes in the perception (white bars) and the action (grey bars) tasks. Each circle represents data from individual participants. The + symbols indicate outliers (values 1.5 times the interquartile range above the third quartile). Error bars indicate standard error. **, $p < 0.01$; ***, $p < 0.001$.

Fig. 3**A** and **B** show the mean perceived and actual MTs, respectively. Solid lines indicate the regression lines in each group. Both the mean perceived and actual MTs increased linearly with ID with high r^2 values in all conditions. [Perception-PD group, $r^2 = 0.91$, $F(1, 4) = 53.3$, $p = 0.0019$; Perception-control group, $r^2 = 0.80$, $F(1, 4) = 20.8$, $p = 0.01$; Action-PD group, $r^2 = 0.92$, $F(1, 4) = 60.6$, $p = 0.0015$; Action-control group, $r^2 = 0.95$, $F(1, 4) = 95.9$, $p = 0.00061$]. This indicates that the results in both the PD and control groups followed Fitts' law.

Levene tests revealed that variances in slope across the two groups were heterogeneous in the action condition ($p = 0.001$), but not in the perception condition ($p = 0.72$). Regarding the slope, we found significant main effects of group [$F(1, 44) = 9.90$, $p = 0.003$, $\eta_p^2 = 0.18$] and task [$F(1, 44) = 83.4$, $p < 0.01$, $\eta_p^2 = 0.66$]. This suggests that the slopes in the PD group were significantly steeper than were those in the control group. Moreover, the slopes in the action condition were significantly steeper than were those in the perception condition. Furthermore, the interaction of group × task was significant [$F(1, 44) = 5.23$, $p = 0.027$, $\eta_p^2 = 0.11$]. The simple main effects of the interaction revealed that the effect of group was significant in the action condition [$F(1, 88) = 15.00$, $p < 0.01$, $\eta_p^2 = 0.145$]. This suggests that the slope in the PD group was significantly steeper compared with that in the control group for the action condition (88.95 vs. 61.73). Moreover, the slopes for the action condition in both the control [$F(1, 44) = 23.45$, $p < 0.01$, $\eta_p^2 = 0.35$; 61.73 vs. 29.70] and PD [$F(1, 44) = 65.21$, $p < 0.01$, $\eta_p^2 = 0.60$; 88.95 vs. 35.54, Fig. 3**C**] groups were significantly steeper than were those for the perception condition.

3. Experiment 2

In Experiment 1, we found that Fitts' law was preserved in both tasks and in both groups of participants when they were instructed to simulate the person on the screen as 'themselves'. This suggests that in the PD group, the ability to understand action using a simulation strategy seems to be preserved. In the subsequent experiment, we explored whether this strategy can be overridden by explicit instructions—to imagine that the person in the display is 'another' person. When planning the experiment, we hypothesized that if the patients with PD have difficulties in simulating the person in the display as 'another' person, so as not to use their own bodily abilities in a simulation strategy, then their performance should be similar to the results found in Experiment 1. However, if the patients with PD do not have difficulties in switching strategies, then their performance would be different from the results in Experiment 1. The experimental settings and analysis of Experiment 2 were identical to those of Experiment 1.

3.1. Methods

3.1.1. Participants

Twenty-three patients with PD and 23 healthy controls participated in this experiment. All patients with PD and 21 of 23 healthy controls were identical with the participants in Experiment 1 (Table 1). Two healthy participants withdrew from the experiment because they felt unwell during the testing. All participants provided written, informed consent prior to the experiment, as in Experiment 1.

Neither the PD patients nor controls were taking any benzodiazepines, antidepressants, antipsychotics, or medication with anticholinergic properties that could affect motor performance.

3.1.2. Procedure

3.1.2.1. Task 2-1: perception task (apparent motion paradigm). Three different ID levels (2, 3, and 4) were used. Because we found that the action performance in the PD group was somewhat unstable in the larger amplitude condition of Experiment 1, we changed IDs by manipulating W with a constant A value (8 cm) (Table 3). The SOAs ranged from 67 to 517 ms in 50-ms intervals. In contrast to Experiment 1, participants were explicitly instructed to imagine that the person onscreen was someone else and then to judge whether the observed apparent motion was possible to perform with no failures to touch the target (simulating 'other' condition). The participants performed two experimental blocks. Each block consisted of the 30 possible trial types (3 IDs × 10 SOAs) in a pseudorandom order that varied from block to block.

3.1.2.2. Task 2-2: action task (reciprocal tapping). Two rectangular targets were displayed with values of both W and A identical to those used in Experiment 1 (Table 3). Both the instructions and tasks were identical to those of Experiment 1. The participants performed 10 experimental blocks and each block consisted of the three possible trial types (i.e. 3 IDs) in a pseudorandom order that varied across blocks. In each trial, participants were asked to touch the targets nine times.

3.1.3. Statistical analysis

The statistical analyses were identical to those of Experiment 1.

3.2. Results

Fig. 4 shows the proportion of 'possible' judgments (**A**) in the PD group, and (**B**) in the control group.

Fig. 5**A** and **B** show the mean perceived and actual MTs in both groups. Solid and dotted lines show the regression lines for the two groups. Both the mean perceived and actual MTs followed Fitts' law in both groups. Although the r^2 values (adjusted) were high in all conditions, significance for ID as an independent variable was found only in the action task [Perception-PD group, $r^2 = 0.92$, $F(1, 1) = 24.24$,

Table 3
Target width (cm) in Experiment 2.

Movement amplitude (cm)	Index of difficulty		
	2	3	4
8	4	2	1

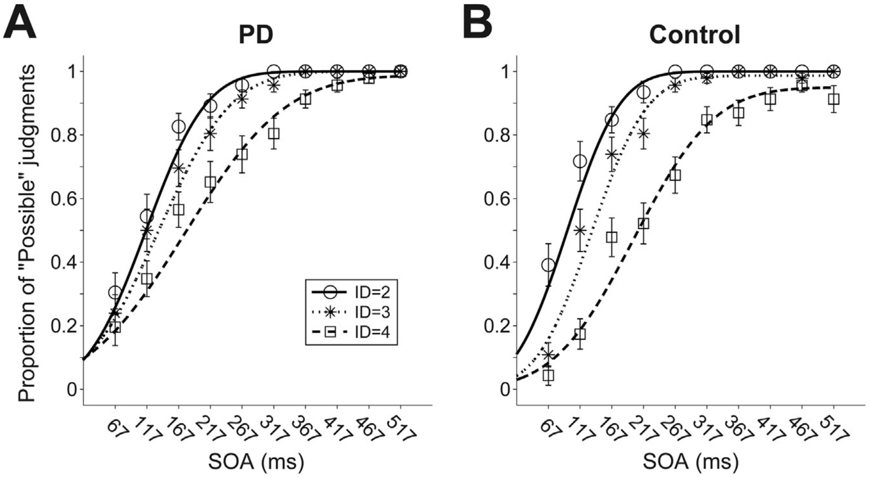

Fig. 4. Perception task results (Experiment 2). Proportion of 'possible' judgements in (A) PD and (B) control groups. In Experiment 2, participants are asked to imagine that someone else is the person shown performing the actions. Error bars indicate standard error.

$p = 0.13$; Perception-control group, $r^2 = 0.95$, $F(1, 1) = 40.83$, $p = 0.099$; Action-PD group, $r^2 = 0.99$, $F(1, 1) = 70{,}760.18$, $p = 0.0024$; Action-control group, $r^2 = 0.99$, $F(1, 1) = 237.87$, $p = 0.041$].

Levene provided no indication that the variances of slopes were heterogeneous across the two groups in the action condition ($p = 0.31$) and the perception condition ($p = 0.75$). Regarding the slope (Fig. 5**C**), the interaction of group × task was significant [$F(1, 44) = 9.36$, $p = 0.0038$, $\eta_p^2 = 0.18$], but no other effects reached statistical significance [$F\text{s} < 0.64$, $p\text{s} > 0.43$]. The simple main effects of the interaction revealed that the effect of group was significant in the perception condition [$F(1, 88) = 6.31$, $p < 0.01$, $\eta_p^2 = 0.07$, Fig. 5**c**]. This suggests that the slope in the control group was significantly steeper compared with that in the PD group for the perception condition (54.72 vs. 32.54). Moreover, the slope for the action condition was significantly steeper than that for the perception condition in the PD group [$F(1, 44) = 7.11$, $p < 0.05$, $\eta_p^2 = 0.14$; 52.99 vs. 32.54, Fig. 5**C**].

4. Discussion

Summarizing the main results, in both experiments, the actual and perceived movement times in the PD group were significantly longer than were those in the healthy control group. In Experiment 1, where participants were explicitly instructed to imagine that the person in the display was the participant him/herself, there were no significant group differences in slope for the perception condition. However, the slopes in the action condition were significantly steeper in patients with PD. In contrast, in Experiment 2 where participants were explicitly instructed to imagine that the person in the display was another person, the slopes in the healthy control group were significantly steeper compared with the PD group in the perception condition, but we found no significant differences in slope between groups in the action condition.

In regard to our initial hypothesis, the results from Experiment 1 suggest that action perception is preserved in both groups when participants adopt a simulation strategy based on their own motor abilities (following the instruction to imagine the person in the display as themselves), as the slopes in the perception condition of the PD group were not significantly different from the slopes in the control group. However, the slopes for the action condition were significantly steeper compared with those for the perception condition in both groups. This suggests that the task difficulty differently affected motor control in the PD group compared with healthy controls. Moreover, the slopes in the action condition were significantly steeper compared with those in the perception condition in both PD and healthy controls, suggesting that both groups underestimated the difficulty of performing movements at high speed when asked to judge whether observed movements were feasible.

In contrast to the results from Experiment 1, when participants were explicitly instructed to imagine that the person in the display was another person, we found that the estimated movement slopes in the

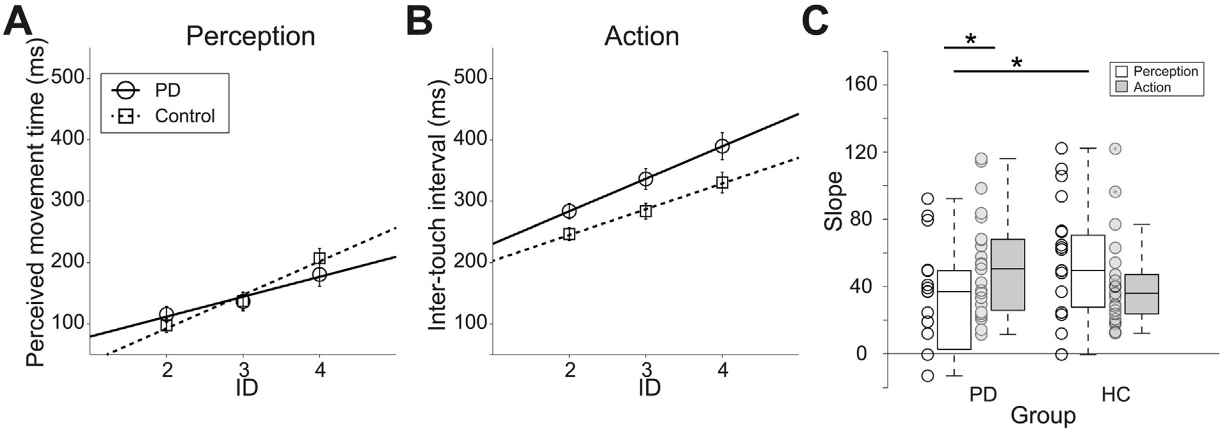

Fig. 5. Comparison of results of perception task and action task (Experiment 2). (A) Mean perceived MT and (B) mean actual MT as functions of ID. (C) Mean Fitts'-law slopes in the perception (white bars) and the action (grey bars) tasks. Each circle indicates data from individual participants. The + symbols indicate outliers (values 1.5 times the interquartile range above the third quartile). Error bars indicate standard error. *, $p < 0.05$.

perception task were steeper in the healthy control group than those in the PD group. Despite the lack of a significant difference of slope for the action and perception tasks, the mean inter-touch interval in the PD group was significantly longer than that in the healthy controls (overall differences in speed only affect the intercept), indicating that the touch action followed Fitts' law. Moreover, the slopes in the action condition were steeper compared with those in the perception condition in the PD group, but not in the healthy control group. These results imply that the strategy for action estimation in the PD group was somewhat different from that in the healthy control group when patients with PD were explicitly required to imagine another person performing the task. This means that the PD group might have a difficulty in switching from simulating 'self' action to 'other' action according to task instruction. In previous neuroimaging studies on self and other judgments, the ventral medial prefrontal cortex (mPFC), left ventrolateral PFC, and dorsal mPFC regions were identified as key to supporting the distinction between self and other (Denny et al., 2012). Because hypoactivation of prefrontal areas in PD has been consistently reported (Dirnberger et al., 2005; Huang et al., 2007; Narayanan et al., 2013), an atypical prefrontal function of regions supporting the self-other distinction might lead to the atypical action estimation pattern found in the PD group across experiments.

Overall, the data show that the healthy control group readily modulated timing parameters for estimating others' actions based on top-down information provided in the instruction, as we found different slope patterns in the two experiments. However, the PD group did not seem to engage in such modulations, as evidenced by the similar slopes across both experiments. Because the two experiments were conducted on separate days, this cannot reflect problems with quickly switching from simulating 'self' action to 'other' action. It is more likely that patients with PD have a bias for utilizing their own motor ability as a basis for simulating others' actions.

Alternatively, it is possible that the results of Experiment 2 are due to difficulties with configuring the task in the PD group (Woodward et al., 2002). Supporting this possibility, it has been shown that in patients with cervical or spinal cord injury with motor difficulty similar to that of our PD group, the judgments of action possibilities are somewhat detached from their own current movement capabilities irrespective of task instructions (Manson et al., 2014). Therefore, it is possible that problems with top-down modulation of perceived action abilities in the PD group are due to the impairment of the predictive mechanisms residing in the motor system (Eskenazi et al., 2009). In light of these studies, the preserved performances of both action and perception tasks in patients with PD would be due to compensation mechanisms mainly performed in cortical regions. As we did not assess the cognitive function of the prefrontal cortex for patients with PD in our current study, further studies are needed to address the relationship between prefrontal cortical function and action estimation.

It should be noted that nine PD patients were most affected on the left side. If these patients had minimal or no symptoms in their right hand or upper arm, it might be expected that they would have performed and thus perceived similarly to the controls. To account for this possibility, we further divided the PD patients into two groups based on the affected side. In this additional analysis, two-way ANOVA was applied to the slopes of the regression lines with affected side in the PD group (left vs. right) as a between-subjects factor and task (perception vs. action) as a within-subject factor. For the results in Experiment 1, we found a main effect of Task, but no other main effect and interaction were significant. A similar tendency was also observed in Experiment 2. These results indicate that the affected side in the PD group does not affect the performance of both the action and perception tasks.

A potential concern with the interpretation of our findings is that measurement error during the action task may have affected our findings, as the maximum amount of error amounted to ± 6 ms for a single trial. However, as there were ten trials in each condition the size of the measurement error is well within the range of precision provided in neuropsychological studies. Importantly it did not differ between the different conditions. Also, note that the estimated maximum error is rather small compared to the inter-touch interval (200–500 ms) and the group difference in slope we obtained (approximately 27 ms). Therefore, we feel that it is safe to assume that the random error in individual slopes could not have created a significant group difference.

We acknowledge that there are several limitations to the present study. First, although we screened participants through the MMSE assessments, several studies have pointed out that elderly participants with cognitive impairments show atypical behavioural patterns in the Fitts'-law task (Poletti et al., 2016). The MMSE score alone is not sufficient to differentiate MCI from a typical cognitive condition (Hoops et al., 2009; Kim et al., 2017). Therefore, we also screened patients based on their clinical records, and selected only those who had not been diagnosed with depression, MCI, or other neurological conditions. We also confirmed that none of the participants had brain atrophy, based on MRI screening, and administered the GDS and MoCA during the medical examination, if necessary. Nevertheless, we cannot fully exclude the possibility that there were subtle cognitive differences between the PD patients and controls. Future studies should consider adding other cognitive assessments to screen participants.

A second limitation is that the two experiments we conducted are not fully comparable. Whereas Experiment 1 varied both amplitude and target width, only target width was varied in Experiment 2 in an attempt to remove the potential effects caused by hypometric movements in patients with PD. Therefore, further studies would be needed to compare the performance across two experiments with identical experimental conditions.

A third limitation is that the variances of the slope data for patients and controls were heterogeneous in the action condition of Experiment 1. Although this might be almost unavoidable when studying patients with motor disorders that they will have higher variance in performing actions than controls, it limits the robustness of the interpretation of the current data. Further studies could attempt to provide experimental tasks that are less prone to generate inhomogeneity of variances across patient and groups. One potential way of achieving this could be to use a manipulation of the index of movement difficulty that does not require participants to perform movements as quickly as possible.

In conclusion, we found that both the perceptually judged action speed of others and the participant's own execution speed were significantly lower in the PD group than in healthy controls. However, the Fitts'-law slopes for the action vs. perception tasks were preserved. These findings suggest that patient's strategies for understanding others' actions are based on their own motor abilities, and that they have difficulty in modulating their simulation based on their own ability to take into account others' ability, even when they are explicitly asked to do so.

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Author contributions

MH, TS, GK, and NS conceived the study and designed the experiments. TS wrote the programs and analysed the data. MH and TS conducted the experiments. SM performed diagnosis and follow-up on study participants with Parkinson's disease. All authors contributed to writing the manuscript, and all approved the final manuscript.

Additional information

The authors declare that they have no competing interests.

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