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Research report

Impaired perception of human movements in Parkinson's disease

Silvie Kloeters, Christian J. Hartmann, Viktoria D. Pundmann, Alfons Schnitzler, Martin Südmeyer, Joachim Lange*

Medical Faculty, Institute of Clinical Neuroscience and Medical Psychology, Heinrich Heine-University Düsseldorf, Germany

HIGHLIGHTS

- Theories have linked motor execution and observation.
- Parkinson patients are impaired in motor execution.
- We hypothesized that Parkinson patients should be impaired in observation of human movements.
- Results confirm the hypothesis that Parkinson patients are impaired in biological motion perception.

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ABSTRACT

Interacting with other individuals in a social world requires fast and accurate perception of other individuals' identity, actions, or intentions. Humans are very efficient in these social tasks, as they can extract social information even if the actor is represented only by a handful of point-lights on an otherwise invisible body. Theories have argued that efficient visual perception of actions is based on intact motor system functioning. The motor system provides visuo-motor action representations shaped by the observer's own movements or motor repertoire. If the observer's motor repertoire is impaired, this should lead to impaired visuo-motor representations and ultimately to impaired visual perception of movements. Here we tested this hypothesis in a behavioral study with patients suffering from Parkinson's disease (PD). PD patients are typically impaired in movement execution. We tested these patients and a matched control group in a visual discrimination task on human movement perception. The results showed that PD patients were significantly impaired in the perception of human movements. This impairment was most prominent for transitive (object-related) movements. The results indicate that impaired movement execution critically influences movement perception. The results support the hypothesis that the motor system plays a causal role for the visual perception of human movements.

1. Introduction

Perceiving and interpreting the movements and actions of other individuals is an important aspect for human social interaction [1,2]. Thus, it is not surprising that humans are very accurate and efficient at recognizing other peoples' movements or gestures. It has been demonstrated already more than 40 years ago that observers can easily recognize the actions of other individuals even if the to-be-observed human body is depicted by only a handful light dots on an otherwise invisible body [3]. The sparse information of these so-called point-light displays has been shown to be sufficient to recognize gender, identity, or mood of the actor [4–6].

Despite many years of research and increasing knowledge about the perception of human movements, the neuronal mechanisms are still not fully understood. While there is mounting evidence that the superior temporal sulcus (STS) and lateral occipito-temporal cortex (LOTC) are critically involved in the process of perceiving human movements [7,8], also other cortical areas have been shown to play a role for the perception of human movements. For example, areas of the motor system, which are typically involved in the execution of movements, have been associated also with movement perception [9][e.g. 9]. In this regard, theories have postulated a link between movement perception and execution of movements [10]. These theories have been supported by behavioral studies demonstrating interference between visual perception of a movement and the observer's own movement or movement capabilities. For example, compared to stationary observers, walking observers were impaired in judging the walking speed of animated persons [11]. Similarly, it has been shown that self-generated movement

* Corresponding author at: Medical Faculty, Institute of Clinical Neuroscience and Medical Psychology, Heinrich Heine-University Düsseldorf, Germany.
E-mail address: Joachim.lange@med.uni-duesseldorf.de (J. Lange).

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of the observers modulates discrimination of body postures and movements [12,13]. Furthermore, observers' ability to judge the weight of a box lifted by another person depends on the weight of a box lifted by the observers [14]. Further evidence for a link between movement perception and execution of actions comes from fMRI studies reporting BOLD responses in the (pre)motor system during action perception [9,15,16]. In addition, EEG and MEG studies reported a suppression of alpha/mu- and beta-activity (8–30 Hz) in sensors over central and motor areas during action observation and imagination [17–20]. This suppression of alpha/beta-band activity was modulated by plausibility and the lateralization of the observed action [19,21,22].

In summary, several behavioral and imaging studies provide converging evidence for a link between action perception and execution. It has been suggested that such a link between action perception and execution reflects the sharing of body representations by the motor and visual system [10]. If the motor system is crucially involved in movement perception, dysfunctions in the shared visuo-motor representations in the motor system should lead to impaired perception of human movements. Indeed, studies have shown that observers with lesions in the human premotor or motor system are impaired in their ability to perceive human movements [23–25]. For example, it has been shown that patients with hemiplegia (a lesion at the motor system that affected the contralesional arm) are impaired in the perception of gestures performed by an arm contralateral to their impaired body site [24]. Another study has shown that paraplegia patients are severely impaired in the perception of human movements [25]. Also, patients with periventricular leukomalacia (PVL; a damage to the periventricular brain found in some prematurely born children) often show impaired motor abilities [26]. These patients also show impaired perception of human movements [27]. However, impaired perception did not correlate with the severity and even patients with early impaired movement production could perceive human movements to a certain degree [26]. Therefore, movement production does not seem to be a necessary prerequisite for movement perception. But impaired movement production seems to affect movement perception.

From the hypothesis of shared visuo-motor representations and the above mentioned studies on the relationship of impaired movement production and perception, it might also follow that people with impaired abilities to execute movements due to impairments in the motor system should also be impaired in the perception of human movements. Parkinson's disease (PD) offers an intriguing model to test this hypothesis and to test a general link between the motor and visual system for human movement perception in general. PD is typically associated with the triad of motor dysfunctions: akinesia, rigor, and tremor [28]. That is, patients suffering from PD are typically impaired in their movement execution. Given the interaction of observers' own movements and their perception of human movements, we hypothesized that patients with PD who are impaired in movement execution should also be impaired in the perception of human movements. In line with this hypothesis, a recent study found that PD patients are impaired in a temporal duration discrimination task on human movements and their scrambled counterparts compared to healthy control subjects, indicating altered processing of human and scrambled movements in PD [29]. Furthermore, PD is often associated with abnormal beta-band activity in the motor and basal ganglia system [30–32]. Since beta-oscillations in the motor system have been shown to play a role during perception of human movements, the abnormal beta oscillations in PD provide further support for our hypothesis of impaired perception of human movements in PD.

We tested this hypothesis in a behavioral study by presenting point-light animations of human movements [3] to a group of PD patients and a matched control group. If PD patients' impairments in motor execution and their abnormal beta-oscillations affect their abilities to perceive human movements, we expected that PD patients also show impaired perception of human movements. Such a finding would provide further evidence for a causal link between movement execution and perception and the interaction of visual and motor systems during movement perception.

Table 1
Characteristics of patient and control groups.

Gender	Patients	Controls
	17 (11 male)	17 (11 male)
Mean Age (±SEM)	60.5 ± 2.4	60.5 ± 2.6
Mean Years of Schooling (±SEM)	11.2 ± 0.4	11.2 ± 0.4

2. Methods

2.1. Participants

20 patients with Parkinson's disease and 23 healthy subjects participated in the experiment. All participants had normal or corrected to normal vision and no history of internal, psychiatric or neurological disorders other than Parkinson's disease. None of the patients had deep brain stimulation treatment. In order to be able to exclude participants suffering from dementia, we used the Mattis Dementia Rating Scale – 2 (MDRS-2) [33] with a cut-off score of 130 points. Three Parkinson's disease patients and six controls had to be excluded from the analysis due to low MDRS scores, inability to complete the testing session, a contested Parkinson's disease diagnosis, as well as symptoms indicative of neurological disorders and vision difficulties that first transpired after testing began. This resulted in a final sample of 17 patients and 17 age, gender and education matched controls (Table 1).

We measured patients' motor symptoms using the UPDRS scale and the Hoehn & Yahr (H&Y) scale [34]. We categorized one patient (6%) into H&Y-stage one, seven patients (41%) into H&Y-stage two and nine patients (53%) into H&Y-stage three.

UPDRS scores were rated by two independent raters. The inter-rater reliability correlation coefficient for UPDRS scores was highly significant ($r_s(15) = 0.86$, $p < 0.001$). Patients' mean UPDRS score was 31.88 ± 2.47 (averaged ratings of both raters).

Written informed consent according to the Declaration of Helsinki was obtained from all participants prior to testing. The study was approved by the local ethics committees of the medical department of the Heinrich Heine-University.

2.2. Procedure

Patients had been instructed not to take any dopaminergic medication 12 h prior to testing, which is a standard time period for medication withdrawal in so-called OFF medication states [e.g., 35–37]. All participants were tested separately and started the testing session with a computer-based motion perception task, followed by UPDRS and MDRS-2 tests (see below for details).

The motion perception task started with written instructions presented on the screen. Each trial started with a blank screen presented for 500 ms followed by presentation of the stimulus (Fig. 1A). Stimuli consisted of point-light animations of natural and different unnatural versions of moving humans, animals, or objects (Fig. 1B; see *Stimuli* for details). Stimuli were presented in blocks, with each block containing an equal number of natural and unnatural stimuli, presented in randomized order. The stimulus presentation length varied between 1.62–2.69 s (see *Stimuli* for details). After each stimulus presentation, response instructions were presented for up to 3 s on the screen. Participants had to decide if the stimulus depicted a natural or an unnatural motion by pressing buttons on a key-

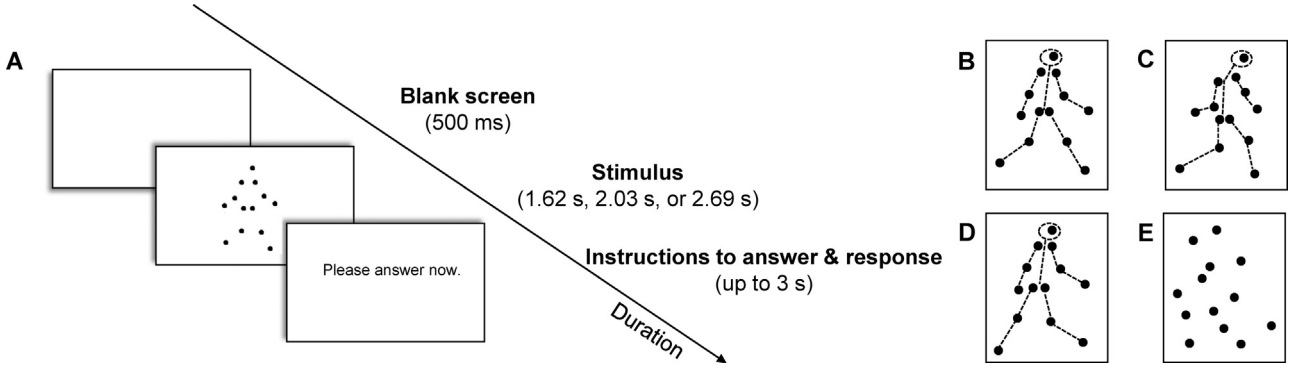

Fig. 1. Experimental setup and example stimuli. A) The experimental paradigm. Subjects were presented with either natural or unnatural human movements (see B-E) and were asked to report their perception. B) Static example image of a natural movement. C) Static example image of an implausible version of B), where the position of dots was shifted to create a biomechanically implausible movement. D) Static example image of an incoherent version of B), where upper and lower body parts face in opposite directions. E) Static example image of a scrambled version of B), where all dots are shifted to random positions to create a meaningless movement of dots. The connecting lines between dots are for illustration only and were not shown to participants.

board in front of them with the index finger of their left or right hand. The response configurations were balanced across subjects. The participants had been instructed to respond as quickly as possible. If there was no response within 3 s, or if there was a response before the presentation of the response instructions, a warning text was presented, the trial was discarded and the respective trial was repeated at the end of the block. After the completion of the motion perception task, each natural motion stimulus was presented again in sequential order and the participants were asked to verbally describe these motions.

The motion perception task was preceded by a trial run in which participants viewed example stimuli of the natural/unnatural motions presented in the upcoming trial and in which they were familiarized with the responses. The motion perception task lasted approximately one hour.

The paradigm was presented on one of two laptops (Medion Akoya E6234 and MSI CR61) at a viewing distance of approximately 80 cm. Both laptops had a display size of 34.5 × 19.6 cm and a resolution of 1366 × 768 pixels.

After the patient group had completed the motion perception task, their symptoms in the "OFF"-state were tested using the motor examination section (Part III) of the Movement Disorder Society-sponsored revision of the Unified Parkinson's Disease Rating Scale (MDS-UPDRS). We also rated participants on the Hoehn & Yahr (H&Y) scale [34]. These ratings took approximately 15 min. Next, patients were tested with the MDRS – 2. The control group participants were only tested with the MDRS – 2, which took approximately 10 min.

2.3. Stimuli

Stimuli were two-dimensional point-light animations of human, animal, and object motion. The animations were offline manipulated to create unnatural versions using MATLAB (Mathworks, Natick, MA; see below). The animation frame was approximately 5 × 7 cm in size. The stimuli were presented as black dots on a white background.

In the present study, we will focus our analysis on human and object motion only. Therefore, we will describe here only the human and object stimuli. The animal stimuli and their respective analysis will be described in a future study.

2.3.1. Natural motion stimuli

We used point-light animations of biomechanically plausible human movements [19]. The point-light stimuli were created by attaching 13 sensors to the head and main joints (feet, knees, hips, hands, elbows and shoulders) of a human actor and recording the sensors' movements while the actor was performing natural movements and actions [38]. The recorded movements were cut into segments representing one cycle of an action. The point-light animations were presented from a side view, with the actor facing to the left or right. Translatory movement components were eliminated, so that all stimuli seemed to move on the spot (Fig. 1B).

In addition to the animations of natural motions, we created unnatural motions. We created three subversions of unnatural movements: Implausible, incoherent, and scrambled movements.

2.3.2. Implausible

Versions of each natural motion animation were created by shifting the position of a few point lights, while their movement trajectory was left unchanged (Fig. 1C). Healthy subjects typically perceive these animations as human, but biomechanically implausible movements [19]. The number of shifted stimuli and the shifting parameters varied between stimuli.

2.3.3. Incoherent

Versions of each natural motion animation were created by manipulating the upper or lower body half of the stimuli so that they faced and moved into opposite directions [Fig. 1D, [39–41]].

2.3.4. Scrambled

Versions of each natural motion stimulus were created by randomizing the starting positions of each point-light (Fig. 1E). That is, the initial position of the point-lights was shifted randomly within the animation frame, while their movement trajectories were left intact [16,18,42]. Healthy subjects typically perceive these scrambled animations as meaningless movements of dots [18].

The original dataset consisted of 20 point-light animations of human actions. In a pretest with 6 healthy students, we presented these 20 animations and their unnatural counterparts (i.e. either implausible, incoherent or scrambled versions of these motions) and asked the students to report whether the stimulus depicted a natural or unnatural action. Based on the responses for each of the three human motion conditions (i.e. the natural/implausible, natural/incoherent and natural/scrambled conditions), we selected seven unique types of natural/unnatural action pairs for which recognition rates were >50% and <100% to avoid bottom or ceiling effects. Based on the pretest, we expected that discrimination between natural and unnatural motions would be most difficult in the natural/implausible condition (lowest recognition rates) and easiest in the natural/scrambled condition.

The natural/implausible motion condition included five different walking motions, one jumping motion and one kickboxing side kick motion. The natural/incoherent motion condition included two different walking motions, one soccer kicking motion, two different ball throwing motions, one jumping motion and one boxing motion. The natural/scrambled motion condition included three different walking motions, two different jumping motions, one baseball catching motion and one ice skating motion. Furthermore, we selected a natural walking motion stimulus that was almost perfectly discriminable from its respective implausible, incoherent and scrambled motion version. This stimulus as well as its unnatural counterparts were used as example stimuli.

Every original stimulus was made up of 140 frames presented with 86 frames/s, i.e. these stimuli lasted for 1.62 s. We additionally created slower versions with 69 frames/s (i.e. 2.03 s) and 52 frames/s (i.e. 2.69 s). These stimuli will be referred to as "fast" (86 frames/s), "medium" (69 frames/s) and "slow" (52 frames/s) speed versions. Note that the natural walking speed is termed "fast". "medium" and "slow" are unnaturally slow conditions. Thus, the natural/implausible, natural/incoherent and natural/scrambled human motion conditions each included seven "fast-speed", seven "medium-speed" and seven "slow-speed" unique natural stimuli as well as their unnatural counterparts. This resulted in 42 unique stimuli per condition (21 natural and 21 unnatural). Each of the 42 stimuli was presented twice. Thus, each condition comprised 84 stimulus presentations in total.

The preceding trial runs included one presentation of every "slow-speed" natural motion animation. In addition, the trial runs included the implausible, incoherent or scrambled counterparts of the natural motion animations. This resulted in a total presentation of 14 stimuli (seven natural, seven unnatural) per trial run.

2.3.5. Object motion stimuli

In order to test object motion perception, we programmed point-light animations of a rotating cylinder [43,44]. These animations were made up of a collection of black dots on a white background that were projected on an imaginary outline of a two-dimensional cylinder. The initial position of the point-lights was chosen randomly. Point-lights then moved coherently clockwise or counterclockwise on this imaginary outline which typically gives the impression of a rotating cylinder. The size of the point-lights was identical to the size of the human point light animations. We used two different types of cylinders. One cylinder was made up of 100 dots and the second one was made up of 200 dots. In addition, we programmed scrambled versions of these two natural motion stimuli by randomly distributing the point-lights on the surface of the cylinder in each frame, i.e. we eliminated the coherent dot motion. This typically destroys the impression of a rotating cylinder.

Concordant with the human point-light stimuli, we created "fast", "medium", and "slow" speed version of the stimuli. This resulted in six different natural object motion animations and six different scrambled motion animations, which were each presented three times in the natural/scrambled object motion condition of the experiment. Thus, there were 36 object motion presentations in total. We used the "slow-speed" version of the 200 dot-animations as example stimuli. The trial run featured one presentation of the two different natural motion animations and their scrambled counterparts.

2.4. Data analysis

In order to analyse participants' perception, we applied signal detection theory to our data. For each of the seven experimental conditions, we calculated every participant's hit and false alarm rates. A response was counted as a hit, when a natural motion stimulus was rated as "natural". A response was counted as a false alarm, when an unnatural motion stimulus (implausible, incoherent or scrambled) was rated as "natural". Hit and false alarm rates were subsequently used to calculate the sensitivity index *d'*.

If there was a significant effect for one condition, we additionally post-hoc analyzed whether participants' *d'*-rates were affected by the type of movement (transitive/intransitive). "Transitive" is a term used to describe any movement in which an object is employed, such as grasping an apple or placing a plate on the table. Intransitive movements do not involve an effector-object interaction. Before using parametric tests, we tested whether data differed significantly from a normal distribution by means of the Kolmogorov-Smirnov-Test (all data $p > 0.05$).

3. Results

We compared patients' and controls' *d'*-rates for human motion in each of the three motion type conditions. The patient group had significantly lower *d'*-rates than the control group in the natural/incoherent condition, ($t(32) = -2.19$, $p = 0.04$; patients: 1.28 ± 0.24 (Mean ± SEM); controls: 1.99 ± 0.22) (Fig. 2A). Patients also showed lower d'-rates for natural/implausible and natural/scrambled conditions, albeit these differences were not statistically significant ($t(32) = -0.69$, $p = 0.50$; $t(32) = -0.53$, $p = 0.60$).

In order to interpret the significant differences between the patient and control group, results in the natural/incoherent condition were analyzed in more detail. First, we compared patients' and control group participants' mean hit and false alarm rates. Mean hit rates were significantly lower in the patient group compared to the control group, ($t(32) = -2.54$, $p = 0.016$; patients: 0.80 ± 0.04, controls: 0.91 ± 0.02). There was no significant difference in false alarm rates, ($t(32) = 0.95$, $p = 0.35$; patients: 0.43 ± 0.04; controls: 0.38 ± 0.04) (Fig. 2B). We additionally tested hit rates in the other conditions: Mean hit rates were lower in the patient group compared to the control group in the plausible/scrambled and in the plausible/implausible condition, albeit the difference did not reach statistical significance scrambled: $t(32) = -0.73$, $p = 0.47$; patients: 0.91 ± 0.03, controls: 0.94 ± 0.02; plausible: ($t(32) = -0.98$, $p = 0.34$; patients: 0.72 ± 0.03, controls: 0.77 ± 0.02).

Furthermore, we analyzed *d'*-rates for transitive and intransitive motions in the natural/incoherent human motion condition. We identified two throwing motions, one soccer kicking motion and a boxing motion as transitive (i.e., object-related) movements. Two walking motions and one jumping motion were identified as intransitive (i.e. non-object related) movements. A 2 (group: patient vs. control) × 2 (movement type: transitive vs. intransitive) ANOVA revealed a significant main effect of group on *d'*-rates ($F(1,32) = 4.48$, $p = 0.04$; controls: 1.99 ± 0.22, patients: 1.34 ± 0.22). There was also a highly significant main effect of movement type ($F(1,32) = 45.66$, $p < 0.001$; intransitive: 2.01 ± 0.16, transitive: 1.32 ± 0.17). In addition, the interaction effect between group and movement type was significant, ($F(1,32) = 5.28$, $p = 0.03$; controls intransitive: 2.22 ± 0.23, controls transitive: 1.76 ± 0.23, patients intransitive: 1.80 ± 0.23, patients transitive: 0.88 ± 0.23). Post-hoc *t*-tests revealed that the control group had significantly higher d'-rates than the patient group for transitive movements ($t(32) = -2.68$, $p = 0.01$; controls: 1.76 ± 0.25, patients: 0.88 ± 0.22). However, there was no significant difference in d'-rates between patients and controls for intransitive movements ($t(32) = -1.31$, $p = 0.20$; controls: 2.22 ± 0.20, patients: 1.8 ± 0.25; Fig. 3).

Additionally, we investigated the influence of animation speed on *d'*-rates in the natural/incoherent motion condition. We found a significant difference between patient and control group *d'*-rates in the "slow motion" condition ($t(32) = -2.59$, $p = 0.01$; controls: 1.80 ± 0.19, patients: 1.08 ± 0.20) and in the "fast

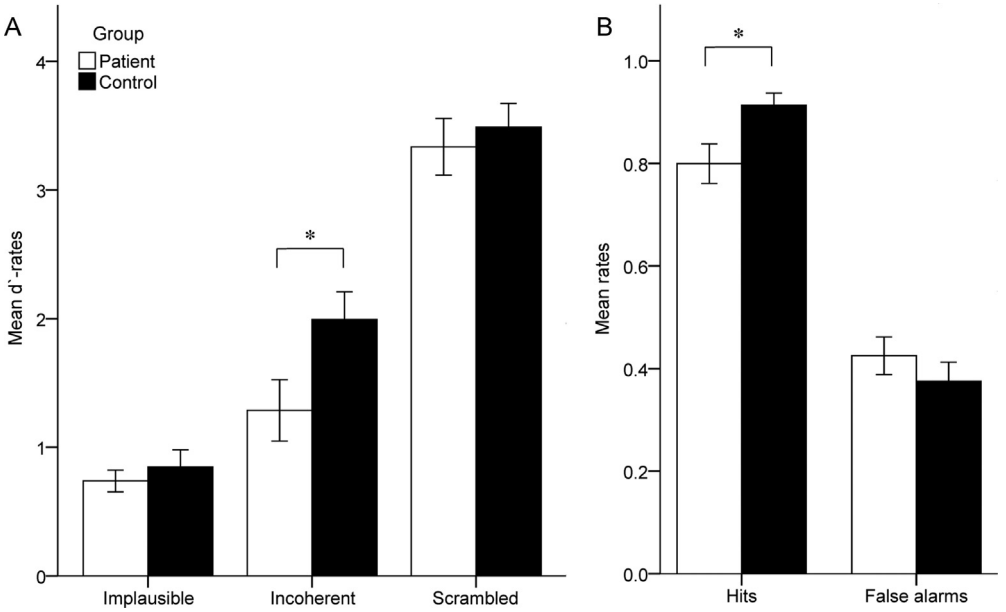

Fig. 2. Results of the discrimination tasks. A) Mean d'-rates for PD patients (white bars) and the control group (black bars) in the different discrimination tasks. The label "Implausible" refers to the natural/implausible motion condition, the label "Incoherent" refers to the natural/incoherent motion condition and the label "Scrambled" refers to the natural/scrambled motion task. B) Mean hit and false alarm rates in the incoherent human motion task. *p < 0.05. Error bars display ±1 SEM.

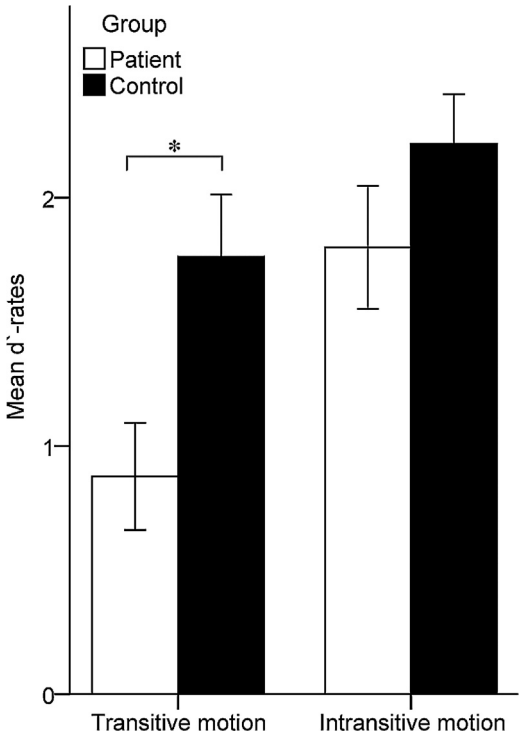

Fig. 3. Mean d'-rates for PD patients (white bars) and the control group (black bars) for transitive and intransitive motion in the natural/incoherent human motion task. *p < 0.05. Error bars display ±1 SEM.

motion" condition, ($t(32) = -2.29$, $p = 0.03$; controls: 1.74 ± 0.16, patients: 1.16 ± 0.20) but not in the "medium motion" condition ($t(32) = -1.04$, $p = 0.31$; controls: 1.50 ± 0.26; patients: 1.15 ± 0.21). That is, patients were significantly impaired in the natural ("fast") walking speed, but also showed lower recognition rates in the unnatural walking speeds ("medium" and "slow"), with the difference being significant for 'slow'. Within both groups, participants' *d*'-rates did not differ significantly between the "slow motion", "medium motion" and "fast motion conditions", (patients: $t(16) > -0.48$, $p > 0.64$; controls: $t(16) > 1.38$, $p > 0.19$; see above for exact d'-values).

When asked to describe the natural actions verbally at the end of the session, participants did not show any severe problems. Only two patients and one healthy control participant did not recognize the kickboxing motion and misinterpreted some walking motions (e.g., as kicking a ball or jumping jack).

3.1. d'-*rates for object motion*

There were no significant differences between patient and control group *d*'-rates for object motion ($t(32) = -0.47$, $p = 0.64$; patients: 3.77 ± 0.03, controls: 3.79 ± 0.03).

4. Discussion

We assessed the perception of human point-light actions in patients with Parkinson's disease (PD) and a healthy control group. We tested the ability to recognize the actions in three tasks in which subjects had to discriminate a natural human movement from different types of unnatural movements. PD patients showed lower recognition rates in all conditions compared to control subjects, albeit only the difference in the natural/incoherent condition was statistically significant. In post-hoc tests, we found that this difference was due to significant lower recognition rates for natural movements, while the recognition of incoherent movements was similar to the control group. Finally, we found that the difference between PD and control groups was significantly stronger for transitive compared to intransitive movements.

The results confirm our hypothesis that PD patients are impaired in the perception of human movements. It is unlikely that the impairment is induced by the medication the patients are regularly taking, because medication was withdrawn for >12 h. 12 h withdrawal is a standard procedure regularly applied in studies and sufficient to reduce the concentration of the medication to a negligible concentration [35–37,45]. The impairment is unlikely to arise from general impairments of visual perception or cognitive abilities, or by a bias to towards reporting unnatural movements,

because both effects should have affected perception of natural and unnatural movements. Rather, we find that the impairment is specific for natural movements. That is, PD patients tend to perceive natural movements more often as unnatural compared to healthy controls, while their perception of unnatural movements is not different from healthy controls. The lower recognition rates for natural movements were found for all contrast conditions (natural/scrambled, natural/incoherent, natural/implausible), but the difference in natural movements between patients and controls reached statistical significance only in the natural/incoherent condition. This is probably due to ceiling/bottom effects: Although patients might be generally impaired in the perception of natural movements, it might still be possible to differentiate the natural stimuli from scrambled stimuli. On the other hand, in the natural/implausible condition, differentiation might also be difficult for the control group, camouflaging any impaired perception in patients. It has been argued that perception of human movements operates via a template-matching approach [46–48]. In this approach, visually perceived stimuli are matched to neuronal templates of human movements. We suggest that these templates might be shaped by a person's own motor repertoire and thus affected by the motor system. If a person's motor repertoire depletes, the number of templates and their sensitivity also decreases. From this follows ultimately that persons with impaired motor repertoire can no longer perceive all human movements accurately and thus will tend to perceive the movements as unnatural movements. We argue that these templates are depleted in PD due to their impaired motor abilities, resulting in less accurate perception of natural human movements. Since in the template-matching approaches templates exist only for natural, but not for unnatural movements, this approach also implies that the perception of unnatural movements should be unaffected in PD. This hypothesis was confirmed by our results that PD patients were impaired in the perception of natural movements while perception of unnatural movements was unaffected. The template-matching approach might also generalize across different movement types. There is evidence that the human motor system shows a certain degree of abstraction. That is, the motor system does not exclusively respond to movements that are completely congruent with the observer's own motor repertoire, but also to movements that are similar to the own motor repertoire.

A different explanation might be that motor areas are involved in motor imagery or an internal replay of an observed action. It has been reported that PD patients show less activity in the motor system during motor imagery [49], but instead increased activity in visual areas [50]. These results suggest that PD patients compensate for their processing deficits in the motor system by recruiting visual areas more strongly. That is, if a discrimination task can be sufficiently performed by visual analysis, PD patients should be less impaired compared to tasks requiring an intact motor system. In addition, [51] suggest that the premotor cortex is important for the analysis of bodily actions whereas visual areas (extrastriate body area) are important for the discrimination of bodily forms. Since scrambled animations do not represent a human form, the natural/scrambled task might be solved by discrimination of the bodily form, i.e. in visual areas. From this follows that PD patients might not be impaired in natural/scrambled tasks. On the other hand, natural/incoherent or natural/implausible tasks cannot be solved based on analysis of static forms, thus they might require intact motor systems for the analysis of bodily actions. From this follows that PD patients should be impaired in these tasks. Both predictions are in general confirmed by our data. In addition, Candidi et al. [52] showed that transcranial magnetic stimulation (TMS) over premotor cortex impairs the perception of biomechanically possible actions, but not the perception of biomechanically impossible actions. This finding is in line with our finding that PD patients were only impaired in the perception of natural movements, but not unnatural movements.

The reason for a lack of significant differences between PD patients and the control group in the natural/implausible task might be simply that the task was too difficult for both groups, so that they only reached chance level in this task. Although we aimed to select stimuli in our pretest that are not too difficult to differentiate, it seems that the selection was not optimal. A potential reason might be that the sample of subjects and the task duration in our pretest differed from our main task, so that it was easier for the subjects in the pretest to differentiate between natural and implausible movements.

Previous studies demonstrated that observers' perception of other humans' movements depended on their own movements [11,14]. Since PD patients are impaired in their walking speed, we hypothesized that the walking speed of the stimuli might affect PD patients' perception [53]. However, we did not find an effect of stimulus speed on motion perception. PD patients were significantly impaired in the natural (termed "fast") walking speed, but also showed (significantly) lower recognition for unnatural ("medium" and "slow") walking speeds. Consequently, recognition rates did not differ significantly across speed conditions, neither for controls nor for patients. A possible reason might be that the speed was not properly adjusted to the observers' impairments. A future study might first measure the individual impairments of the PD patients with regard to walking speed and then adjust the speed of the stimuli accordingly.

We did, however, find an influence of the motion type. Compared to the control group, PD patients were more strongly impaired for transitive movements (i.e., related to an object) relative to intransitive movements (i.e., not related to an object). One reason might be that natural transitive movements were more difficult to differentiate from their incoherent counterparts than natural intransitive movements. This might be due to the fact that all intransitive motions turned out to be periodic, i.e., the movement repeated smoothly and seemingly continuous, because the final posture of a cycle was identical to the starting posture of the next cycle. In contrast, all transitive movements were non-periodic, i.e., the movement repeated discontinuously and interrupted, because there was an abrupt jump from the final posture of one cycle to the starting posture of the next cycle. Thus, the overall impaired perception of human movements in PD patients might be amplified for the more difficult transitive movements. Another reason might be that motor cortex is more sensitive to transitive movements. The original studies on mirror neurons in monkeys revealed that neurons in the mirror-neuron-system were only activated, if the monkey saw a transitive movement, while intransitive movements did not trigger mirror neuron activity [54,55]. The findings in humans are less clear. There is, however, increasing evidence that human motor cortex is especially sensitive for perceiving goal-directed movements [56][see 56 for a review]. Perception of our transitive, goal-directed movements should thus more strongly rely on intact processing in motor areas. The significantly decreased perception of transitive movements in PD patients might therefore be due to impaired processing capabilities in motor areas that more strongly affect the perception of transitive than intransitive movements.

In conclusion, we find that PD patients are impaired in the perception of human movements. The impaired perception is most pronounced for transitive, goal-directed movements. We argue that this impairment of perception is directly related to the impaired abilities in motor execution of the PD patients. The motor execution impairment critically affects visuo-motor representations of human movements in the motor cortex, thus leading to impaired perception of human movements. Future imaging studies

might investigate the exact mechanisms and cortical areas leading to the impaired perception of human movements in PD patients.

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