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RESEARCH ARTICLE

Submovements during pointing movements in Parkinson's disease

Natalia Dounskaia · Laetitia Fradet · Gyusung Lee · Berta C. Leis · Charles H. Adler

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Abstract Velocity irregularities frequently observed during deceleration of arm movements have usually been interpreted as corrective submovements that improve motion accuracy. This hypothesis is re-examined here in application to movements of Parkinson's disease (PD) patients in which submovements are specifically frequent. Pointing movements in patients and age-matched controls to large and small targets in three movement modes were studied. The modes were discrete (stop on the target), continuous (reverse on the target), and passing (stop after crossing the target). Two types of submovements were distinguished, gross and fine. In both groups, gross submovements were more frequent during the discrete and passing than continuous mode, specifically for large targets. This suggested that gross submovements were fluctuations accompanying motion termination (stabilization at the target) that was included in discrete and passing but not continuous movements. Gross submovements were specifically frequent in patients, suggesting that PD causes deficiency in smooth motion termination. Although in both groups fine submovements were more frequent for small than large targets, this relation was also observed in passing movements after crossing the target, i.e., when no corrections were needed. This result, together with higher jerk of the entire trajectory found for smaller targets, indicates that fine submovements may also be not corrective adjustments but rather velocity fluctuations emerging due to low speed of movements to small targets. This interpretation is consistent with the recognized inability of PD patients to promptly change generated force as well as to quickly re-plan current motion. The results suggest a need to re-examine the traditional interpretation of submovements in PD and the related theory that the production of iterative submovements is a strategy used by patients to compensate for a decreased initial force pulse.

Keywords Kinematics · Velocity profile · Movement termination · Reaching · Basal ganglia disfunction

N. Dounskaia · L. Fradet · G. Lee · B. C. Leis
Movements Control and Biomechanics Laboratory, Arizona State University, Tempe, AZ 85287, USA

C. H. Adler
Parkinson's Disease and Movement Disorders Center, Mayo Clinic, Scottsdale, AZ 85259, USA

N. Dounskaia (✉)
Motor Control and Biomechanics Laboratory, Arizona State University, P.O. Box 870404, Tempe, AZ 85287-0404, USA
e-mail: natalia.dounskaia@asu.edu

Introduction

Although the most portion of the velocity profile during pointing and reaching movements usually has a smooth bell shape, small irregularities often emerge during the deceleration stage. Originally described by Woodworth (1899), these irregularities have been interpreted as feedback-guided secondary submovements performed to improve the accuracy of the primary, ballistic submovement (Abrams and Pratt 1993; Chua and Elliott 1993; Crossman and Goodeve 1983; Elliott et al. 2001; Keele 1968; Khan and Franks 2003; Meyer et al. 1988; Novak et al. 2002; Pasalar et al. 2005; Pratt and Abrams 1996; Pratt et al. 1994; Walker et al. 1997; Woodworth 1899). This intuitively appealing interpretation is consistent with the increased frequency of submovements usually observed with decreases in target size. The interpretation of submovements as corrective adjustments is important because it offers an explanation for the mechanism of movement accuracy regulation.

Other submovement interpretations have also been proposed. They suggest that submovements are a property of movement control. For instance, a lognormal law of control of movement kinematics predicts submovements (Plamondon 1995). Studying "fragmented" movements of stroke patients, Krebs et al. (1999) suggested that submovements are primitives used as building blocks of normal movements. Although submovements in these interpretations usually become more frequent when target size decreases, these interpretations do not necessarily imply the corrective function of submovements, suggesting that they may emerge without a direct relation to accuracy requirements.

Existence of non-corrective submovements was explicitly proposed by our research group (Dounskaia et al. 2005a; Fradet et al. 2008; Wisleder and Dounskaia 2007). It was argued that many of submovements represent irregular fluctuations of velocity, emerging because of various sources of noise in the kinematic output, such as muscle elasticity, co-activation, non-smooth activation of motor units, and noise in the neural circuitry involved in movement control.

Although it is apparent that both corrective and non-corrective submovements may emerge during arm movements to a target, it is important to establish whether corrective submovements are frequent because, if they are rare, the interpretation of corrective submovements as a major mechanism of movement accuracy regulation needs to be re-considered. However, it is difficult to distinguish corrective and non-corrective submovements based on kinematic analyses. Both have the same kinematic features, being represented by inflections in the velocity profile, and therefore, by zerocrossings of the first three (Meyer et al. 1988) or four (Novak et al. 2000) displacement derivatives. Other proposed methods distinguish submovements by fitting movement trajectory with series of bell-shaped functions of scaled duration and amplitude (Milner 1992; Novak et al. 2002; Rohrer et al. 2004; Rohrer and Hogan 2006). Submovements extracted with these methods can also be either corrective or non-corrective. Analysis of whether submovements bring the trajectory closer to the target may also be not informative of the submovement nature since noisy motion towards the target may look as a series of corrective submovements.

Dounskaia et al. (2005a) and Wisleder and Dounskaia (2007) approached the problem of distinguishing non-corrective submovements using specific experimental manipulations. These studies were driven by a hypothesis that motion termination, which is an inherent component of discrete movements (that terminate on the target), may cause submovements. Indeed, motion termination requires total dissipation of mechanical energy and stabilization of the arm at the target. This movement component results in nullification of both velocity and acceleration. Motion termination is not performed during continuous movements that reverse without dwelling on the target, in which case only velocity, and not acceleration, is nullified at the target. Accordingly, kinematic energy is not fully dissipated but converted to elastic energy of tissues surrounding the joints and then recovered as kinematic energy of the reversal motion (Guiard 1993; Meulenbroek and Thomassen 1993; Meulenbroek et al. 1998; Smits-Engelsman et al. 2002). The stabilization of the limb at the target in the discrete mode may cause motion irregularities, i.e., submovements, that would be absent in continuous movements (Scheidt and Ghez 2007).

This hypothesis was tested by comparing submovement incidence between discrete and continuous movements. Submovements were distinguished with an analysis of zerocrossings in the first three derivatives of displacement, following the traditional method of submovement detection (Meyer et al. 1988). It was found that the majority of submovements revealed with the lower derivatives (gross submovements) were caused by motion termination. Indeed, incidence of these submovements was substantially greater during discrete than continuous movements, and it was independent of target size. Unlike gross submovements, submovements revealed with the higher derivatives of motion (fine submovements) were more frequent during movements to small than to large targets equally in the two modes. However, the interpretation of fine submovements as corrective was also questioned by a finding that during cyclical movements, incidence of fine submovements depended on cyclic frequency and not on target size (Wisleder and Dounskaia 2007). It was discussed that movements of low speed may be prone to irregularities observed as fine submovements, and therefore, the commonly observed dependence of fine submovements on target size may be a by-product of the speed-accuracy tradeoff.

To further test the nature of fine submovements, Fradet et al. (2008) included a passing mode in the experiment, in addition to the discrete and continuous mode. During the passing mode, subjects crossed the target in a sweeping motion. Similar to the discrete mode, the passing mode ended with motion termination but this task was performed not simultaneously with accuracy regulation but after it. Again, the role of the accuracy requirements was further accentuated using two target sizes, small and large. Although fine submovements were more frequent during movements to small than to large targets in all modes, these submovements were observed (with the same dependence on target size) in the passing mode after the target crossing, i.e., where corrective submovements were not needed. This result supported the finding of the other two studies that fine submovements may be non-corrective, even though their frequency increases with decreases in target size. Together, the results for gross and fine submovements suggested that all three submovement types may be non-corrective irregularities, which questions submovements as a major mechanism of movement accuracy regulation.

The above conclusions were formulated for movements of healthy young adults. It is important to investigate whether these conclusions are applicable to other subject groups in which submovements are specifically frequent. This study examines the nature of submovements in Parkinson's disease (PD) in which secondary submovements and a shortened primary submovement are consistent features of goal-directed movements (Adamovich et al. 2001; Doan et al. 2006; Flash et al. 1992; Flowers 1978a, b; Phillips et al. 1994; Rand et al. 2000; Romero et al. 2003; Teasdale et al. 1990; Weiss et al. 1997). The frequent submovements in movements of PD patients have usually been interpreted as corrective movement adjustments through which the arm gradually approaches the target. The underlying reasoning is that these subjects have decreased ability to plan and execute accurate movements to the target, and; therefore, corrective submovements could be a mechanism that compensates for this deficiency.

The interpretation of submovements in PD as corrective adjustments is appealing because it seems to be consistent with some features of Parkinsonian movements, such as variability, prolonged deceleration phase, dependence on vision, and a proprioceptive deficit (Adamovich et al. 2001; Flash et al. 1992; Keijsers et al. 2005; Ketcham et al. 2003; Klockgether and Dichgans 1994; Poizner et al. 1998; Sheridan and Flowers 1990; Sheridan et al. 1987). Also, movements in PD are often hypometric and are initiated with decreased acceleration force (Berardelli et al. 1996; Hallett and Khoshbin 1980), and; therefore, submovements seem to be needed to cover the full distance to the target. However, other deficits caused by PD challenge the ability of patients to perform a series of corrective submovements to the target. Indeed, corrective submovements imply a capability to promptly assess the error at the end of the current submovement and to generate a new, corrective motion without a delay. Evidence suggests that the production of non-smooth corrections of motion, such as submovements, is drastically impaired in PD (Castiello and Bennett 1994; Desmurget et al. 2004; Montgomery et al. 1991; Plotnik et al. 1998). This deficit questions the interpretation of segmented movements of PD patients as a sequence of corrective submovements. Here, we exploit the experimental paradigm of Fradet et al. (2008) to investigate the nature of frequent velocity fluctuations observed in PD. If a dominant portion of these fluctuations represents non-corrective submovements, the view that submovements compensate for the inability of patients to accurately propel the limb to the target needs to be re-considered.

Methods

Participants

Sixteen healthy control subjects (12 males, 4 females, mean age 72.4 years, SD = 6.4 years) and 13 subjects with idiopathic PD (8 males, 5 females, mean age 70.3 years, SD = 9.9 years) participated in the experiment. All subjects were right-handed. After an explanation of the experiment, subjects signed informed consent approved by the Human Subjects Institutional Review Board (IRB) of Arizona State University. Patients and controls met study criteria as follows: normal or corrected vision, and the presence of full range of motion in the finger, wrist, and elbow joints, and functional range of motion in shoulder joints. In addition, patients and controls met a cutoff score of 25 on the mini-mental state examination (Folstein et al. 1975). Elderly controls did not have a history of any central nervous system (CNS) disease.

Patients diagnosed with idiopathic PD as designated by a history of levodopa responsiveness and the presence of two of four cardinal symptoms of PD (tremor, bradykinesia, rigidity, postural stability) were eligible to participate (Calne et al. 1992). In addition, eligible patients could not have a history of any other CNS disorder. All patients were tested at least 12 h following their last intake of PD medication. Patients were Hoehn and Yahr stages 2 or 3 (Hoehn and Yahr 1967) and averaged 24.5 (SD = 5.5) points on subscale III (motor exam) of the unified PD rating scale [UPDRS, (Fahn and Elton 1987]. Since the study focused on submovements not related to symptomatic tremor, patients who had any noticeable action tremor and/or severe resting tremor (quantified by a score of 3 or greater on the UPDRS motor exam) were excluded from the analysis. Patient characteristics are summarized in Table 1.

Procedure

The procedure was similar to that described by Fradet et al. (2008). The experimental setup is schematically presented in Fig. 1. Subjects sat comfortably at a horizontal table with a Wacom Intuos 12 × 18 digitizer positioned on the top of the table in front of them. The height of the table was adjusted to provide right arm movements in the horizontal plane at the shoulder level right above the table. Movements were restricted to shoulder and elbow rotations. The movement of the trunk was prevented by the chair-back

Table 1 PD patient characteristics

No.	Age (years)	Gender	Disease duration (years)	Hoehn and Yahr stage	UPDRS	Symptoms
1	69	M	7	2	24.0	T, R, B
2	80	M	10	3	33.5	T, R, B
3	60	F	15	2	23.5	R, B
4	74	M	8	2	21.0	R, B
5	72	F	15	2	19.5	T, R, B
6	49	M	4	2	16.5	R, B
7	81	M	9	2.5	27.5	T, R, B
8	61	F	7	2	19.5	T, R, B
9	69	F	5	2.5	25.0	R, B
10	77	M	2	3	32.5	T, R, B
11	81	M	3	2	19.0	R, B
12	62	F	5	2.5	28.5	T, R, B
13	79	M	15	3	27.5	T, B

M male, *F* female, *T* tremor, *R* rigidity, *B* bradykinesia

and the front edge of the table. The wrist was fixed with a brace. The index finger was extended and a pen was attached beneath it. To reduce friction, the upper arm was supported by a sling and a piece of low friction Velcro tape was wrapped around the index finger.

Subjects executed pointing movements by sliding the pen tip across the digitizing tablet from the home position to a target. The home position was located 34 cm from the trunk on the body midline. Four targets were placed on a 20 cm radius circle around the home position. Motion of

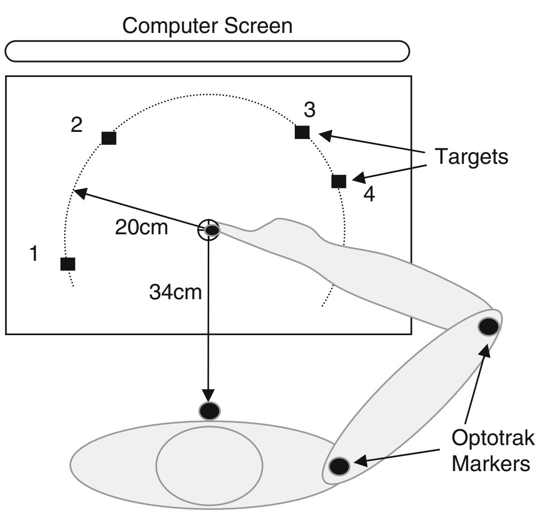


Fig. 1 Schematic representation of the experimental setup. Subjects moved the fingertip to one of the four targets on the horizontal table. The arm was positioned horizontally above the table. Movements were performed with shoulder and elbow rotations. The trunk and wrist were immobilized. Although the targets are shown in the plane of motion, they were presented on the computer screen and not on the table. The computer screen also showed a cursor that represented motion of the fingertip

the pen tip was represented by a cursor on a large (24 inches) vertical computer screen positioned behind the digitizer at 70 cm distance from the subject. The home position and the targets were also shown on the screen. The distance between the home position and the targets on the screen was the same as on the digitizer.

The targets were chosen to require distinct shoulder and elbow coordination patterns. Target 1 required only shoulder flexion, Target 2 required a combined elbow extension and shoulder flexion, Target 3 required elbow extension only, and Target 4 required elbow and shoulder extension. The order of target presentation was randomized across subjects. The purpose of the target manipulations was to test whether inter-segmental dynamics influence submovement production. No evidence for this influence was found in our previous studies with young adults that used the same target locations (Dounskaia et al. 2005a; Fradet et al. 2008; Wisleder and Dounskaia 2007). Similarly, preliminary analysis in the present study did not reveal any significant effect of joint coordination pattern on submovement production either in PD patients or in age-matched controls. The results of this analysis are not reported here since they do not add any new knowledge compared with the results of a similar analysis reported in detail in Dounskaia et al. (2005a). The data from the four targets were combined in the further analyses in the present study.

In order to test the effect of spatial accuracy requirement on the submovement production, two square target sizes were used, small (1.0 × 1.0 cm) and large (3.5 × 3.5 cm). Movements to the targets were performed in three different modes: discrete, continuous, and passing. Discrete movements started from the home position and ended in the target area. In the continuous mode, movements started from the home position, reached the target, and returned to the home position without dwelling on the target. During passing movements, the pen tip passed through the target and stopped after that within the digitizer boundaries. At least, 18 cm of the digitizer space was available in each direction for the movement after passing the target. Subjects were instructed to perform passing movements in a single action as if they were "wiping" the target with a sweeping action. Later analysis confirmed that the velocity profile had the bell shape observed during movements performed as a single stroke. The three modes were exploited to distinguish submovements related to pointing accuracy constraints and to motion termination. A comparison between the discrete and continuous movements allowed the distinction of submovements caused by motion termination, since only discrete and non-continuous movements included this component. Additionally, the passing mode was informative about the influence of both motion termination and accuracy requirements on submovement production by dissociating the two factors from each other in the time domain. In this mode, submovements emerging after passing the target could not be accuracy adjustments since the target was achieved before emergence of these submovements. The small and large targets and the three movement modes were randomized across subjects. The manipulations of movement mode together with the target size manipulations provided an efficient experimental paradigm for studying dependence of submovements on the two factors.

An auditory signal was provided to initiate movement. Subjects were instructed to accurately point to the target, moving to it as fast as possible. Previous studies of submovements have practiced predominantly two different types of accuracy requirements. One type encourages accurate target achievement but allows missing the target and terminating motion nearby. The other type includes an ultimate requirement to reach the target. Dounskaia et al. (2005a) and Wisleder and Dounskaia (2007) employed the first type of accuracy requirements. In the study by Fradet et al. and in this study, the second, more stringent type of accuracy requirements was used. Namely, subjects were required to terminate motion strictly within the target in the discrete mode, to reverse motion inside the target without dwelling in the continuous mode, and to cross the target area in the passing mode. If these requirements were not fulfilled, an auditory signal was produced to inform the subject that he/she failed to perform the task, and that the trial had to be repeated. Practice trials were performed in each condition, and data recording was initiated only after the subject had demonstrated the stable ability to perform the task. If the subject accidentally performed an inaccurate movement during the main session, the data were not preserved for future analysis, and this movement was repeated. The exclusion of inaccurate movements from the analysis was justified because the task was not performed in these trials. It also increased the average probability of emergence of corrective submovements, since accuracy regulation mechanisms apparently were not sufficiently activated during inaccurate trials. Data from eight successful trials were collected for each condition.

The control for valid trials was performed with a computer program that verified fulfillment of the following requirements. During the discrete mode, the pen tip velocity and acceleration had to be nullified within the target area and stay below 5% of the velocity peak for at least 150 ms. During the continuous mode, the pen had to reach the target with zero velocity. However, velocity could not stay below 5% of its peak for a period longer than 60 ms. During the passing mode, the pen had to pass the target while its velocity remained higher than 5% of the preceding peak velocity.

Data recording and analysis

Pen motion was recorded by the digitizer at a sampling frequency of 100 Hz. These data were employed to present motion on the computer screen. Motion analysis was performed with the use of data collected with a three-dimensional, optoelectronic tracking system (Optotrak, Northern Digital) at 100 Hz. Four reflective markers were attached to the sternum, shoulder, elbow and tip of the index finger. Data from the markers were used to control for joint movement patterns corresponding to the four target locations and to analyze fingertip motion. Velocity, acceleration, and jerk were computed as derivatives of fingertip displacement. Signed velocity was computed positive values of which corresponded to motion away from the home position. Since PD patients sometimes failed to produce sharp reversals, which resulted in low but not zero velocity at the reversal, velocity was computed along the line connecting the home position and the target to avoid discontinuity in signed velocity. A differentiation method that simultaneously smoothes data was used. This method is based on a sliding window technique. In this method (see Hoffman 2001 for details), the data are approximated within the window with a quadratic polynomial. The coefficients of the quadratic polynomial were then used for calculating the derivative at the window's center.

The start of the movement was determined as the moment of time at which the unsigned velocity of the fingertip exceeded 5% of peak velocity after being below this threshold for at least 150 ms. A backward-tracing algorithm was then used to determine the last preceding moment at which signed velocity was zero. Similarly, the end of the discrete and passing movements was determined based on the moment of time at which unsigned velocity was lower than 5% of peak velocity and stayed under this threshold for at least 150 ms. The moment at which signed velocity became zero after crossing the 5% threshold was considered as the movement end. Continuous movements were analyzed only from the home position to the target. To define the end of this movement, two peak velocities were detected, during the motion to the target and during the reversal stroke. Starting from the second peak velocity, a backwards-tracing algorithm was used to detect the last moment when the unsigned velocity became lower than 5% of the first peak.

Each movement to the target was parsed into the primary and secondary submovement with the use of a method suggested by Meyer et al. (1988). Although other methods of submovement detection have also been suggested (Milner 1992; Novak et al. 2002; Rohrer et al. 2004), the majority of studies promoting the interpretation of secondary submovements as corrective adjustments employed the method of Meyer et al. (1988). Since the goal of the present study was to re-examine this interpretation, we also used this method. According to this method, the beginning of a secondary submovement is notified by the first of any of the following events: a zero-crossing from positive to negative value occurs in the velocity profile (submovements of type 1); a zero-crossing from negative to positive value occurs in the acceleration profile (type 2); a zero-crossing from positive to negative value appears in the jerk profile (type 3). Defined in this way, type 1 submovements correspond to reversals in the trajectory, type 2 submovements represent re-accelerations towards the target, and type 3 submovements signify decreases in the rate of deceleration. The portion starting from this event up to the end of the movement was considered a secondary submovement and the movement portion prior to the secondary submovement was considered a primary submovement. Thus, each trajectory fluctuation was not analyzed. Rather, the analysis focused on the interruption of the smooth velocity profile and onset of irregular motion. Only secondary submovements emerging during the deceleration phase were analyzed, since corrective adjustments are likely to emerge during this phase. Examples of the three submovement types during discrete movements are shown in Fig. 2. Submovements in the passing mode were analyzed only in the movement portion after passing the target. By this way, we isolated submovements not related to accuracy regulation. The time moment of passing the target was defined as the instant when the distance between the fingertip and the target center was minimal. As reported in the "Results" section, the target passing always occurred during the deceleration phase.

Total incidence of submovements of all three types was computed as the number of movements with a secondary submovement divided by eight, i.e., by the total number of movements performed in this condition. Total submovement incidence has usually been analyzed in studies developing the interpretation of submovements as corrective adjustments. However, many of those studies did not

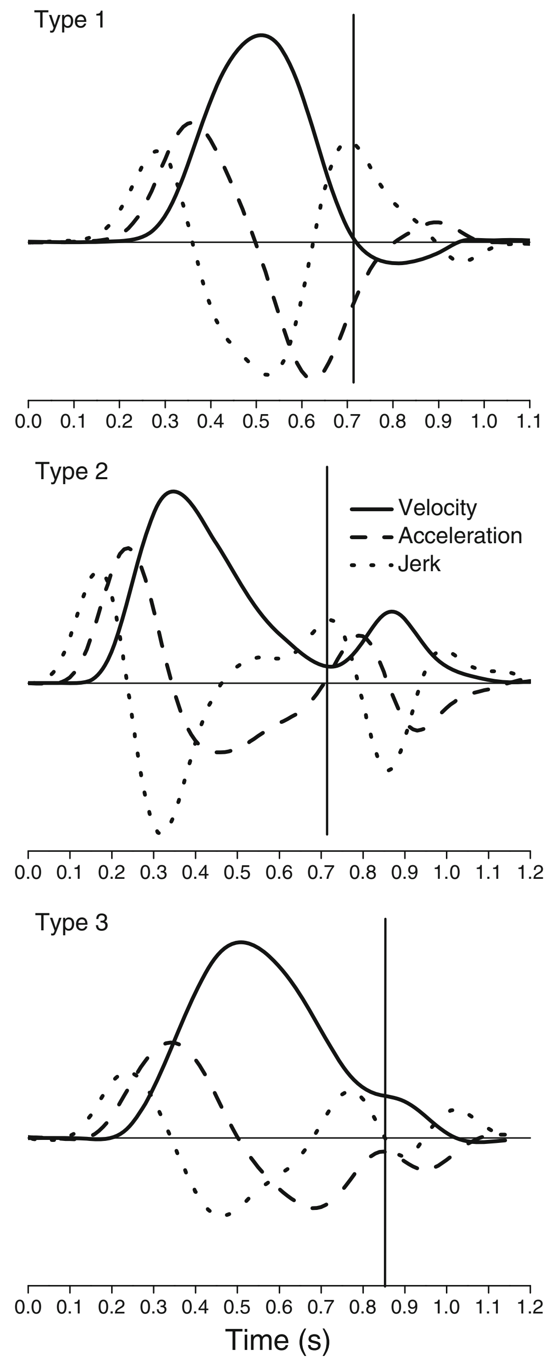


Fig. 2 Examples of movements with submovements of type 1, 2, and 3. Movements were performed by a control subject. The *vertical line* marks a velocity zero-crossing from positive to negative values in case of the type 1 submovement, an acceleration zero-crossing from negative to positive values indicating the type 2 submovement, and a jerk zero-crossing from positive to negative values when the submovement was of type 3

use all three types of submovements for analysis, focusing either on type 1 and 2, or on type 2 only, or on type 2 and 3. This divergence in the types of analyzed submovements makes it difficult to compare the results across the studies. For this reason, we analyzed total submovement incidence and submovement incidence separately for each type. The separate analysis of the three submovement types was also justified by a consideration that different factors may cause different degrees of disturbance in the velocity profile represented by the three submovement types. This expectation has been supported in our previous studies (Dounskaia et al. 2005a; Fradet et al. 2008; Wisleder and Dounskaia 2007) with a finding that submovements of the three types can be divided in gross and fine submovements based on the distinct dependence of their incidences on the conditions for motion termination and accuracy regulation. Incidence of submovements by type was computed for each condition and each subject as the number of movements with a secondary submovement of the respective type divided by the total number of movements performed in this condition. Thus, the sum of the incidences of the three submovement types was equal to the total submovement incidence.

Additionally, normalized jerk score (NJS) was computed to assess the variability of movement trajectory with the formula $\mathrm{NJS} = \sqrt{\left(0.5 \times \mathrm{duration}^5/\mathrm{length}^2 \times \int \mathrm{j}^2 \mathrm{dt}\right)}$ (Teulings et al. 1997). Here j is the jerk, i.e., the third derivative of displacement, duration is the movement time, and length is the movement distance. The NJS was computed separately for the acceleration phase (NJSacc) and deceleration phase (NJSdec).

Statistical analysis

A $2 \times 2 \times 3$ (group $\times$ target size $\times$ movement mode) repeated measures factorial analysis of variance (ANOVA) was applied to the majority of the computed characteristics. Bonferroni post hoc tests were conducted to perform pairwise comparisons between the modes. Primary submovement distance was analyzed only during the discrete and continuous mode with the use of a $2 \times 2 \times 2$ (group $\times$ target size $\times$ movement mode) ANOVA. Passing movements were not included in this analysis because their distance was not restricted.

Verification of the dependence of submovements on the filtering procedure

As was described in this section, the differentiation method used for computation of velocity, acceleration, and jerk of the pen motion included a smoothing procedure. It was analyzed whether the differentiation and smoothing procedures influenced the emergence of the three types of submovements. With this purpose, results obtained for the total submovement incidence and submovement incidence by type with use of this method were compared with results obtained with use of two other smoothing methods and a MATLAB 2-point signal differentiation procedure. The first smoothing method was a 5th order dual-pass low-pass Butterworth filter with a cutoff frequency of 7 Hz. The second method was a MATLAB cubic smoothing spline procedure *csaps*. Although using the different smoothing procedures resulted in slight variations in the values of submovement incidence in each condition, the statistically significant main effects and interactions were the same for all three methods. This demonstrated that the majority of submovements of all three types were not an artifact of the differentiation and smoothing procedure. Instead, they were inherent features of movement kinematics and their emergence depended on movement conditions, as presented next.

Results

Primary submovement distance

Average distance travelled during the primary submovement in discrete and continuous mode is shown in Fig. 3. The primary submovement distance was significantly lower during movements to small than to large targets [$F(1, 27) = 37.1$, $p < 0.001$] and during continuous than during discrete movements [$F(1, 27) = 41.7$, $p < 0.001$]. Interaction between target size and movement mode was also significant [$F(1, 27) = 10.4$, $p < 0.001$] because the difference in the distance between the two modes was substantially greater for large than small targets. The group effect was significant [$F(1, 27) = 10.9$, $p < 0.001$]. PD

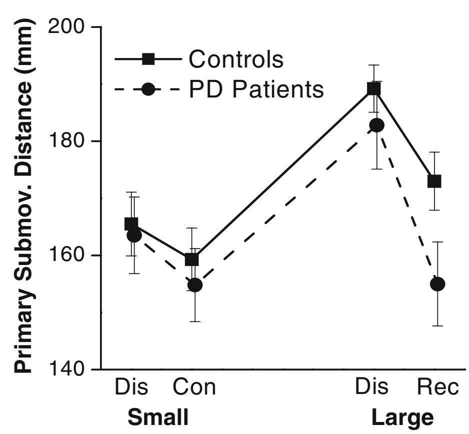
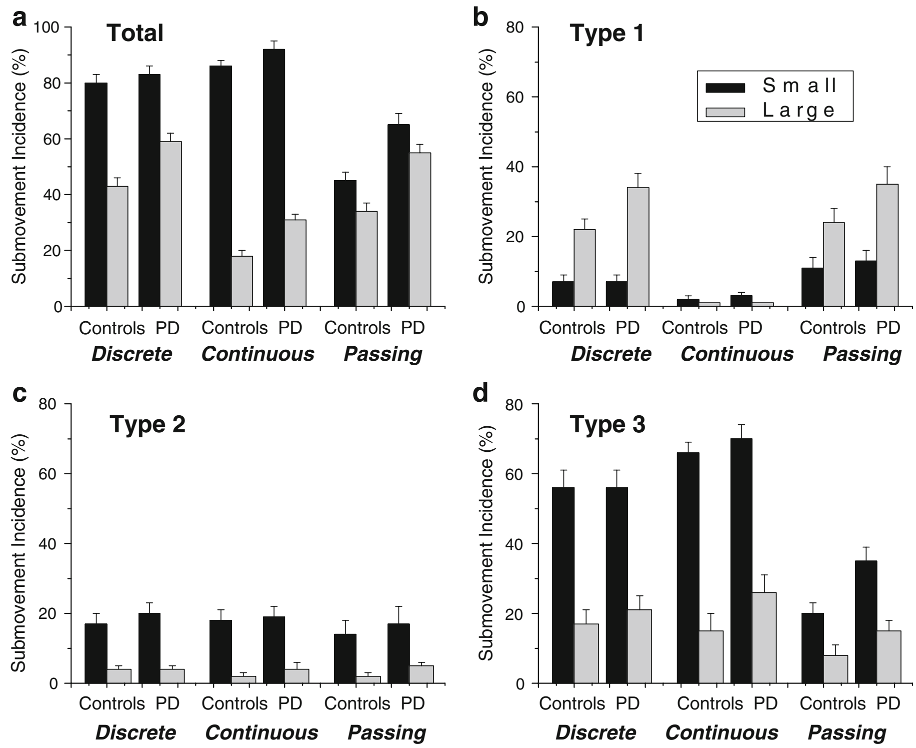


Fig. 3 Distance covered in the primary submovement during discrete (*Dis*) and continuous (*Con*) movements in the two target size conditions, small and large. Here and in the other figures, the *error bars* represent standard error (SE)

Fig. 4 Total submovement incidences (a) and by type (b–d) expressed in percentage of the total number of movements in the discrete, continuous, and passing mode. The sum of the incidences of the three submovement types in each condition is equal to the total incidence of submovements in this condition



patients covered shorter distance during the primary submovement than controls. This result is consistent with the previous observations of a shortened primary submovement in PD (Rand et al. 2000; Romero et al. 2003). Interactions of group with target size and movement mode and the three-factor interaction were not significant.

Total submovement incidence

The major purpose of this analysis and the subsequent analyses of submovement incidence by type was to contrast the influence of the two factors, accuracy regulation and motion termination on submovement production in patients and controls. It should be taken into account in these comparisons that submovements in the passing mode were analyzed not within the entire deceleration phase but within a portion of it because the target passing usually occurred after the peak velocity was achieved. For small targets, the percentage of the deceleration duration elapsed before the target passing was 35% (±4.2%) and 32% (±3.3%) for PD patients and controls, respectively. This percentage was 12% (±1.5%) and 3% (±0.3%) for the two groups during movements to large targets. The analysis of submovements only after passing the target could decrease submovement incidence during the passing mode, as compared to the other two modes.

Total submovement incidence (a sum of incidence of the three submovement types) is presented in Fig. 4a. Table 2 shows the results of ANOVA for this and other characteristics that were analyzed for all three modes. In agreement with previous observations, the decreases in target size bolstered submovement production in both subject groups. This result may suggest the influence of accuracy requirements on submovement production. However, submovements were frequent during the passing mode. Furthermore, submovement incidence depended on target size during the passing mode in the same way as in the other two modes. This result is remarkable because these submovements were revealed after passing the target, and; therefore, they could not be corrective adjustments performed to accurately achieve the target.

The main effect of movement mode was also significant. Post hoc testing revealed that submovement incidence was greater during the discrete than the other two modes. In addition, interaction between target size and movement mode was also significant. Figure 4a shows that for both groups, submovement incidence was lower during continuous than during discrete and passing movements when targets were large. A possible reason for this result may be that submovements caused by motion termination during discrete and passing movements were specifically frequent for large targets because movement speed, and hence, energy to dissipate would be higher for these targets as compared to small targets. Also, submovement incidence was lower during passing than during discrete and continuous movements when targets were small, possibly because of detecting submovements only after the target passing that occurred during movements to small targets after more than

Table 2 Statistical results (*F* values)

	Size	Mode	Group	Size × mode	Group × size	Group × mode	Group × size × mode
Degrees of freedom	1, 27	2, 26	1, 27	2, 26	1, 27	2, 26	2, 26
SM incidence, total	267.0***	23.0***	5.7*	68.1 ***	2.1	2.2	1.1
SM incidence, type 1	71.7***	49.0***	3.0°	39.3 ***	5.6*	1.5	3.6*
SM incidence, type 2	53.2***	1.2	0.8	1.3	0.2	0.4	0.6
SM incidence, type 3	137.3***	56.2***	3.4°	26.3***	0.0	1.8	1.7
NJSacc	6.9*	1.8	1.6	0.4	0.3	0.3	0.3
NJSdec	24.0***	3.3°	2.9	4.5*	0.4	7.4*	0.4
Vpeak	97.2***	21.7***	10.6**	16.0***	6.5*	2.8°	1.9

SM submovement

° $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

30% of the deceleration phase has elapsed. Total submovement incidence was greater in PD patients than in controls, which is consistent with findings of previous studies of submovements in PD. Interactions of group with target size and movement mode were not significant.

The results for total submovement incidence suggest that at least a portion of submovements produced by each group cannot be interpreted as corrective adjustments performed to fulfill pointing accuracy requirements. Sources of submovements were further investigated by analyzing submovement incidence separately for each type.

Submovement incidence by type

Mean values of type 1, 2, and 3 submovement incidence are shown in Fig. 4b, c, and d, respectively. The main effect of target size was significant for all three types. However, while type 2 and 3 submovement incidence was greater for small targets, the effect of target size was opposite for type 1. This result demonstrates that the interpretation of submovements as corrective adjustments is not applicable to type 1 submovements. Furthermore, this interpretation is questionable even with respect to type 2 and 3 submovements because they frequently appeared during passing movements. As in the other modes, incidence of type 2 and 3 submovements in the passing mode was significantly greater for small than for large targets, even though these submovements could not be corrective adjustments. Similar to the corresponding finding for total submovement incidence, this result shows that the inverse relationship between target size and submovement incidence does not necessarily mean that type 2 and 3 submovements served to improve pointing accuracy, as suggested by the traditional interpretation.

The effect of movement mode was significant for submovement incidence of type 1 and 3 but not of type 2. Type 1 submovements were more frequent during discrete and passing than continuous movements, especially when targets were large as was attested by a significant interaction between target size and movement mode. These findings point to motion termination as a primary source of type 1 submovements in both groups of subjects. The effect of movement mode on type 3 submovements was opposite to that on type 1 submovements, causing lower type 3 submovement incidence during discrete and passing than during continuous movements. In addition, these submovements emerged more frequently during discrete than during passing movements. The interaction between target size and movement mode was also significant for type 3 submovements. Although type 3 submovement incidence increased with decreases in target size for all movement modes, these increases were more pronounced during the continuous than during the other two modes (see Fig. 4d). The results point to principal differences between mechanisms causing type 1 and type 3 submovements both in PD patients and controls.

There were group differences for incidence of type 1 and 3 submovements that did not reach the significance level ($p < 0.1$). The result for type 1 submovements was clarified by significant group by target size interaction and by the three-factor interaction, showing that PD was associated with an increased type 1 submovement incidence during discrete and passing movements performed to large targets, as observed in Fig. 4b. The non-significant group effect for type 3 submovements was clarified by post hoc testing that revealed a significant group effect for the passing mode but not for the discrete and continuous mode. Other main effects and interactions were not significant. These results explain the effect of PD found for the total submovement incidence. During discrete movements, the increases in total submovement incidence in PD patients should be attributed solely to the more frequent type 1 submovements in patients than in controls during movements to large targets. During continuous movements, the difference between the two groups was minor and it may have emerged due to non-significant difference in type 3 submovements (Fig. 4d). Incidence of both type 1 and 3 submovements was greater in patients than in controls during passing movements.

Trajectory variability

The analyses of submovement incidence show that although type 2 and 3 submovements became more frequent with decreases in target size, these submovements, as well as their inverse dependence on target size, were also observed during the passing mode after crossing the target. This result suggests that at least some of type 2 and 3 submovements may be non-corrective. To account for the origin of these non-corrective submovements, a hypothesis can be formulated that mechanisms involved in accurate pointing to small targets result in velocity fluctuations represented by type 2 and 3 submovements. Moreover, the presence of these submovements after the target crossing in the passing mode suggests that the decreases in target size affected smoothness of the entire velocity profile and not only its portion during the deceleration phase.

To verify this observation, NJS, a characteristic sensitive to trajectory irregularities, was computed separately for the acceleration and deceleration phases. The results are shown in Fig. 5. The NJS was much higher during the deceleration than acceleration phase, as observed from the scale difference between the vertical axes in Fig. 5a and b. Nevertheless, the score was significantly higher for small than for large targets during both phases. The movement mode effect was marginally significant for NJS during deceleration. This characteristic was non-significantly higher during the passing than continuous mode. Although the NJS was systematically higher for PD patients than for controls, these differences did not reach the significance level. The only significant interaction was the group by mode interaction for NJS during deceleration. This characteristic was higher for PD patients than controls during the passing mode as compared to the continuous mode. It is noteworthy that the increased NJS in patients during the passing mode may be related to the increases in type 1 submovement incidence that was also observed in patients in the same mode.

The NJS data show that satisfying more stringent accuracy requirements was accompanied with increased trajectory variability during entire motion, including the acceleration phase. Regulation of accuracy of target achievement would hardly cause submovements yet in the acceleration phase. The alternative interpretation is that irregularities in the entire velocity profile emerged more frequently during slower movements performed to smaller targets. This interpretation accounts for the emergence of type 2 and 3 submovements during passing movements and for the finding that these submovements were more frequent for smaller targets. It also shows that at least some of type 2 and 3 submovements observed during discrete and continuous modes may also have been non-corrective velocity fluctuations directly related to low movement speed, while the higher incidence of these submovements for small than large targets was a consequence of the speed-accuracy tradeoff (Fitts 1954).

An analysis of peak velocity (shown in Fig. 6 and denoted by Vpeak in Table 2) confirmed that the speed-accuracy tradeoff was maintained in the present experiment. Peak velocity was significantly lower during movements to small than to large targets. Also, peak velocity was greater during the discrete mode than during the continuous mode and lower than during the passing mode. PD patients were significantly slower than controls in all conditions. In addition, increases in peak velocity with the increase of target size were lower in patients than in controls, as revealed by significant group by target size interaction. The other interactions did not reach significance.

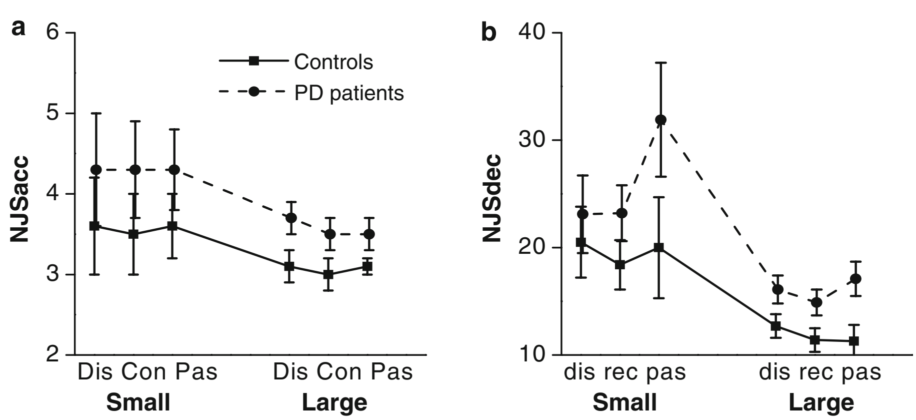


Fig. 5 Normalized jerk score during **a** the acceleration phase (*NJSacc*) and **b** the deceleration phase (*NJSdec*) for discrete (*Dis*), continuous (*Con*), and passing (*Pas*) movements. The *error bars* represent standard error (SE). No units are indicated because NJS is a normalized characteristic. Both NJSacc and NJSdec were higher for small than for large targets

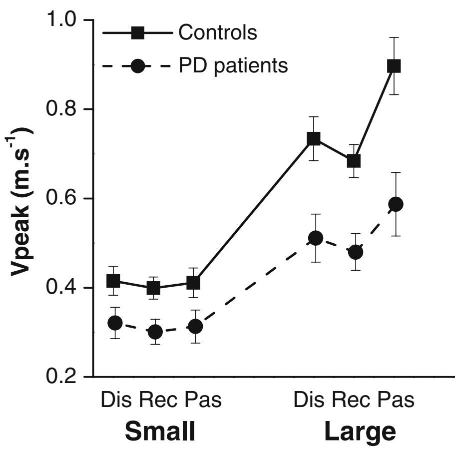


Fig. 6 Peak velocity (*Vpeak*) during discrete (*Dis*), continuous (*Con*), and passing (*Pas*) movements in PD patients and controls. The *error bars* represent standard error (SE)

Discussion

A dominant interpretation of secondary submovements that has been employed in motor control studies for longer than a century is that they are corrective adjustments purposefully generated to satisfy pointing accuracy requirements (Meyer et al. 1988; Woodworth 1899). Accordingly, a conclusion has been derived that the production of secondary submovements is one of the major mechanisms of movement accuracy regulation frequently employed during movements of young adults (Houk et al. 2007; Milner 1992; Novak et al. 2002) and more so in movements of subjects with a declined motor function due to aging (Bellgrove et al. 1998; Darling et al. 1989; Pratt et al. 1994; Seidler-Dobrin et al. 1998; Walker et al. 1997) or PD (Flash et al. 1992; Teasdale et al. 1990). The primary support for the interpretation of submovements as purposefully generated corrective adjustments stems from an observation that decreases in target size are usually accompanied with shortening of the primary submovement and increases in the incidence of secondary submovements.

The fact that submovements can be purposefully produced to correct movement trajectory is apparent. Segmented trajectories in movements of infants during reaching (Berthier 1996; Thelen et al. 1993) and in adults during tracking tasks (Pasalar et al. 2005; Roitman et al. 2004) provide convincing examples of corrective submovements. However, non-corrective submovements representing fluctuations in movement velocity can also emerge. Our previous studies have demonstrated that the majority of submovements in pointing movements of young adults may be non-corrective, irregular fluctuations of velocity emerging in the process of motion termination and during motion of low speed. Here, we examined whether the same conclusion is applicable to movements of PD patients during which submovements are abundant (Flash et al. 1992; Flowers 1978a; Phillips et al. 1994; Rand et al. 2000; Romero et al. 2003; Teasdale et al. 1990; Weiss et al. 1997). The control group used in this study represented normal aging that has also been recognized for frequent submovements. The corrective nature of submovements has been accepted for both groups because it seems to offer explanation of how subjects compensate for specific deficits experienced by each group in planning and executing goal-directed movements. Our results question this interpretation of submovements both in PD patients and in the control group of healthy adults in advanced age. Results obtained for both groups and those obtained specifically for PD are discussed next.

Results common for the two subject groups

The results of the target size manipulations were consistent with those obtained in studies that promoted the traditional submovement interpretation. Decreases in target size were accompanied by increases in total submovement incidence and by shortening of the primary submovement. Nevertheless, other results question the traditional submovement interpretation. First, type 1 submovements cannot be qualified as corrective adjustments because their incidence increased with increases in target size. Furthermore, type 1 submovements emerged almost exclusively during discrete and passing and not during continuous movements. This result points to the emergence of type 1 submovements from motion termination that was not performed during continuous movements. The motion termination factor also accounts for the increases in type 1 submovement incidence with target size. Indeed, movements to large targets were faster than to small targets, and therefore, larger amount of mechanical energy had to be dissipated in the process of motion termination, which increased the probability of type 1 submovements. Type 1 submovements may emerge due to active control responsible for motion termination, e.g., antagonist co-activation near the target during the third phase of the tri-phasic pattern of muscle activity (Berardelli et al. 1996). Also, type 1 submovements may be a result of passive elasticity of muscles that may cause oscillations of the limb around the target during energy dissipation.

The conclusion that type 1 submovements emerged due to motion termination in the two studied groups is consistent with that obtained by Fradet et al. (2008) for young adults. However, in addition to type 1, type 2 submovements were also qualified as emerging from motion termination in studies of Dounskaia et al (2005a) and Wisleder and Dounskaia (2007). The different results for type 2 submovements may be attributed to several differences in movement conditions in these studies. Namely, motion and the targets were presented on a vertical computer screen and there was an ultimate requirement to terminate motion within the target in this study and the study by Fradet et al. In contrast, movements were performed in natural vision conditions in the first two studies. Also, subjects were instructed to achieve the target as accurately as possible but were allowed to end motion anywhere near the target in those studies. In spite of the differences in the results for type 2 submovements, all our studies agree on a common finding that the majority of gross submovements (revealed by the first and sometimes also the second derivative of motion) are not corrective submovements performed to improve pointing accuracy. Rather, they are trajectory irregularities emerging during motion termination.

The second finding questioning the traditional interpretation is related to type 2 and 3 submovements. Although incidence of these submovements was inversely related to target size (as predicted if submovements are corrective), this dependence was also observed in the passing mode in which type 2 and 3 submovements were also frequent. In the passing mode, only submovements emerging after the target crossing were analyzed, and therefore, they could not be corrective adjustments for pointing accuracy. This result shows that the inverse relationship between submovement incidence and target size does not necessarily imply the traditional interpretation. Instead of representing corrective adjustments, submovements may be irregular fluctuations in the velocity profile that, for some reason, emerge during accuracy regulation. The analysis of the NJS supported this hypothesis. Although the NJS was low during the acceleration phase as compared to the deceleration phase, it proportionally increased in both phases with decreases in target size. This result shows that type 2 and 3 submovements could emerge as trajectory irregularities that were more pronounced when accuracy requirements were more stringent. As discussed further, type 2 and 3 submovements may be a characteristic feature of slow motion, and their dependence on target size is a result of the speed-accuracy tradeoff (Fitts 1954).

To summarize, the results obtained from the two groups reveal two origins of non-corrective submovements. Motion termination was responsible for the majority of type 1 (gross) submovements, and irregular fluctuations in velocity gave rise to type 2 and 3 (fine) submovements. These two origins of non-corrective submovements were also revealed for young adults in our previous studies, suggesting that factors causing non-corrective submovements were similar across the different subject groups.

Although our data do not exclude a possibility that some of submovements were corrective, they show that a substantial portion of submovements of each type may have been non-corrective. Moreover, there is a principal possibility that none of the submovements observed in this experiment were purposefully generated corrective submovements. Further, additional evidence is discussed that supports this possibility with respect to submovements in PD.

Effect of PD

In agreement with previous findings, distance covered in the primary submovement was shorter and the total submovement incidence was greater in patients than in controls. The analysis of submovement incidence by type clarified that the major group difference was in type 1 submovements that were more frequent in patients than in controls, but only during movements to large targets. This result points to a specific deficiency of PD patients in performance of smooth motion termination. Indeed, movements were faster to large than to small targets, thus making the deficiency in the production of smooth motion termination more apparent. The inability of patients to smoothly terminate relatively fast movements is consistent with PD-related deficits in movement control. Indeed, smooth motion termination synchronized with the approach to the target requires fine regulation of muscle activation. Impairments in muscle activation caused by PD have been well recognized in electromyographic studies (Pfann et al. 2001; Robichaud et al. 2002). Behavioral studies have also provided evidence for deficiency of fine control in PD (Dounskaia et al. 2005b; Teulings et al. 1997). In addition, evidence for the involvement of basal ganglia in performance of motion deceleration and termination has been reported by Kato and Kimura (1992). They demonstrated impairments in deceleration and stopping at a target during visually guided, step-tracking elbow movements in monkeys as a result of reversible blockage of the putamen. The study reported co-activation and abnormal increases in the antagonist activity during the final movement portion, both of which may cause brief reversals represented by type 1 submovements.

The reduced capability to produce termination of motion to large targets without type 1 submovements suggests that movement slowness in PD might partially be a result of this factor. Patients may have a tendency to reduce movement speed because they are not capable to cope with disturbances caused by fast motion termination. This assumption is consistent with a prolonged deceleration phase typical of discrete movements in PD (Rand et al. 2000). Slow approach to the target may be a compensatory strategy employed by patients to reduce submovements associated with motion termination.

No group differences were found with respect to type 2 submovements. Submovements of type 3 were more frequent in PD patients than in controls, but this difference was significant only during passing movements. Although the influence of PD on fine submovements was modest, these data show that PD patients produced fine submovements at least as frequently as controls. This finding is important because it argues against the interpretation of type 2 and 3 submovements as purposefully generated corrective adjustments, at least in movements of PD patients. Indeed, corrective type 2 and 3 submovements imply an ability to produce rapid re-arrangement of movement control in response to visual and/or proprioceptive feedback about current motion. Multiple studies suggest that this ability is drastically impaired in PD. For example, when a change in direction and magnitude of generated force is required (as it is in the case of type 2 and 3 submovements, respectively), PD patients demonstrate increased latencies and decreased rate of force change (Godaux et al. 1992; Jordan et al. 1992). Desmurget et al. (2004) have shown that although PD patients are mildly impaired in visually guided smooth modifications of movement to a slightly shifted target position, they are dramatically delayed when production of a corrective submovement is required. Consistent findings that PD patients have difficulties to reorganize reaching and grasping movements during motion in response to various types of perturbations have been repeatedly reported (Castiello and Bennett 1994; Montgomery et al. 1991; Plotnik et al. 1998; Tunik et al. 2004).

Furthermore, PD patients experience significant difficulty when required to string together successive motor acts (Agostino et al. 1992; Benecke et al. 1987; Cools et al. 1984), which would be required during the production of a series of iterative, corrective submovements. In particular, patients are impaired in switching from one coordinated movement to another (Almeida et al. 2003; Giladi et al. 1992, 1997; Weiss et al. 1997). This impairment worsens when the movement sequence is not known in advance (Curra et al. 1997), which is the case when a corrective submovement has to be generated in response to error detected at the end of the primary submovement. The role of vision in submovement production has also been challenged by an observation that submovements were more frequent without than with vision in movements of PD patients (Romero et al. 2003). Similarly, the reliance of patients on proprioception during production of fine submovements does not agree with reduced capacity to use proprioceptive information well-documented in PD (Klockgether et al. 1995; Moore 1987; Rickards and Cody 1997). Together, these considerations suggest that the production of fine corrective submovements in PD is highly unlikely. Since the majority of gross submovements were also non-corrective, a conclusion should be made that the overwhelming majority of submovements in movements of PD patients were not corrective but rather represented irregular fluctuations of velocity.

Origins of fine submovements

A question remains what could be the origin of velocity fluctuations represented by fine (type 2 and 3) submovements. We hypothesize that the dependence of fine submovements on target size is a secondary effect, and that the primary factor influencing incidence of these submovements is movement speed that depends on target size (Fitts 1954). It is well recognized that increases in movement speed may be associated with increased variability of motor output emerging from increases in variability of force generated for movement production (Schmidt et al. 1979). However, our data suggest that the opposite effect is also possible, i.e., fluctuations represented by submovements of type 2 and 3 become more frequent with decreases in movement speed. This suggestion is consistent with a finding of Doeringer and Hogan (1998) that smoothness of movement trajectory decreases with decreases in movement speed.

There are a number of factors that may cause motion fluctuations in the form of fine submovements during slow movements. First, the natural effect of muscle activation on movement kinematics predicts velocity fluctuations during slow motion. Indeed, slow motion is characterized by low acceleration and therefore requires steady production of low muscle force. This task may be difficult even for young adults, as confirmed by Doeringer and Hogan (1998) who reported inability of subjects to perform smooth motion with constant speed. It may require a series of small force pulses generated through muscle activation and de-activation or through interplay of co-activated antagonistic muscles. This control would result in velocity fluctuations, i.e., in type 2 and 3 submovements. This possible source of submovements is consistent with the interpretation of them as movement units or building blocks of goal-directed movements proposed in healthy adults (Burdet and Milner 1998) and in stroke patients (Krebs et al. 1999). These studies suggest that young adults may be capable to blend submovements by providing fine regulation of motor unit activation that decreases fluctuations and results in fairly smooth motion. In contrast, stroke patients may be unable to blend submovements to provide smooth velocity profile. A similar deficit may result in frequent submovements in other groups of individuals characterized by reduced capability to provide fine regulation of muscle force, including elderly adults and PD patients (Enoka et al. 2003; Galganski et al. 1993; Teasdale et al. 1990).

In addition to small muscle force pulses generated to keep acceleration low, non-corrective submovements of type 2 and 3 may also randomly emerge due to increased variability of motor output. One possible source of variability is associated with effect of normal aging on muscle activation represented by abnormalities in motor unit synchronization and in discharge rate specifically apparent during slow movements (Carnahan et al. 1993; Enoka et al.

2003; Galganski et al. 1993; Kornatz et al. 2005; Vaillancourt et al. 2003). Increased muscle co-activation and production of multiple muscle activity bursts in PD (Berardelli et al. 1996; Pfann et al. 2001; Robichaud et al. 2002) may further contribute to production of fine submovements. Exacerbation of these disruptions during slow movements has been confirmed by Teasdale et al. (1990). This study reported PD-related increases in the number of distinct agonist activity bursts with decreases in movement speed. Tremor may also contribute to submovement production in PD, although the irregular emergence of submovements in movements of PD patients argues against this possibility (Flash et al. 1992).

Finally, submovements are predicted by a hypothesis that pointing accuracy is achieved via regulation of arm stiffness (Gribble et al. 2003; Osu et al. 2004; Selen et al. 2006). According to this hypothesis, increased stiffness prevents deviations from motion to the target due to possible external perturbations and noise in the neuromuscular control signals. Greater limb stiffness also slows motion down, which accounts for the speed-accuracy tradeoff (Fitts 1954). It also increases the signal-to-noise ratio of forces that drive the limb to the target, making velocity fluctuations in the form of type 2 and 3 submovements more frequent.

In conclusion, our findings suggest that the interpretation of submovements as corrective adjustments constituting an iterative process of target achievement may be not applicable for movements in PD. This conclusion raises questions with respect to a theory that PD patients are unable to transport the limb to the target with a single force pulse, and therefore, they produce iterative submovements to achieve the target (Hallett and Khoshbin 1980). This theory finds support in the typical EMG pattern in PD which is characterized by a decreased initial burst of agonist activity and several cycles of alternating agonist-antagonist activity (Hallett and Khoshbin 1980; Kelly and Bastian 2005). This type of muscle activity has usually been interpreted as submovements performed by patients to compensate for the deficiency of the initial activity burst that is insufficient to propel the limb to the target. The results of the present study question this interpretation, suggesting that submovements may be not a part of the motor strategy but a result of inability of PD patients to provide smooth muscular control.

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