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## RESEARCH ARTICLE | *Control of Movement*

# Vigor of reaching, walking, and gazing movements: on the consistency of interindividual differences

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<sup>1</sup>Complexité, innovation, activités motrices et sportives (CIAMS), Université Paris Sud, Université Paris-Saclay, Orsay, France; <sup>2</sup>CIAMS, Université d'Orléans, Orléans, France; and <sup>3</sup>Institut Universitaire de France, Paris, France

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**Labauve O, Deroche T, Teulier C, Berret B.** Vigor of reaching, walking, and gazing movements: on the consistency of interindividual differences. *J Neurophysiol* 123: 234–242, 2020. First published November 27, 2019; doi:10.1152/jn.00344.2019.—Movement vigor is an important feature of motor control that is thought to originate from cortico-basal ganglia circuits and processes shared with decision-making, such as temporal reward discounting. Accordingly, vigor may be related to one's relationship with time, which may, in turn, reflect a general trait-like feature of individuality. While significant interindividual differences of vigor have been typically reported for isolated motor tasks, little is known about the consistency of such differences across tasks and movement effectors. Here, we assessed interindividual consistency of vigor across reaching (both dominant and nondominant arm), walking, and gazing movements of various distances within the same group of 20 participants. Given distinct neural pathways and biomechanical specificities of each movement modality, a significant consistency would corroborate the trait-like aspect of vigor. Vigor scores for dominant and nondominant arm movements were found to be highly correlated across individuals. Vigor scores of reaching and walking were also significantly correlated across individuals, indicating that people who reach faster than others also tend to walk faster. At last, vigor scores of saccades were uncorrelated with those of reaching and walking, reaffirming that the vigor of stimulus-elicited eye saccades is distinct. These findings highlight the trait-like aspect of vigor for reaching movements with either arms and, to a lesser extent, walking.

**NEW & NOTEWORTHY** Robust interindividual differences of movement vigor have been reported for arm reaching and saccades. Beyond biomechanics, personality trait-like characteristics have been proposed to account for those differences. Here, we examined for the first time the consistency of interindividual differences of vigor during dominant/nondominant arm reaching, walking, and gazing to assess the trait-like aspect of vigor. We found a significant consistency of vigor within our group of individuals for all tested tasks/effectors except saccades.

dominant and nondominant arm reaching; eye saccades; movement vigor; walking

## INTRODUCTION

In everyday life, we perform a multitude of movements involving different effectors, such as the eyes, the legs, or the arms. For instance, we may walk to the coffee machine, gaze

at the desired knob, and press it with the fingertip. Those movements are all performed with a certain vigor, e.g., with a certain speed, which is self-selected and chosen by the central nervous system. As simple as this daily task may sound, it raises fundamental questions in movement neuroscience: what are the underpinnings of movement invigoration? Does vigor reflect an individual trait, i.e., a quite stable and distinctive attribute of individuality?

The first question has received a great deal of attention with investigations at neural, behavioral, and theoretical levels (see Carland et al. 2019; Dudman and Krakauer 2016; Shadmehr et al. 2019 for reviews). Seminal studies on movement vigor were motivated by abnormalities observed in patients with Parkinson's disease, who typically exhibit slower, rarer, and smaller movements with increased delay before their initiation (Mazzoni et al. 2007; Panigrahi et al. 2015). These alterations do not seem to originate from biomechanical deficiencies, but mainly from a dopaminergic deficit in the basal ganglia (BG) (Desmurget and Turner 2010; Turner and Desmurget 2010).

Yet, in relation to the second question, significant differences of vigor have been reported also between healthy individuals, mostly for eye and arm movements (Berret et al. 2018; Choi et al. 2014; Reppert et al. 2018a). The vigor of walking is less well known, but interindividual differences of preferred walking speed, going beyond simple anthropomorphic factors, have been documented (Bohannon 1997; Seethapathi and Srinivasan 2015; Summerside et al. 2018). Despite such differences, there is, nevertheless, a common behavior exhibited by everyone: the speed of movements tends to increase with their extent for movements with a start and a stop (see Berret et al. 2018 for reaching, Choi et al. 2014 for saccades, and Seethapathi and Srinivasan 2015 for walking). This characteristic trend led researchers to model vigor as the outcome of processes shared with decision-making ones, in the frame of temporal reward discounting or cost of time theories (Shadmehr 2010; Shadmehr et al. 2010). Accordingly, vigor may be related to one's relationship with time, which may, in turn, reflect an individual's trait. The extent to which certain personality traits (e.g., impulsivity or boredom proneness) could account for the above-mentioned interindividual differences of vigor was tested for eye and arm movements but such an explicit approach is tricky as it requires to define a priori certain putative traits and test a large number of participants

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with validated questionnaires (Berret et al. 2018; Choi et al. 2014).

However, if vigor represents a general trait-like aspect of individuality, then people who move fast in one task should also move fast in another task comparatively to the rest of the population. Therefore, the trait-like aspect of vigor can also be tested more implicitly by assessing the consistency of interindividual differences across various movement modalities (i.e., different motor tasks and/or different effectors). In this vein, within and across sessions consistency has been verified for eye saccades and arm reaching separately (Berret et al. 2018; Choi et al. 2014). Consistency of vigor across various modalities (eye, head, and dominant arm reaching movements) was further tested in Reppert et al. (2018a). The rationale is that consistency of interindividual differences of vigor despite the involvement of distinct neuromechanical systems would suggest that common neural processes underlie movement invigoration at large, in agreement with the hypothesis of its relationship with some individuality traits. Reppert et al. found a good consistency of interindividual differences of vigor between arm and head movements, but not saccades. The present study complements this previous approach by adding two other movement modalities that have been extensively studied in motor control but not through the vigor spectrum: reaching with the nondominant arm and walking. For instance, do people who reach faster than others with their dominant arm also tend to reach faster than others with their nondominant arm? And do they tend to walk faster than others as well? To answer these questions, we compared the consistency of movement vigor within the same group of individuals for the following elementary motor tasks: reaching (interlimb), walking, and gazing. To our knowledge, vigor has not been investigated previously in all these tasks at once. The goal was to examine the extent to which movement vigor is idiosyncratic despite discrepancies in task/effector biomechanics and associated neural circuits.

## MATERIALS AND METHODS

**Participants.** Twenty young adults with no known neuromuscular disease and with normal or corrected-to-normal vision participated in the experiment (12 females, 19 right-handed,  $22.6 \pm 3.3$  yr old,  $1.71 \pm 0.09$  m tall,  $62.80 \pm 10.20$  kg,  $21.41 \pm 2.16$  kg/m<sup>2</sup> of body mass index (BMI),  $0.73 \pm 0.04$  cm of fully extended arms' length,  $0.93 \pm 0.05$  cm of fully extended legs' length; means  $\pm$  SD values). The experimental protocol was approved by the Comité d'Ethique de la Recherche, the local Ethics Committee of Université Paris-Saclay (CER-Paris-Saclay-2018-36-R), and it conformed to relevant guidelines and regulations. Written informed consent was obtained from each participant in the study, as required by the Helsinki Declaration.

**Experimental design and materials.** The experimental protocol was divided into three distinct motor tasks related to 1) arm pointing movements (referred to as "reaching" and denoted by R), 2) locomotion (referred to as "walking" and denoted by W), and 3) eye saccades (referred to as "gazing" and denoted by G).

Our goal was to make the three tasks as comparable as possible despite the differences in the effectors they mostly involve (i.e., arms, legs, or eyes). For each motor task, the independent variable was motion amplitude. In all cases, the instruction was to move from a given initial position to a given final target with a "natural speed" (i.e., a spontaneous, preferred, or comfortable pace). No other instruction was given about the accuracy of the movement end point or any other aspect of the motor strategy. In particular, the pace of movement was unconstrained and self-selected. The successive appearance of targets,

determining the upcoming amplitude of each discrete movement, was automatized via a program specifying the time interval between two target illuminations. This time interval was significantly longer than the maximal time needed to produce each movement (using pilot data and known literature, see below). It enabled the participants to move without temporal pressure, at their own pace. Thus, each motor task lasted a fixed amount of time regardless of the movement speed chosen by the participants. Participants were informed about the total duration of the experiment.

The order of the three motor tasks was pseudo-randomized to prevent learning, habituation or fatigue effects from impacting the results. Importantly for our purpose, the same group of 20 participants performed the three motor tasks described in detail hereafter.

**Reaching (one-degree of freedom, horizontal arm pointing).** The two arms were tested separately: dominant arm movements (denoted by DR) and nondominant ones (denoted by NDR) were recorded in a randomized order for each participant. The reaching (R) task consisted of visually guided single-joint arm pointing movements, with the arm fully extended in the horizontal plane (rotation around the shoulder joint; targets were placed at the shoulder's height to get horizontal movements). Oral instruction to keep the chest as still as possible was given to make the participants remain globally stable while the arm moved. The participant stood in front of a large vertical screen where a sequence of targets was displayed (3-cm wide white dots) by means of a projector placed behind. The participant had to point toward the target that was illuminated without touching it, as it would otherwise imply trunk bending, and to keep this position until the next target appeared. The final position of a movement was then the initial position of the following one. Once a target disappeared, the next one appeared immediately to inform the participant about the next movement. The resultant reaching movement could be 5°, 15°, 25°, 35°, 45°, 55°, 65°, 75°, 85° or 95° wide (10 amplitudes, both rightward and leftward directions tested). The stimuli were produced with MATLAB using Psychtoolbox (Kleiner et al. 2007). The time interval between two target illuminations was significantly longer than the maximal time needed to produce each movement (using pilot data and known literature; ranging between 3.04 and 4.14 s). The task began with an initial familiarization sequence of 20 reaching movements. Then five blocks of 20 reaching movements were recorded (10 movements per amplitude, both rightward and leftward directions tested). The order of appearance of the targets was pseudo-randomized (same blocks for every participants, their order being randomized). Participants had breaks between each block to rest and relax their arm to reduce fatigue effects. After another break, the movements of the second arm were recorded. Data were acquired with a motion capture system (OptiTrack S250e). Three reflective markers (9 mm in diameter) were placed on the acromial process, humeral lateral condyle and apex of the index finger of the studied arm. Six OptiTrack cameras were used to record marker displacements at a rate of 250 Hz. The total duration of R task was ~40 min.

**Walking (standard bipedal locomotion).** In this task, 13 FitLights were used as targets, the lighting sequences of which were programmed on a FitLight Trainer tablet computer. They were aligned on the ground and positioned every 50 cm. The FitLight targets lighted up in a pseudo-random order, resulting in seven amplitudes of movement (0.5 m, 1 m, 2 m, 3 m, 4 m, 5 m, or 6 m). Participants were asked to walk parallel to the FitLight line and to stop when they reached the target that was lighted up. Once they stopped, they had to wait for the extinction of the FitLight target and turn around. After a time during which all the FitLights were off, the next FitLight target lighted up somewhere in front of them to inform them about the next target to walk to. The time interval between two target illuminations was significantly longer than the maximal time needed to produce each movement (using pilot data and known literature; ranging from 16 s to 23 s). The task started with a familiarization sequence of 14 movements where participants experimented with the 7 amplitudes. Five blocks of 14 randomized movements were then recorded (10 of each

amplitude, 5 of each direction). Data were acquired with a motion capture system Qualisys. Six reflective markers (9 mm in diameter) were placed bilaterally on the head of the fifth metatarsal, lateral malleolus, and greater trochanter (hip markers). Eight Qualisys cameras were used to record marker movements at a rate of 100 Hz. Total duration of walking (W) task was ~50 min.

**Gazing (eye saccades).** In this task, the participant sat in front of a computer screen. Head position was standardized using a wooden support for participants' chins. Eye-level height was, therefore, largely consistent across participants, and the distance between the eyes and the screen was 56 cm. Oral instruction to keep the head and the neck as still as possible was given to make the participants remain globally stable while their eyes moved. Only the eyes were moving in the gaze (G) task. An Eye Tracker device (SR Research EyeLink 1000) was used to track the right eye of every participant at a rate of 1,000 Hz. Stimuli in the G task were run with MATLAB using Psychtoolbox. After the calibration sequence, 14 blocks of 10 rightward saccades were recorded and analyzed. Initially, the gaze was fixed on the target at the center of the screen (0.5-cm-wide white dot). As soon as the target disappeared, the next target appeared at one of the possible locations on the horizontal line passing through the center of the screen (in the rightward direction). Then, a return saccade was performed to a target that served as the new starting position. The resultant horizontal saccades were 4°, 8°, 12°, 16°, 20°, 24° or 28° wide (7 amplitudes tested). Order of appearance of the targets was pseudo-randomized with the constraint of each amplitude being repeated 20 times in total. The participants were told to look at the target that appeared and to maintain fixation until the next one appears. The time interval between two target illuminations was significantly longer than the maximal time needed to produce each movement (using pilot data and known literature; 2 s and a random additional time ranging from 1 to 2 s). The participants had breaks between each block to rest and reduce fatigue effects. They were asked not to move their heads off the wooden support during those breaks to keep stable the distance between the eyes and the screen. Total duration of G task was ~20 min.

**Data processing.** Data processing of the three tasks was performed with custom software written in MATLAB, from the recorded three-dimensional positions of markers for R and W and from the recorded pupil positions for G. Recorded signals of the three tasks were low-pass filtered using a digital fifth-order Butterworth filter, with cutoff frequencies of 20 Hz, 2 Hz, and 50 Hz for R, W, and G, respectively (MATLAB butter/filtfilt functions). Since the recording files contained several point-to-point discrete movements, they had to be segmented to isolate each movement of interest for further analysis.

For R task, data files were segmented using known time intervals between two appearances of the targets. Once time intervals containing each pointing movement were found, peaks of angular velocity (in deg/s) were located (joint angle was between the acromial-index line and the horizontal line orthogonal to the screen passing through the shoulder). Then, the start and the stop of each movement was found using a threshold method (5% of angular peak velocity of each individual movement). With this method, peak velocity, mean velocity, absolute value of amplitude, and duration of each reaching movement were calculated.

For the W task, segmentation was done by identifying each half-turn. To do so, angular velocity profile between the hip markers in the direction of the displacement ( $x$ -axis) was studied. Peak velocity of each movement was gathered from the speed of a participant's reference point (defined between the two hip markers). The absolute value of feet's speed was determined by adding together the absolute value of right and left metatarsal markers' speed. This method was used to resolve issues related to which leg began or ended the walking movement. The beginning ( $t_0$ ) and the end ( $t_1$ ) of the movement were determined by a threshold method (5% of peak velocity of each individual movement). Duration of the movement was computed subtracting  $t_0$  from  $t_1$ . Metatarsal markers positions were studied on

the  $x$ -axis to estimate the real amplitude of movements. The minimal position between those right and left markers at  $t_0$  and the maximal position between them at  $t_1$  were used. Mean velocity (in m/s) of each movement was computed with their duration and amplitude values. Here, speed was further normalized according to body size (Bohannon 1997). This allowed us to compute an analog of an angular velocity also for walking (thus expressed in deg/s).

For G, data files were segmented using time interval between two appearances of the targets. When this method failed to isolate the principal saccade (e.g., blink during time interval of interest), segmentation was manually done after visual inspection of gaze displacement during this interval. Once time intervals containing each saccade were found, velocity profile of the saccade was determined by differentiating gaze angular position on the horizontal axis with respect to time. Then, velocity peaks were located, and the primary saccade was isolated via a threshold method (5% of peak velocity of each individual movement). With this method peak velocity (in deg/s), mean velocity, absolute value of amplitude and duration of each saccade were gathered using the custom software.

In all cases, the obtained amplitude-velocity data were fitted with a rational function of the form (see also Berret et al. 2018; Reppert et al. 2018a):

$$g_n(x) = \alpha \left( 1 - \frac{1}{1 + \beta x} \right) = \frac{x}{ax + b} \quad (1)$$

where  $x$  is the amplitude and  $g_n(x)$  is the corresponding peak velocity for subject  $n$ . The parameters  $a = \alpha^{-1}$  and  $b = (\alpha\beta)^{-1}$  were adjusted to fit experimental data (see Fig. 1). The shape of this curve is compatible with previous experimental observations for the three tasks (Berret et al. 2018; Choi et al. 2014; Seethapathi and Srinivasan 2015). Fitting was applied separately for each participant and each task.

**Vigor scores.** Following an approach similar to Choi et al. (2014) and using a custom software written in MATLAB, movements were clustered by their amplitudes for each participant for each task (10 clusters in R task, 7 clusters each in W and G tasks). Peak velocities associated with each amplitude were averaged to reduce the effect of trial-to-trial variability due to sensorimotor noise occurring during movement execution. This resulted in a mean peak velocity for each amplitude, each task, and each participant. Z-scores of these data were computed across participants. This allowed us to define relative vigor scores at the individual level, which could be compared across different tasks and/or amplitudes. Thus, a null vigor score meant that the participant had an "average" peak velocity for that amplitude and task (with respect to the 20 tested participants). A single vigor score could also be computed from the grand mean of peak velocities across all amplitudes, for each task and each participant separately. Therefore, we could obtain four vigor scores per participant (for the RD, RND, W, and G tasks, normalized as z-scores and hence comparable despite the different nature of the tasks). We also tested an approach like Reppert et al. (2018a). For each task, from the mean peak velocity ( $v$ ) for each amplitude ( $i$ ) and each participant ( $n$ ), vigor scores ( $k$ ) were computed at the participant level based on the canonical function that mapped each amplitude ( $x$ ) to the mean peak velocity of the population ( $g(x)$ ), as follows:

$$k_n = \frac{\sum_i v_{n,i} g(x_i)}{\sum_i g(x_i)^2} \quad (2)$$

Vigor scores for each participant were also computed with this method for each task. It allowed us to test the interindividual consistency of vigor scores across tasks using an alternative quantitative definition of vigor. However, different from Choi's method, this maximum likelihood approach does not allow to test the consistency of vigor across amplitudes.

**Statistical analyses.** Data analyses were performed on 20 participants with MATLAB and IBM SPSS Statistics software. Significance



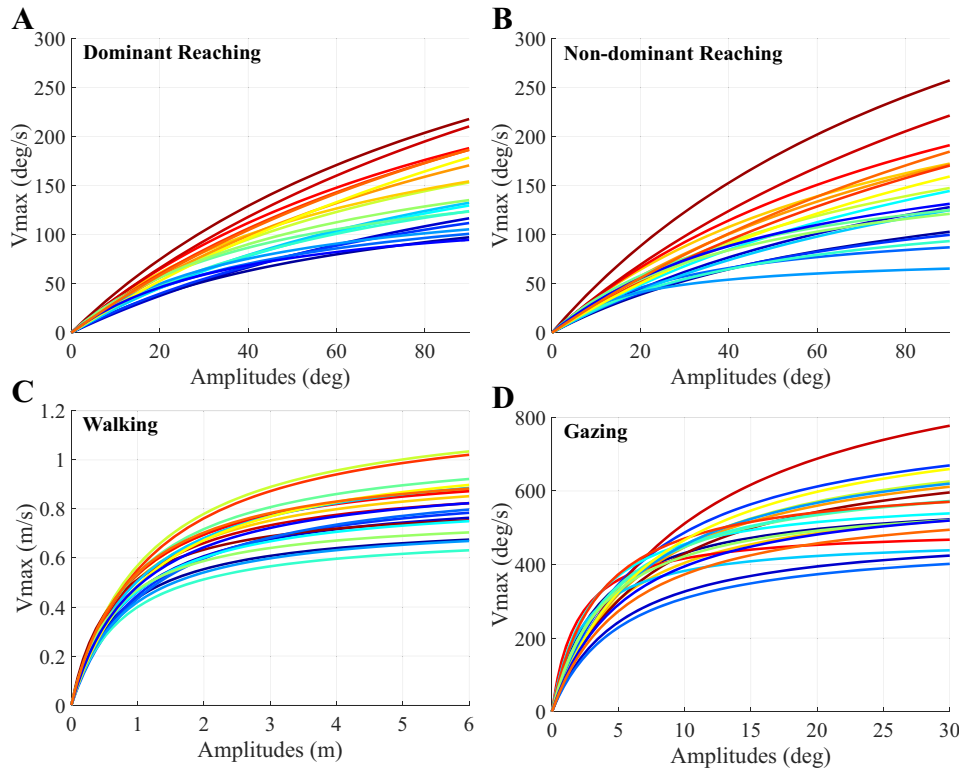


Fig. 1. Peak velocity as a function of movement amplitude. Each color stands for one participant (color code is kept fixed throughout the paper). A rational function (Eq. 1) was used to fit the data of each participant separately. *A*: peak velocity as a function of movement amplitude (dominant arm reaching). *B*: peak velocity as function of movement amplitude (nondominant arm reaching). *C*: peak velocity as function of displacement amplitude (walking). *D*: peak velocity as function of saccade amplitude (gazing).

level was set at  $P = 0.05$  for every test. Hierarchical linear models (HLM) were used to obtain a statistical decomposition of variance of vigor scores between the interamplitude level, the intertask level, and the interindividual level. These analyses relied on the empty model described in a similar context in Berret et al. (2018). Linear correlation analyses were performed to study the relationships between the vigor scores in the different tasks (R, W, vs. G) and with the different effectors for R. Finally, multiple linear regressions analyses were performed to study the potential effect of biomechanical factors (height, weight, and BMI) on the relationship between the vigor scores of R and W tasks. Multiple linear regressions analyses followed the general equation:

$$V_{W,i} = \beta_0 + \beta_1 V_{RD,i} + \beta_2 C_i + \varepsilon_i \quad (3)$$

where  $V_{W,i}$  is the vigor score of W,  $\beta_0$  the intercept,  $\beta_1$  the coefficient associated with the vigor score of RD ( $V_{RD,i}$ ),  $\beta_2$  the coefficient associated with the tested covariate ( $C_i$ , being height, weight or BMI), and  $\varepsilon_i$  the residual error. The subscript  $i$  denotes each participant.

**RESULTS**

*Evolution of peak velocities across amplitudes and individual vigor scores.* As expected, a common tendency was observed for all tasks and all participants. Peak velocity tended to increase as a function of movement amplitude. These relationships are shown in Fig. 1 for each task and each participant (each color represents a participant, and this color code is kept constant throughout the study). Goodness of fit using function  $g(x)$  was as follows:  $r^2 = 0.99 \pm 0.01$  for DR,  $r^2 = 0.98 \pm 0.04$  for NDR,  $r^2 = 0.99 \pm 0.02$  for W and  $r^2 = 0.96 \pm 0.09$  for G (means  $\pm$  SD values). Regarding vigor scores (computed using Choi’s method), they were sorted in ascending order and are reported for all participants and each task separately in Fig. 2. Positive vigor scores stand for individuals more vigorous than the average in the task.

*Decomposition of variance of vigor scores.* A statistical decomposition of variance was performed with empty hierarchical linear models (HLM) to determine which level of analysis could explain the greatest part of variance in vigor scores between amplitude, task and individual levels (see *Vigor scores* in MATERIALS AND METHODS). Interamplitude differences represented 10.3% [6.6; 15.0], intertask differences represented 51.1% [42.3; 57.8] and interindividual differences represented 38.6% [27.2; 51.1] of the total variance of vigor scores. Confidence intervals are given between brackets. Those results indicated that the variance in movement vigor was mainly rooted at the task and individual levels rather than the amplitude level. Indeed, vigor scores were much more consistent across amplitudes than across participants and modalities, suggesting that for a given modality participants who had relatively large vigor scores for one amplitude also had relatively large vigor scores for the other amplitudes.

This HLM analysis showed that the variability of vigor scores between modalities of movement was  $\sim 5$  times bigger than the variability of vigor scores of each participant between amplitudes, even if their peak velocity increases with it. It also showed that the variability of vigor scores between individuals was  $\sim 4$  times bigger than the variability of vigor scores of each participant between amplitudes.

From now on, we focus, thus, on mean vigor scores (4 vigor scores per participant corresponding to the DR, NDR, W, and G tasks). Here, only the results obtained from the method of Choi et al. (2014) will be presented in details because similar results and the same conclusions were obtained using the alternative method of Berret et al. (2018) or Reppert et al. (2018a).

*Interindividual correlation analyses of vigor scores.* A linear correlation analysis was performed to determine whether in-

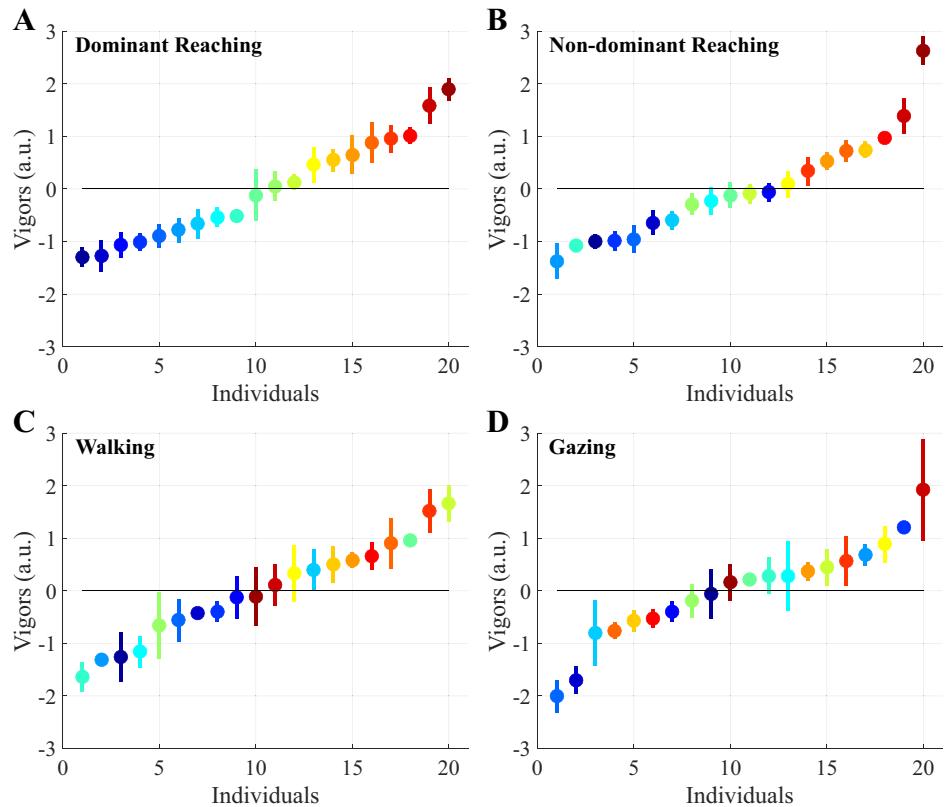


Fig. 2. Vigor scores computed for each task/effector. Each color stands for a single participant according to the color code defined in Fig. 1. Participants are ordered by ascending vigor scores. Bars show standard deviations arising from variability across amplitudes. The horizontal black line represents the mean vigor of the population ( $z$ -scores). *A*: reaching vigor scores (dominant arm). *B*: reaching vigor scores (non-dominant arm). *C*: walking vigor scores. *D*: gazing vigor scores.

terindividual differences of vigor scores were consistent between DR and NDR (same reaching task but with the dominant arm or nondominant arm). The correlation coefficient was high,  $r = 0.899$  ( $P < 0.001$ ) (see Fig. 3). The depicted regression line further suggests that the dominant and nondominant means were also similar. Grand mean velocities (in deg/s) were computed for each participant in DR and NDR by averaging the mean peak velocities of each amplitude. A paired  $t$  test was performed to test the difference between DR and NDR grand mean velocities ( $t(19) = -0.575$ ;  $P = 0.572$ ). We could not conclude about a difference of angular velocities between these two sets of data. These analyses revealed a high interlimb consistency of vigor for reaching movements, and that the vigor of the dominant arm may be a good predictor of the vigor

of the nondominant arm across individuals. On the basis of these findings, we decided to use only the results of DR in the subsequent analyses for intertask comparisons. Nevertheless, we also considered averaging data from both arms or using only NDR, and it did not affect the main results and conclusions of the study.

Linear correlation analyses were finally performed to determine whether interindividual differences of vigor were consistent across the three tasks under investigation, R, W, and G. Vigor scores of DR and W tasks were significantly correlated ( $r = 0.536$ ,  $P = 0.015$ ; Fig. 4A). We checked the robustness of this result to slight changes of data processing. Normalization according to square root of leg size was tested because it is relevant for mechanical reasons (related to step frequency in a compass-gait walking model, e.g., Usherwood 2005) to check whether it affected or not the main results and conclusions of the study. But even in this case, vigor scores of DR and W tasks were significantly correlated ( $r = 0.570$ ,  $P = 0.009$ ). Correlation between vigor scores of NDR and W tasks were also significantly correlated ( $r = 0.482$ ,  $P = 0.031$ ). We further tested the correlation between vigor scores computed with Reppert's method for DR and W tasks, which was significant as well ( $r = 0.478$ ,  $P = 0.033$ ). Overall, this result seems to be robust. Otherwise, no significant correlation was found with the G task (see Fig. 4B and Fig. 4C). These results show that the interindividual differences of vigor were relatively consistent between reaching and walking, but that the vigor of saccades was distinct and not related to the vigor of reaching and walking.

Although the vigor scores in the previous analyses were computed from velocities normalized in units of angular velocities to avoid simple morphological confounds related to

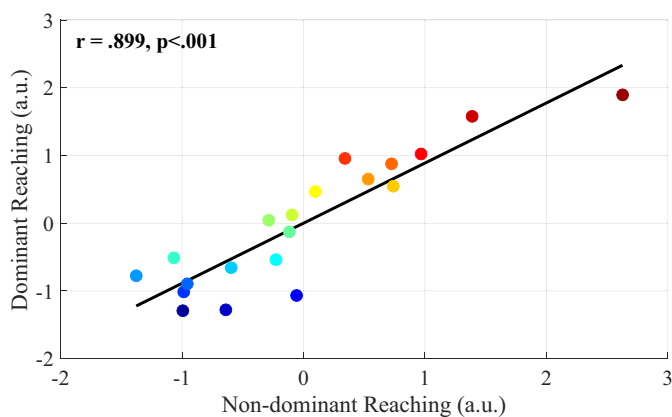


Fig. 3. Relationship between reaching vigor scores for the dominant and nondominant arms. Each color stands for a single participant according to the color code defined in Fig. 1. A linear correlation analysis was used to quantify the relationship. For visualization purpose, we also display the regression line.

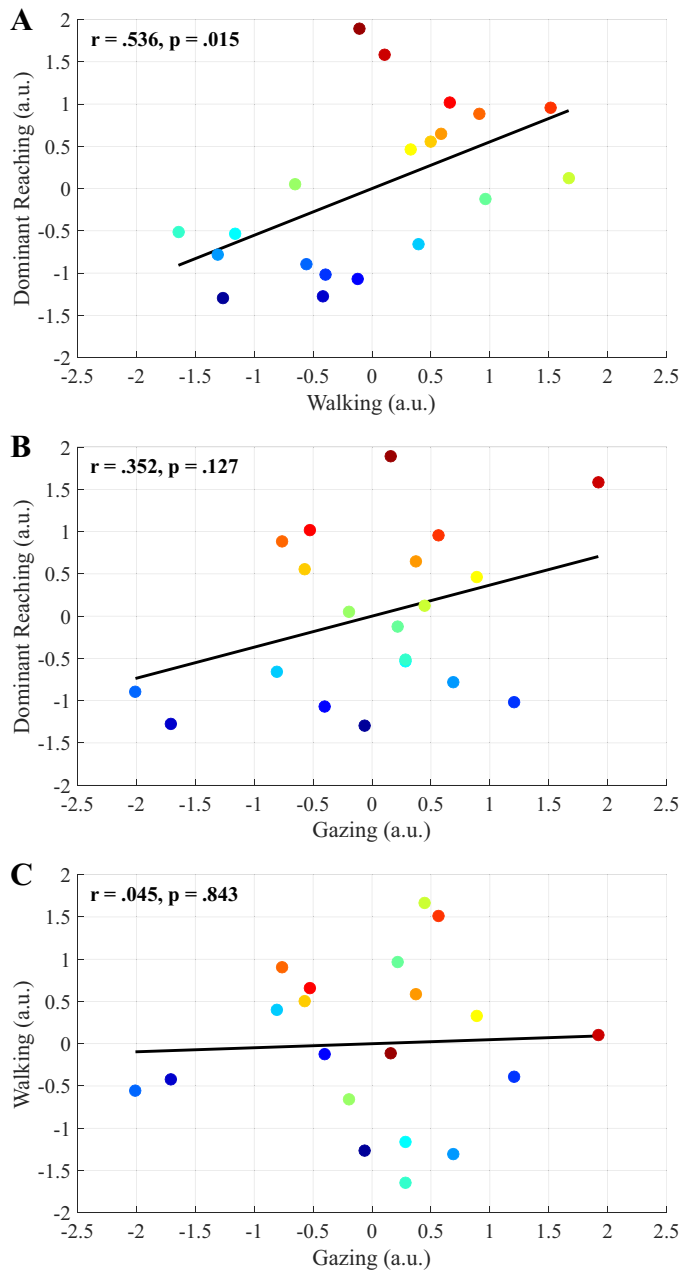


Fig. 4. Relationships between vigor scores across motor tasks. Each color stands for a single participant, according to the color code defined in Fig. 1. Linear correlations were used to quantify the relationships. For visualization purpose, we also display the regression line. *A*: relationship between walking and reaching (dominant arm) vigor scores. *B*: relationship between reaching (dominant arm) and gazing vigor scores. *C*: relationship between walking and gazing vigor scores.

segment lengths, we wanted to further check the potential impact of other biomechanical factors on the relationship between vigor scores in R and W. For the subsequent analyses, vigor scores were recomputed with the same method as previously described (see *Vigor scores* in MATERIALS AND METHODS) but without any length-related normalization this time (i.e., peak velocities were expressed in m/s before computing vigor scores in R and W tasks). The linear correlation analyses were then repeated on these data. First, the vigor scores of DR and W tasks were still significantly correlated ( $r = 0.528$ ,  $P =$

0.017), and nonnormalized vigor scores of DR and NDR tasks were also significantly correlated ( $r = 0.854$ ,  $P < .001$ ), thereby, reaffirming previous findings. To further investigate a potential link between segment length and vigor, three additional linear correlation analyses were performed. Results showed that despite the significant correlation between leg length and arm length ( $r = 0.914$ ,  $P < 0.001$ ), RD vigor scores were not significantly correlated with arm length ( $r = 0.105$ ,  $P = 0.661$ ) and W vigor scores were not significantly correlated with leg length ( $r = 0.108$ ,  $P = 0.649$ ). To consider other biomechanical covariates, we switched to multiple regression analyses. As the R and W tasks were concerned, we considered global biomechanical parameters, such as height, weight, and BMI. Multiple linear regressions analyses were performed to verify whether the inclusion of basic biomechanical covariates could affect the significance of the relationship between R and W. First, we recovered the significant relationship between vigor scores in RD and W mentioned above ( $\beta_1 = 0.528$ ,  $P = 0.017$ ,  $r^2 = 0.279$ ). Second, we added different biomechanical covariates to test their potential effect over and above RD contribution ( $\beta_2$ , coefficient associated with the tested covariate, i.e., height, weight, or BMI). Results showed that none of the covariates had a significant effect on the relationship, whether it was height ( $\beta_1 = 0.529$ ,  $P = 0.021$ ;  $\beta_2 = -0.006$ ,  $P = 0.975$ ), weight ( $\beta_1 = 0.527$ ,  $P = 0.020$ ;  $\beta_2 = -0.092$ ,  $P = 0.659$ ) or BMI ( $\beta_1 = 0.507$ ,  $P = 0.023$ ;  $\beta_2 = -0.175$ ,  $P = 0.401$ ). Overall, these analyses indicate that the interindividual consistency of vigor scores in the R and W tasks is not strongly dependent on common biomechanical factors related to length and mass.

**DISCUSSION**

In this study, we compared the vigor of elementary reaching (dominant vs. nondominant arms), walking (for different distances) and gazing (fixed-head eye saccades) movements within the same group of 20 participants. We assessed the consistency of interindividual differences of vigor previously reported in separate studies to test the extent to which vigor may be a general trait-like feature of individuality. The dependence of vigor on the task and movement effector was, therefore, investigated. Empirical vigor scores were calculated on the basis of peak velocities, which were known to increase with amplitude for the type of self-paced discrete movements considered here. Decomposition of variance showed that defining a single vigor score per participant and per modality was pertinent. Correlation analyses then revealed a highly significant consistency of interindividual differences of vigor during reaching with either limb, and a significant consistency between reaching and walking. In contrast, the interindividual differences of vigor during eye saccades were unrelated to those of reaching and walking.

*Interlimb consistency of vigor for reaching movements.* Neuroanatomical and behavioral arm asymmetries have been extensively documented in the literature (e.g., Goble and Brown 2008 for a review). In particular, existing studies have emphasized that neural control of movement is largely lateralized and relies on different control mechanisms between the two arms (Sainburg 2005; Schaefer et al. 2007, 2012). Differences also exist regarding the muscle characteristics of both arms. For instance, the dominant arm seems to be composed of

more slow-twitch fibers than the nondominant arm, which are recruited for a lower threshold of stimulation and are less fatigable (Williams et al. 2002). Despite marked central and peripheral differences underlying the control of each arm, we found a strong interlimb consistency of vigor between individuals. This may suggest a common control of vigor shared by both arms. This common root might be linked with the left motor cortex which was found to be substantially activated for movements of both left and right hands (Kim et al. 1993) and to cortico-BG-thalamocortical loops, which are known to be involved in the control of vigor and its dependence on reward outcome/expectancy, i.e., the motivational aspect of movement (Desmurget and Turner 2010; Dudman and Krakauer 2016; Opris et al. 2011; Panigrahi et al. 2015; Turner and Desmurget 2010). Interestingly, there is evidence that both ipsilateral and contralateral BG systems are involved in the control of unilateral movements (Scholz et al. 2000). This bilateral activation of BG could explain the high correlation ( $r \sim 0.9$ ) between the vigor exhibited by both arms, which may actually constitute a useful feature for bimanual tasks where both upper limbs must function in synergy.

*Relation between vigor of reaching and vigor of walking.* We found consistent interindividual differences of vigor between reaching and walking tasks. While the vigor of walking has not been thoroughly documented in the literature for this type of “discrete” task with a start and a stop, modulation of preferred walking speeds has been studied in many studies, as reviewed by Shadmehr et al. (2019). Generally, the preferred walking speed seems to be related to a minimization of metabolic cost or temporal cost of the displacement (Seethapathi and Srinivasan 2015; Summerside et al. 2018). As metabolic cost can depend on speed variations during walking (Seethapathi and Srinivasan 2015), the preferred walking speed of people may vary with walking distance. In our study, walking speed increased with distance in an idiosyncratic way, which was found to be related to the vigor of reaching (significant  $r \sim 0.5$ ).

This result is interesting because the control of walking differs a lot from the control of reaching. Besides obvious biomechanical differences, locomotor behaviors may imply the activation of central pattern generators (CPGs) rooted in the spinal cord (Grillner 2006). One role of CPGs, suggested by animal studies, is their capacity to be activated from higher centers to modulate locomotor speed (Kiehn 2006). The exact nature of CPGs remains elusive in humans (Minassian et al. 2017) but in any case, there are major differences in the neuro-anatomical systems controlling walking and reaching movements. It may be hypothesized that certain common structures influence the control of vigor for both reaching and walking movements despite the well-defined somatotopy for “arm” and “leg” movement effectors at all stages of the cortico-BG-thalamocortical circuitry. According to Grillner (2006), BG may be responsible for the control and coordination between the different CPGs. At rest, locomotor CPGs are inhibited by the pallidum. To activate them, the striatal neurons need to inhibit the pallidum. Striatal neurons can themselves be stimulated by thalamic or dopaminergic inputs. In particular, striatal dopaminergic denervation is associated with a reduction of gait speed (Cham et al. 2008). Some of these elements are common with those modulating the speed of reaching movements (Berardelli et al. 2001). Recent studies have also

highlighted the role of the BG in the control of exploratory, slow-paced locomotor behaviors in animals, which resemble the goal-directed, self-paced movements considered here with human subjects (Gatto and Goulding 2018). In contrast, fast escape movements were found to be mediated by another pathway involving the superior colliculus (SC).

*Singularity of the vigor of saccades.* Interindividual correlations of vigor scores between gazing and reaching or walking movements were not significant. This may be because the oculomotor system is fundamentally different from the other motor systems controlling self-paced limb movements, both anatomically and functionally. Nevertheless, like reaching and walking, control of saccade vigor seems to be rooted in cortico-BG pathways and modulated by analog reward-related mechanisms (Choi et al. 2014; Hikosaka et al. 2000; Shadmehr 2010; Shadmehr et al. 2010; Xu-Wilson et al. 2009). However, the oculomotor territory in BG is well distinct from the skeletomotor territory (Alexander et al. 1991; Nambu 2011; Wichmann and DeLong 2006). In particular, BG receives inputs from the frontal eye field (FEF) and projects to SC, which plays a critical role in activating the brainstem saccade-generating machinery (Shires et al. 2010). Recently, it was found that activity of SC but not of FEF varied with saccade peak velocity (Reppert et al. 2018b).

SC has also been shown to be involved in eye-hand coordination reaching tasks (Lünenburger et al. 2001) but mainly for hastened arm movements (Pruszynski et al. 2010). Given the involvement of SC in fast escape movements in locomotor behaviors, one may speculate that differences in vigor are related to a distinction between the voluntary self-paced movements for reaching/walking (not relying strongly on SC) and the “reflexive” saccades (relying more on SC) we considered here. Indeed, it was shown that voluntary saccades, such as antisaccades and saccades to the remembered target, have longer reaction times and smaller peak velocities than reflexive saccades (Smit et al. 1987; Walker et al. 2000). Thura et al. (2014) also showed a positive relationship between decision urgency and the vigor of saccades during a reaching task in which the oculomotor behavior of monkeys was not controlled (head and neck free). Yet, in Reppert et al. (2018a), the subjects were instructed to “reach and touch the target as quickly and as accurately as possible”, and eye and arm movements were simultaneously recorded. Nevertheless, the authors did not find a link between the vigor of (reflexive) saccades or reaching. It is possible that this instruction did not induce enough “urgency” to involve SC, and the rapid visuomotor pathway pointed out by Pruszynski et al. (2010) for reaching. It would be interesting in future studies to compare the interindividual consistency of vigor between voluntary self-paced and “as fast as possible” movement responses, be it for gazing, reaching, or walking movements.

In summary, the present study suggests that common neural processes may underlie, in part, movement invigoration of different limb movements. Yet, the specific neural circuits and biomechanical peculiarities of each effector clearly play a nonnegligible role on one’s movement invigoration. Indeed, while the vigor scores of the dominant and nondominant arms shared a large part of variance ( $\sim 80\%$ ), reaching and walking shared much less variance ( $\sim 30\%$ , although significant). It is likely that movement vigor is also influenced by mechanistic factors, such as metabolic energy, effort, or accuracy (Berret et



al. 2018; Summerside et al. 2018; Wang et al. 2016). This suggests that a modeling study is needed to disentangle the part of vigor that is due to mechanistic reasons from the part that is due to high-level traits, such as one's relationship with time (temporal discounting). For a given task, such as reaching, the strong consistency we found (e.g., interamplitude and interlimb) at least highlights that there must exist a common root for arm movement control, which is not too sensitive to neuromuscular peculiarities and rather reflects higher-level individual characteristics. However, it seems illusory to find a high-level personality trait that could explain why some individuals are more vigorous than others since at least a part of the answer would be task dependent.

**Future work.** To go further, it would be interesting to test whether interindividual differences of vigor depend on whether movement is executed at a comfortable pace or with some urgency (e.g., a “move as fast as possible” instruction). One could predict that vigor scores from “Fitts’ like” protocols may not necessarily be consistent with those from “comfortable-pace” protocols. However, dedicated studies are required to answer such questions, especially because movement accuracy may come into play as a moderator variable of vigor (e.g., findings may depend on other factors like the target width for instance). Note that Reppert et al. (2018a) already demonstrated that the vigor of reaching movements performed “as quickly and accurately as possible” was not related to the terminal accuracy.

Future work could also investigate whether certain personality traits such as boredom proneness or impulsivity could resist to the intertask variability of vigor scores found for reaching and walking movements. Since the vigor of saccades was found to be uncorrelated with those of reaching and walking, it seems, however, unlikely that the same traits could account for the interindividual differences of vigor during both saccade and limb movements. Nonetheless, the consistency of the vigor of saccades in various conditions (head free or fixed, reflexive, or voluntary) deserves to be tested to better understand the case of eye movement invigoration.

Finally, besides motor aspects, other aspects of behavior may be related to vigor (e.g., Carland et al. 2019 for a review). For instance, Reppert et al. (2018a) showed that reaction time is linked with movement vigor, that is, participants moving with higher vigor than others also tend to have shorter reaction times. While our present data did not allow us to investigate reaction times, future work could attempt to establish a link between vigor and reaction time for movements performed at a comfortable pace. In this work, since participants were instructed to perform movement at a comfortable pace, they also reacted to stimuli accordingly. Hence, it is not clear whether a link between vigor and reaction time would have been found, as in Reppert et al. (2018a). Some of these questions that are left open by the present study will be part of upcoming investigations.

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#### DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

#### AUTHOR CONTRIBUTIONS

O.L., T.D., C.T., and B.B. conceived and designed research; O.L. performed experiments; O.L. analyzed data; O.L., T.D., and B.B. interpreted results of experiments; O.L. prepared figures; O.L. and B.B. drafted manuscript; O.L., T.D., C.T., and B.B. edited and revised manuscript; O.L., T.D., C.T., and B.B. approved final version of manuscript.

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