A control policy can be adapted to task demands during both motor execution and motor planning

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Running Head: Tuning feedback gains during motor planning and execution

Abstract

Movement planning consists of several processes related to the preparation of a movement such as decision making, target selection, application of task demands, action selection and specification of movement kinematics. These numerous processes are reflected in the reaction time, which is the time that it takes to start executing the movement. However, not all the processes that lead to motor planning increase reaction time. In this paper, we wanted to test whether tuning feedback gains to task demands contributes to reaction time. Taking into account that the tuning of feedback gains differ for narrow and wide targets, we used a timed response paradigm in order to track the amount of time needed to tune feedback gains appropriately to task demands. We discovered that it does not take any time during motor planning and even that it can occur indistinguishably during motor planning or during motor execution. That is, the tuning of feedback gains was equally good when the narrow or large target was displayed before than when it was displayed after. These results suggest that the frontier between motor planning and execution is not as clear cut as it is often depicted.

New & Noteworthy

Movement preparation consists of different processes such as target selection, and movement parameters selection. We investigate the time that it take to tune movement parameters to task demands. We found that the brain does this instantaneously and that this can even happen during movement. Therefore, this suggests that there exist an overlap during movement planning and execution.

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Disclosure

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Introduction

Movement preparation involves the integration of multiple sources of sensory information to allow the execution of coordinated and efficient actions, and has been conceptualized as a two-stage process (Wong et al. 2015). The first stage involves a non-motor perceptual "decision making" process through which the goal of the movement is selected, involving the sub-processes of detecting relevant stimuli and identifying the target of the action, both of which can be modified by relevant task constraints. This is followed by a second "motor planning" phase wherein the action to execute is selected, relevant movement kinematics are applied, and the final movement to be executed is specified via a motor command. Classical studies indicate that the time required for movement preparation increases with the complexity of the task demands (Henry and Rogers 1960). In line with this suggestion, contemporary work has proposed that the majority of the time required for movement preparation is in fact consumed by the decision-making process, arguing that motor planning itself can be achieved almost instantaneously (Wong et al. 2015). This is, however, at odds with the finding that adapting the control policy to task demands carries a switching cost (Orban de Xivry 2013; Orban de Xivry and Lefèvre 2016), which typically directly influences the reaction time (Monsell 2003).

The motor planning phase of movement preparation is often examined within the framework of optimal control theory (Todorov 2004; Todorov and Jordan 2002). Optimal control theory proposes that movement selection minimizes a cost function that balances a tradeoff between movement accuracy and energy expenditure. This has widely been studied by examining whether movements respect the 'minimum intervention principle' in the presence of perturbations or of natural movement variability (Dingwell et al. 2010). If a perturbation does not interfere with the goal of the movement (i.e. it introduces 'task-irrelevant variability'), the response will be relatively minor; by contrast, perturbations that interfere with the goal of the movement (i.e. that introduce 'task-relevant variability') will be met with more robust corrections (Diedrichsen 2007; Nashed et al. 2014; Scott 2004). Alternatively, the absence of correction for task-irrelevant dimensions has also been linked to an uncontrolled manifold (Latash et al. 2001, 2002; Scholz and Schöner 1999; but see Giulio et al. 2013). The uncontrolled manifold corresponds to a space of movement parameters that are irrelevant to task success and that are left uncontrolled by the motor system. When reaching to a narrow target, both optimal control theory and the uncontrolled manifold hypothesis would predict that any perturbation that affects hand trajectory and impedes task success should be strongly resisted. In contrast, if the target is wide and the perturbation does not reduce task success, the response to the perturbation should be much smaller as found in numerous studies (De Comite et al. 2021, 2022, 2023; Nashed et al. 2012; Orban de Xivry 2013; Orban de Xivry and Lefèvre 2016). The minimum intervention

principle extend to error correction mechanisms as well as error are only corrected in task-relevant dimensions (van Beers et al. 2013; Orban de Xivry 2013; Orban de Xivry and Lefèvre 2016). In the context of the optimal feedback control theory, the reaction to a perturbation or to natural movement variability is determined by feedback gains, which are presumably determined during the motor planning stage, hence during the reaction time period (Wong et al. 2015).

The computation occurring during the reaction time period can be assayed via timed response paradigms that limit response preparation time (Schouten and Bekker 1967). Using such an approach, it has been demonstrated that movement preparation and initiation are two separate processes (Haith et al. 2016). This paradigm allows one to force participants to initiate their movement before movement planning is fully completed (Haith et al. 2015, 2016). For instance, forcing participants to move before full movement preparation leads to the expression of habitual behaviors (Hardwick et al. 2019).

Here we used the timed response paradigm to investigate how fast feedback gains can be tuned to task demands, i.e. to their ability to implement the minimum intervention principle (Todorov and Jordan 2002). If the time required for computing optimal feedback gains is truly negligible (Wong et al. 2015), then limiting the time participants have to prepare movements should have a discrete, stepwise effect on the adjustment of feedback gains to task demands; all movements prepared with less than the minimal time should not reflect task demands in how they deal with perturbations, while all movements prepared with times above this minimum should. By contrast, if the time available to prepare movements does influence the tuning of feedback gains in function of task demands, we could instead expect that changes in feedback gains in response to task demands would gradually increase with the amount of time available.

Materials and Methods

Participants

Forty healthy subjects (29 female, 11 male, mean age±SD = 21.1±2.0 years) participated to this experiment. Participants were right-handed according to the Edinburgh Handedness Inventory (Oldfield 1971), and free from neurological dysfunctions. All participants provided written informed consent prior to the experiment. All procedures were approved by SMEC (Sociaal-Maatschappelijk Ethische Commissie) of the KU Leuven (G-2019 02 1536).

Setup

Participants sat in front of a robotic arm (Endpoint Kinarm; Kinarm, Kingston, ON, Canada), and held the right handle with their right hand. A force transducer was placed below the handle in order to record the force applied by the hand against the robot. The participant's own right hand was hidden from view by a mirror that reflected the image of a monitor placed above the mirror. The distance from the hand to the mirror was equal to the distance between the mirror and the display, making the cursor appear in the same position as the participant's hand. The computer that controlled the robotic manipulandum stored hand position, velocity, and force at 1000Hz for later offline analyses.

Protocol

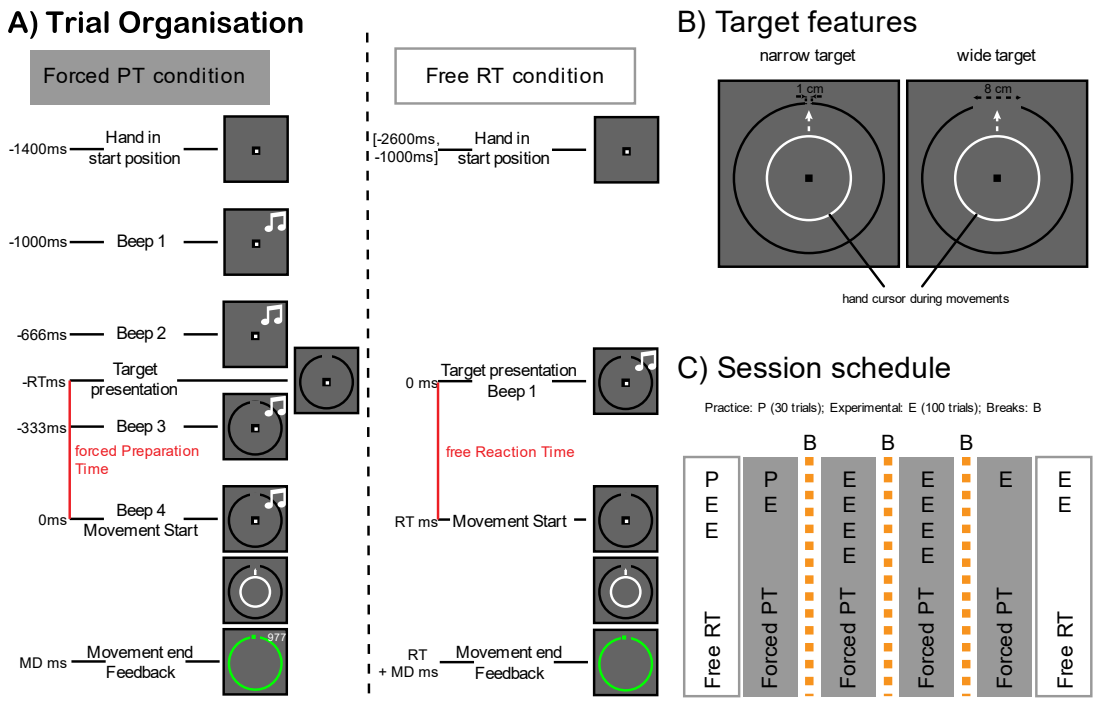

Fig.1: **A) Trial organization: 1. Forced preparation time (PT) trials.** The participant had to first bring their hand cursor (white square) inside the starting position (red square of 0.6x0.6 cm, represented by the black square). After having remained inside the start position for 400ms, a series of four beeps were delivered at a 333ms interval for a total duration of 1s. The target appeared in one of the ten possible forced PT during this interval. Subjects were trained to start their movement at the time of the fourth beep. Their movement ended when they travelled 15cm away from the start position in any direction.

At that location, an imprint was presented to provide participants with feedback about the accuracy of their movement. If the imprint was within the target region delimited by the circle, this circle became green. The color of the imprint indicated to the participant whether they moved too fast (yellow), too slow (blue) or at the right speed (green). Finally, feedback about the timing of the start of the movement with respect to the first beep (in ms) was presented to the participant just above the target region. A perfect timing corresponded to 1000ms. **2. Free RT trials:** After placing their hand cursor within the starting position, participants waited between 1000 to 2600ms for the display of the target. The target presentation was accompanied by a beep. In response to this event, participants had to elicit a reaching movement to the target. As in the forced PT trials, they then received feedback on movement accuracy and movement speed, but not on reaction time. **B) Target features:** The target consisted of a circle (radius of 15cm) with a gap that was either narrow (1.0cm) or wide (8.0cm). The location of the target remained identical for all trials. During the reaching movement, the cursor changed into an expanding circle that provided feedback on the distance (extent) of the movement, but not its direction. **C) session schedule:** Participants first performed one practice block of free RT trials followed by two blocks of 100 free RT trials. Then then performed 30 practice trials of forced PT trials followed by one block of 100 forced PT trials. After a break, four more blocks of 100 forced PT trials were performed, followed by another break, and another four blocks of forced PT trials. After the last break, one last block of forced PT trials was performed and two blocks of free RT trials.

Forced preparation time condition

In a forced preparation time (PT) trial (Fig.1A), participants moved first the white hand cursor within the starting position (red square of 0.6cm^2). After a time period of 400 ms, four consecutive tones were played every 333ms for a total time interval of 1s. Participants were instructed to start of their movement at the time of the fourth tone. The target always appeared at the same location (15cm above the start position) at the time of one of the ten possible instructed preparation times: between 594 and 1ms before the last tone, by step of 66ms. The target consisted of an aperture within a white circle (Fig.1B, radius of 15cm, centered on the starting position). The size of the aperture could be either narrow (1cm) or wide (8cm). The participants were instructed to bring the cursor outside of the circle via the aperture and to stop their movements when they were outside of the circle. During the movement, the small hand cursor was replaced by a white circle that was centered on the starting position and whose radius was equal to the distance between the hand and the starting position. This expanding circle provided thus information about the extent of the ongoing movement, but not about its direction.

Crossing the 15cm circle corresponded to the end of the movement. At that time, the location of the hand was recorded and displayed as an imprint (small circle of radius of 1mm). In the forced PT trials, three pieces of information were provided as feedback at the end of the trial. The color of the imprint indicated whether the movement was too fast (shorter than 300ms, yellow imprint), too slow (longer than 500ms, blue imprint) or correct (green imprint). The location of the cursor provided feedback about the accuracy of the movement. If the cursor was within the aperture, the target circle turned green. The time interval in milliseconds between the first beep and the start of the movement was also displayed right above the aperture in order to provide feedback about the timing of the

movement with respect to the first beep. A timing of 1000ms (1ms after the fourth beep) would be considered perfect. Additional verbal feedback was given by the examiner to start earlier or later depending on whether they were ± 75 ms from this target time. Participants earned one point when the movement was accurate and one point when the movement had the right speed.

Free reaction time condition

Free reaction time (RT) trials are a simplified version of the forced PT trials. In these trials, once the participant had bought their hand into the starting position, the target appeared together with a beep after a delay of between 1000 and 2600ms. Participants were instructed to start moving as soon as possible after the appearance of the target. Once the movement started, the free RT trials were identical to the forced PT trials except that no feedback about their reaction time was provided.

Perturbation trials

A subset of forced PT and free RT trials consisted in perturbation trials. During these trials, the hand was deviated from the center of the target by virtual walls that were created by applying a stiff unidimensional spring (spring stiffness: 1000 N/m; viscosity: 10 N·s/m) and acted as a mechanical guide that directed the hand 2 cm to either the left or the right of the center of the target. During these trials, the imprint was always displayed in the center of the target to hide the fact that a perturbation was applied. Given the use of the expanding circle during the movement, no visual information about the perturbation was provided to the participants.

Session schedule

The session was divided into practice and experimental blocks (Fig.1C). Two practice blocks gave participants the opportunity to familiarize themselves with the task, and to make sure that the instructions were clearly understood. Practice blocks were 30 trials long and contained no perturbation trials, and data from these blocks was not analyzed.

Experimental blocks of free RT and forced PT conditions contained 100 trials, 20% of which included perturbations. To ensure that we had an equal number of perturbation trials per target size (2 levels) and instructed preparation times (10 levels), we created 10 different forced PT blocks that contained a defined trial order. The order of these 10 blocks was then randomized for the different participants. These 10 blocks contained 10 perturbation trials and 40 unperturbed trials per instructed PT and target size.

Each session began and ended with 2 blocks of free RT trials. The first two experimental blocks were preceded by a practice block and followed by one practice and 10 experimental blocks of forced PT trials. Short breaks were inserted after the first, the fifth and the ninth experimental block of forced PT trials to allow the participants to stand up and stretch his arms and legs and to drink if necessary.

Data processing

Data processing was based on the data processing used in previous papers (Orban de Xivry 2013; Orban de Xivry and Lefèvre 2016). Our primary outcome was the force applied against the perturbation when the hand was 13cm away from the starting position (perturbation trials only). This outcome was obtained from the low-pass filtered force profiles (second-order Butterworth filter with cutoff: 50 Hz). For right perturbation trials, the perpendicular force was sign-reversed in order to pool the data across perturbation direction. For unperturbed trials, we measure the horizontal position of the hand with respect to the straight trajectory connecting the start position to the center of the target. This position is measured when the movement extent was 13cm. All measures were taken at 13cm to ensure that trials where participants anticipatively stopped before the target could be included. A strong correlation (R > 0.8) between the lateral deviation at 13cm and at the end of the movement has previously been reported (Orban de Xivry and Lefèvre 2016). In an exploratory investigation of how early in the movements the reported effects were present, values of the force were also measured 2cm, 4cm and 5cm into the movement.

The time of movement onset was measured in both perturbed and unperturbed trials based on a velocity threshold of 0.02m/s. In both forced PT and free RT trials, the reaction time corresponds to the time between the appearance of the target and the start of the movement.

Data processing was conducted in Matlab (readKinTiPR.m, AnalyzeTiPR.m and ExtractTiPR.m on the github page) to process the raw data and extract the relevant parameters. Further data processing steps were done in Python (Beep_v1.py on the github page) to prepare the data for statistical analyses.

Data Analysis

Statistical analysis was carried out in R. R scripts to reproduce the statistical analysis are available on the OSF page: doi: 10.17605/OSF.IO/8YAHE

Analysis 1:

This analysis aimed to compare the application of the minimum intervention principle in forced PT and free RT trials. Three outcomes were examined: 1) the mean and 2) standard deviation of the lateral deviation, and 3) the mean force applied against the perturbation. These outcomes were submitted to a 2x2 ANOVA with the factors condition (forced PT vs free RT) and target size (narrow vs wide) as within-subject factors. The aov_car function from the afex package (Singmann et al. 2022) was used to fit the ANOVA model. The implemented analysis can be found in the file FreevsForced_all.R on OSF (doi: 10.17605/OSF.IO/8YAHE)

Analysis 2:

To determine the effect of preparation time on the planning of an optimal movement, we submitted the outcomes to an 2x2 ANOVA with PT categories (see below) and Target Size (narrow vs

wide) as within-subject factors. PT categories were made by pooling trials in function of one of five different preparation time intervals: [-1000ms,50ms], [50ms,200ms], [200ms,350ms], [350ms,500ms] and [500ms,650ms]. Greenhouse-Geisser correction was applied because the sphericity assumption was violated (Degrees of freedom were then multiplied by GG epsilon). Although we recognize that categorizing a continuous variable is not optimal, this was necessary to be able to look at the evolution of the standard deviation in function of PT. For the analysis of the force outcome, 6 participants were not taken into account because they did not have datapoints in all PT categories. Analysis 3 deals with the preparation time as a continuous factor for the force outcome. The implemented analysis can be found in the file AnalysisRTSub.R on OSF (doi: 10.17605/OSF.IO/8YAHE)

Analysis 3:

To investigate the influence of the reaction on the force outcome without discretizing the preparation time variable, we used a linear mixed model with Force as dependent factor and target size as fixed effect and reaction as continuous random effect. Because the influence of the preparation time on force could be subject-dependent, we also added a random slope for the effect of preparation time. This gave us the following model: Force ~ TarSize*PT + (TarSize*PT|Sub) where the variable Sub refers to the participants, PT to the preparation time and TarSize to target size. The variable PT was z-normalized before being entered into the mixed model using the scale() function from R. This linear mixed model was fitted using the “lme4” package of R (Bates et al. 2015). The implemented analysis can be found in the file MixModelForce_all.R on OSF (doi: 10.17605/OSF.IO/8YAHE)

Data availability statement

The pre-processed data (position,velocity and force over time for each trial and each participant) and the processed data (lateral deviation at 13cm, force at 13cm and reaction time for each trial and each participant) are available on the OSF page (doi: 10.17605/OSF.IO/8YAHE). Raw data are available upon request from the first author.

Results

In this experiment, we asked participants to reach to either a narrow or wide target while either asking them to initiate their movement as quickly as possible (free RT condition) or imposing a preparation time (PT) by requiring them to initiate their movement in synchrony with the last beep of a series of four beeps (forced PT condition). As illustrated in Fig,2, the participants were able to time their movements in synchrony with the last beep although they tended to slightly lead the go-cue by around 40ms for short preparation time to around 140ms for longer instructed PT. Therefore, participants tended to start slightly earlier than the instructed PT. Across all trials, participants were able to time their movement to the go cue. For the short preparation times (<330ms), the movement was initiated less than 100ms before or after the go cue in 70% of the trials or more (from 68% for PT=1ms to 92% for PT=264ms). Given the earlier movement initiation discussed above, the adherence plummeted for longer instructed PT, averaging around 20% (from 25% for instructed PT of 396ms to 15% for instructed PT of 594ms. Note that this does not influence the results presented below as we took the actual preparation time instead of the instructed one. As can be seen on Fig.2, the pattern is very similar for both perturbed and unperturbed trials.

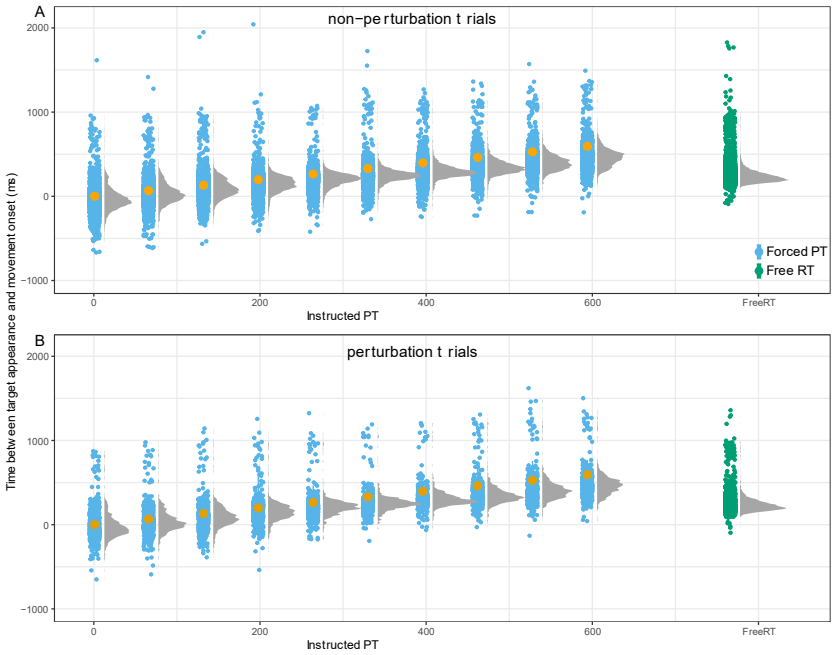

Fig.2: distribution of preparation time of each instructed preparation time for both unperturbed (panel A) and perturbed (panel B) trials. Blue dots correspond to preparation time in the forced PT condition for the different instructed preparation times (orange dots, between 1 and 594ms by steps of 66ms). Green dots represent the trials in the free RT condition. Grey histograms represent the preparation time distribution for each instructed preparation time and for the free RT condition.Panel

Before looking at the effect of preparation time on our outcomes, we wanted to make sure that the overall behavior was broadly consistent with the minimum intervention principle. That is, we expect

that the force applied against a perturbation will be larger for narrow than for wide targets. We also expect that participants will be more accurate with a narrow target than for a wide target and that the variability of this error will be larger for wide than for narrow targets. We measured these outcomes 13cm into the movement as in our previous publications (Orban de Xivry 2013; Orban de Xivry and Lefèvre 2016). In the free RT condition, when preparation time was unconstrained, this distance was travelled in approximately 400ms (perturbed trials: 396±4ms, unperturbed trials: 384±4ms, mean ± SE). In the forced condition, these timing remained unchanged (perturbed trials: 408±5ms, unperturbed trials: 398±5ms, mean ± SE).

Fig. 3A shows that the force was indeed larger for the narrow target than for the wide target (Analysis 1, main effect of Target size: $F(1,39)=84.25$, $p<0.001$). The force applied in the free RT condition was also larger than in the forced PT condition (main effect of condition: $F(1,39)=11.02$, $p=0.002$). Even though the average force across target was larger in the free RT condition than in the forced PT condition, we did not find evidence that this influenced the modulation of force by the target size (interaction between target size and condition: $F(1,39)=0.003$, $p=0.96$). Importantly, we found a modulation of force by target size both for the free RT condition (Fig.3B) and the forced PT condition (Fig.3C) independently. In short, the behavior of the participants followed the minimum intervention principle in perturbed trials.

In unperturbed trials, the results were mixed. We did not find evidence that the accuracy of the reach movement (reflected by the position error) was modulated by target size (Fig.3D-F, Analysis 1: main effect of target size: $F(1,39)=0.13$, $p=0.72$). Unexpectedly, participants were more accurate in the forced PT condition than in the free RT condition (main effect of condition: $F(1,39)=25.78$, $p<0.001$, mean+stdev for Free response condition = -0.39+-0.36cm, Forced response condition –0.22+-0,23cm), but the difference in accuracy was actually small and represents a difference of less than 2mm. This behavior was not different for the narrow or wide target (interaction between target size and condition: $F(1,39)=0.17$, $p=0.68$). This suggests that the position error cannot reflect the implementation of the minimum intervention principle and will not be investigated further. In contrast, we found that the variability of the reach endpoint error was modulated by target size (Fig.3G, Analysis 1: main effect of target size: $F(1,39)=13.83$, $p=0.0006$) and by the condition (main effect of condition: $F(1,39)=11.09$, $p=0.002$). Interestingly, the modulation of the variability of reach endpoint by target size was more pronounced in the forced PT condition (Fig.3I) than in the free RT condition (Fig.3H, interaction between target size and condition: $F(1,39)=8.89$, $p=0.005$). Further analysis demonstrate that, in the forced condition, the variability of the reach endpoint error was larger for the wide target than for the narrow target ($t(39)=-6.23$, $p<0.001$, $d=-0.99$). We did not find evidence that this was the case in the free RT condition ($t(39)=-0.96$, $p=0.34$, $d=-0.15$).

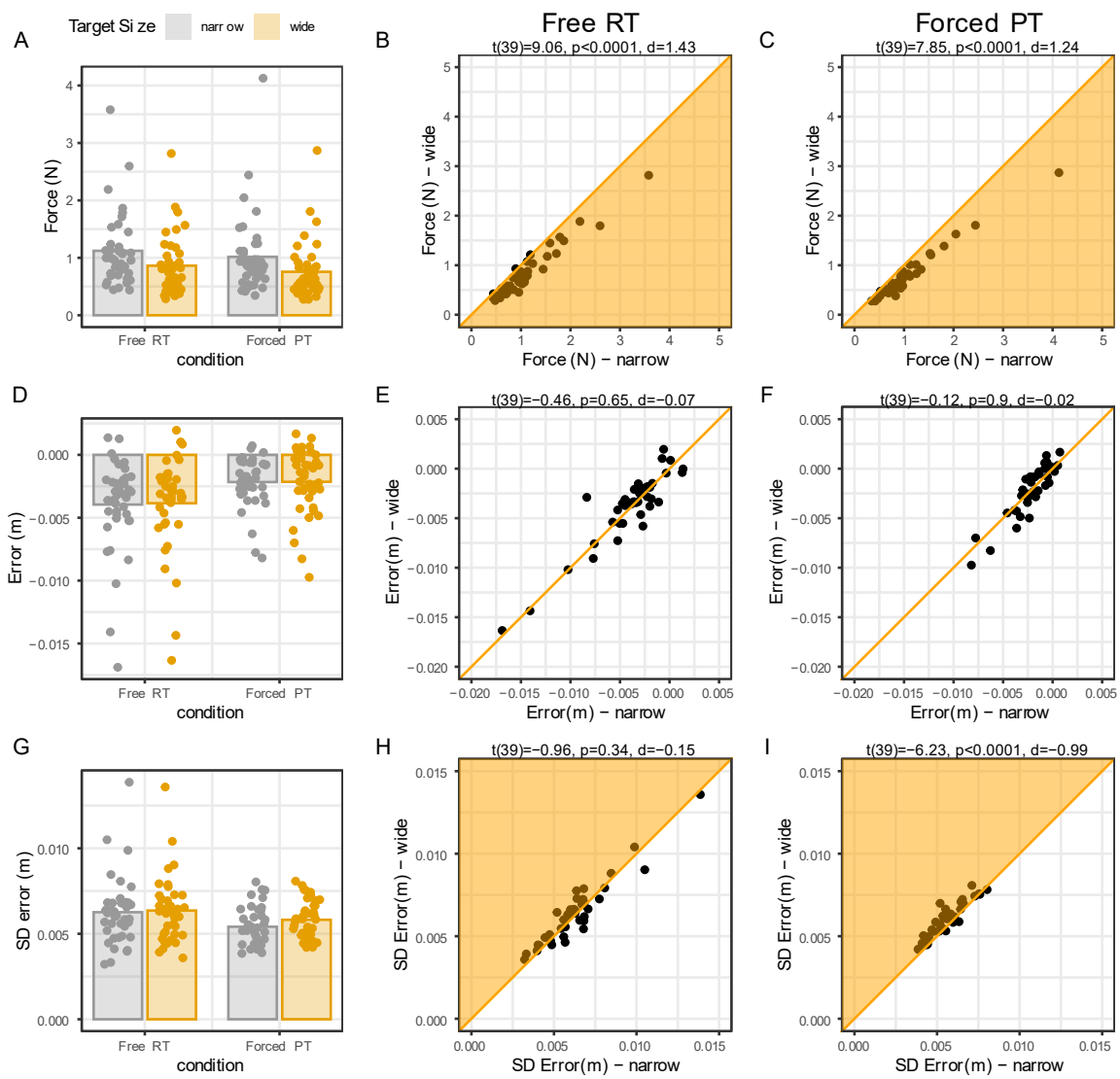

Fig.3: comparison of the free RT and forced PT condition. First, second and third rows illustrate the force applied in perturbed trials, the average error in unperturbed trial and the standard deviation (SD) of the error in unperturbed trials, respectively. In the first column, the average outcome is represented for each target size and each condition. Individual datapoints represent the individual datapoints of each participant. Second and third column represent the average value of the outcomes for the narrow target (horizontal axis) vs the wide target (vertical axis) in the free RT and forced PT conditions, respectively. Each datapoint represents the average of the outcome for an individual participant. For the force, points under the diagonal are consistent with the intervention principle. For the standard deviation of the error, individual points above the diagonal are consistent with this principle. Statistics above the panels reflect the outcome of paired t-test between the values for the wide target vs the values for the narrow target. Orange areas correspond to areas compatible with the minimum intervention principle.

Influence of preparation time on the optimality of movements

Our key question is whether the amount of preparation time that is given to the participants will influence the optimality of their movements. If preparation time influence this optimality, we expect that 1) the difference in force between the narrow and wide targets will be increase with longer

preparation time and that 2) the difference in variability of reach endpoint error between the narrow and wide targets will also increase with preparation time.

Our first approach was to categorize the preparation time of the individual trials into five different categories and to see whether the optimality of the movement was influence by these categories (Fig.4). We did not find any evidence that the preparation time influenced the modulation of the force applied for the two different target sizes (Analysis 2: interaction between target size and preparation time category: F(2.81,92.81)=0.89, p=0.44) even though there was a clear modulation of the force by target size (main effect of target size: F(1,33)=48.95, p<0.001). As shown on Fig.4, more force was applied for the narrow target than for the wide target for each preparation time categories. Effect size (Cohen's d) of the effect of target size on the force were large and ranged between 0.67 and 1.14. Interestingly, this effect was also true for movement starting less than 50ms before the target appeared (Fig. 4A). In those movements, the movement was initiated before the visual feedback about the target size could influence their control policy. Yet, by the end of the movements, those movements were optimal.

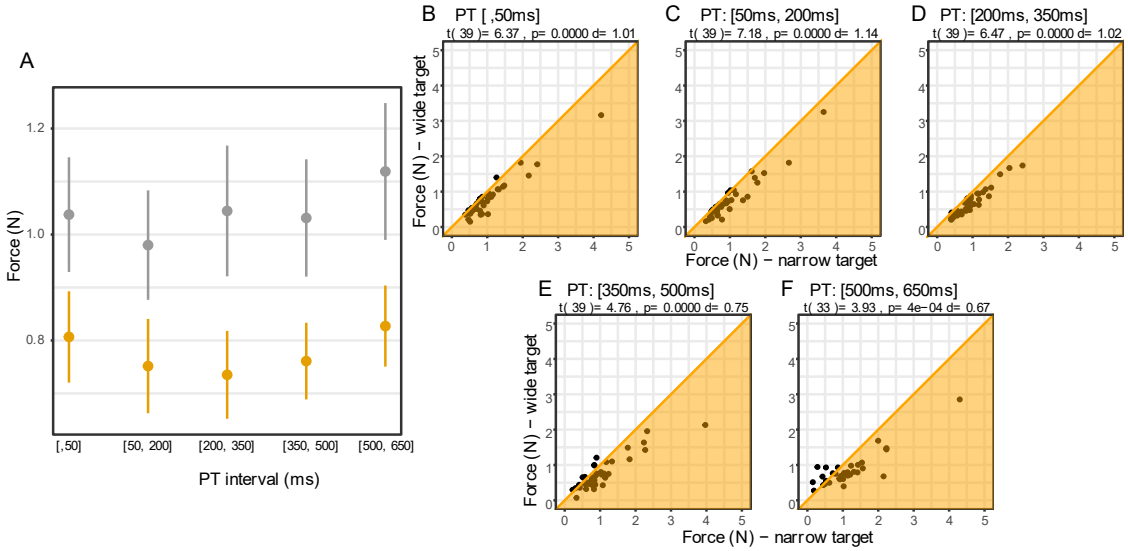

Fig.4: A) Force exerted against the perturbation for the narrow and wide target for each instructed preparation time bin. Each dot represents the mean force for that target width and the error bar represents the standard error of the mean. B) Force exerted against the perturbation for the wide target vs. for the narrow target. Each dot represents the data of an individual participant. Orange areas correspond to areas compatible with the minimum intervention principle.

To take the full spectrum of preparation time into account and to avoid losing power due to the categorization of a continuous variable, we ran a mixed model analysis on the force data (Fig.5, Analysis 3). As expected, the mixed model revealed a strong effect of target size on the force applied against the perturbation (coefficient of the effect of target size: t(38.5)=-7.75, p<0.001) confirming earlier analyses. Again, there was no evidence that preparation time influenced the modulation of force by target size (coefficient of the interaction between target size and PT: t(336)=-0.307, p=0.76).

Upon close inspection of Fig.5, there seems to be a small effect of preparation time on target size whereby the two regression lines appear to diverge with preparation time. Yet, this effect is too small to be detected despite the 40 participants and their 200 perturbation trials each.

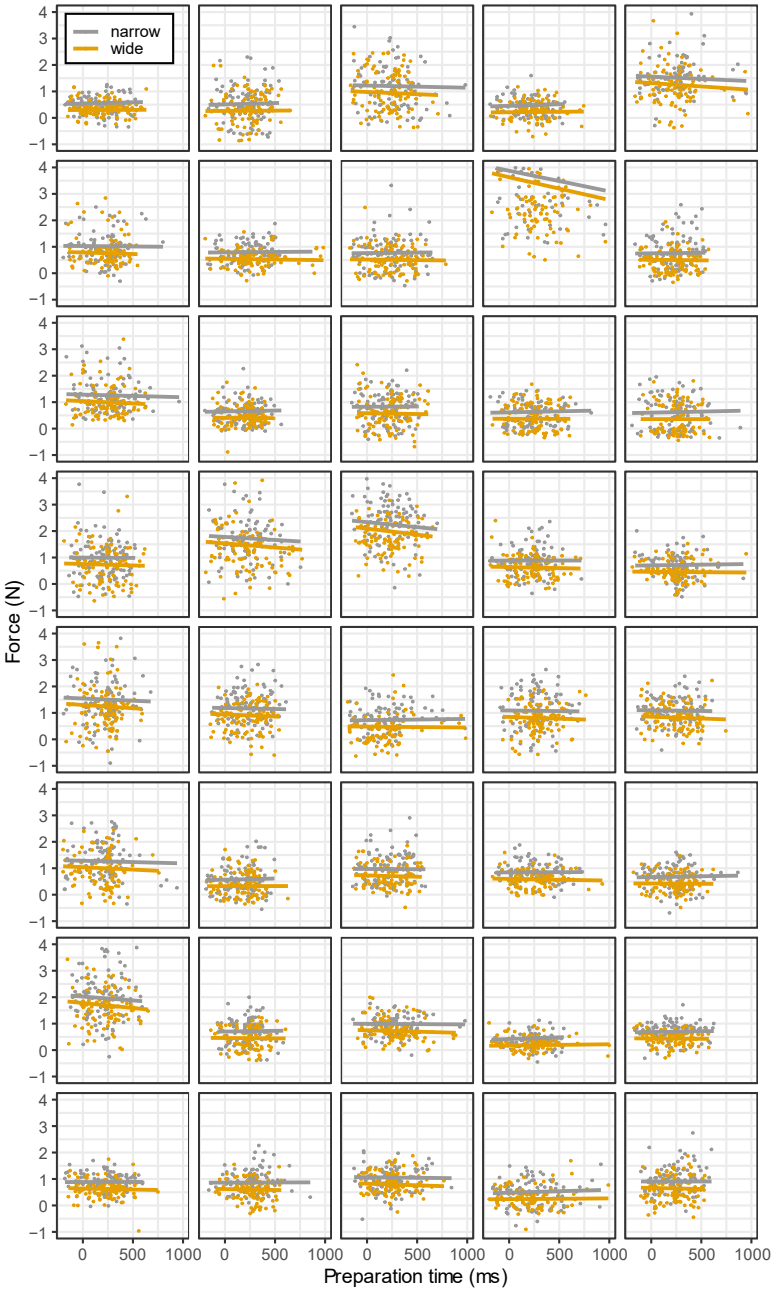

Fig.5: prediction from the linear mixed model (regression lines) superimposed on the force (N) data for each individual trial in function of preparation time (ms). Each panel represents the data of a single participant. Each dot represents a single perturbation trial.

Qualitatively similar results were obtained for the standard deviation of the reach endpoint error (Fig.6). This outcome was modulated by target size (Analysis 2: main effect of target size: $F(1,39)=19.16$, $p<0.0001$), and we did not find evidence that this modulation differed across preparation time categories (interaction between target size and preparation time categories:

F(2.13,83.39)=1.31, p=0.27). In contrast to our results with the force, the effect size were much smaller, ranging from 0.14 to 0.82. In addition, the modulation of the variability of reach endpoint error with target size did not reach significance for the early (earlier than 50ms) and late preparation time categories (later than 500ms). Those are also the categories with the least amount of trials per participant, making the estimation of variability more difficult.

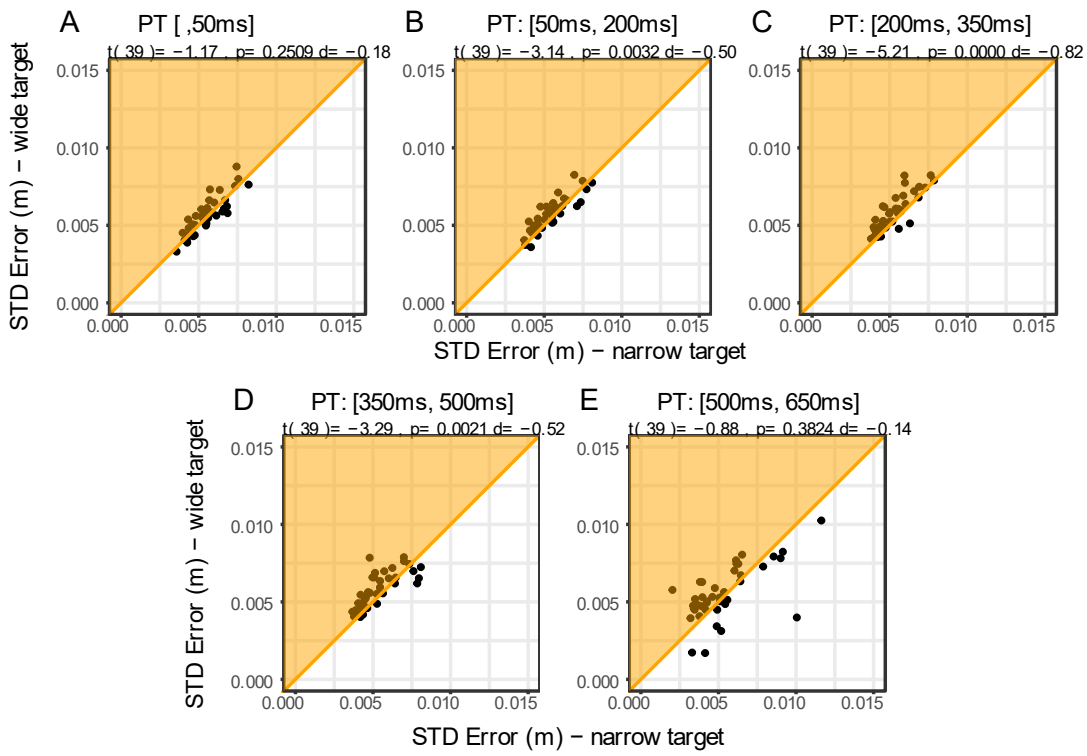

Fig.6: Standard deviation of the lateral position of the end at 13cm for the wide target vs. for the narrow target. Each dot represents the data of an individual participant. Orange areas correspond to areas compatible with the minimum intervention principle (more variability for the wider target).

In the outcomes reported up to now, force were measured when the hand had travelled 13cm. This measure of performance occurs around 400ms after movement onset, leaving ample time for online tuning. Yet, measuring the force earlier in the movement further support the finding that target size but not preparation time influences the force applied against the perturbations. Indeed, measuring it earlier (5cm) into the movement (around 230ms after movement onset) does not change any of the results. However, at that time, the size of the perturbation is much smaller, reducing the signal to noise ratio. Focusing on the force outcome measured at 5cm, we found that the modulation of the force by target size was absent in the Free RT condition ($t(39) = -0.60$, $p = 0.5550$ $d = -0.09$) but still present in the forced PT condition ($t(39) = 3.53$, $p = 0.0011$ $d = 0.56$), yielding an interaction between target size and condition ($F(1,39) = 5.64$, $p = 0.023$). This absence of difference in the free RT condition is potentially due to the decreased signal-to-noise ratio in that condition and to the lower number of trials in free RT compared to forced PT.

As for the force measured at 13cm, we submitted the force values computed 5cm into the movement from forced PT condition to an Anova (analysis 2) and to the linear mixed model in order to look at the effect of preparation time onto the force. These analyses yielded qualitatively similar results as at 13cm in the forced PT condition despite the time in the movement being much shorter. When preparation time were separated into different categories (analysis 2), we found that target size influenced the force applied by the participants against the perturbation (main effect of target size: $F(1,33)=9.18$, $p=0.005$) but did not find evidence that this difference was modulated by preparation time (interaction between target size and PT: $F(4,132)=0.34$, $p=0.85$). Similarly, in the mixed model (analysis 3), target size modulated force at 5cm ($t(313.5)=-3.46$, $p=0.0006$). We did not find any evidence that preparation time influenced the difference in force between the two target widths ($t(3118)=-0.245$, $p=0.81$), again consistent with the results at 13cm.

But there is a limit to what we can do because it is unknown when the perturbation is detected by the brain and this could vary trial-by-trial. We did not find any evidence that target width influenced force outcomes when this was measured at 2 or 4cm in the forced PT condition (different in force applied between the narrow and wide target measured at 2cm into the movement: $t(39) = -1.24$, $p = 0.22$ $d = -0.2$; measured at 4cm into the movement: $t(39) = 0.88$, $p = 0.38$ $d = 0.14$).

Discussion

In the present study participants were asked to reach for either a narrow or wide target, initiating their movement as quickly as volitionally possible (free RT condition), or in a manner that allowed us to experimentally manipulate the time they had available to prepare their movement (forced PT condition). Across both conditions, when participants experienced a perturbation, their behavior generally followed the minimum intervention principle; they applied greater forces and were more accurate for narrow targets, while the variability of their endpoint error was greater for wide targets.

In contrast to our expectation, the modulation of force with target width did not change in function of the amount of time participants were given to prepare their movements in the forced PT condition. Strikingly, even when the movement started *before* the information on target width was presented, participants were able to modulate the force applied against the perturbation as well as in the when preparation time was unconstrained. That is, we did not observe any difference in the adaptation of feedback gains to task constraints when these feedback gains were tuned during movement planning or during ongoing movement. Together, these results suggest that the tuning of feedback gains is instantaneous and can occur both during movement preparation and execution.

How long does it take to tune feedback gains?

Our present results are consistent with the proposal that the tuning of feedback gains to task demands does not impact reaction time; while participants had more time available to prepare their movements in forced PT trials with long preparation times, the movements they performed did not differ significantly from those performed with shorter preparation times. This is broadly consistent with previous theories of movement preparation (Wong et al., 2015), which suggest that movement preparation does not affect reaction time.

Yet, this does not mean that the tuning of the feedback gains is instantaneous. It is possible that the movement is being initiated while the tuning of the feedback gains is not fully finished but that this can occur during ongoing movement. A modelling effort on understanding movement preparation suggests that this can be the case (Kao et al. 2021). In addition, previous studies have demonstrated that it is possible to adapt the tuning of the feedback gains during ongoing movement (De Comite et al. 2021, 2022, 2023), yet is currently unclear how much time this takes. De Comite and colleagues (2021) showed that the tuning of the feedback gains representing the adaptation of the control policy to the task demands was completed within 150ms. Given visuomotor delays, they estimated that it takes 50ms to update the control policy during ongoing movement. Yet, the timing was not systematically investigated in this task. In a postural task, Yang and colleagues systematically vary the

timing of the presentation of task instruction and found that long-latency stretch reflex can reflect the right instruction within 90ms of its presentation (Yang et al. 2011). Our data does not allow us to estimate the amount of time necessary to adjust the control policy more accurately than in the previous studies. Indeed, we do not know when the perturbation was detected by the brain as the size of the perturbation increases gradually with the distance travelled by the hand. If we hypothesize that it takes 50-100ms for the brain to detect the perturbation, that on average people initiate their movements at the time of the go cue, and that sensorimotor delays amount 100ms, the observed response at 5cm (around 230ms after movement onset) would be consistent with a delay of 80-100ms to adjust feedback gains to task demands.

Why is this at all surprising?

Both the theory (Wong et al. 2015) and previous study (De Comite et al. 2021) suggested that it took little time to adjust the control policy to feedback gains. The framework of Wong et al. (2015) even predicted that it would not affect reaction time. Yet, we were willing to confirm this experimentally because of the existence of a switching cost for switching between two control policies (Orban de Xivry and Lefèvre 2016). When wide or narrow targets are presented for many trials in a row, the force exerted against a perturbation is more influenced by target width than when target width varies from trial to trial (Orban de Xivry 2013; Orban de Xivry and Lefèvre 2016). This suggests that adapting the control policy to task demands is an effortful process, yet this effortful process does not impact reaction time as is typical for switching cost in the cognitive domain (Monsell 2003).

Does motor planning actually exist?

A surprising result of our study is that there was absolutely no advantage in tuning the feedback gains before movement onset compared to during movement execution. That is, the tuning of the feedback gains was similar for trials where the movement started after the presentation of the target and for those where the movement was initiated before the visual information about target width was displayed. This is consistent with the idea that there can be a large overlap between planning and execution (Lara et al. 2018; Orban de Xivry et al. 2017) and that movements can be initiated before movement preparation is finished (Haith et al. 2016). One can also prepare the next movement during ongoing movement (Kashefi et al. 2023). Yet, the present result and the aforementioned studies ask the question whether the computation of the -optimal- motor control policy is actually part of the motor planning stage or whether this embedding results from the use of delayed reaching task paradigms where movement planning and execution are artificially separated. Indeed comparing delayed to quasi-automatic reaches, Lara and colleagues (2018) suggested that the motor preparatory stage was present for both types of trials but that the motor preparatory stage was taking very little time in quasi-automatic reaches. They estimated that the motor preparatory stage could take as little

as 40ms, which would be undetectable in the present experiment. In summary, the present study adds on a series of recent results that demonstrate that the frontier between motor planning and motor execution is not as clear cut as was once thought and that the motor preparation stage can happen during movement.

How does this view fit with motor preparation in the brain?

In the motor cortex, preparation and execution of movements are well segregated at the neural levels. In the dynamical system framework (Shenoy et al. 2013), motor preparation results in setting the population state at a given point reflecting the initial conditions (Afshar et al. 2011) that is followed by rotational dynamics linked to movement execution (Churchland et al. 2012). In addition, movement preparation and execution live in orthogonal subspaces (Kaufman et al. 2014). In the idea that movements can be initiated before motor preparation is fully completed, it has been reported and theorized that different endpoints in movement preparatory activity can be reached when movement are initiated without loss of movement accuracy (Ames et al. 2014; Kao et al. 2021). Even with quasi-automatic movements, the motor preparation stage takes place but partially overlap with movement execution (Lara et al. 2018). Yet, it is unclear how modulation of the control policy by task demands will influence these mechanisms. Would a change in feedback gains be reflected in different neural activity in preparatory dimensions or in different rotational dynamics/movement execution dimensions?

The efficacy of measurements of performance in forced PT conditions is critically dependent upon participant's adherence to task instructions. In the present experiment, participants were generally able to time their movements in synchrony with the last tone, but tended to start slightly earlier than the instructed time with the forced PT was longer. Informal examination of prior experiments indicates that participants are more likely to delay the initiation of their movements when a very short time to prepare an action is imposed (Hardwick et al., XXXX, Vleugels et al., XXXX).

In conclusion, the present study indicates that increasing the amount of time available for movement preparation does not lead to significant differences in movement planning. This is consistent with previous work which suggests that motor plans can be generated almost instantaneously. Moreover, our results indicate that movements prepared volitionally (in free RT conditions) and with limited time (in forced PT conditions) are broadly equivalent, as both are in general accord with the principles of optimal control. These results point to the fact that the frontier between movement planning and execution is not as clear as is often depicted.

Bibliography

Afshar A, **Santhanam G**, **Yu BM**, **Ryu SI**, **Sahani M**, **Shenoy KV**. Single-trial neural correlates of arm movement preparation. *Neuron* 71: 555–64, 2011.

Ames KC, **Ryu SI**, **Shenoy KV**. Neural Dynamics of Reaching following Incorrect or Absent Motor Preparation. *Neuron* 81: 438–451, 2014.

Bates D, **Mächler M**, **Bolker B**, **Walker S**. Fitting linear mixed-effects models using lme4. *J Stat Softw* 67: 1–48, 2015.

van Beers RJ, **Brenner E**, **Smeets JBJ**. Random walk of motor planning in task-irrelevant dimensions. *J Neurophysiol* 109: 969–77, 2013.

Churchland MM, **Cunningham JP**, **Kaufman MT**, **Foster JD**, **Nuyujukian P**, **Ryu SI**, **Shenoy KV**. Neural population dynamics during reaching. *Nature* 487: 51–6, 2012.

De Comite A, **Crevecoeur F**, **Lefèvre P**. Online modification of goal-directed control in human reaching movements. *J Neurophysiol* 125: 1883–1898, 2021.

De Comite A, **Crevecoeur F**, **Lefèvre P**. Continuous Tracking of Task Parameters Tunes Reaching Control Online. *eNeuro* 9: ENEURO.0055-22.2022, 2022.

De Comite A, **Lefèvre P**, **Crevecoeur F**. Continuous monitoring of cost-to-go for flexible reaching control and online decisions. bioRxiv: 2022.11.16.516793, 2023.

Diedrichsen J. Optimal task-dependent changes of bimanual feedback control and adaptation. *Curr Biol* 17: 1675–9, 2007.

Dingwell JB, **John J**, **Cusumano JP**. Do Humans Optimally Exploit Redundancy to Control Step Variability in Walking? *PLOS Comput Biol* 6: e1000856, 2010.

Giulio ID, **Baltzopoulos V**, **Maganaris CN**, **Loram ID**. Human standing: does the control strategy preprogram a rigid knee? *J Appl Physiol* 114, 2013.

Haith AM, **Huberdeau DM**, **Krakauer JW**. Hedging Your Bets: Intermediate Movements as Optimal Behavior in the Context of an Incomplete Decision. *PLOS Comput Biol* 11: e1004171, 2015.

Haith AM, **Pakpoor J**, **Krakauer JW**. Independence of Movement Preparation and Movement Initiation. *J Neurosci* 36: 3007–3015, 2016.

Hardwick RM, **Forrence AD**, **Krakauer JW**, **Haith AM**. Time-dependent competition between goal-directed and habitual response preparation. *Nat Hum Behav* 3: 1252–1262, 2019.

Henry FM, **Rogers DE**. Increased Response Latency for Complicated Movements and A "Memory Drum" Theory of Neuromotor Reaction. *Res Q Am Assoc Health Phys Educ Recreat* 31: 448–458, 1960.

Kao T-C, **Sadabadi MS**, **Hennequin G**. Optimal anticipatory control as a theory of motor preparation: A thalamo-cortical circuit model. *Neuron* 109: 1567-1581.e12, 2021.

Kashefi M, **Reschechtko S**, **Ariani G**, **Shahbazi M**, **Die-drichsen J**, **Pruszynski JA**. Interaction of multiple future movement plans in sequential reaching. bioRxiv: 2023.05.24.542099, 2023.

Kaufman MT, **Churchland MM**, **Ryu SI**, **Shenoy KV**. Cortical activity in the null space: permitting preparation without movement. *Nat Neurosci* , 2014. doi:10.1038/nn.3643.

Lara AH, **Elsayed GF**, **Zimnik AJ**, **Cunningham JP**, **Churchland MM**. Conservation of preparatory neural events in monkey motor cortex regardless of how movement is initiated. *eLife* 7: e31826, 2018.

Latash ML, **Scholz JF**, **Danion F**, **Schöner G**. Structure of motor variability in marginally redundant multifinger force production tasks. *Exp Brain Res* 141: 153–165, 2001.

Latash ML, **Scholz JF**, **Danion F**, **Schöner G**. Finger coordination during discrete and oscillatory force production tasks. *Exp Brain Res* 146: 419–432, 2002.

Monsell S. Task switching. *Trends Cogn Sci* 7: 134–140, 2003.

Nashed JY, **Crevecoeur F**, **Scott SH**. Influence of the behavioral goal and environmental obstacles on rapid feedback responses. *J Neurophysiol* 108: 999–1009, 2012.

Nashed JY, **Crevecoeur F**, **Scott SH**. Rapid Online Selection between Multiple Motor Plans. *J Neurosci* 34: 1769–1780, 2014.

Oldfield RC. The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia* 9: 97–113, 1971.

Orban de Xivry J-J. Trial-to-Trial Reoptimization of Motor Behavior Due to Changes in Task Demands Is Limited. *PloS One* 8: e66013, 2013.

Orban de Xivry J-J, **Lefèvre P**. A switching cost for motor planning. *J Neurophysiol* 116: 2857–2868, 2016.

Orban de Xivry J-J, **Legrain V**, **Lefèvre P**. Overlap of movement planning and movement execution reduces reaction time. *J Neurophysiol* 117: 117–122, 2017.

Scholz JP, **Schöner G**. The uncontrolled manifold concept: identifying control variables for a functional task. *Exp Brain Res* 126: 289–306, 1999.

Schouten JF, **Bekker JAM**. Reactlon tine and accuracy. *Acta Psychol (Amst)* 27: 143–153, 1967.

Scott SH. Optimal feedback control and the neural basis of volitional motor control. *Nat Rev Neurosci* 5: 532–46, 2004.

Shenoy KV, **Sahani M**, **Churchland MM**. Cortical control of arm movements: a dynamical systems perspective. *Annu Rev Neurosci* 36: 337–59, 2013.

Singmann H, **Bolker B**, **Westfall J**, **Aust F**, **Ben-Shachar MS**. afex: Analysis of factorial experiments [Online]. https://CRAN.R-project.org/package=afex.

Todorov E. Optimality principles in sensorimotor control. *Nat Neurosci* 7: 907–15, 2004.

Todorov E, **Jordan MI**. Optimal feedback control as a theory of motor coordination. *Nat Neurosci* 5: 1226–35, 2002.

Wong AL, **Haith AM**, **Krakauer JW**. Motor Planning. *The Neuroscientist* 21: 385–398, 2015.

Yang L, **Michaels J a**, **Pruszynski JA**, **Scott SH**. Rapid motor responses quickly integrate visuospatial task constraints. *Exp Brain Res* 211: 231–42, 2011.