

Increase in grasp force reflects a desire to improve movement precision

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Increase in grasp force reflects a desire to improve movement precision

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Grasp force is positively correlated with precision.

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AT Designed Research, Performed Research, Analyzed data, Wrote the paper; HK Wrote the paper; YK Wrote the paper.

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Statement - 96

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55 Abstract

56 Grasping is an action engraved in the human genome, enabling newborn infants to hang
 57 from a monkey-bar immediately after birth. The grasp force provides rich information about the
 58 brain's control of arm movements. In this study, we tested the hypothesis that the grasp force
 59 increases to improve the hand's movement precision during reaching. In two reaching
 60 experiments, subjects increased grasp force to suppress movement imprecision that arose from
 61 both self-generated motor noise and from an unpredictable environment. Furthermore, the grasp
 62 force did not increase constantly, but increased specifically along the movement where the
 63 hand's deviation was greatest. The increased grasp was premeditated and wasn't a reaction to
 64 environmental forces, suggesting that the central nervous system has a predictive, state-
 65 dependent model of movement precision during reaching. The grasp force provides a high
 66 temporal resolution and calibration-less estimate of movement precision adaptation.

67 Significance Statement

68 Humans use their hands on a daily basis to interact with the environment. Many tasks
 69 require the hand's movement to be precise. Standard measures of movement precision resort to
 70 measuring the stiffness of the arm, which is notoriously difficult to measure during motion. We
 71 show that the power grasp force is correlated with movement precision, and that it provides a
 72 real-time measure of movement precision adaptation. Furthermore, the grasp force measure
 73 reveals that the brain has a state-dependent adaptation of movement precision, such that it
 74 increased grasped force in locations where the hand's deviation was greatest.

75 Introduction

76 Grasping with the hand is a fundamental motor action in humans that can be evoked in
 77 infants (McGraw, 1940), alongside the traction response, where the passive stretching of the
 78 shoulder abductors and the arm's flexors cause the fingers, elbow and shoulder flexors to flex in
 79 synergistic response (Twitchell, 1965). As infants mature, their arm movements become
 80 smoother and more precise (Thelen et al., 1996). As adults, humans rarely make mistakes when
 81 moving the arm, like when reaching to grab a mug. However, some skilled movements that
 82 require precision are difficult even for adults.

83 Taking hammering as an example, the hammer must strike the nail head precisely, which
 84 is challenging due to self-generated motor noise (Selen et al., 2009), and the head of the hammer
 85 must remain flat against the nail during contact, which is difficult as unpredictable contact forces
 86 can destabilize the hammer (Ganesh et al., 2012). Failure at such tasks occurs when the hand's
 87 movement is perturbed unpredictably because the central nervous system (CNS) uses delayed
 88 sensory feedback to correct its movement (Pew et al., 1967). Thus, both unpredictable self-
 89 generated motor noise and environmental interactions result in reduced *movement precision* that
 90 cannot be corrected immediately by the CNS. It should be noted that precision is different from
 91 accuracy, as precision relates to variance whereas accuracy refers to bias.

92 A vast literature exists on how humans adapt to a force field that perturbs the accuracy of
 93 the hand's motion when reaching towards a point target (Shadmehr et al., 2010). The pioneering
 94 study of (Shadmehr and Mussa-Ivaldi, 1994) revealed the ability of the CNS to learn to move in
 95 a velocity-dependent force field. Prior to the introduction of the force field, the hand moves from
 96 one point to another in a straight but somewhat curved trajectory. When the force field is
 97 introduced, the hand's trajectory curves outward and causes the subject to miss the intended

98 target. Movement accuracy is regained by learning the dynamics of the force field and
 99 countering the force field's effects on the hand via appropriate forces produced by the hand
 100 (Conditt et al., 1997).

101 To recover movement accuracy in the force field, a forward model of the force field's
 102 dynamics is learned by the CNS. However, if the external forces are unpredictable and cause
 103 movement imprecision, the CNS uses a different strategy of coactivating the muscle pairs in the
 104 arm, increasing its stiffness, which reduces the impact of unpredictable forces on the movement
 105 of the arm (Burdet et al., 2001; Hogan, 1984; Wong et al., 2009). Thus, the CNS' adaptation of
 106 movement precision in the presence of unpredictable external forces has been estimated by
 107 measuring the stiffness or the cocontraction of the arm (Franklin et al., 2008).

108 A recent study reported another method of measuring the CNS' adaptation to
 109 unpredictable forces. The authors of this study measured increases in the pinch grip force when
 110 subjects reached in an unpredictable force field (Hadjiosif and Smith, 2015). They found a
 111 positive correlation between the pinch grip force and the variability of the external forces. One
 112 issue with the pinch grip methodology is the strong coupling between the pinch grip force and
 113 the load force, which may confound the interpretation of the data. Furthermore, (Hadjiosif and
 114 Smith, 2015) did not test whether subjects increase pinch grip force when increased movement
 115 precision is desired in the absence of external forces.

116 In this study, we hypothesize that the power grasp force positively correlates with the
 117 desire to increase movement precision. We test two predictions based on this hypothesis in two
 118 experiments. First, we test the hypothesis that the grasp force increases when subjects want to
 119 improve movement precision. This hypothesis is tested by asking subjects to keep their hand
 120 within a wide or narrow visual track whilst reaching towards a target, and measuring the changes
 121 in the grasp force. Second, we hypothesize that changes in grasp force reflect a desire to improve
 122 movement precision, and do not reflect the actual movement precision per se. This second
 123 hypothesis is tested by asking subjects to reach in a diverging force field that pushed their hand
 124 laterally from the center line. As subjects were unaware of when the force field would activate,
 125 we predicted that the grasp force would not increase in response to the force field on the first
 126 trial. We also predicted that in catch trials, where the force field was unexpectedly turned off, the
 127 grasp force would not decrease even though the actual movement precision was high.

128

129 **Materials and Methods**

130 10 male subjects, who all gave their informed consent, participated in the study. The
 131 experiment was carried out in accordance with the Declaration of Helsinki, and the study was
 132 approved by the Ethical Review Board for Epidemiological Studies at the authors' institution.

133 The subjects were seated facing the KINARM planar robotic manipulandum from BKIN
 134 Technologies (see Figure 1). Subjects held onto the KINARM interface via a handle that was
 135 affixed with a three axis force sensor (Tec Gihan) to measure the grasp force from the palm of
 136 the hand during reaching movements. An Edero Armon arm support was used under the elbow to
 137 support the arm's weight when using the robotic interface. Visual feedback was provided on a
 138 monitor that was placed upside-down such that subjects viewed a reflection of the monitor on a
 139 thin film mirror placed directly above the hand, which obscured the hand from view. The

position of the hand was visible as a white circular cursor during both the visual track and the divergent force field experiments.

Visual track reaching experiment

Subjects moved their hand to reach a target of radius 2cm placed 25cm away from their initial starting position. Subjects were instructed to prevent the cursor from deviating off a red visual track that was displayed between the initial and target positions (see Figure 1B).

The experimental structure consisted of 7 blocks that consisted of 15 trials. The first block consisted of training trials, where the red region was absent. Blocks 2, 4 and 6 were the ‘Wide’ condition that demanded low movement accuracy blocks as the visual track was ± 4 cm wide. On the other hand, the ‘Narrow’ condition was tested in blocks 3, 5 and 7 that required high movement accuracy due to a narrow visual track with a width of ± 0.4 cm. The cursor in this experiment had a diameter of 0.4 cm. Feedback of the movement duration was provided to the subject on a trial-by-trial basis. Movements that were faster than 900ms and longer than 1100ms triggered a feedback message of ‘fast’ or ‘slow’, respectively, to ensure that subjects reached with the same movement speeds in both the Wide and Narrow conditions. No feedback was given of the lateral deviation after the trial.

As we observed a linear relationship between both the lateral deviation and the grasp force as a function of trials, we fitted these data from the visual track experiment using the linear mixed-effects model of the form

$$Y = \beta_{0s} + \beta_{1s}C + \beta_{2s}T + \beta_{3s}(T \cdot C) + \varepsilon_s \quad (1)$$

where the response Y is either the vector of data from grasp force F_G or from the lateral deviation x_{LD} , T is the trial number, C is the visual track condition (narrow or wide), β_{0s} is the intercept, β_{1s} to β_{3s} are the parameters for each predictor, and ε_s is the unexplained variance of the response Y for each subject s .

A likelihood ratio test was employed to examine the significance of the condition parameter C on explaining the data. If deemed significant, this implied that the width of the visual track had a significant impact on the grasp force and the lateral deviation.

If the condition was deemed to significantly influence the grasp force or the lateral deviation, a one-sample t-test was conducted on the data, which was grouped separately for the wide and narrow conditions. This enabled us to test our hypothesis of whether the grasp force increased when reaching alone a narrow visual track, and whether a reduction in lateral deviation was observed in the narrow track. However, these tests alone were not sufficient to establish a relationship between the grasp force and the lateral deviation as they only examine the effect on a group level. We examined how each subject’s lateral deviation changed as a function of the change in their grasp force. Here, a non-parametric sign-test was employed as this data was observed to violate normality. The normality of all data sets was tested using an Anderson-Darling test prior to post-hoc testing.

Divergent force field experiment

The same 10 subjects that took part in the first experiment participated in the divergent force field task (see Figure 2A). Subjects were instructed to reach a target 20cm away from the starting position. The diameter of the cursor was 1cm in this experiment. Feedback was provided

182 on a trial-by-trial basis about the duration of the movement, which had to be between 500-600ms.
 183 Each participant practiced a standard reaching task for 15 training trials, after which they
 184 experienced 25 divergent field blocks. The divergent force field was designed to amplify lateral
 185 reaching errors by applying the following force to the hand,

$$186 \quad F_x = kx \text{ for } |x| < 0.04\text{m} \quad (2)$$

187 where the stiffness $k = 400\text{N/m}$ and x is the lateral position of the hand such that the initial and
 188 target positions are at $x = 0$. Each divergent field block was composed of 4 trials where the last
 189 trial was a catch trial where the force field was switched off, i.e. $F_x = 0$. The catch trials tested
 190 whether subjects were simply grasping the handle as a reaction to the forces from the robot, or
 191 were increasing their grasp force to improve their movement precision. If the hand's lateral
 192 deviation was greater than $\pm 4\text{cm}$ in a force field trial, it was switched off and the subjects were
 193 shown a 'failed' trial message.

194 Post-hoc one-sample t-tests were carried out to examine the difference between the last
 195 training trial and the first force field trial, and the difference between the catch trials and the
 196 force field trials. If the grasp force is different in either of these cases, our hypothesis must be
 197 rejected.

198

199 Results

200 *Experiment 1: reaching along a wide or narrow visual track*

201 In the first experiment, subjects had to make point-to-point reaching movements towards
 202 a circular target of radius 2cm that was placed 25cm away from the initial starting position.
 203 Subjects were instructed to prevent the cursor from deviating off a red visual track that was
 204 displayed between the initial and target positions (see Figure 1B).

205 The literature reports that, with a pinch grip, significant correlation is observed between
 206 pinch grip force and load force (Flanagan and Wing, 1997). Such a correlation could undermine
 207 our study as the grasp force may simply reflect the load experienced by the hand during
 208 reaching. The grasp force and the load force are plotted as a function of normalized time in
 209 Figure 1C. The data from every trial's whole movement was selected for this analysis, where the
 210 start of the trial was when the target appeared, and the end was when the hand stopped inside the
 211 target. We calculated the Pearson correlation coefficient in all trials between the grasp force and
 212 the load force supplied by the subject against the robotic interface. If the load force has a
 213 significant impact on the grasp force measurement, this must be taken into account in subsequent
 214 analysis as it may influence the results. However, we found that the group mean correlation
 215 between the grasp and load force was $\rho = 0.26 \pm 0.12$ (mean and standard error), which was not
 216 significantly different from zero (one-sample t-test, $t(9)=2.09$, $p>0.07$). Thus, no significant
 217 coupling was observed between the grasp force and load force in this experiment.

218 Next, we examined whether the variance in the reaching movement was different
 219 between the Wide and Narrow conditions. We normalized all trajectories in time, and calculated
 220 the mean trajectory for each Wide and Narrow condition using the trials from all 3 blocks. We
 221 then calculated the *lateral deviation*, defined as the absolute distance halfway into the movement
 222 between the cursor's x -axis position and the mean trajectory, for each trial, which is plotted as a
 223 function of trials for the population mean on Figure 1D. The lateral deviation appeared to be

functionally dependent on the width of the visual track. We employed a fit with a linear mixed-effects model (see eq. (1) in the Methods) on the data from all trials, which was labelled by subject, trial number and track condition. A likelihood ratio test revealed a significant effect of the visual track condition on the lateral deviation ($\chi^2(2)=21.95$, $p<10^{-4}$). Using the regressed linear model, we calculated the difference in the lateral deviation between the Wide and Narrow track conditions for the trial range 16 to 115, i.e. blocks 2 to 7. A one-sample t-test on the lateral deviation showed that the subjects' mean lateral deviation, shown in Figure 1E, was significantly smaller in the Narrow ($0.17\pm0.02\text{cm}$) than the Wide ($0.23\pm0.03\text{cm}$) condition ($t(9)=-4.32$, $p<0.0019$), indicating that the subjects' trajectories were more precise in the Narrow condition. What facilitated the subjects' ability to improve their lateral movement precision in the narrow track?

If the grasp force is correlated with movement precision during reaching, a selective increase in grasp force should be observed in the Narrow condition where smaller lateral deviation was observed. The population mean grasp force from each trial is plotted as a function of trials in Figure 1B, where the blue and red points are from the Wide and Narrow conditions, respectively. The average grasp force from a single trial was calculated using data from the entire movement, where the start of the trial was when the target appeared, and the end of the trial was when the hand stopped inside the target. Upon visual inspection, there appeared to be a functional dependence of the grasp force on the visual track condition and the trial number. The grasp force data from all trials and all subjects was fit with a linear mixed-effects model with the trial number and track condition as predictors (refer to eq. (1) in the Methods). A likelihood ratio test showed that the grasp force was significantly affected by the visual track condition ($\chi^2(2)=118$, $p<10^{-15}$). We calculated the mean grasp force in the Wide and Narrow conditions from the linear model fits, and a one sample t-test showed that the grasp force was significantly higher in the Narrow than in the Wide condition ($t(9)=4.41$, $p<0.0012$).

To directly assess the effect of the grasp force on the movement, we plotted the lateral deviation as a function of the grasp force for each subject in the Wide (blue) and Narrow (red) conditions in Figure 1F, with a black line connecting the data from the same subject. The data from each subject was averaged across all three blocks in the Wide and Narrow conditions to yield one data point per subject per condition. An increase in grasp force was observed to reduce the hand's lateral deviation, and a non-parametric sign test, which was employed since the data violated normality according to an Anderson-Darling test, found this relationship to be significant ($p<0.022$). In summary, these results suggest that the grasp force is related to the hand's movement precision during reaching.

Experiment 2: divergent force field

In the second experiment, we tested subjects reaching in a divergent force field. The force field applied a force that pushed the hand laterally away from the center-line if it deviated laterally from the straight line between the initial and target positions (see Figure 2A). The same 10 subjects that took part in the first experiment participated in the divergent force field task (see Figure 2A). The trajectories from the first 15 trials inside the divergent force field from a sample subject are plotted in Figure 2B. The grasp force, averaged over each trial, is plotted as a function of trials in Figure 2C, where the points are the group mean and the shaded area is the standard error from all 10 subjects. In the 15 training trials, where subjects reached towards the target without the force field, the grasp force was generally low (black dots of Figure 2C) and continually declined with practice. On trial 16, when the force field was first experienced by

subjects, the grasp force was effectively the same as the last training trial. The grasp force increased rapidly in the second and third force field trials, and peaked at approximately the fourth force field trial, after which the grasp force declined exponentially, but not to the original level observed in the training trials.

Recall that the second prediction from our hypothesis dictates that increases in the grasp force should only be related to a desired increase in movement precision. Thus, the grasp force should not change even if the actual movement precision increases or decreases. The movement precision in this force field experiment is denoted by the perpendicular distance, defined as the absolute distance from the line at $x=0$,

First, we examined how the grasp force and the perpendicular distance changed from the last training trial (dashed trace in Figure 2D) to the first force field trial (solid trace). The group mean grasp force and the group mean perpendicular distance are plotted, in Figure 2D, as a function of normalized time, where time zero was the time of target onset and the end was where the subject reached the target. The perpendicular distance was observed to increase dramatically on the first force field trial. The group mean grasp force in the last training trial was $3.1 \pm 0.7\text{N}$ (mean and standard error) and for the first force field trial it was $2.9 \pm 0.7\text{N}$. A paired sample t-test found that the difference in the grasp force between the last training trial and the first force field trial was not statistically significant ($t(9)=2.20$, $p>0.055$). Even though the perpendicular distance increased dramatically, the grasp force did not change.

Next, we examined if the grasp force was different on catch trials in comparison to the force field trials. The group mean grasp force (blue traces) and the perpendicular distance (dashed traces) from all catch trials (dashed traces) and all force field trials (solid traces) is plotted as a function of normalized time. Notably, the grasp force profile is different from the training trial in Figure 2D, where it was constant throughout the movement. The grasp force appears to increase in tandem with the perpendicular distance in the force field trials. We found the mean grasp force, taken over the whole trial, and calculated the difference between the mean grasp force in catch trials with the neighboring force field trials. This difference was $0.08 \pm 0.12\text{N}$, which was statistically not different from zero (one-sample t-test, $t(9)=0.65$, $p>0.53$). Hence, the grasp force did not change in catch trials, even though the perpendicular distance clearly decreased.

Discussion

In this study, we measured the power grasp force whilst subjects completed two reaching tasks. The first task asked subjects to stay within a visual track during reaching, and the second task had subjects reach to a target whilst their hand was perturbed by a diverging force field that amplified lateral reaching errors. The results from both experiments support our hypothesis that the grasp force is positively correlated with the desire to increase movement precision. Namely, the grasp force increased when the visual track was narrower and required higher movement precision. Furthermore, the grasp force in the force field did not change in tandem with changes in the actual perpendicular distance, but the desire to change it.

The latter observation, that the grasp force was not significantly correlated with the load force from the force field, is of importance. Several studies have reported the high correlation between the pinch grip force and the load force from the environment (Flanagan et al., 2006;

Flanagan and Wing, 1997). This coupling had to be taken into account when subjects adapted their pinch grip force when reaching in a variable force field (Hadjiosif and Smith, 2015) to avoid the confound where a change in the grip force may be mistaken for an adaptation to the variability of the force field, when the change may have been due to the increased load force from the variable force field. In our experiment, we employed a divergent force field, which has a similar effect to the variable force field used in (Hadjiosif and Smith, 2015), namely that unpredictable forces are imposed on the subject's hand that cause movement variability. Unlike the pinch grip force, the power grasp force during reaching was not correlated with the load force from the force field. The power grasp force thus avoids confounds when interpreting changes in the grasp force. However, this may be valid only when the forces from the force field are approximately orthogonal to the placement of the grasp force sensor, and so caution is still required when interpreting the changes in the grasp force.

In both experiments, the grasp force increased from the initial exposure to a visual or force field condition, but gradually decayed as a function of trials. As reported in (Hadjiosif and Smith, 2015), two opposing adaptation phenomena are likely at play. The first is a fast and sensitive adaptation that increases grasp force to rapidly improve movement precision due to a task demand. The second is a slower adaptation process that optimizes grasp force to conserve effort (Emken et al., 2007; Todorov and Jordan, 2002). The summed contributions of both fast and slow adaptation processes explains why grasp force increases rapidly from initial exposure, but continually decays throughout our experiment. This decay can be observed in the training trials in both experiments, implying that the gradual decay in the grasp force must be taken into account when interpreting the data. In our first experiment, this was accounted for by the linear mixed-effects model that included a trial gradient. The decay in the grasp force does not contradict our hypothesis, but it shows that an effort conservation process is continually working to reduce excessive grasp force production.

In addition to these adaptation processes, we observed that the increase in grasp force, when switching from a wide to a narrow visual track, was less pronounced in the later trials. Subjects may have learned to update their motion plan to move straighter without having to rely on increasing grasp force to remain inside the visual track (Wong et al., 2009). Such a strategy was likely possible when staying inside the narrow visual track, but was infeasible when reaching in the diverging force field that punished even minor lateral deviations. This may explain why the grasp force plateaus to a value above the nominal level observed in the training trials.

The changes in the grasp force observed when subjects learned to reach in the diverging force field are similar to the results of another study that examined the adaptation of arm cocontraction during the learning of a DF (Franklin et al., 2008). In their study, they also found an initial, rapid increase in cocontraction, followed by a slow and gradual decay, which plateaued above the baseline observed in the training trials. The similarity between the grasp force observed in our study, and the arm cocontraction observed in the study of (Franklin et al., 2008), raises the possibility of using the grasp force as a tool to probe the CNS' desire to improve movement precision in rapid movements, such as during a golf swing (Komi et al., 2008), where the delay introduced by the processing of the electromyography data may be detrimental to the analysis. As such, the grasp force methodology could complement existing methods to measure the cocontraction of muscles to further our understanding of the CNS' desire to improve movement precision.

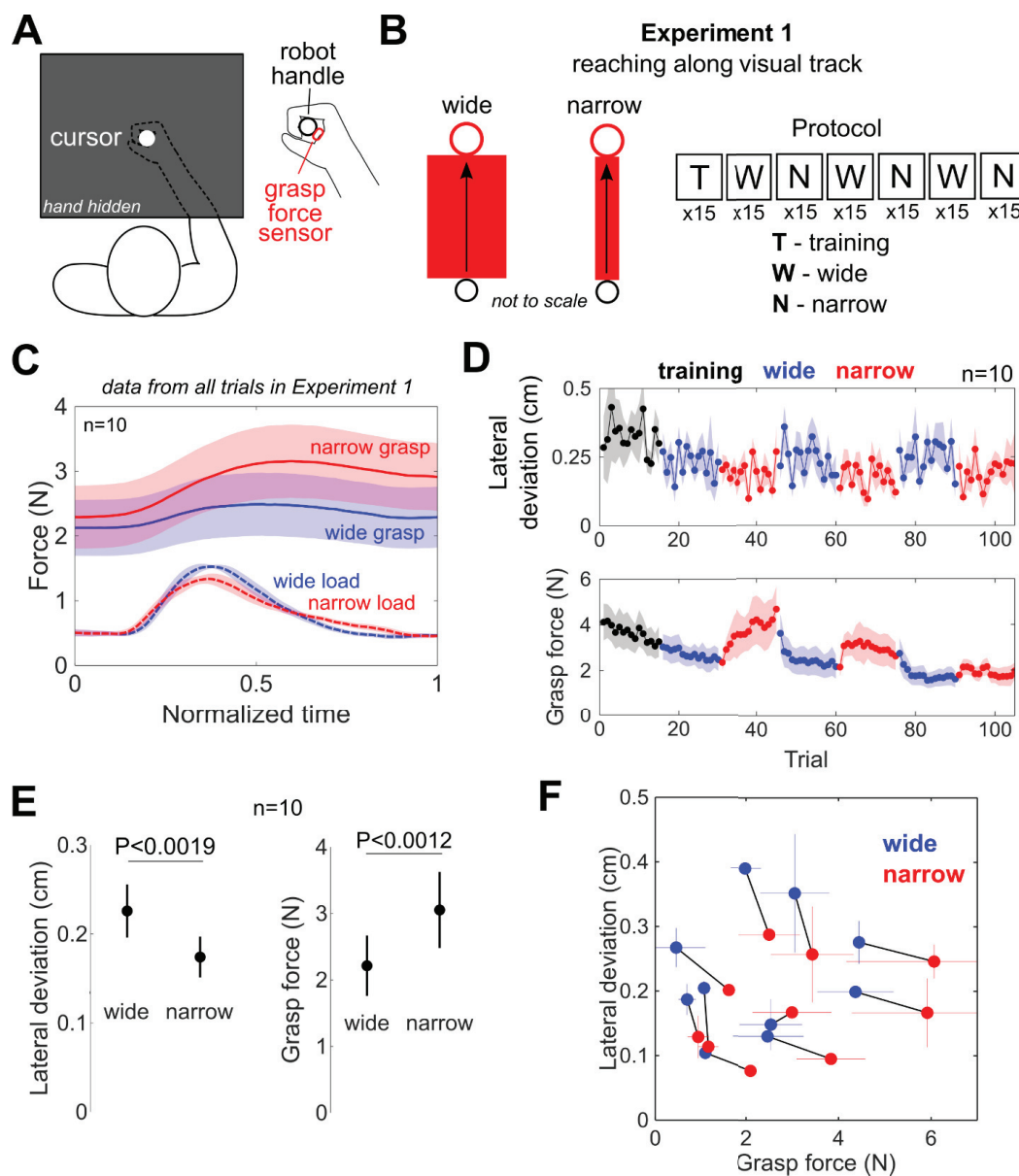
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402

403 **Competing interests**

404 The authors have no competing financial or non-financial interests.



405

406 **Figure 1.** Experimental setup, protocol and results from the first experiment where subjects
 407 reached along a visual track (A) Subjects held the handle of a robotic manipulandum, where the
 408 position of their arm was hidden behind a screen mirror. Subjects received visual feedback of the
 409 position of their hand as a cursor on the monitor such that it could be seen above the hand. The
 410 elbow was supported such that the hand, elbow and shoulder were level along a horizontal plane.
 411 A force sensor was placed between the palm of the hand and the handle to measure the grasp
 412 force. (B) In the first experiment of reaching along a visual track, subjects were presented with

413 two visual feedback conditions showing either a wide or a narrow track. Subjects were instructed
414 to keep their cursor inside the track and reach the circular target at the end of the track. Subjects
415 first made reaching movements without a visual track in a training block, after which they
416 experienced wide and narrow blocks in consecutive sequence for three repetitions per condition.
417 (C) The group mean grasp force (dotted traces) and load force (solid traces) are plotted as a
418 function of normalized time, where the shaded area is one standard error. The data were
419 separated into the Wide (blue) and the Narrow (red) conditions. The Pearson correlation
420 coefficient between the grasp and load forces was not significantly different from zero. Thus, no
421 significant correlation between grasp and load force was observed when reaching along a visual
422 track. (D) The lateral deviation and the grasp force of the population mean and standard error are
423 plotted as a function of trials with the plot color indicating the training trials (black), Wide track
424 (blue) and Narrow track (red) conditions. (E) The mean lateral deviation and the mean grasp
425 force from the population is shown for the Wide and Narrow conditions. The lateral deviation
426 was lower and the grasp force was higher when the visual track was narrow. (F) The lateral
427 deviation is plotted as a function of the grasp for every subject in the Wide and Narrow
428 conditions, with a line connecting the data from the same subject. The thin lines show standard
429 deviation from the linear mixed effects model fits. An increase in grasp force was observed to
430 subsequently reduce the lateral deviation.

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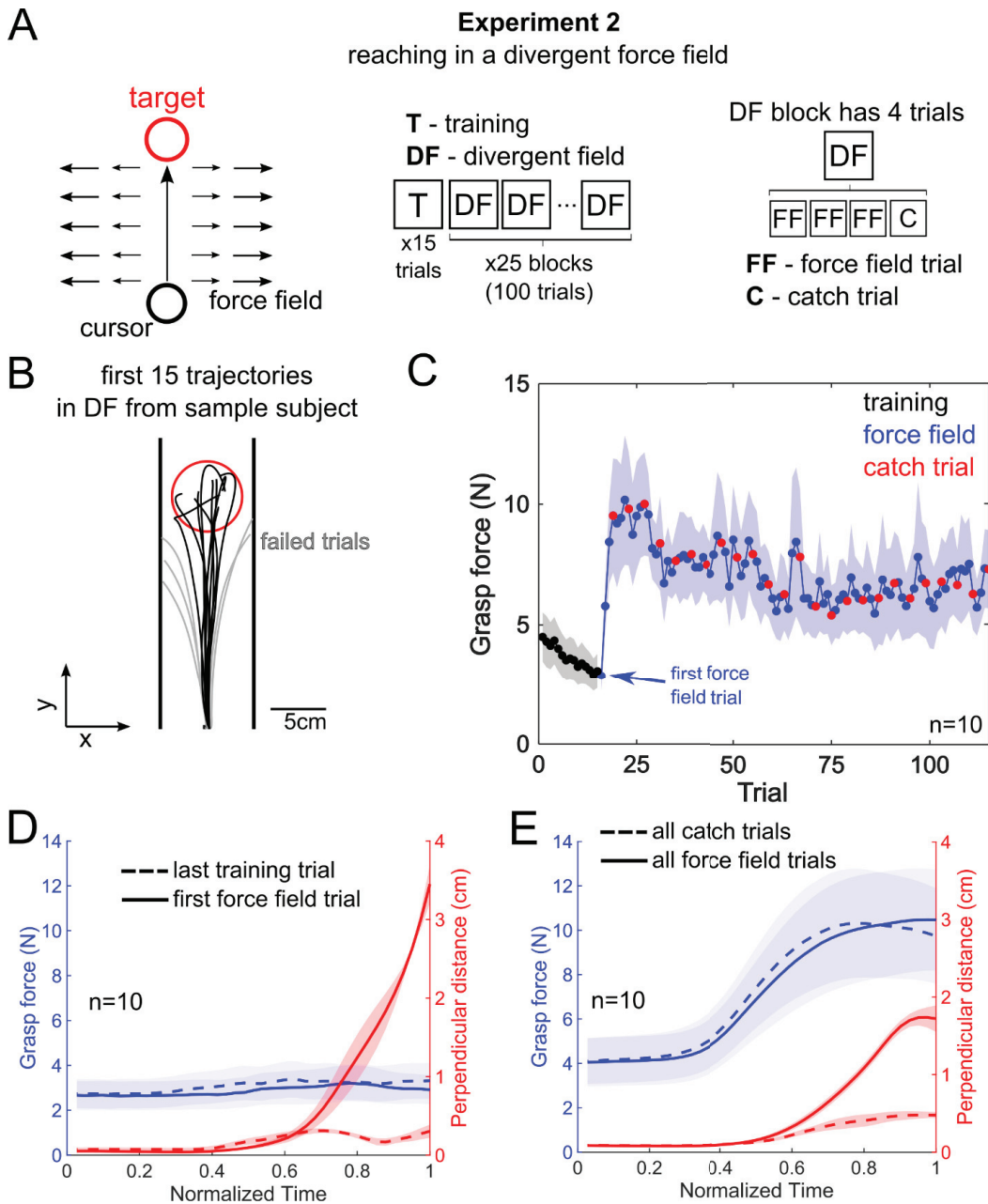
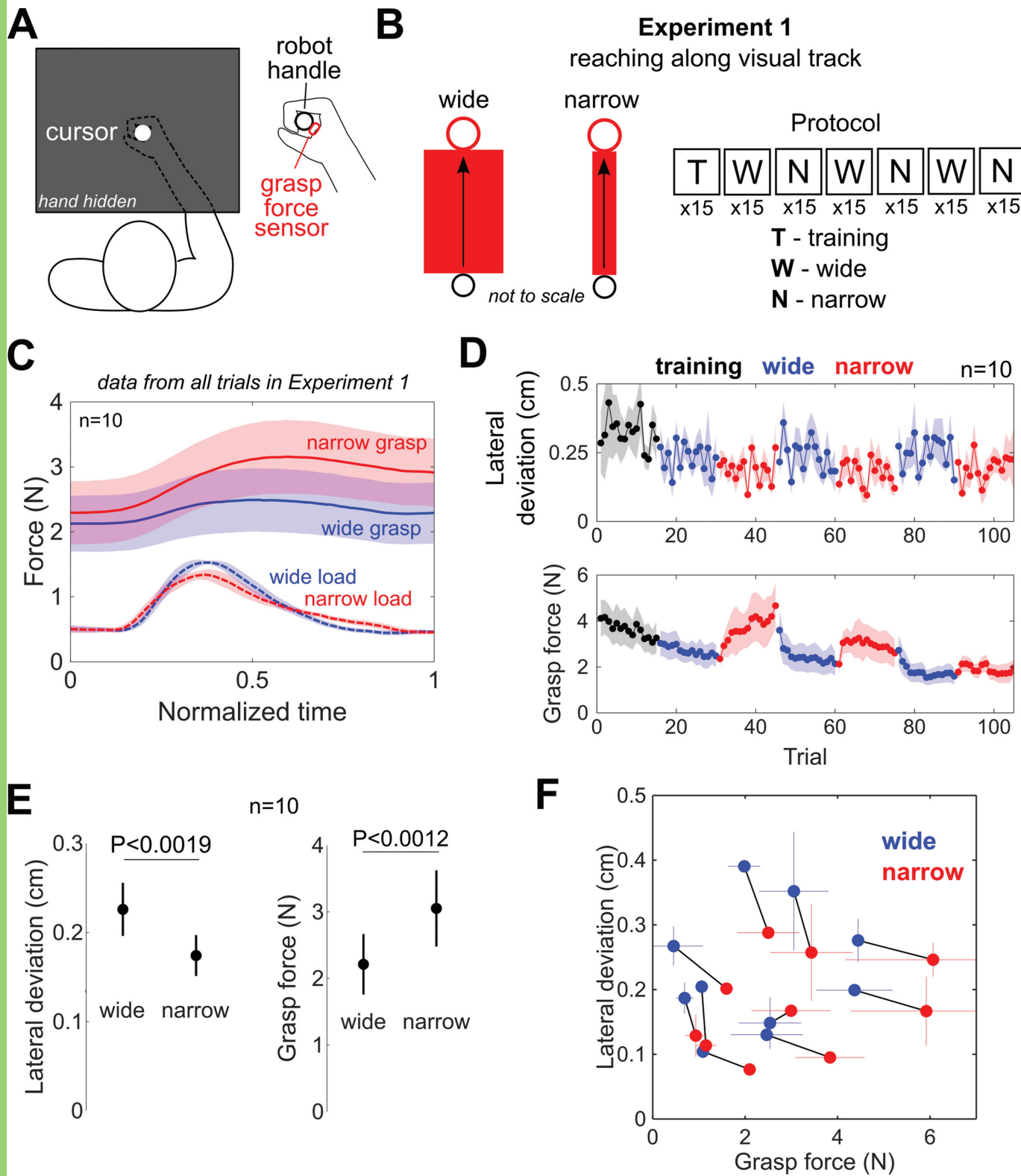
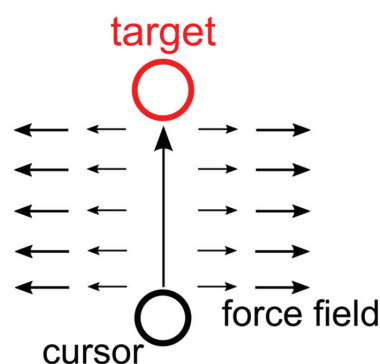


Figure 2. The divergent force field reaching experiment supports the hypothesis that the grasp force increases when better movement precision is desired, and not when the actual movement precision changes. (A) A schematic of the experiment and its protocol. The force field pushed the hand away laterally if it deviated from the line that connected the start and the target positions. To succeed, a subject must reach as straight as possible with minimum lateral

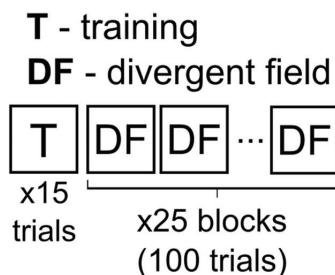
439 deviation. Subjects experienced 15 training trials in the null field conditions, after which they
440 experienced 100 force field trials. Of these 100 trials, every fourth trial was a catch trial where
441 the force field was switched off. (B) The first 15 trajectories in the force field trials from a
442 sample subject are shown, where the gray trajectories show failed trials where their hand hit the
443 safety margins placed 4cm to the left and right of the center line. A trial was successful when
444 subjects stopped inside the red target. (C) The mean grasp force from all subjects, averaged over
445 each trial, is plotted as a function of trials. In training trials (black), the grasp force continually
446 declines. The grasp force in the first force field trial is similar to the level observed in training
447 trials, but begins to increase until it peaks at approximately the 4th force field trial. Although the
448 grasp force declines during the force field trials, it never reaches the same level as the training
449 trials. Furthermore, the grasp force in catch trials is indistinguishable from the force field trials,
450 revealing that the grasp is not a reaction to the forces from the force field, but is premeditated.
451 (D) The group mean grasp force from the last training trial (dashed blue trace) and the first force
452 field trial (solid blue trace) are plotted as a function of normalized time. On the same figure, the
453 group mean perpendicular distance from the last training trial (dashed red trace) and the first
454 force field trial (solid red trace) are plotted as a function of normalized time. Even though the
455 perpendicular distance increased dramatically due to the force field, the grasp force remained
456 constant. (E) The group mean grasp force (blue traces) and the group mean perpendicular
457 distance (red traces) from all catch trials (dashed blue trace) and all force field trials (solid blue
458 trace) are plotted as a function of normalized time. The grasp force was similar between the
459 catch trials and the force field trials, even though the perpendicular distance was smaller in catch
460 trials where the force field was switched off.
461



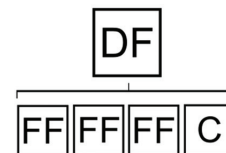
A



Experiment 2 reaching in a divergent force field



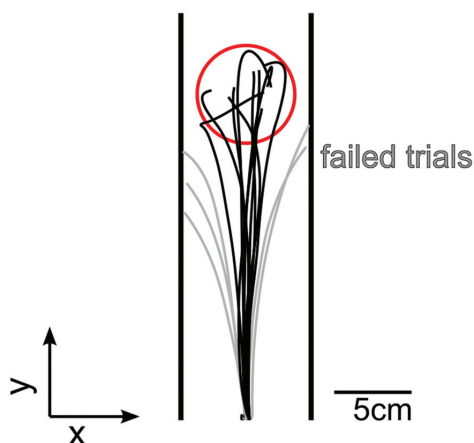
DF block has 4 trials



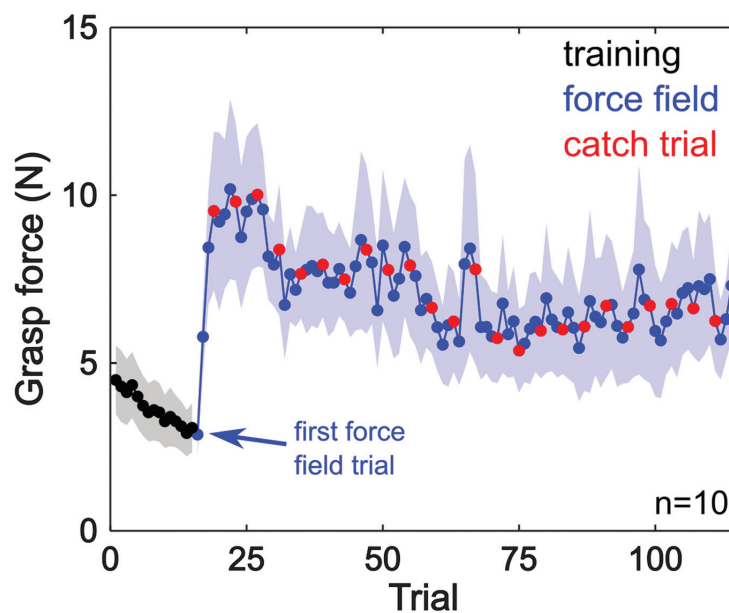
FF - force field trial
C - catch trial

B

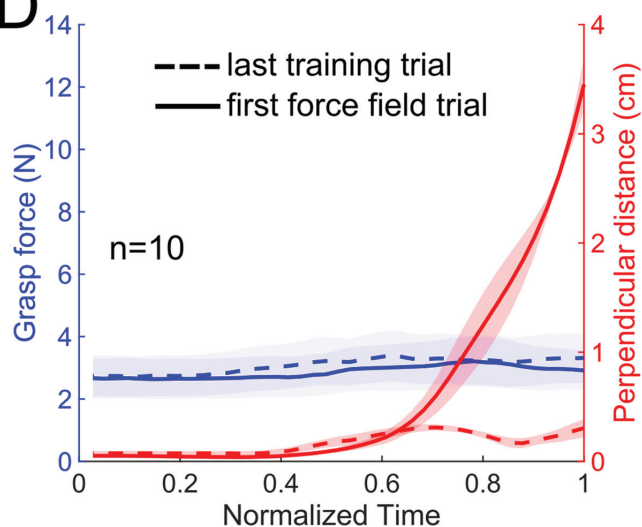
first 15 trajectories
in DF from sample subject



C



D



E

