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Hand Interactions in Rapid Grip Force Adjustments Are Independent of Object Dynamics

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White O, Dowling N, Bracewell RM, Diedrichsen J. Hand interactions in rapid grip force adjustments are independent of object dynamics. *J Neurophysiol* 100: 2738–2745, 2008. First published September 3, 2008; doi:10.1152/jn.90593.2008. Object manipulation requires rapid increase in grip force to prevent slippage when the load force of the object suddenly increases. Previous experiments have shown that grip force reactions interact between the hands when holding a single object. Here we test whether this interaction is modulated by the object dynamics experienced before the perturbation of the load force. We hypothesized that coupling of grip forces should be stronger when holding a single object than when holding separate objects. We measured the grip force reactions elicited by unpredictable load perturbations when participants were instructed to hold one single or two separate objects. We simulated these objects both visually and dynamically using a virtual environment consisting of two robotic devices and a calibrated stereo display. In contrast to previous studies, the load forces arising from a single object could be uncoupled at the moment of perturbation, allowing for a pure measurement of grip force coupling. Participants increased grip forces rapidly (onset ~70 ms) in response to perturbations. Grip force increases were stronger when the load force on the other hand also increased. No such coupling was present in the reaction of the arms to the load force increase. Surprisingly, however, the grip force interaction did not depend on the nature of the manipulated object. These results show fast obligatory coupling of bimanual grip force responses. Although this coupling may play a functional role for providing stability in bimanual object manipulation, it seems to constitute a relatively hard-wired modulation of a reflex.

INTRODUCTION

To lift an object, our fingers have to apply grip forces to the object that are sufficient to counteract both the gravitational and the inertial components of the load force acting on the fingertips (Johansson and Westling 1984). Often grip forces can be adjusted in a predictive fashion; for example, we increase grip forces just before we accelerate an object (Flanagan and Wing 1997; Flanagan et al. 2003) or before the object impacts a known obstacle (Johansson and Westling 1988; Serrien et al. 1999). However, in numerous situations, we must cope with unpredictable perturbations, and grip forces must increase very rapidly to prevent slippage. For example, when using a screwdriver on an unstable object, or when transporting a food item in a crowd of people, rapid and strong increases in grip forces may be needed to restore stability. Experimentally, participants respond with a grip force increase that peaks 80–100 ms after a sudden increase in load force (Johansson and Westling 1988; Turrell et al. 1999). This reflex response comprises a short-latency component of spinal origin (Johansson et al. 1994) and then a long-latency supra-spinal component (Cole and Abbs 1988; Johansson and Westling 1988).

In daily life, we often manipulate objects bimanually. When our two hands are linked through an object, the forces generated by one hand are transmitted through the object to the other hand. In these situations, we maintain stability by actively opposing these interaction forces through predictive increases in load and grip forces. Previous experiments have shown bimanual interaction in grip force control, indicated by a positive correlation between the grip forces of the two hands, both during voluntary and unpredictable load increases when holding a single object (Bracewell et al. 2003). In these experiments, however, the authors needed to account for the grip force coupling that was caused by the mechanical transmission of load forces through the object using a partial correlation. The authors found a positive intermanual correlation of grip forces in both the voluntary and reactive conditions; even once the effects of load force correlation were partialled out. This correlation was even stronger in the reactive condition.

During voluntary object manipulation, predictive grip force increases are observed on a hand holding an object, when the other hand acts on it. This predictive grip force control is strongly modulated by task requirements and prior experience (Blakemore et al. 1998; Witney and Wolpert 2003; Witney et al. 2000). When the intermanual dynamics change, this anticipatory mechanism adapts rapidly to maintain accurate predictions (Blakemore et al. 1998; Witney and Wolpert 2003, 2007; Witney et al. 2000). Here, we address the question of whether the reactive grip force coupling is also adaptive and dependent on the nature of the object that is manipulated or whether the grip force coupling is a fixed and immutable element of the human motor system. A number of prior studies have reported that the way we respond with both hands to a perturbation applied to one hand is dependent on task instruction and prior experience (Diedrichsen 2007; Marsden et al. 1981; Ohki et al. 2002). We therefore hypothesize that, when holding a single object, the system should increase the grip force of both hands when a perturbation is sensed on either of the hands, because a force perturbation to one hand is likely to be transmitted to the other. In contrast, this reaction would not be necessary when holding two separate objects. Thus the

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strength of grip force coupling may depend on the intermanual dynamics experienced just before the perturbation.

In this study, we measured the grip force reaction elicited by unpredictable load perturbations when participants held one object with two hands, or two separate objects. The visual and mechanical feedback from the objects was simulated using a virtual environment consisting of two robotic devices and a calibrated stereo display. Our apparatus allowed us to completely unlink the load force at the moment of perturbation even when a single object was simulated. Compared with previous studies (Bracewell et al. 2003), we therefore obtained a pure measure of grip force coupling independent of load force coupling. Furthermore, the technique allowed for a strong comparison between the one- and two-object conditions, which otherwise have very different dynamics. In *experiment 1*, we perturbed one or both hands with a rapid increase in load force in the downward direction. In *experiment 2*, the load force perturbation was applied in line with the principal axis of the object(s), such that the horizontal perturbation on one side was maximally transmitted to the other side.

METHODS

Participants

All experimental and consent procedures were approved by the ethics committee of the School of Psychology at Bangor University (United Kingdom). All participants had normal or corrected to normal vision and did not report any motor disabilities. Twelve volunteers (5 males; mean age, 23.5 yr) participated in the first experiment, and 10 new participants (mean age, 25.1 yr; 4 males) were recorded in the second experiment. They were naïve as to the purpose of the experiment and were debriefed after the experimental session.

Apparatus and stimuli

Participants were comfortably seated in front of the virtual environment equipment with their head on a chin rest. A horizontal crossbar stabilized the upper body and minimized interaction torques between left and right arm movements. Strain gauges transducers (Honeywell) embedded in a black Plastic-disk (material: Delrin, 30 mm thick, 40 mm diam) were mounted at the end of two robotic devices (Phantom 3.0, Sensable Technologies) (Fig. 1*A*) to record grip forces (range, 0–15 N; 0.01-N resolution). Participants looked into two mirrors that were mounted at 90° to each other, such that they viewed one LCD screen with the right eye and one LCD screen with the left eye. This stereo display was calibrated such that the physical locations of the robotic arms were consistent with the visual disparity information. Throughout the experiment, the position of the hands was indicated as three-dimensional (3D) gray spheres (8 mm diam) in the display (Fig. 1, *B* and *C*).

The 3D positions and forces of the robotic arms were controlled at 1,000 Hz to simulate either two separate objects (6 × 4 × 3 cm, 150 g) in each hand (Fig. 1*B*) or one object (12 × 4 × 3 cm, 300 g) held between the two hands (Fig. 1*C*). These objects could be translated and rotated without constraint and were simulated using Newtonian rigid-body dynamics (Baraff 1997). To allow for the stable simulation of inertial objects, the endpoint of the robot was attached to the virtual object via a simulated spring (stiffness, 800 N/m). Furthermore, the low-level routines of the robotic devices were rewritten, such that position and velocity were estimated using a Kalman filter. In this way, participants experienced the natural inertial and gravitational forces while manipulating the objects in the workspace. When a single object was simulated, participants also experienced the intermanual dynamics, i.e., a force applied by the left hand was transmitted through the object to the right hand.

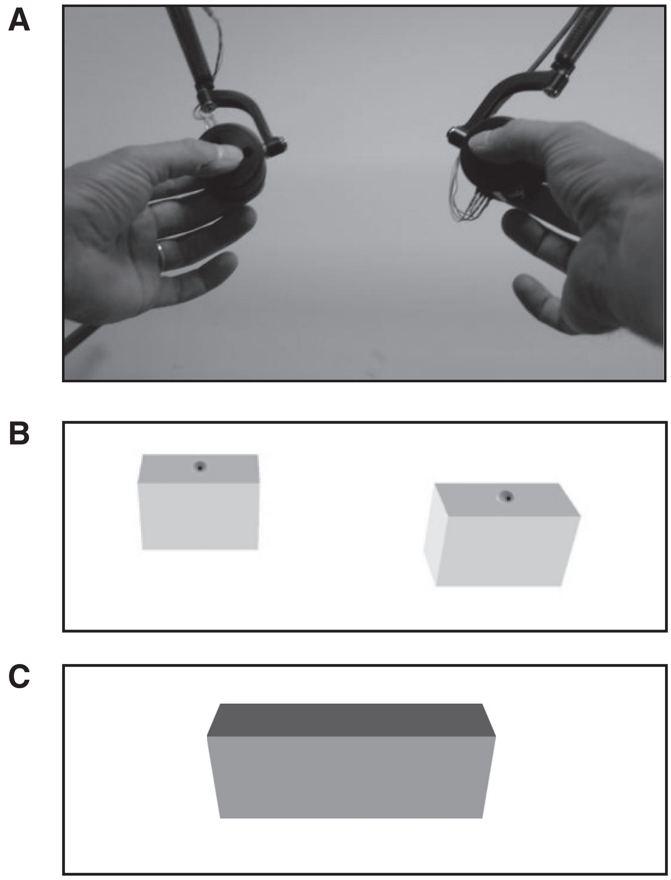

FIG. 1. Experimental apparatus. *A*: the participant held each grip force sensor attached to the robot arms with a precision grip (index finger opposing the thumb). During the experiment, the participants could see either 2 separate objects (*B*) or 1 object (*C*), and the corresponding object dynamics was simulated to calculate the forces produced by the robotic arm. The small spheres represent the location of the link between the object and the hand (hands not visible in *C*).

Experiment 1: vertical perturbations

To start a trial, participants moved their two hands into two gray starting spheres (8 mm diam), displayed 6 cm to the left and right of the body midline at breast height. In the two-object condition, two objects were attached to the hands, whereas in the one-object condition, a single object was suspended between the hands. In both conditions, two target spheres (gray, 8 mm diam) appeared simultaneously 12 cm above the home position. Participants were instructed to move the block(s) upward on to the target spheres. Once the participant had reached the target spheres, they were asked to hold the object(s) steady in that position using a relaxed grip. To ensure that participants did not increase the grip forces during this waiting period in anticipation of the perturbation, the color of the object turned red when either hand exceeded a grip force of >3 N. After a randomly assigned time period between 500 and 1,000 ms, a vertical force perturbation was applied to each side of the object. This perturbation was designed to mimic a rapid increase in the weight of the object by 0 (no perturbation), 33, 66, 100, and 133% (Fig. 2*C*). Load forces peaked ~80 ms after perturbation onset, followed by an oscillation induced by the simulated spring dynamics. When hand position changed by <25 mm, the participant was awarded a point, and the cumulative score was presented on the screen.

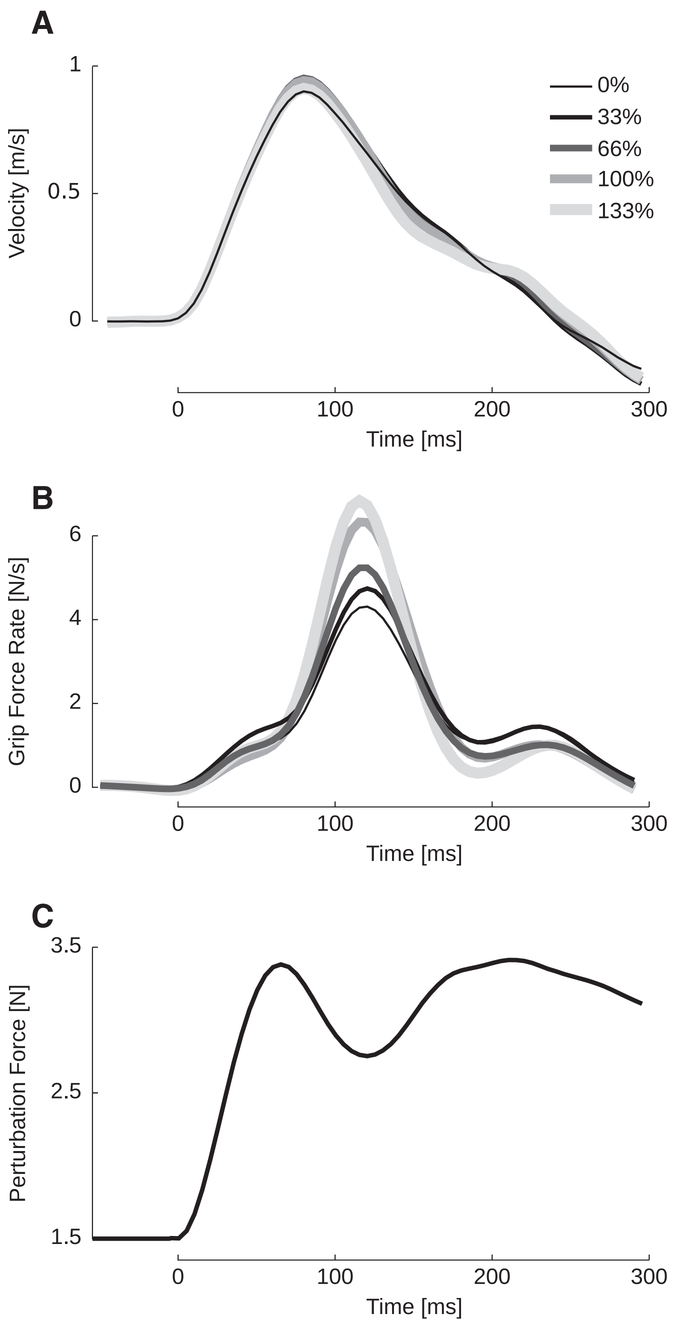

FIG. 2. Velocity (*A*) and grip force rate (*B*) profiles as a function of time when the hand is perturbed at a level of 100%. Profiles are averaged across participants, object conditions, and hands. Each line corresponds to a different level of perturbation of the other hand. *Time 0* is the onset of perturbation. *C*: force profile of the 100% vertical perturbations applied in *experiment 1*. The downward increases in load force for the 5 levels of perturbations (0, 33, 66, 100, and 133%) are scaled versions of this 100% force profile.

All 25 combinations of the five perturbation levels on the right and on the left hand were repeated twice each in a block. In a training block, participants familiarized themselves with the task and apparatus. They performed 20 trials in the one-object and 20 trials in the two-object condition. In these blocks, they experienced the natural object dynamics even after the perturbation. This was followed by six blocks of 50 trials, in which load forces were always decoupled during the perturbation. The object condition alternated between blocks, and their order was counterbalanced across participants.

Experiment 2: horizontal perturbations

Ten different volunteers participated in *experiment 2*. The apparatus, instructions, and task were identical to those used in *experiment 1*. However, because we did not find a modulation of grip force coupling based on the object dynamics in *experiment 1*, we made two changes. First, the perturbations were applied horizontally, in line with the principal axis of the single object, such that they would be maximally transmitted through the object. Second, catch trials in which the natural object dynamics was interrupted at the moment of perturbation were embedded in trials in which the natural object dynamics persisted. We used eight different patterns of horizontal perturbations (Fig. 4*A*). In Unilateral trials, only the left hand or the right hand was perturbed sideways, resulting in four combinations. In the two Opposite trials, the forces applied to each hand were in opposite directions. The two Same trials induced perturbations of both hands in the same direction. We used a sigmoidal perturbation profile (Fig. 4, *B* and *C*, dashed line) that was similar in the first 80 ms to the one used in *experiment 1*.

Each of the eight perturbations was presented six times per block, and participants performed 16 blocks of 48 trials. In every block, 16 trials were randomly chosen to be catch trials in which the physical link between the two hands was removed. In the remaining 32 trials, the natural object dynamics remained intact. The object condition was alternated every two blocks, and the order was counterbalanced across participants. As in *experiment 1*, the participant was awarded a point when hand position was perturbed by <25 mm.

Data analysis

Position and grip forces were recorded at 200 Hz. The load forces were inferred from the commands to the robot motors. In a control experiment in which we pushed the grip force transducers against a stiff surface using the robot motors, we determined the internal delay between sending the force command and the force and kinematic measurements to be 15 ms. Therefore the load force trace was shifted in time accordingly. Grip force rate and velocity were obtained using a central-difference algorithm. All trials were aligned to the onset of the perturbation. We averaged the grip force and velocity traces for each participant, hand, and condition and determined the time and value of the maximal grip force rate and velocity on these averaged traces. By convention, velocity was positive in the direction of the perturbation.

A three-way repeated-measures ANOVA was conducted on peak grip force rates and peak velocities to assess the effects of perturbation level on one hand, perturbation level on the other hand, and object condition. The data were tested for sphericity with Mauchly's test. If sphericity was violated, the degrees of freedom were adjusted as necessary with the Greenhouse-Geisser method. Paired *t*-test of individual subject means were used to investigate differences between object conditions on the above variables. The values reported in the text are mean ± SD. The statistical analysis was done using the SPSS package (SPSS, Chicago, IL).

RESULTS

In the first experiment, we simulated the interaction forces arising from either a single object or from two separate objects in a virtual environment. We perturbed one or both of the hands with a rapid increase in vertical load force. At the moment of perturbation, the load forces of the two hands were always uncoupled, allowing us to assess grip force coupling in the absence of any load force coupling.

The load force increases led to a rapid downward perturbation of the hand. Figure 2*A* shows the downward velocity of the right hand for the 100% perturbation, averaged over hands, object conditions, and participants. The downward velocity was independent of the perturbation level of the other hand, as shown by the overlapping lines in Fig. 2*A*. To quantify this observation, we determined the peak velocity for each participant, hand, perturbation, and object condition on the average trace. Peak velocity occurred on average 85.3 ± 4.3 ms after the onset of the perturbation. The mean peak velocities (Fig. 3*A*) were submitted to a repeated-measures ANOVA with the factors perturbation level, perturbation level on the other hand, hand (left vs. right), and object condition (1 vs. 2 objects). As expected, the peak velocity increased with increasing perturbation level ($F_{4,44} = 440$, $P < 0.001$). We found that the left hand showed on average higher peak velocities than the right hand ($F_{1,11} = 112.6$, $P < 0.001$). However, the peak velocity was independent of the object condition ($F_{1,11} = 0.06$, $P = 0.817$), and most importantly, was also independent of the level of perturbation to the other hand ($F_{4,44} = 1.4$, $P = 0.234$). These findings show that the two arms reacted independently to the load force perturbation, making the physical situation on the finger–object interface identical across different perturbation and object conditions. Therefore any modulation or coupling of grip forces has to arise from grip force control per se, rather than being caused indirectly by differences in the sensory input to the fingertips, such as the occurrence of microslips.

Given the independence of the perturbations to the arms, we now turn to the main focus of this experiment, the coupling of grip forces. The average grip force rate for a 100% perturbation of the right hand, averaged over object conditions and participants, shows the rapid and stereotypical increase, starting ~70 ms following the perturbation. The peak grip force rate was observed on average 131 ± 12 ms after perturbation onset. The slightly slower time course in comparison to previous studies is likely because of the less rapid increase in load force used here.

In contrast to the velocity of the arm, grip force rates showed a clear dependence on the level of perturbation to the other hand: the higher the perturbation on the contralateral side, the more rapidly grip forces increased (Fig. 2*B*, separate lines). To determine the strength of the influence of one hand onto the other, we plotted the peak grip force rates as a function of the perturbation level of the other hand (Fig. 3*B*). The slope of the lines can be interpreted as a measure of the coupling strength and was estimated separately for participants, hands, object conditions, and perturbation levels. Consistent with previous results, we found positive slopes ($t_{11} = 4.6$; $P = 0.001$) in the one-object condition. Furthermore, the strength of the interaction between grip force rates increased with increasing levels of perturbation; an ANOVA showed a significant increase of the slope with increasing perturbation levels on the hand ($F_{4,44} = 4$; $P = 0.008$). Thus our experiment provides clear evidence for coupling of grip force in the absence of load force coupling and shows that this interaction—at least as measured by grip force rate—is nonlinear rather than purely additive.

Importantly, if the coupling between grip force reactions was dependent on the participant's current estimate of object dynamics, we would have expected less coupling when holding two objects. However, we also observed positive slopes in the two-object condition ($t_{11} = 3.9$; $P = 0.002$), which did not differ from the slopes observed in the one-object condition ($F_{1,11} = 1.7$; $P = 0.217$). Thus the overall strength of bimanual coupling did not depend on the estimated dynamics of the held object.

Unexpectedly, however, we found an interaction between object and perturbation level on the hand ($F_{4,44} = 3.8$; $P = 0.01$). Indeed, the slopes for the one- and two-object conditions were identical for the lower levels of perturbations but diverged beginning with the 100% perturbation level. In other words, the interaction was driven by the fact that when both hands were perturbed strongly, grip forces increased less rapidly when the participants held a common object than when they held two separate objects.

In sum, grip force coupling was not modulated by the object condition. We had hypothesized that grip force coupling would have been reduced in the two-object condition, but we found that strength of the coupling was even slightly higher for the two-object condition for the stronger perturbation levels.

Before considering possible reasons for these findings, we addressed two limitations of the first experiment that might have prevented us from observing the predicted modulation. First, at the moment of perturbation, the load forces were always uncoupled (all trials were catch trials). It is therefore possible that participants learned that it did not matter whether they held one or two objects, hence attenuating any differences in grip force control. Second, because we applied the perturbations downward, the object could rotate freely in reaction, preventing a transmission of the forces to the other side. Therefore, although the object never slipped out of the grasp,

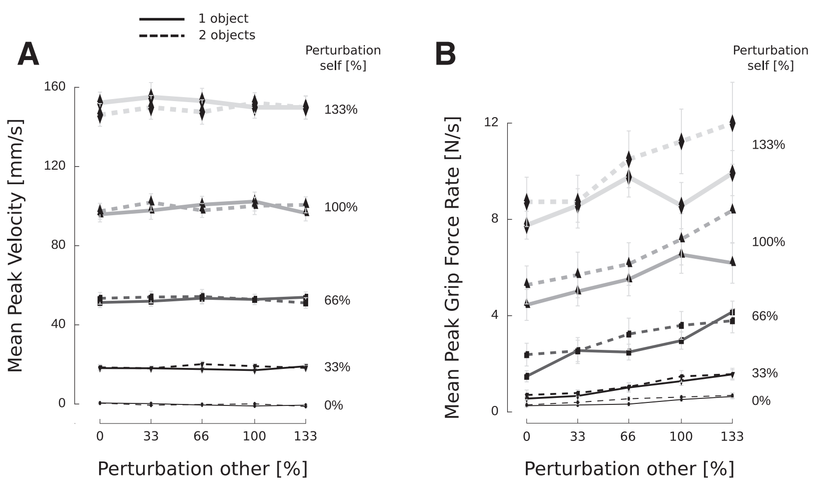

FIG. 3. Mean peak velocities (*A*) and peak grip force rates (*B*) of the perturbed hand, categorized by level of perturbation (*right*) as a function of the perturbation on the other hand. The 1-object and 2-object conditions are represented by solid and dashed lines, respectively. Error bars are between-subject SE.

bilateral grip force increases were suboptimal to prevent slippage. One might predict stronger grip force coupling in a situation in which load forces are transmitted maximally through the object.

In the second experiment, we addressed these two issues. First, we left the natural object dynamics intact on two thirds of the trials and only used one third of the trials as catch trials in which the load forces were artificially uncoupled to test the grip force interactions. Even if grip force interactions could adapt rapidly to the combination of perturbations on the last trial, participants would experience a difference in dynamics during most of the trials and any difference between the one- and two-object conditions should now become apparent. Second, we wanted to create a situation in which one would predict a strong and specific modulation of the grip force coupling with changing object dynamics. Therefore the load force perturbations were applied laterally, in line with the major axis of the virtual single object. Specifically, the robots either perturbed one hand (Fig. 4*A*, Unilateral), or both hands either in the same direction (Same) or in opposite directions (Opposite). These perturbations lead to very different consequences depending on the nature of the object. In the two-object condition, the resulting load forces were independent of the perturbation on the other hand, as shown by the overlapping lines (Fig. 4*B*). In contrast, in the one-object condition, pulses were transmitted through the object (Fig. 4*A*). Opposing force pulses quickly cancelled each other out after the simulated springs between the hands and object started to be stretched. This was not the case when the force pulses were applied in the same spatial direction. Catch trials were identical in the two object conditions (Fig. 4, dashed lines). Therefore we can make specific predictions about the optimal grip force modulation in the one-object condition: grip force should increase less for perturbation in opposite directions compared with perturbations in the same direction.

Figure 5 shows the average grip force rate profiles for the three different types of perturbations. When holding one object under natural dynamic conditions, the average grip force rate response was maximal when the object was perturbed on both sides in the same direction (Fig. 5*A*, Same, gray solid line; 16.7 ± 9.9 N/s). When the load forces opposed each other (Fig. 5*A*, Opposite, gray dotted line), the perturbations cancelled out and grip force increases were minimal (3.5 ± 3.3 N/s). When the object was perturbed only on one side, the perturbed (Fig. 5*A*, Unilateral, black solid line; 7 ± 6.4 N/s) and the nonperturbed (Fig. 5*A*, Unilateral, black dotted line; 6.1 ± 5.8 N/s) hands both increased their grip force as the forces were transmitted through the object. In the two-object condition (Fig. 5*B*), there was no mechanical link between both sides. Grip force rate responses were equivalent in the Opposite and Same perturbations ($t_9 = -1.1$; $P = 0.289$, 17.2 ± 10.2 vs. 16.3 ± 8.9 N/s, respectively). In sum, under natural dynamics, participants showed a clear difference in the grip force increases when holding a single versus two separate objects.

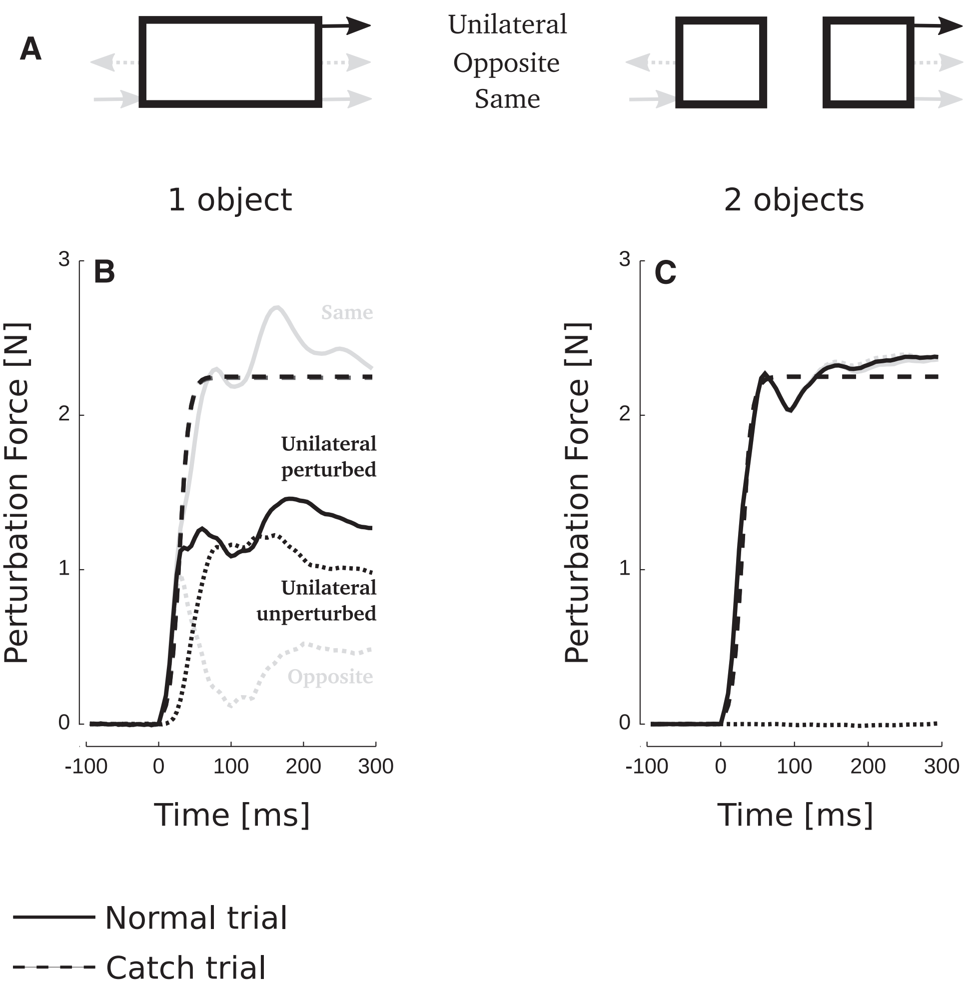

FIG. 4. *A*: sketch of the patterns of horizontal perturbations in *experiment 2*. Force perturbation profiles in the 1-object (*B*) and 2-object conditions (*C*). The Unilateral, Opposite, and Same perturbations are represented in black, dotted gray, and solid gray lines, respectively. For the Unilateral perturbation, the perturbed (solid line) and unperturbed hand (dotted line) are shown separately. The perturbation in catch trials are shown in dashed black lines and are similar in the 2 object conditions. Perturbations are averaged across hands and perturbation directions.

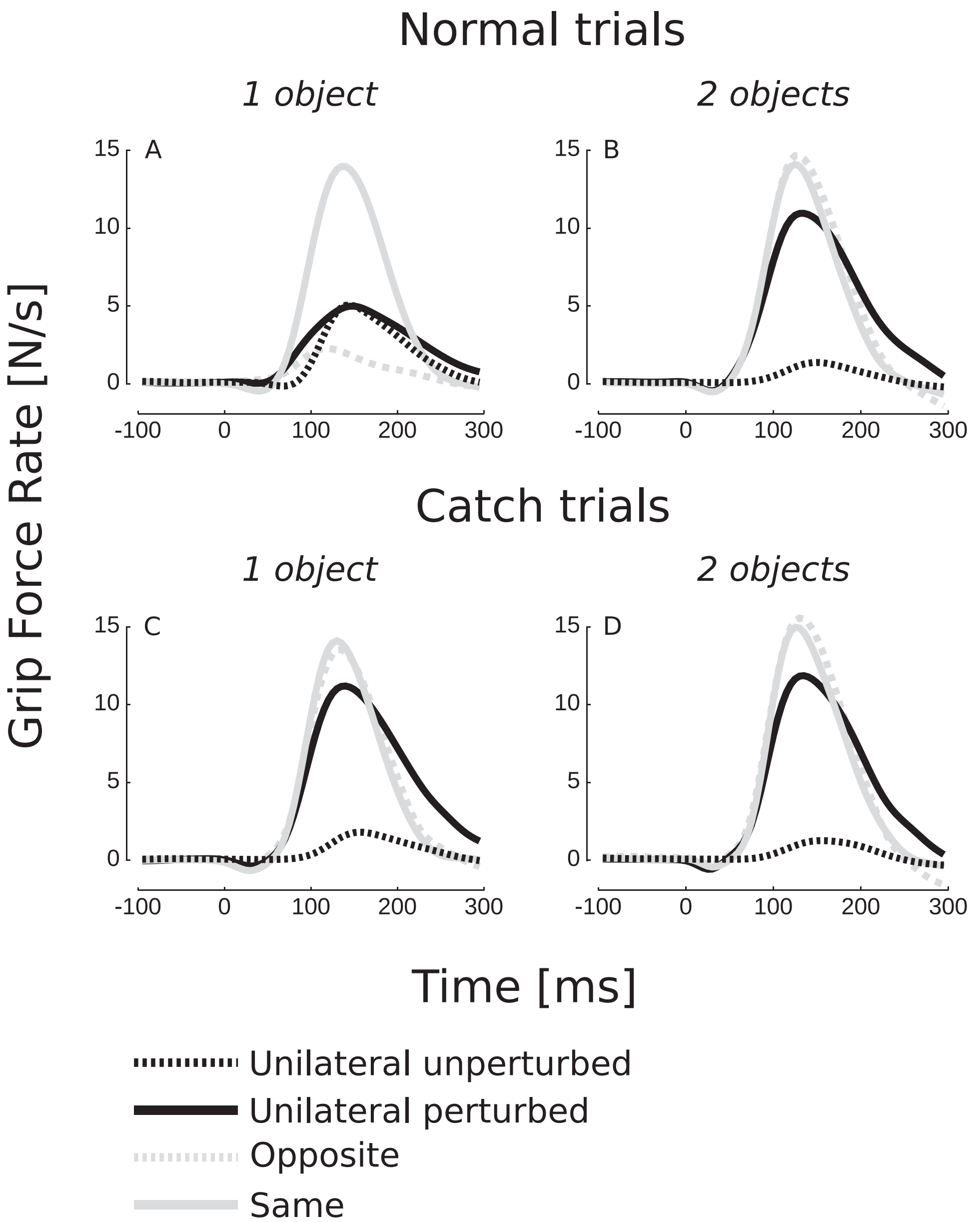

FIG. 5. Averaged grip force rate profiles as a function of time in normal trials (*A* and *B*) and catch trials (*C* and *D*) for the 1-object (*A* and *C*) and 2-object conditions (*B* and *D*). Unilateral, Opposite, and Same conditions are represented in black, dotted gray, and solid gray, respectively. In the Unilateral case, the unperturbed hand is shown in black dotted lines. *Time 0* is the onset of perturbation.

On catch trials, the natural dynamics of the simulated object was interrupted (Fig. 5, *C* and *D*). In this way, we were able to measure any object-dependent change in grip force rate control under identical load force conditions at the moment of perturbation. As in *experiment 1*, the induced displacement of the hands was independent of the perturbation to the other hand. Peak velocity occurred on average 118.2 ± 8.2 ms after perturbation onset. The average peak velocities were the same across the three perturbation conditions, Unilateral, Opposite, or Same ($F_{2,18} = 2.1$; $P = 0.152$), and across object conditions ($t_9 = 0.9$; $P = 0.379$).

The results for the average peak grip force rate confirm and extend our findings in *experiment 1*. The peak grip force rates were observed on average 135 ± 19 ms after perturbation onset. We found higher grip force rates when both hands were perturbed (Same and Opposite conditions, 17 ± 9.3 vs. 17 ± 10.3 N/s, respectively) than when only one hand was perturbed (Opposite vs. Unilateral: $t_9 = 6.2$, $P < 0.001$; Same vs. Unilateral: $t_9 = 6.8$, $P < 0.001$; 14.6 ± 11 N/s). In contrast, we found no difference between Opposite and Same perturbations ($t_9 = 0.1$; $P = 0.96$). We also again found a small increase in grip force on the unperturbed side (Fig. 5*B*, Unilateral, black dashed line; $t_{39} = 4.8$, $P < 0.001$, 1.8 ± 3.37 N/s). These results replicate the coupling of grip forces, again consistent with the results found in *experiment 1*.

This grip force coupling was not modulated by the type of object because object condition did not interact with the type of perturbation ($F_{2,18} = 1.9$; $P = 0.18$). Therefore our second experiment also failed to find a specific modulation of bilateral grip force coupling based on estimated object dynamics. However, when both hands were perturbed, grip force increased less rapidly in the one-object than in the two-object condition (16.2 vs. 17.9 N/s; $F_{1,9} = 5.6$; $P = 0.043$).

In *experiment 2,* we analyzed two additional aspects of grip force coupling. First, we found a significant positive correlation between peak grip force rates on the left and right hand within each perturbation condition ($r = 0.54$). In line with our other findings, this correlation was the same for the one-and two-object conditions (t_{19} = 1.5; P = 0.147). Second, we thought to determine whether the grip force increase on the current trial was influenced by the immediate history of perturbation. We analyzed the peak grip force rates on the perturbed hand, depending on whether the previous perturbation was on the same, the other, or both hands. The ANOVA failed to show an effect of the previous perturbation ($F_{2,18}$ = 1.7; P = 0.208) or an interaction between the previous trial and the current trial ($F_{4,36}$ = 1.1; P = 0.92).

To summarize, *experiment 2* confirmed the observations made in *experiment 1*. First, grip force reactions of the two hands interact through a very rapid mechanism. Although this coupling was nonlinear and more apparent for higher levels of load force perturbations, it was visible already when only one hand was perturbed. Second, we did not find evidence that the strength of the grip force coupling was modulated in an object- or directional-specific fashion. However, for trials in which both hands were perturbed, we observed in the two experiments that grip force increases were slightly slower when one object rather than two objects were manipulated.

DISCUSSION

In two experiments, we studied whether the fast coupling between reactive grip force increases of the hands is a fixed element of the human motor system or whether it is adaptive and dependent on the nature of the object that is manipulated. When our hands are linked through an object, the forces generated by one hand are transmitted through the object to the other hand. Therefore it is reasonable to assume that we maintain stability in these situations by increasing grip forces of both hands when a perturbation is only experienced on one of the hands.

We replicated and extended previous results showing a clear bimanual grip force interaction when holding a single object that underwent a sudden vertical load force increase (Bracewell et al. 2003). In that earlier study, grip force coupling was not directly observable; the authors needed to take into account the load force coupling by using a partial correlation analysis. Here, we showed that grip forces are still coupled even when the load forces are unlinked at the moment of perturbation. Furthermore, we also showed that bimanual grip force interactions are present when only one hand is perturbed (e.g., Unilateral perturbations in *experiment 2*) and that this interaction increases nonlinearly with the strength of the perturbation.

We hypothesized that the strength of coupling between grip force reactions would depend on the intermanual dynamics experienced just before the perturbation. Specifically, we tested two predictions about the possible modulation of grip force across hands. First, we expected that this modulation would be reduced when manipulating two separate objects; in this case, increasing grip force on the unperturbed hand would not improve overall stability. Second, we hypothesized that grip force coupling in the one-object condition would be directionally specific. In particular, opposing lateral perturbations to both sides of a single object should not require any grip force increases, whereas lateral perturbations in the same direction should require grip force increases. We failed to find evidence to support our two predictions. This indicates that reactive grip force coupling arises from a relatively fixed mechanism that could be attributed to the existence of a strong neuronal coupling at a low level of the motor control hierarchy (Bracewell et al. 2003).

These findings contrast strongly with the flexibility of bimanual grip force coupling during voluntary object manipulation where predictive grip force control is highly modulated by task requirements and prior experience (Blakemore et al. 1998; Witney and Wolpert 2003; Witney et al. 2000). Predictive grip force responses are also modulated by the prior experience of external perturbations to one of the hand (Witney and Wolpert 2007), whereas our results indicate that the opposite is not true; reactions to external perturbations were not modulated by the prior experience of object dynamics. Therefore our findings clearly indicate separate mechanisms for grip force coupling during these voluntary actions and in reaction to perturbations.

Furthermore, our results also contrast with a number of findings that show that medium-latency reflex responses can be changed depending on prior instruction (Kimura et al. 2006) and task goals (Pruszynski et al. 2008). More specifically, previous work has highlighted how the nature of the task can alter the coupling of bilateral feedback responses. For example, the fast feedback correction of an arm in response to a perturbation of the other arm can be changed, depending on whether both hands control one common or two separate visual cursors (Diedrichsen 2007) or depending on the object held in the unperturbed hand (Marsden et al. 1981). In a study by Ohki et al. (2002), participants were instructed to prevent motion of plates with the index fingers of the two hands by pressing down on them. The two plates could be translated together or one at a time. The participants showed fast bilateral responses to unilateral perturbations, but only if they had experienced many bilateral perturbations on previous trials. The difference between these prior studies (Diedrichsen 2007; Marsden et al. 1981; Ohki et al. 2002) and this experiment suggests a qualitative difference between the coupling of grip force reactions and the coupling of feedback responses that involve the production of net force in a specific spatial direction.

We can only speculate why grip force coupling seems to be task independent, whereas directional reaction to perturbations can be flexibly modulated (Diedrichsen 2007; Diedrichsen et al. 2003; Marsden et al. 1981; Ohki et al. 2002). Tight grip force coupling may have had advantages during our evolutionary history, in which the two forelimbs were often used to support the body weight or for bimanual grasp of objects. As we evolved to perform more independent actions with the two hands, there was strong benefit to be able to guide arm movements independently toward separate spatial targets. In contrast, the cost of superfluously increasing grip force on a hand that is not affected by a perturbation is negligible. Thus it remains an open question whether humans can modulate the bilateral coupling of grip forces when there are strong costs attached to the failure to do so.

There was, however, one task-dependent modulation in bimanual grip force control: in both experiments, for high perturbation levels on both hands, grip forces increased more rapidly when participants manipulated two separate objects than holding a single object. One likely explanation for this effect is that reflex gains were regulated differently in the one- and two-object conditions, because the cost of a slip is different in these two situations. The consequence of losing grip on an object held with one hand is likely to be more severe than that of losing only one side of one object, because in the latter case, the other hand can still potentially prevent the object from falling. Thus our results may provide some evidence for a modest modulation of the gain of grip force reflexes with task demands.

Finally, our findings raise the question of where in the neural hierarchy these bilateral interactions arise. The short latency of unimanual grip force reactions of about 60–70 ms suggests a subcortical origin of the reflex. However, Kourtis et al. (2008), recently showed that the evoked EEG response in sensorimotor cortex peaks 58 ms after the onset of an unpredictable perturbation, early enough to make a major contribution to the early EMG activity in hand muscles. Thus it seems that grip force reactions have a strong cortical component, additionally to contributions of spinal, brain stem, and cerebellar circuits (Ehrsson et al. 2007; Johansson et al. 1994).

Where in this hierarchy does the coupling between the two hands occur? Coupling of grip force reflexes may be caused dominantly by bilateral cross-talk in subcortical structures such as the reticular formation or the cerebellum. Alternatively, coupling may be established through cross-talk between two cortical areas across the corpus callosum. The very early onset of the coupling and the apparent inflexibility to changes in object dynamics may be counted as evidence in favor of a subcortical origin. The critical test, however, would be to show that coupling of grip force responses as measured in *experiment 1* is preserved after transection of the corpus callosum. Such a finding would contrast with grip force coupling during voluntary force production, during which force coupling between the fingers is strongly reduced or absent in callosotomy patients (Diedrichsen et al. 2003).

Previous findings also indicate that grip force coupling was stronger in reactive than in predictive tasks (Bracewell et al. 2003), and we show here that reactive coupling is not modulated by the nature of the manipulated object. Together these findings suggest a relatively low-level and inflexible mechanism of reactive grip force coupling that has matured during evolution to ensure stability during bimanual object manipulation. The theoretical challenge in the future, not only for theories of grip force control but for theories of motor control in general, is to explain how task-dependent and voluntary control interacts with faster and less flexible control structures.

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