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Predictive Mechanisms Control Grip Force after Impact in Self-Triggered Perturbations

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ABSTRACT. Impulsive loadings during object grasping are common in everyday life. In predictable conditions, the grip force (GF) increases before the impact to anticipate the perturbation and reaches a maximum after the perturbation. In the present study, the authors addressed the predictive or reactive nature of this late GF component. The load of a handheld object was briskly increased by dropping a mass attached to the object (impact trials). The drop was self-induced, but for one third of the trials, the mechanism was blocked and no impact occurred (blank trials). Evidence that the late GF component is programmed as a predictive action emerged from a systematic comparison between impact and blank trials. The authors conclude that the GF increase occurring after a predictable impulsive loading is essentially of a predictive nature.

Keywords: collision, motor control, precision grip, programming

Sudden changes in force when grasping an object, such as when a dog kept on a leash catches sight of a cat a few meters away or when a heavy bag tears apart in a supermarket, are common in everyday life. These changes in force can be unpredictable or expected, depending on whether an individual can anticipate the perturbation and adapt the motor behavior to minimize disturbances.

The ability to anticipate rapid load increases has been widely studied in the field of precision grip during the past 20 years (Eliasson et al., 1995; Johansson & Westling, 1988b; Turrell, Li, & Wing, 1999; Witney, Goodbody, & Wolpert, 1999). Holding an object between the thumb and index fingers requires good coordination of the grip force (GF) and tangential load force (LF; Westling & Johansson, 1984). This precise coordination is due to (a) predictions of the movement to generate an adequate GF (Blakemore, Goodbody, & Wolpert, 1998; Flanagan & Wing, 1997; Witney, Wing, Thonnard, & Smith, 2004) and (b) the ability to update these predictions by way of reactive mechanisms (Gordon, Forssberg, Johansson, & Westling, 1991; Johansson & Wesling, 1984, 1988a). However, in the context of rapid force changes that can be considered transient perturbations, the short duration of the LF increase does not allow a reactive correction to ensure a secure grasp (Delevoye-Turrell, Li, & Wing, 2003). Therefore, any strategy for avoiding slippage must be anticipative.

It is generally accepted that well-timed anticipation should allow a perfect synchronization between the impact (LF maximum) and the maximal GF (Witney et al., 1999). In addition, the ability to anticipate a collision can be closely linked to visual cues available to the subject (Delevoye-Turrel et al., 2003). However, in situations in which a self-generated collision was applied to a participant's static arm, the maximal GF often occurred later than the maximal LF (Delevoye-Turrell et al.; Eliasson et al., 1995; Johansson & Westling, 1988b; Nowak & Hermsdorfer, 2006; Serrien, Kaluzny, Wicki, & Wiesendanger, 1999). This reactive response to the impact, a late component of GF, is called an *automatic long-latency response.* (Delevoye-Turrell et al.; Johansson & Westling; Serrien et al.).

Using a drop-ball task to investigate rapid load changes, Johansson and Westling (1988b) described this GF component as "triggered by somatosensory input elicited by the impact" under both predictive and reactive conditions (p. 73). Consequently, they suggested that similar neural pathways are engaged in predictive and reactive conditions. Johansson and Westling recorded stronger responses on EMG when the participant could not anticipate the drop of the ball. They suggested that, in predictive conditions, the preparatory actions "caused a decreased excitation of the motoneurones" (p. 83). Surprisingly, although Johansson and Westling presented this response as having been triggered by the impact, some trials under predictive conditions in which the impact was prevented still led to an increase in GF after impact (see Figure 4). Although they did not specifically address this result, their results call into question the reactive nature of the response. This is further supported by the irregular occurrence of this GF component after a collision under certain conditions (Delevoye-Turrell et al., 2003).

The aim of the present study was to unambiguously assess the predictive nature of this late component of GF. To this end, we designed a task in which participants had no visual cues to anticipate the collision, allowing for the use of unexpected blank trials during which no collision occurred. If the response is purely reactive, as described in the literature, an unexpected absence of collision should lead to an absence of GF increase after impact. Conversely, we hypothesized that the unexpected lack of collision should lead to a persistent GF increase after impact in blank trials, which should demonstrate the predictive nature of this response. The originality of our study is the characterization of this response by the thorough study of its delay, amplitude, and other features in the absence of stimulus.

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Method

Participants

Participants were 30 adults aged between 22 and 58 years (*M* age = 34.6 years, *SD* = 11.2 years; 15 men, 15 women) who presented no hand disease or injury. This study was authorized by the Ethical Committee of the Université catholique de Louvain. Participants gave their informed consent.

Materials: Grip Task Apparatus

The instrumented object used to measure fingertip forces was a cylindrical object (80-mm diameter, 30-mm height, 220-g mass) equipped with two brass circular grip surfaces (40-mm diameter) placed on two parallel lightweight force-torque sensors (Mini40 F/T transducer, ATI Industrial Automation, NC). Normal GF and tangential LF were calculated on the basis of the three force components (Fx, Fy, Fz) measured by each sensor (Figure 1A). Fx, Fy, and Fz sensing ranges were ±40, ±40, and ±120 N, with 0.002, 0.002, and 0.006 N resolution, respectively. LF was defined as $LF = LF_1 + LF_2$, where $LF = \sqrt{F_x^2 + F_y^2}$ for each sensor (i = 1, 2).

This instrumented object was placed on an open table (see Figure 1B), and a steel mass (100 g) was attached to the instrumented object by way of a Kevlar string (1.5 mm diameter). The mass was then placed on an electromagnet. Once the electromagnet was on and the mass was placed on it, the string was free and the object could be lifted without any influence of the additional mass.

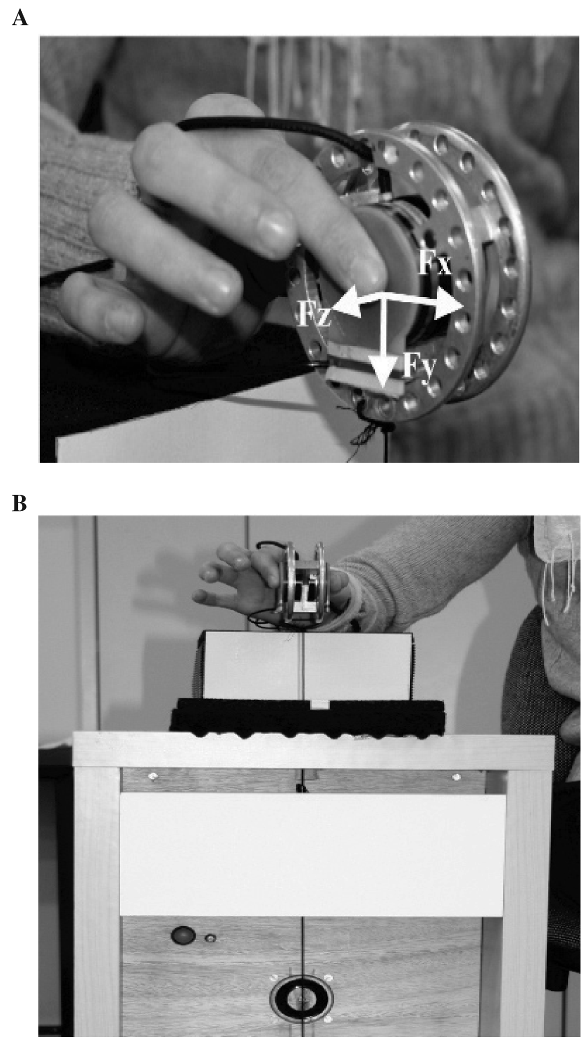

FIGURE 1. (**A**) The three force (Fx, Fy, Fz) components measured by each sensor of the hand-held object and (**B**) the apparatus showing the object, arm support, open table, Kevlar string, additional mass, and electromagnet.

Procedure and Experimental Protocol

Participants were first asked to wash and dry their hands. The task was then clearly described to them. Participants sat next to the table that provided support to the forearm of their dominant hand (see Figure 1B). While keeping their forearm on the support, the participants were asked to grasp the instrumented object with a precision grip and maintain it in a given position.

Participants held a push-button switch with the nondominant hand. When participants pressed this switch in response to an auditory signal it instantaneously turned off the magnetic field and led to a 4-cm drop of the mass followed by a sudden increase in LF (impact trials). For one third of the trials, the release mechanism was unpredictably blocked and no drop occurred (blank trials).

Each participant performed 15 consecutive trials with the dominant hand according to the following sequence: 5 impact trials, 5 blank trials, and 5 impact trials. The 5 consecutive trials allowed us to study the evolution of the responses within each block. More important, the participants were not aware that a transition between blank and impact trials would occur. Therefore, we considered Trials 1, 6, and 11 *catch trials*.

Data Acquisition and Analysis

The analysis focused on the *impact phase*, which we defined as the period including the impact time and the modulations of GF preceding and following the impact. Dynamic and temporal variables were measured on each trace. A typical trace (see Figure 2) illustrates the different variables.

The following temporal variables were studied with the impact (t_0) as a reference time: anticipatory delay between the onset of GF increase and the impact (see Figure 2A), delay between the impact and the maximal GF (delay to GF max; Figure 2–B), and delay between the impact and maximal rate of GF (see Figure 2C).

To compute an estimate of the impact occurrence (t_0) in blank trials, an average delay between the switch and the impact was calculated for each participant for all impact

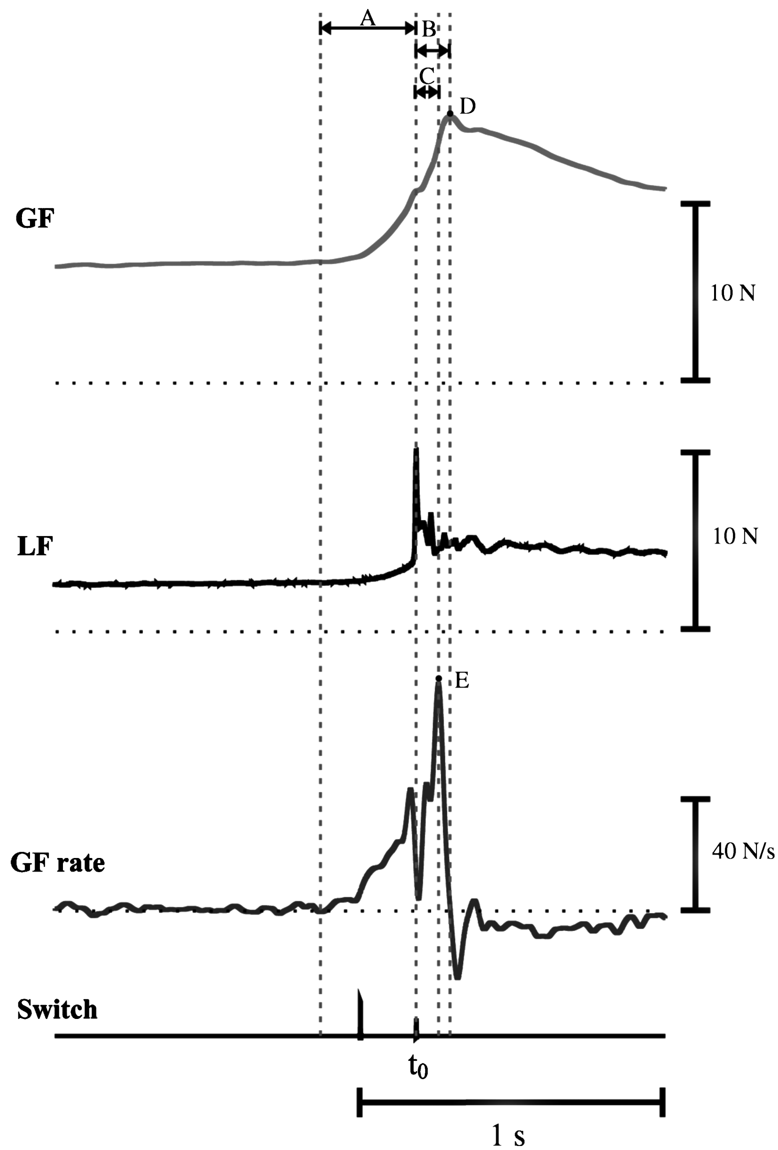

FIGURE 2. A typical trace showing (**A**) the anticipatory delay, (**B**) the delay between impact and grip force (GF) max, (**C**) the delay between impact and GF rate max, (**D**) the GF max, and (**E**) the GF rate max. The vertical bar indicates the moment the participant pressed the button-switch. The moment the impact occurs is considered reference time (t_0). LF = load force.

trials. This average delay (~200 ms) was added to the time at which the participants pressed the switch in each blank trial, providing an estimate of impact time.

The dynamic variables included the maximal GF (GF max; Figure 2D) and the maximal GF rate after the impact (GF rate max; Figure 2E). GF and GF rate were filtered with a low-pass filter at 25 Hz. GF rate max, GF max, and the impact (LF max) were designated on each trial by the absolute maxima in the impact phase.

Statistics

Trial effects on dynamic and temporal variables were tested among the 30 participants throughout the 15 trials using Friedman analysis (repeated-measures analysis of variance on ranks). Post hoc values were analyzed using Tukey tests. Spearman correlations were used to test the link between one trial and the preceding one. All means presented in the Results section are grand means (for all participants).

Results

Figure 3 shows the GF and LF for 1 participant during 15 consecutive trials. Each row represents a series of 5 consecutive trials in the same condition. Series of impact trials (Rows 1 and 3) were alternated with blank trials (Row 2). Because no training trials were permitted, the participant was unable to correctly anticipate the impact during the first trial.

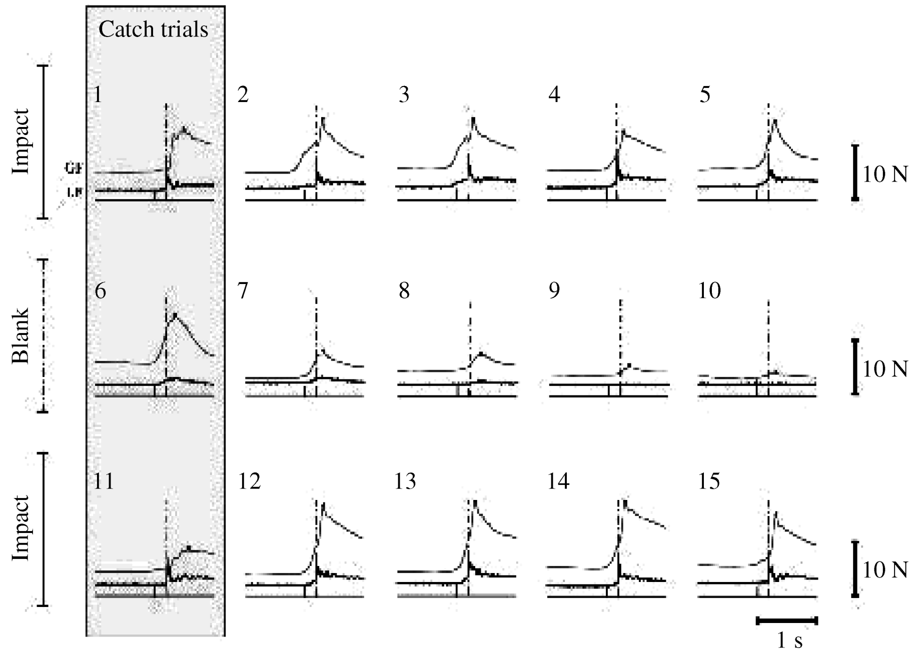

FIGURE 3. Series of 15 trials for 1 participant. The vertical bar indicates the moment the participant pressed the push-button switch. The dotted vertical line (t_0) indicates the moment the impact occurred (impact trials) or should have occurred (blank trials). Black circles highlight each maximum of grip force (GF). LF = load force.

From the 2nd to 5th trial, an anticipative GF increase preceded the impact; the GF continued to rise to a maximum, which occurred after the impact. The first blank trial (6th trial) was recognizable by the absence of impact. Because of the inertial component of the LF (slight postural adjustment of the wrist), it sometimes increased slightly just prior to the anticipated moment of impact. This first blank trial (6th trial) was similar to the four preceding impact trials (2–5) because the GF max was not significantly different from previous trials and was reached within identical delays. In contrast, GF max was significantly decreased during the four following blank trials. The 11th trial was the first unexpected impact trial (catch trial) after a series of 5 blank trials (6–10). The 11th trial's GF max was significantly lower than that of the other impact trials (2–5); moreover, it occurred later. A classical GF profile with values similar to those observed during Trials 2–5 reappeared for Trials 12–15.

These observations were confirmed by a statistical analysis performed across the 30 participants throughout the 15 trials. The anticipatory delay was significantly shorter, Friedman, $\chi^2(14, N = 30) = 38.374$, $p < .001$, and more variable for the first trial ($M = -121$ ms, $SD = 205$ ms) compared with all other trials ($M = -339$ ms, $SD = 134$ ms). Figure 4A shows the mean GF max. This variable was significantly lower during all blank trials, Friedman, $\chi^2(14, N = 30) = 163.104$, $p < .001$, except on the first trial (Trial 6). This first blank trial was not significantly different from the five preceding impact trials (Tukey test, $p > .05$). In the same way, the mean GF max measured during the 11th trial was not significantly different from the one measured during the four preceding blank trials. In addition, GF max of consecutive trials was well correlated (Spearman $\rho = .753$, $n = 420$, $p < .001$). This correlation was reduced when performed with the penultimate trial (Spearman $\rho = .590$, $n = 390$, $p < .001$) and weak when calculated between one trial and the antepenultimate (Spearman $\rho = .384$, $n = 360$, $p < .001$). This revealed a clear influence of history on the GF trace.

In most trials (92%), GF max occurred after the impact or the expected impact. On these trials (Figure 4B), the delay between the impact and GF max was not significantly different between impact trials ($M = 179$ ms, $SD = 91$ ms) and blank trials ($M = 171$ ms, $SD = 100$ ms). Interestingly, during the two catch trials with impact, GF max occurred significantly later ($M = 336$ ms $SD = 246$ ms) and ($M = 271$ ms. $SD = 147$ ms) for the 1st and 11th trial, respectively; Friedman, $\chi^2(14, N = 30) = 59.153$, $p < .001$). This finding suggests that impact does not influence the time to reach GF max unless its occurrence is unpredictable (catch trials with impact).

The GF rate max was closely related to the occurrence of the impact. The GF rate max was significantly lower during blank trials ($M = 13.3$ N/s, $SD = 16.6$ N/s)—including the first one—than impact trials ($M = 113.3$ N/s, $SD = 83.9$ N/s); Friedman, $\chi^2(14, N = 30) = 193.939$, $p < .001$, demonstrating a reactive component. However, regardless of the condition (impact or blank trials), the average GF rate

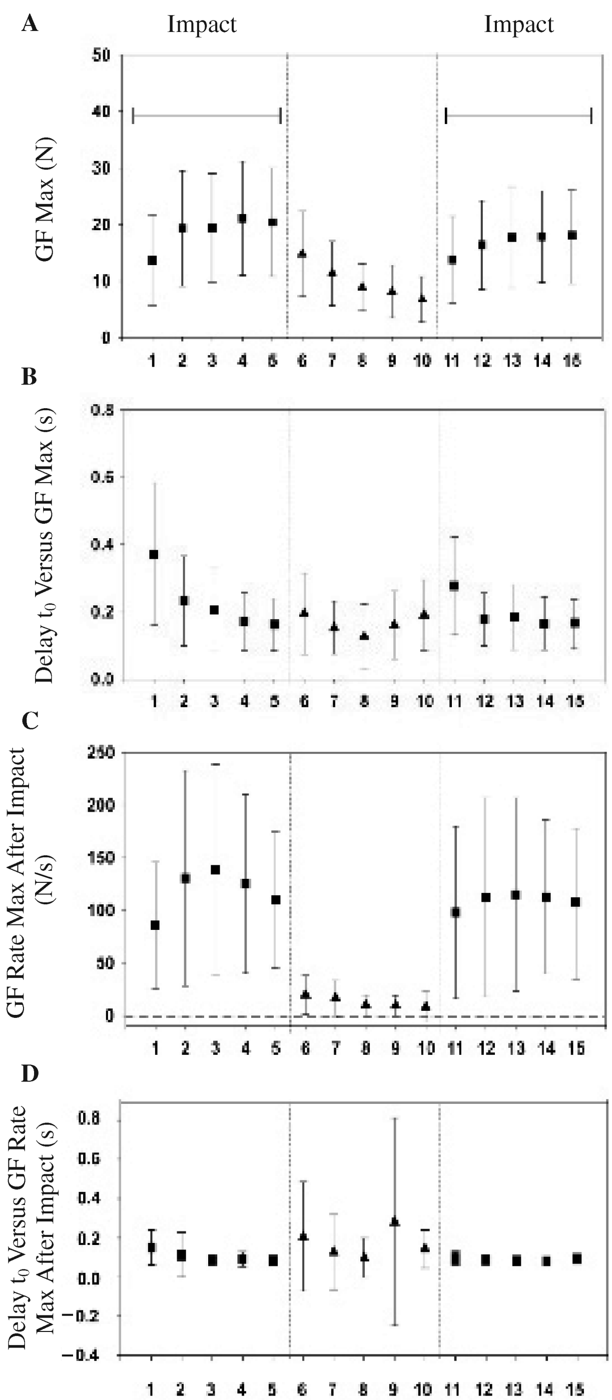

FIGURE 4. Mean grip force (GF) max (**A**) and the mean delay between impact and GF max (**B**) for all participants during each trial. (**C**) The mean GF rate max after impact for all participants during one impact trial and (**D**) the mean delay between impact and GF rate max after the impact for all participants during one impact trial. The trials are presented in chronological order. Black squares represent the impact trials, and triangles represent the blank trials. For all graphs, values given as $M \pm SD$.

remained positive after t_0 and led to a global GF increase after the impact time. The fact that this was the case for blank trials suggests a predictive nature for the response. Under blank conditions, the delay to reach GF rate max after impact was highly variable ($M = 163$ ms, $SD = 273$ ms). As illustrated in Figure 4D, this delay was much more reproducible in impact conditions ($M = 86$ ms, $SD = 13$ ms), which was compatible with the presence of a reactive component in the response.

Discussion

The late component of the GF during predictable load increases has long been described as an automatic long-latency response. Although an attenuating influence of preparatory actions on this post-impact GF increase has been observed in previous studies (Johansson & Westling, 1988b; Serrien et al., 1999), this component has always been considered an automatic and reflexive adjustment triggered by the collision (Delevoye-Turrell et al., 2003; Johansson & Westling, 1988b; Serrien et al., 1999). In the present study, we questioned the triggered nature of this component. We showed that this component is essentially of a predictive nature and integrates a reactive component.

Occurrence of GF Max: Evidence for a Predictive Mechanism

In most trials, the maximum GF arises after the impact. The delay between the impact and GF max was measured throughout the trials. This delay was not different between blank trials and impact trials, which supports the idea that the response timing is programmed using a predictive process. A purely reactive response should have led to the absence of a GF increase after the expected impact in blank trials, but this was clearly not the case. In particular, catch Trial 6 is of interest because it immediately follows a series of impact trials and reveals the predictive nature of the response after the expected time of impact. The time of GF max was identical to the value observed during impact trials.

Amplitude of GF Max: A Prediction Based on Previous Trials

The amplitude of GF max was significantly lower during blank trials than during impact trials. An exception to this pattern was seen in the GF max values of catch trials (i.e., the first blank after a series of impacts or the first impact after a series of blanks). Values in these trials were not different from those observed in the respective previous trials. These results suggest that the magnitude of GF max is not related to the occurrence of an impact in the current trial but rather to the conditions of the preceding trial. This finding demonstrates the predictive nature of the response. The result is confirmed by the high correlation between the GF max amplitude of consecutive trials. The influence of the previous trial on the predictive GF has been shown in classical grip-lift tasks (Jenmalm & Johansson, 1997; Johansson & Westling, 1984; Quaney, Rotella, Peterson, & Cole, 2003), as well as in bimanual tasks in which anticipatory and reactive forces can be dissociated (Witney, Vetter, & Wolpert, 2001; Witney & Wolpert, 2007). Such a modulation with respect to the previous trial has been described as either (a) an effect of a sensorimotor memory for fingertip forces only (Quaney et al., 2003) or (b) a typical anticipatory behavior resulting from a prediction of the consequences of movement (Witney et al., 2001).

GF Rate Max: Evidence for a Triggered Component in the Response

As the maximum of GF arose after impact, the average GF rate after the impact remained positive until that time. However, all blank trials including the first one presented significantly lower GF rate max values than did impact trials. This finding suggests that GF rate max after the impact time was at least partly related to the occurrence of an impact. This could be linked either to a strong mechanical effect of the impact or to the presence of a triggered component. Because sudden load increases under unpredictable conditions undoubtedly give rise to a triggered response, which shows a modulation of the GF rate max as a function of the impact magnitude (Johansson & Westling, 1988b), the last hypothesis is the most likely. Therefore, a significantly reduced GF rate maximum from the first blank trial strongly suggests a triggered component in the response. In addition, the presence of this triggered component is evidenced in our results by the highly reproducible delay between the impact and the GF rate max after the impact in impact trials. The longer delay needed to reach GF max in Trial 11 also supports the presence of a triggered component. For this condition, the first impact trial after a series of five blank trials, it can be hypothesized that the interaction between the predictive response and an unexpected triggered component because the impact alters the timing of GF max.

Although these results supplied evidence for the presence of a triggered component, it seems that the triggered component influenced neither the amplitude nor the timing of the GF profile after the expected impact. We suggest that in predictable conditions, the increase of GF after impact is essentially of a predictive nature. Although our results are consistent with those of previous studies (Delevoye-Turrell et al., 2003; Johansson & Westling, 1988b), our conclusion is the opposite. Whereas it was generally accepted that this late component of the GF can be modulated by the preparatory actions, it has been systematically described as a reactive response triggered by the perturbation (Delevoye-Turrell et al., 2003; Johansson & Westling, 1988b). Delevoye-Turrell et al. suggested that the reflex response could either be inhibited or maintained "on alert" to optimize behavior. This was consistent with Johansson and Westling's hypothesis, which suggested that the preparatory actions decreased the excitation of the motoneurones responsible for the triggered response. In contrast, we suggest that the movement is planned as a whole: The GF increment after impact is programmed in a predictive way as evidenced by the delay and amplitude of GF max, which are not different in the first blank trial compared with the previous impact trials. In this context, the reactive component, which is still present in impact trials, is integrated in the predictive mechanisms that control the movement. In addition, researchers can argue that this predictive control until the maximum of GF allows a well-adapted behavior to manage impulsive loadings, even in situations in which sensory feedback is missing or of poor quality. This is consistent with a study showing that in a drop-ball task, the presence of an increase of GF after impact in one deafferented patient suggests that the GF adjustment up to the maximum is not dependent on sensory feedback (see Nowak & Hermsdorfer, 2006, Figure 5). Our study demonstrates that this increment of GF after impact is not a strategy specific to pathological subjects but a predictive motor program present in normal subjects.

Neurophysiological studies support the idea that triggered responses can be integrated in and eventually dominated by the predictive process. In a task in which predictable LF perturbations were applied to an object held with a precision grip by monkeys, Monzée and Smith (2004) showed that a perturbation systematically evoked a reflex-like GF increase. The latency of this increase was between 50 and 100 ms, which closely matches the latency of our triggered component. Monzée and Smith recorded single cell activity in the cerebellum (interpositus and dendate nuclei) that was related to grasping and lifting tasks. Interestingly, most of the cells that displayed peak discharge for the anticipation of the perturbation also displayed a peak discharge corresponding to the reflex-like response. This finding suggests that both anticipation and reactive responses are processed by the same structures in the cerebellum. This is further supported by injections of muscimol in the monkey cerebellum (anterior interpositus nucleus) that produced an inability to anticipate and react to a predictable LF increase, though isolated movements of the fingers and wrist remained functional (Monzée, Drew, & Smith, 2004).

In a previous human fMRI study, researchers reported that sudden unexpected load increases that trigger an automatic response evoke activity in the contralateral primary motor and somatosensory cortices and also in the lateral and medial cerebellum (Ehrsson, Fagergren, Ehrsson, & Forssberg, 2007). Ehrsson et al. hypothesized that this activation may be caused by cerebellar involvement in GF changes as a consequence of changes in the sensory feedback. This supports the idea that automatic triggered responses are driven and integrated in the cerebellum, which is classically considered the cradle of predictive mechanisms where skilled motor action is planned (Kinoshita, Oku, Hashikawa, & Nishimura, 2000), sensory consequences of movement are predicted (Blakemore, Frith, & Wolpert, 2001), and online correction is processed (Desmurget & Grafton, 2000).

We conclude that the predictive programming of the movement controls self-triggered impulsive loadings and is able to integrate the reactive component that plays no major role in the motor response. The motor control required for generating a preparatory GF prior to the impact, and an increase of GF after the impact, is thus planned as a whole to optimally stabilize the manipulated object around the collision.

REFERENCES

Blakemore, S. J., Frith, C. D., & Wolpert, D. M. (2001). The cerebellum is involved in predicting the sensory consequences of action. *NeuroReport*, *12*, 1879–1884.

Blakemore, S. J., Goodbody, S. J., & Wolpert, D. M. (1998). Predicting the consequences of our own actions: the role of sensorimotor context estimation. *Journal of Neuroscience*, *18*, 7511–7518.

Delevoye-Turrell, Y. N., Li, F. X., & Wing, A. M. (2003). Efficiency of grip force adjustments for impulsive loading during imposed and actively produced collisions. *Quaterly Journal of Experimental Psychology*, *56*, 1113–1128.

Desmurget, M., & Grafton, S. (2000). Forward modeling allows feedback control for fast reaching movements. *Trends in Cognitive Sciences*, *4*, 423–431.

Ehrsson, H. H., Fagergren, A., Ehrsson, G. O., & Forssberg, H. (2007). Holding an object: Neural activity associated with fingertip force adjustments to external perturbations. *Journal of Neurophysiology*, *97*, 1342–1352.

Eliasson, A., Forssberg, H., Ikuta, K., Apel, L., Westling, G., & Johansson, R. (1995). Development of human precision grip V: Anticipatory and triggered grip actions during sudden loading. *Experimental Brain Research*, *106*, 425–433.

Flanagan, J. R., & Wing, A. M. (1997). The role of internal models in motion planning and control: Evidence from grip force adjustments during movements of hand-held loads. *Journal of Neuroscience*, *17*, 1519–1528.

Gordon, A. M., Forssberg, H., Johansson, R. S., & Westling, G. (1991). Visual size cues in the programming of manipulative forces during precision grip. *Experimental Brain Research*, *83*, 477–482.

Jenmalm, P., & Johansson, R. S. (1997). Visual and somatosensory information about object shape control manipulative fingertip forces. *Journal of Neuroscience*, *17*, 4486–4499.

Johansson, R. S., & Westling, G. (1984). Roles of glabrous skin receptors and sensorimotor memory in automatic control of precision grip when lifting rougher or more slippery objects. *Experimental Brain Research*, *56*, 550–564.

Johansson, R. S., & Westling, G. (1988a). Coordinated isometric muscle commands adequately and erroneously programmed for the weight during lifting task with precision grip. *Experimental Brain Research*, *71*, 59–71.

Johansson, R. S., & Westling, G. (1988b). Programmed and triggered actions to rapid load changes during precision grip. *Experimental Brain Research*, *71*, 72–86.

Kinoshita, H., Oku, N., Hashikawa, K., & Nishimura, T. (2000). Functional brain areas used for the lifting of objects using a precision grip: a PET study. *Brain Research*, *857*, 119–130.

Monzée, J., Drew, T., & Smith, A. M. (2004). Effects of muscimol inactivation of the cerebellar nuclei on precision grip. *Journal of Neurophysiology*, *91*, 1240–1249.

Monzée, J., & Smith, A. M. (2004). Responses of cerebellar interpositus neurons to predictable perturbations applied to an object held in a precision grip. *Journal of Neurophysiology*, *91*, 1230–1239.

Nowak, D. A., & Hermsdorfer, J. (2006). Predictive and reactive control of grasping forces: on the role of the basal ganglia and sensory feedback. *Experimental Brain Research*, *173*, 650–660.

Quaney, B. M., Rotella, D. L., Peterson, C., & Cole, K. J. (2003). Sensorimotor memory for fingertip forces: Evidence for a task-independent motor memory. *Journal of Neuroscience*, *23*, 1981–1986.

Serrien, D. J., Kaluzny, P., Wicki, U., & Wiesendanger, M. (1999). Grip force adjustments induced by predictable load perturbations during a manipulative task. *Experimental Brain Research*, *124*, 100–106.

Turrell, Y. N., Li, F. X., & Wing, A. M. (1999). Grip force dynamics in the approach to a collision. *Experimental Brain Research*, *128*, 86–91.

Westling, G., & Johansson, R. S. (1984). Factors influencing the force control during precision grip. *Experimental Brain Research*, *53*, 277–284.

Witney, A. G., Goodbody, S. J., & Wolpert, D. M. (1999). Predictive motor learning of temporal delays. *Journal of Neurophysiology*, *82*, 2039–2048.

Witney, A. G., Vetter, P., & Wolpert, D. M. (2001). The influence of previous experience on predictive motor control. *NeuroReport*, *12*, 649–653.

Witney, A. G., Wing, A., Thonnard, J. L., & Smith, A. M. (2004). The cutaneous contribution to adaptive precision grip. *Trends in Neurosciences*, *27*, 637–643.

Witney, A. G., & Wolpert, D. M. (2007). The effect of externally generated loading on predictive grip force modulation. *Neuroscience Letters*, *414*, 10–15.

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