



The grasping side of post-error slowing

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ARTICLE INFO

Keywords:

Post error slowing
Error processing
Kinematics
Reach-to-grasp
Reaching

ABSTRACT

A common finding across many speeded reaction time (RT) tasks is that people tend to respond more slowly after making an error. This phenomenon, known as post-error slowing (PES), has been traditionally hypothesized to reflect a strategic increase in response caution, aimed at preventing the occurrence of new errors. However, this interpretation of PES has been challenged on multiple fronts. Firstly, recent investigations have suggested that errors may produce a decrement in performance accuracy and that PES might occur because error processing has a detrimental effect on subsequent information processing. Secondly, previous research has been criticized because of the limited ecological validity of speeded RT tasks. In the present study, we investigated error-reactivity in the context of goal-directed actions, in order to examine the extent to which PES effects impact on realistic and complex movements. Specifically, we investigated the effect of errors on the reach to grasp movement (Experiment 1). In addition to RTs, we performed a kinematical analysis in order to explore the underlying reorganization of the movements after an error. The results of the present study showed that error reactivity strategically influences the grasping component of the action, whereas the reaching component appears to be impermeable to PES. The resistance of the reaching component to PES was confirmed in a second 'only reaching' experiment (Experiment 2). These findings support the hypothesis that error reactivity is a flexible process whose effects on behavior also depend on the motor components involved in the action.

1. Introduction

Error commission is associated with several physiological and behavioral changes. In first instance, heart rate deceleration (Danev & Winter, 1971), pupil dilation (Critchley, Tang, Glaser, Butterworth, & Dolan, 2005) and a larger skin conductance response (O'Connell et al., 2007) following an error have been observed. In second instance, behavioral studies have shown that after making an erroneous decision people tend to slow down on the next decision. This empirical regularity is known as post-error slowing (PES; Jentsch & Leuthold, 2006) and it has been observed in a variety of tasks, including Stroop (Gehring & Fencsik, 2001), forced-choice and go/no-go (Jones, Cho, Nystrom, Cohen, & Braver, 2002), Simon (Fan, Flombaum, McCandliss, Thomas, & Posner, 2003), and categorization (Jentsch & Dudschig, 2009) tasks.

To explain PES two theoretical accounts have been put forward, namely *functional* and *non-functional* (Houtman & Notebaert, 2013). Functional accounts, such as the conflict monitoring (Botvinick, Braver, Barch, Carter, & Cohen, 2001), the inhibition (Marco-Pallarés, Camara, Münte, & Rodríguez-Fornells, 2008; Ridderinkhof, 2002), and the reinforcement learning (Holroyd & Coles, 2002) theories propose that PES

is the product of a compensatory control mechanism serving the purpose of improving subsequent performance. PES is thus interpreted as the result of a more cautious response strategy aimed at producing a *post-error improvement of accuracy* (PIA). However, PES might not necessarily be the expression of an adaptive mechanism. In this perspective, *non-functional accounts* explain PES in terms of reduced cognitive processing after errors (Notebaert et al., 2009). Notebaert et al. (2009) suggested that PES reflects an orienting response to an unexpected event. Since errors are usually rare, they represent unexpected, motivationally salient events that automatically capture attention and thus distract the participant from the task, producing both PES and a decrease in post-error accuracy. According to this theory, it is not the error *per se* that causes the slowing, but rather the attentional orientation toward that event.

Despite the majority of studies on error reactivity have found PES, empirical evidence concerning post-error accuracy is mixed, sometimes supporting the functional accounts (e.g., Neubert, Mars, Buch, Olivier, & Rushworth, 2010), sometimes supporting the non-functional accounts (e.g., Gehring & Fencsik, 2001). In their review, Danielmeier and Ullsperger (2011) point out that there is evidence for both functional

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and non-functional accounts of error reactivity and that these accounts are not necessarily mutually exclusive. Indeed, the functional and non-functional aspects of error reactivity may follow different time courses. Recent investigations indicate that PES tends to decay over time (Danielmeier & Ullsperger, 2011; Jentzsch & Dudschig, 2009). In particular, short inter-trial intervals (ITIs) (< 500 ms) are usually associated with a larger PES and a post-error decrease in accuracy. Instead, long ITIs (> 1000 ms) tend to elicit a post error increase in accuracy and a decrease of PES. A possible explanation for these findings is that at short ITIs, the non-functional aspects of error reactivity are predominant, and thus, attentional reorientation may be the main responsible for PES. Instead, at longer ITIs, strategic influences become more effective since more time is available to adjust behavior after error detection, and PES may be mainly determined by strategic change in speed-accuracy tradeoff (Dutilh et al., 2012b; White, Ratcliff, Vasey, & McKoon, 2010). In support of this suggestion, Dutilh et al. (2012b), using drift diffusion model analysis, found that with ITIs longer than 1000 ms, PES can be attributed almost entirely to a strategic increase in response caution.

Generally, with just a few exceptions (see Anguera, Seidler, & Gehring, 2009; Krigolson & Holroyd, 2006; Vocat, Pourtois, & Vuilleumier, 2011), error reactivity has been investigated by means of speeded reaction time (RT) tasks and most studies have measured only arbitrary button-press responses (Gehring, Liu, Orr, & Carp, 2011). However, as pointed out by Gehring et al. (2011), most daily life movements have a slower time course than speeded RT response, and more realistic and ecologically valid tasks may afford a better opportunity to investigate error-reactivity. Moreover, since the functional meaning of PES is yet unclear, it might be useful to explore error-reactivity by using richer measures than RT, which limit the investigation to pre-movement processes. For instance, the consequences of self-generated errors on the kinematics of goal directed actions has yet to be investigated. Here, we fill this gap by testing PES theories looking at the kinematics underlying the organization of the reach-to-grasp movement, one of the most common goal-directed actions performed in daily life.

Reach-to-grasp behavior has been described as the act of coordinated reaching and grasping (Castiello, 2005; Grafton, 2010; Jeannerod, 1981). The reaching component concerns the transport of the hand toward the target, whereas the grasping component consists in a progressive opening of the hand, followed by a gradual closure of the grip until it matches the object's size. This characterization of prehension dates back to Jeannerod's seminal studies, in which he proposed the *visuomotor channel hypothesis* (Jeannerod, 1981). This hypothesis suggests that the visuomotor mechanisms involved in reaching and grasping are independent, even if temporally coupled. More recently, the visuomotor channel hypothesis has been challenged by a number of studies, showing that the control mechanisms underlying reaching and grasping can be affected by the same spatial and intrinsic properties of the target (e.g., Gentilucci et al., 1991; Jakobson & Goodale, 1991).

Reach-to-grasp behavior is not only constrained by spatial and intrinsic properties of the stimulus (*direct effects*), but also by preceding motor events (*sequential effects*), a phenomenon termed *hysteresis* (Kelso, Buchanan, & Murata, 1994). Hysteresis has been supported by several studies showing its effects on a variety of reaching and grasping parameters. For example, Jax and Rosenbaum (2007) demonstrated that participants, after avoiding an obstacle in order to reach for a target, tended to use a similar trajectory in the following trial, even when the obstacle was no longer present (*hand path priming*). Dixon and Glover (2009) found a potent tendency to perseverate in grip aperture during the latter portion of a movement to grasp a disc. Similarly, Kent, Wilson, Plumb, Williams and Mon-Williams (2009) found that reach-to-grasp movements are susceptible to movement history effects, both in adults and in children. Recent studies have suggested that the hysteresis effect arises due to priming of action plan elements in the motor system (Dixon, McAnsh, & Read, 2012; Glover & Dixon, 2013).

A point worth noting is that until now research on hysteresis has focused the investigation on sequential effects arising from sequences of correct movements. In daily life, however, carrying out a task does not always run smoothly and people can fail to perform a reach-to-grasp movement, which begs the question - how and to what extent the failure to grasp an object influences the following movement?

With this in mind, the overarching aim of the present study is to investigate the consequences of self-generated errors in the context of goal directed actions. To do this we investigate error reactivity effects on both the preparation and the execution of reach-to-grasp movements. Movement preparation includes the relevant sensory and perceptual processes preceding movement initiation (Haith, Pakpoor, & Krakauer, 2016). Traditionally, it is assessed through measurement of RT (Wong, Haith, & Krakauer, 2015). Instead, movement execution is customarily assessed via kinematical analysis and allows investigating the added benefit of monitoring and occasionally adjusting motor programs in flight (Erlhagen & Schöner, 2002). A further aim of the present study is to verify whether error-reactivity has a different impact on the grasping and reaching components or whether it produces an unspecific slowing of the whole movement execution.

2. Experiment 1

In Experiment 1, participants were asked to reach out and grasp a steel ball, without knocking the wooden support over. In order to correctly accomplish this task, participants had to carefully transport the hand near the target and accurately close the fingers upon the steel ball.

In addition to RTs, we also examined the kinematics of the reach-to-grasp movement in terms of both temporal and amplitude measures. And, in order to emphasize the strategic planning that may occur in natural settings after an error, which may differ from the responses elicited by the speeded RT tasks, we used relatively long inter-trial intervals (ITIs).

We hypothesize that if error reactivity processes extend to movement execution, we should find evidence of post-error adjustments also at kinematical level. Functional and non-functional accounts offer the opportunity to put forward different predictions with respect to post-error accuracy as investigated here. If errors lead to a more cautious movement execution, then we should find a post-error improvement of accuracy. Conversely, if error processing has a detrimental effect on subsequent information processing, then we expect a decrease in post-error accuracy.

2.1. Methods and materials

2.1.1. Participants

As there were no previous studies investigating error reactivity in the context of goal directed actions upon which to refer for an a priori power analysis, we selected a target sample size of 15 subjects (8 females, 7 males) with a mean age 26 (SD = 3.5 yrs), which would give 82.1% power to detect a large effect ($f = 0.4$) at an α level of $p = .05$ (GPOWER 3.1; Erdfelder, Faul, & Buchner, 1996). All participants were right-handed, had normal or corrected-to-normal vision and were naive as to the purpose of the experiment. All subjects gave informed consent to participate in the study. The experimental procedure was approved by the Institutional Review Board at the University of Padua and was in accordance with the declaration of Helsinki. The participation was voluntary.

2.1.2. Apparatus

The experimental setup is represented in Fig. 1A. Participants were tested individually in a well-lit room, and were seated on a height adjustable chair so that the thorax pressed gently against the front edge of the table (90 × 90 cm) and the feet were supported. Head movements were restricted by the use of a head-chin-rest in order to maintain a constant viewing distance from the target. The target object consisted of

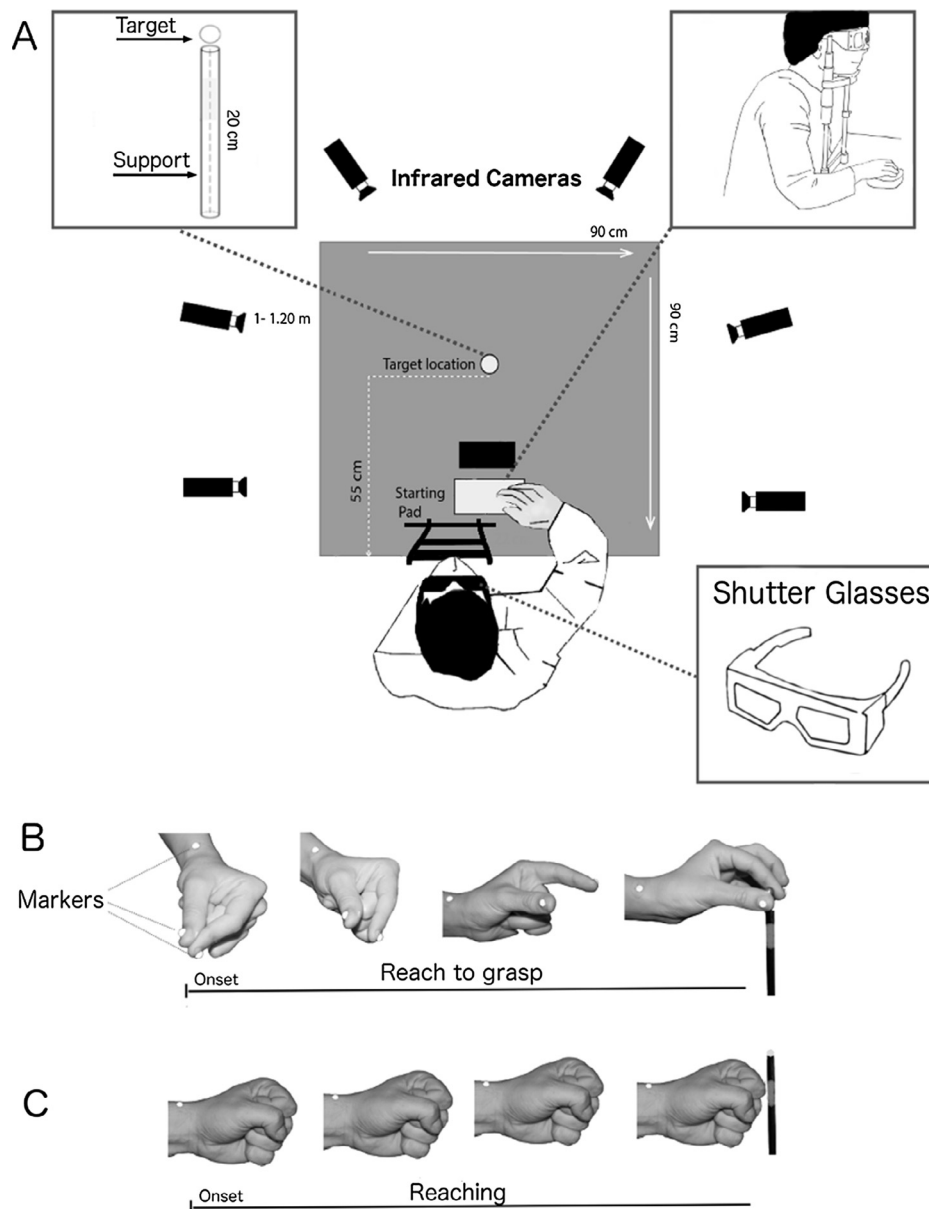


Fig. 1. Graphical representation of the experimental set-up (A) and the designated start position for reach-to-grasp (B) and reaching movements (C).

a steel ball (0.5 cm Ø), positioned on a wooden support measuring 1 cm in width and 20 cm in length. The target object was placed 55 cm away from the edge of the table, along the mid-sagittal plane of the participant. During the experiment, participants' vision was controlled by means of liquid-crystal shutter goggles (PLATO Translucent Technologies), which prevented vision during the inter-trial interval, by changing from a transparent to an opaque state. Before each trial, participants rested their hand on a starting switch (11 × 8 cm) aligned to the participants' body midline and placed 22 cm away from the edge of the table. A container (11 × 8 cm), into which the steel ball had to be placed once grasped, was positioned 4 cm from the starting pad.

2.1.3. Kinematic recording

To track the kinematics of the participants' right hand, we used the 3D-optoelectronic SMART-D system (Bioengineering Technology & Systems, B|T|S). Three infrared reflective markers (0.25 mm Ø) were taped to the following points on participants' right upper limbs (see Fig. 1B): (1) wrist (radial aspect of the distal styloid process of the radius), (2) thumb (ulnar side of the nail) and (3) index finger (radial side

of the nail). The index finger and the thumb markers were used to measure the grasping component of the movement, whereas the wrist marker was used to measure the reaching component. To record the movement, six video cameras (sampling rate 140 Hz) detecting the infrared reflective markers were placed in a semicircle at a distance of 1–1.2 m from the table (Fig. 1A). To optimize accurate tracking of all markers, the system was calibrated before data collection by adjusting the camera position, roll angle, zoom, focus, threshold and brightness. These procedures were followed by static and dynamic calibration. For the static calibration, a three-axes frame of 5 markers at known distances from each other was placed in the middle of the table. For the dynamic calibration, a three markers wand was moved throughout the workspace of interest for 60 s. The spatial resolution of the recording system was 0.3 mm over the field of view. The standard deviation of the reconstruction error was 0.2 mm for the x, y and z axes.

2.1.4. Procedure and design

Before each trial the shutter goggles were closed and the participant held the ulnar side of the hand placed upon the starting switch with the

tip of the index and the tip of the thumb in contact with each other (Fig. 1B). As soon as the shutter goggles became transparent, participants were asked to reach out and grasp the steel ball by means of a precision grip (Fig. 1B), lift it and deposit it into the container. The task required executing the movement as fast and accurately as possible, without knocking the wooden support over. If the wooden support was dropped the trial was considered as an error. During the inter-trial interval, when the shutter goggles were opaque, the experimenter put the steel ball (and the wooden support in the case of error) back in the correct position. The inter-trial interval varied randomly from 6500 to 8500 ms. Each session consisted of 3 blocks of 40 trials separated by a 3-min break. Participants underwent a practice session of 10 trials before the experimental session began. The experiment lasted approximately 50 min.

2.1.5. Data processing

RT was defined as the time between the opening of the shutter glasses and the release of the starting switch, which corresponded to the movement onset. Each trial was individually checked for correct marker identification and the SMART-D Tracker software package (B|T|S) was used to provide a 3-D reconstruction of the marker positions as a function of time. The data were then filtered using a finite impulse response linear filter (transition band = 1 Hz, sharpening variable = 2, cut-off frequency = 10 Hz; D'Amico & Ferrigno, 1990; D'Amico & Ferrigno, 1992). Movement onset was calculated as the time at which the tangential velocity of the wrist marker crossed a threshold (5 mm/s) and remained above it for longer than 500 ms. End of movement was defined as the time at which the hand made contact with the target and quantified as the time at which the hand opening velocity crossed a threshold (5 mm/s) after reaching its minimum value and remained under it for longer than 500 ms. The time from the onset to the end of the movement was defined as total movement time. For the reaching component (see Fig. 2A) we considered reaching time (the interval between the onset of the movement and the time at which the wrist velocity reached its minimum value after the peak of wrist velocity), the amplitude of maximum peak velocity (the maximum velocity of the wrist during the reaching phase), the amplitude of peak wrist deceleration (the amplitude of maximum deceleration of the wrist during the reaching phase), and the time of maximum peak wrist deceleration (the time at which the maximum wrist deceleration occurred). The grasping component was computed based on the relative distance between the markers located on the index finger and the thumb. For this component (see Fig. 2B), grasping time (the time from the beginning of fingers opening up to their contact with the target), the amplitude of maximum opening velocity (the maximum velocity reached during the opening phase with reference to the distance between the thumb and the index finger), the amplitude of maximum closing velocity (the maximum velocity reached during the closing phase with reference to the distance between the thumb and the index finger), and the time of peak grip aperture (the point in time at which the index finger and the thumb reached the maximum distance) were considered.

2.1.6. Principal component analysis

A principal component analysis (PCA) with Oblimin rotation was applied to decompose the data into their underlying factors and reduce the number of temporal and kinematic variables so as to obtain a protection against the Type I error. RTs were not included in this analysis. On the basis of Kaiser's rule (Kaiser, 1960) we selected three components having eigenvalues above 1, which accounted for 82% of the variance (40%, 21%, 21%, respectively). Weights of the kinematic parameters for the first three components are reported in Table 1.

The first component had positive weights for total movement time, reaching time, grasping time, the time of peak grip aperture and the time of peak wrist deceleration. This component can be interpreted as a global descriptor of the *reach-to-grasp timing*. The amplitude of peak wrist velocity and the amplitude of peak wrist deceleration showed a

positive correlation with the second component. This component can be interpreted as a descriptor of *reaching kinematics*. Finally, the amplitude of maximum opening velocity and the amplitude of maximum closing velocity weighted substantially on the third component, suggesting that it can be interpreted as a *gripping velocity* component. The three components were positively correlated with each other, ranging from .20 to .44. All analyses were performed using the R package 'psych' (Revelle, 2012).

2.1.7. Data analysis

Post-error adjustments were computed, with respect to the three kinematic components' scores and RT, using the robust method (PES_{robust}) proposed by Dutilh et al. (2012a, 2012b). This method compares the performance on post-error trial with the performance on the immediately preceding pre-error trial. PES_{robust} metric describes the fluctuation of performance surrounding an error and it is not confounded by long-term effects like distraction, low motivation or fatigue. Post-error analyses were restricted to sequences of trials comprising $E - 1$ and $E + 1$ correctly performed trials. For comparison purpose, in a similar manner to PES_{robust} , we also computed post-correct adjustments considering triplets of correct trials. Linear mixed-effects (LME) models were used to compare post-error and post-correct adjustments for each kinematic component and for RTs. Error rates were analyzed using a Generalized mixed-effects (GLME) models with a binomial link function (Pinheiro & Bates, 2000) after coding error and correct responses with 1 and 0, respectively. LME and GLME models offer several advantages over the traditional linear approach models (Baayen, Davidson, & Bates, 2008; Gelman & Hill, 2007), in particular: (a) allow simultaneously consideration of the standard fixed-effects factors controlled by the experimenter and also the random-effects, (b) provide a greater statistical power for the analysis of repeated observations, (c) provide a flexible method of dealing with missing data. Statistical analysis was performed using the computing environment R (R Core Team, 2014), and the packages lme4 (Bates, Maechler, Bolker, & Walker, 2015) and lmerTest (Kuznetsova, Brockhoff, & Christensen, 2013). For the LME and GLME models used in this study, random effects consisted of Participants and Blocks. The random structure was selected by means of the Bayesian information criterion (BIC) weights (see Wagenmakers & Farrell, 2004), using the R package 'cogmod' (Stojic, 2015). Given a set of models with a different random structure, BIC weights represent the probability of each model being the best (Clavijo-Baquet et al., 2014).

Models were fitted using maximum likelihood (ML). p -values were estimated by likelihood ratio tests of the full model against the null model. Visual inspection of residual did not show any obvious deviation from normality or homoscedasticity. A further t -test analysis (one-tailed) was performed to test whether post-error and post-correct effects were significantly different from 0. p -values were corrected via Bonferroni correction. For LME and t -tests analyses we reported Cohen's d indices as measure of effect sizes (Cohen, 1988), whereas for GLME analysis we reported the odds ratio statistic (OR, see Szumilas, 2010). Outliers were eliminated by refitting the model after removing data points with absolute standardized residuals exceeding 3 standard deviations (less than 2%). We discarded 67 of the total of 1.800 trials because of technical problems. In addition to the null-hypothesis significance testing, we also performed statistical comparisons using the Bayesian approach implemented in the BayesFactor package for R (Morey, Rouder, & Jamil, 2014). We used a Cauchy distribution centered on zero with rate $[r] = .707$ (Rouder, Morey, Speckman, & Province, 2012). The Bayesian Factor (BF) allows calculating the probability that a particular hypothesis is true. Here, we report BFs in favor of the alternate hypothesis, that is the relative evidence for the alternative hypothesis (H_1) compared to the null hypothesis (H_0). The conventional cut-off for the interpretation of Bayes (Jeffreys, 1961) factors suggests that a BF greater than 100 represents a strong evidence for the alternate hypothesis, values greater than 3 represent a sufficient

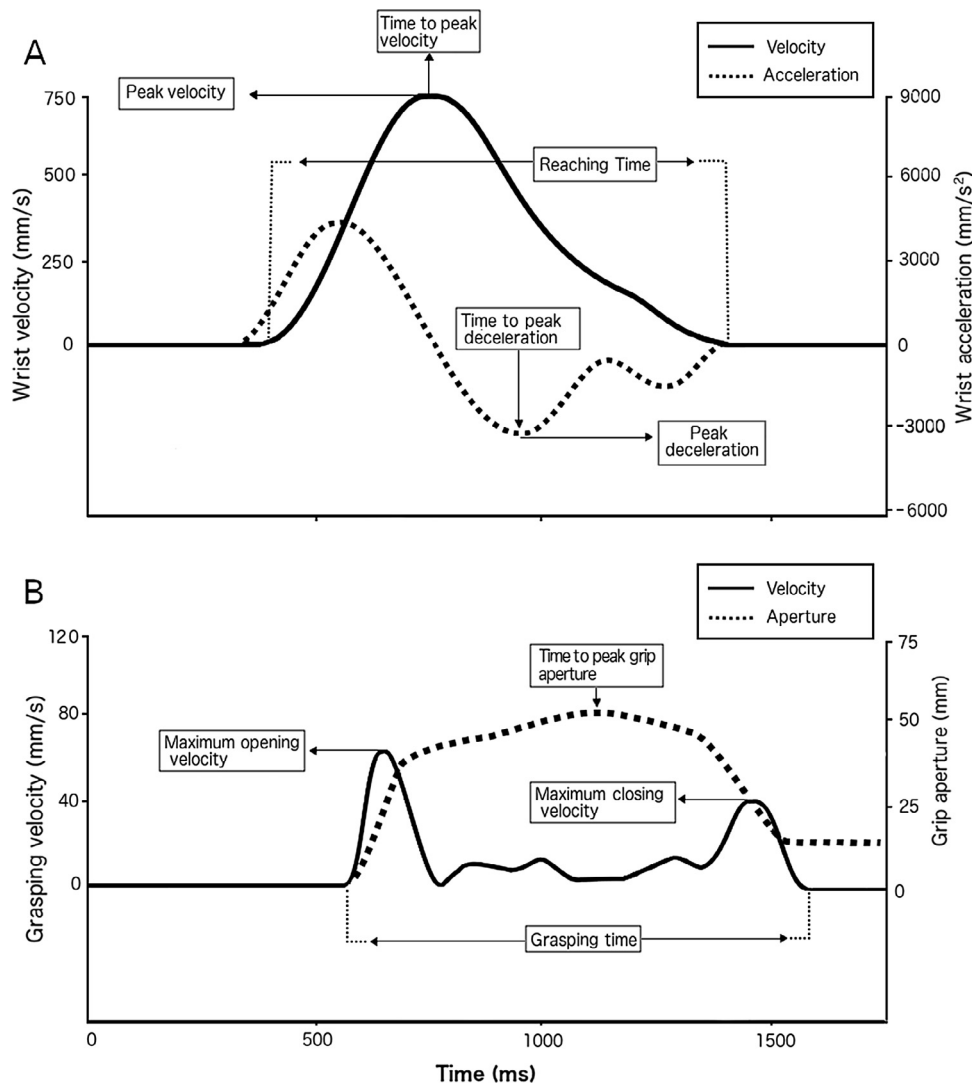


Fig. 2. Graphical representation of the experimental variables. Panel A: plot of wrist velocity (solid line) and wrist acceleration (dashed line). Panel B: plot of grasping velocity (solid line) and grip aperture (dashed line).

Table 1
Weights of the kinematic parameters for the first three components of the reach to grasp movement.

	Component 1	Component 2	Component 3
Movement time (ms)	.972	.001	-.015
Reaching time (ms)	.918	.011	.082
Grasping time (ms)	.959	.004	-.002
Time of peak grip aperture (ms)	.536	-.011	-.441
Time of peak wrist deceleration (ms)	.650	-.097	-.040
Maximum opening velocity (mm/s)	.071	.012	.965
Maximum closing velocity (mm/s)	-.072	-.004	.780
Peak wrist velocity (mm/s)	.114	.998	-.052
Peak wrist deceleration d((mm/s²)	-.181	.894	.083

support for the alternative hypothesis, whereas values less than 1 indicate that the data support the null-hypothesis.

2.2. Results and discussion

2.2.1. Accuracy

The overall error percentage was 18%. Post-error changes in error-rate were evaluated by comparing post-error error rates with post-correct error rates. A GLME analysis, with random intercept for Participants and Blocks, showed that subjects were more accurate following an error (16.2% error-rate) than following a correct response (20% error-rate), $z = -2.23$, $p = .025$, $OR = 0.68$.

2.2.2. Reaction times

The mean post-correct and post-error RT adjustments are shown in Fig. 3. A LME analysis, with random intercept for Participants (modeling both slopes and intercepts) and Blocks (modeling intercepts only), revealed a significant difference between post-correct and post-error adjustments $\chi^2 = 6.37$, $p = .011$, $BF > 100$, $d = 0.44$. Contrast analysis showed a significant post-error slowing ($PES_{robust} = 42.80 \text{ ms} \pm 12.21$), $t(193) = 3.50$, $p < .001$, $BF = 56.73$, $d = 0.25$. After a correct response, subjects showed a post-correct speeding, that is, a statistically significant decrease in RTs

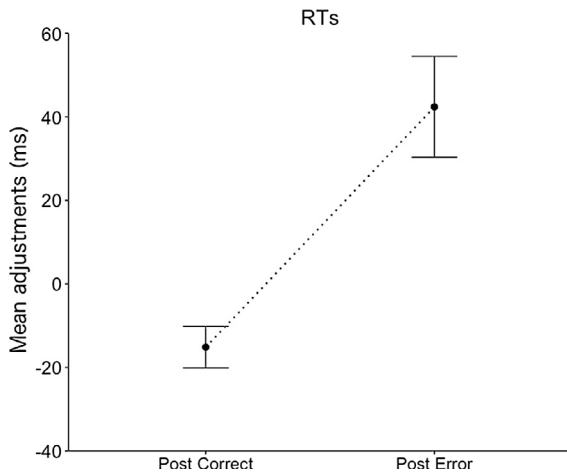


Fig. 3. Mean post-correct and post-error adjustments in RTs. Vertical bars indicate standard error of the mean. Positive values indicate a slowing down.

($-15.18 \text{ ms} \pm 4.96$) on the following trial, $t(810) = -3.06$, $p = .002$, $BF = 8.20$, $d = 0.10$.

2.2.3. Reach-to-grasp timing

The mean of post-correct and post-error adjustments of the Reach-to-grasp timing are shown in Fig. 4A. A LME analysis, with random

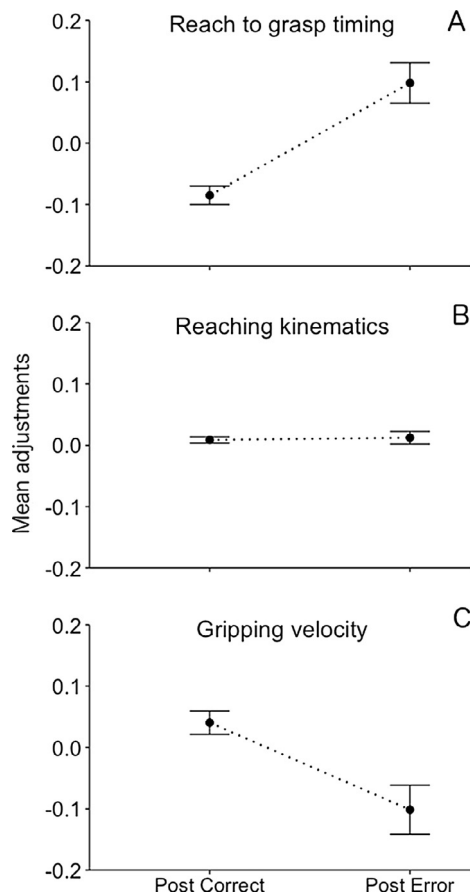


Fig. 4. Mean post-correct and post-error adjustments of the reach to grasp timing (panel A), the reaching kinematics (panel B), and the gripping velocity (panel C) components. For the reach to grasp timing, positive values indicate a slowing down. For the reaching kinematics and the gripping velocity component, negative values indicate a slowing down. Vertical bars represent standard error of the mean.

intercept for Participants and Blocks (modeling intercepts only), revealed a significant difference between post-correct and post-error adjustments $\chi^2 = 27.85$, $p < .001$, $BF > 100$, $d = 0.21$. After an error, subjects showed a significant post-error slowing ($PES_{\text{robust}} = 0.097 \pm 0.032$), $t(195) = 2.98$, $p = .003$, $BF = 11.80$, $d = 0.21$, whereas after a correct trial a post-correct speeding was present (-0.851 ± 0.015), $t(806) = -5.64$, $p < .001$, $BF > 100$, $d = 0.20$.

2.2.4. Reaching kinematics

The mean of post-correct and post-error adjustments of the Reaching Kinematics component are shown in Fig. 4B. A LME analysis, with random intercept for Participants (modeling both slopes and intercepts) and Blocks (modeling intercepts only), revealed no significant difference between post-correct and post-error adjustments $\chi^2 = 0.04$, $p = .829$, $BF = .09$, $d = 0.02$. Neither a significant post-error slowing ($PES_{\text{robust}} = 0.012 \pm 0.010$, $t(200) = 1.20$, $p = .228$, $BF = 0.03$, $d = 0.08$) nor a post-correct adjustment (0.008 ± 0.005 , $t(815) = 1.72$, $p = .082$, $BF = .33$, $d = 0.06$) was found.

2.2.5. Gripping velocity

The mean of post-correct and post-error adjustments of the Gripping velocity are shown in Fig. 4C. A LME analysis, with random intercept for Participants and Blocks (modeling intercepts only), revealed a significant difference between post-correct and post-error adjustments, $\chi^2 = 10.88$, $p < .001$, $BF = 17.1$, $d = 0.26$. After an error, subjects showed a significant reduction of gripping velocity ($PES_{\text{robust}} = -0.101 \pm 0.040$), $t(199) = -2.53$, $p = .012$, $BF = 3.60$, $d = 0.18$. After a correct trial, a significant post correct speeding was found (0.040 ± 0.018), $t(804) = 2.13$, $p = .033$, $BF = 0.75$, $d = 0.07$.

In summary, these findings suggest that after an error accuracy performance tended to increase, and that error-reactivity processes impact on both motor preparation and execution. In terms of motor preparation, results are in line with previous evidence concerned with arbitrary responses, suggesting that errors prompt people to adaptively change their response thresholds and to accumulate more information before movement initiation (e.g., Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999). In terms of motor execution, kinematical analysis revealed that only the reach-to-grasp timing and the gripping velocity were affected by post-error adjustments, whereas no post-error effects were found at the level of the reaching kinematics. This might suggest that PES effects are confined to the programming of the time allotted to unfold the movement and to the scaling of grasping kinematics within such time. In other words, error-reactivity seems to be chiefly confined to the control of the grasping component of the action.

A possible explanation for these results may reside in the task we employed for this study, in which grasping kinematics were directly involved in error commission. In fact, in our task all errors occurred during the grip closure phase, when fingers made contact with the target. This might lead to the implementation of strategic post-error adjustments confined to the grasping component, and it may be aimed to improve the control of digit placement upon the target as to ensure successful completion of the task. In these terms, error-reactivity could be considered as a very efficient process, which, instead of inducing a general slowing of the movement, limits its effects in a targeted manner to the component which is directly involved in error commission.

To test this idea, we performed a second experiment in which an ‘only reaching’ condition was included in order to verify whether the reaching component is impermeable to error-reactivity effects even when the reaching movement is not embedded in a prehension movement involving also the grasping component.

3. Experiment 2

In Experiment 2 participants performed two conditions namely a reach-to-grasp and a reaching condition. The reach-to-grasp condition

was the same as for Experiment 1. For the reaching condition participants were asked to reach out and touch the wooden support with their fist, without knocking it over. In this experiment, the accuracy of the reaching component not only was investigated in terms of error-rates, but also in terms of submovements' organization and endpoint variability. In terms of submovements we know that reaching movements consist of two consecutive phases: a primary submovement, and a homing-in phase (e.g., Elliott, Helsen, & Chua, 2001; Khan & Franks, 2003; Meyer, Abrams, Kornblum, Wright, & Keith Smith, 1988). The primary submovement is represented by a bell-shaped velocity profile, and it has been interpreted as a ballistic movement portion driven by the initial control plan. The inaccuracy of the initial control plan and neuromuscular noise during motion can be corrected during the homing-in phase, at the time proprioceptive and visual feedback are used to reduce any spatial discrepancy between hand and target positions. This is done by means of corrective adjustments, termed as *secondary submovements*. The more the primary movement is inaccurate, the more secondary submovements are necessary to adjust the reaching movement (and viceversa). Accordingly, the production of secondary submovements has been traditionally considered as one of the major mechanisms of movement accuracy regulation (e.g., Houk et al., 2007; Novak, Miller, & Houk, 2002). Endpoint variability of the reaching movement, which measures the variability of wrist position at the end of the reaching movement (Eliasson, Rösblad, & Forssberg, 2004; Gordon, Ghilardi, Cooper, & Ghez, 1994), reflects the precision of the reaching endpoints. In particular, if participants increase the range of the distribution of their movement endpoints, it indicates that their movements are less accurate.

At the level of motor preparation, we expected to find a PES for both the reaching and the grasping conditions as for Experiment 1. As concerns motor execution, if the influence of error-reactivity processes is only evident at the level of the grasping component, then the results for the reach-to-grasp condition should mirror those obtained for Experiment 1. If error reactivity processes strategically slow down the component directly involved in error commission, then for the reaching condition kinematic parameterization should be modulated by PES effects. Alternatively, if reaching is impermeable to PES effects, then no changes at the level of kinematics (including the number of submovements as well as the endpoint variability of the reaching movement) and error-rates should be evident.

3.1. Methods and materials

All methodological aspects were the same as for Experiment 1 except for what follows.

3.1.1. Participants

A total of 15 subjects participated in the experiment, eleven women and four men, with a mean age of 23.1 years ($SD = 2.8$). All participants were naive to the purpose of the study and had normal or corrected-to-normal vision. Participation was voluntary. None of them had participated in Experiment 1.

3.1.2. Procedure, design, data processing

In Experiment 2, two conditions were performed: a reach-to-grasp condition and a reaching condition. The reach-to-grasp condition was the same as for Experiment 1. Procedure and sequence of events for the reaching condition were the same as for the reach-to-grasp condition except that participants were asked to reach out and touch the wooden support with their fist, hitting with the metacarpophalangeal index joint a target area (1×3 cm) placed 3 cm from the top of the support (see Fig. 1C). Participants had to execute the movement as fast and accurately as possible, without knocking the wooden support over. Each subject performed a total of 240 trials. The two experimental conditions (reach-to-grasp and reaching) were presented in blocks of 40 trials. Order of blocks was counterbalanced across participants. The

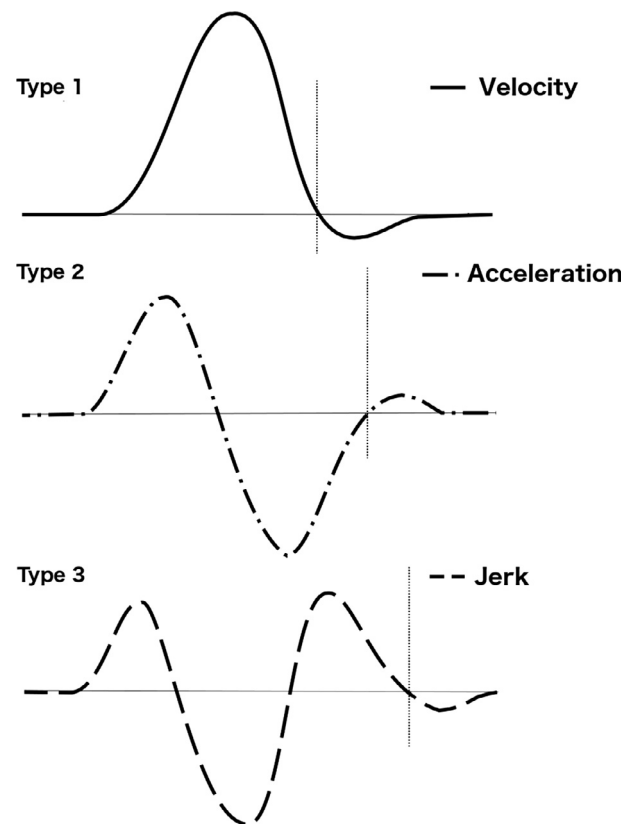


Fig. 5. Examples of discrete movements with secondary submovements of type 1, 2, and 3. The vertical line represents the hypothetical end of the primary submovement.

experimental session was preceded by 20 practice trials. The experiment lasted approximately 100 min. RTs and error-rates were computed as for Experiment 1.

For the determination of whether in post error and post correct trials the reaching component differed with regard to the total number of secondary movements we performed a submovements analysis. The end of the primary submovement was identified by the first of any of the following secondary submovements (see Meyer et al., 1988, Fig. 5): reversals in the trajectory (Type 1 submovement), defined as a zero-crossing from positive to negative value occurred in the velocity profile; reaccelerations toward the target (Type 2 submovement), defined as a zero-crossing from negative to positive value occurred in the acceleration profile; decreases in the rate of deceleration (Type 3 submovement), defined as a zero-crossing from positive to negative value appeared in the jerk profile. Only secondary movements emerging during the deceleration phase were considered, because corrective adjustments usually emerge in close proximity to the target (Fradet, Lee, & Dounskaia, 2008).

The endpoint variability of the reaching movement was defined as the mean Euclidean distance between the endpoint of each trial and the overall average endpoint position of each participant (Darling & Gilchrist, 1991; Rossetti, 1998).

For the reach-to-grasp condition we extracted the same dependent kinematic variables as for Experiment 1, whereas for the reaching condition, we considered the reaching time, the time and the amplitude of peak wrist velocity, the time and the amplitude of peak wrist deceleration. Furthermore, for both conditions, the reaching component was also investigated considering the *primary submovement length* (distance covered in the primary submovement, calculated as a percentage of the total movement length), and the *homing-in phase duration* (the time from the end of the primary submovement to the end of the entire movement).

Table 2

Weights of the kinematic parameters for the first four components of the reach to grasp condition.

	Component 1	Component 2	Component 3	Component 4
Movement time (ms)	.963	-.005	-.009	-.007
Grasping time (ms)	.823	.102	.086	-.119
Reaching time (ms)	.957	.006	.025	-.013
Time of peak grip aperture (ms)	.641	-.143	-.141	-.116
Time of peak wrist deceleration (ms)	.610	-.283	-.117	.083
Maximum opening velocity (mm/s)	.045	.043	.049	.893
Maximum closing velocity (mm/s)	-.166	-.036	-.041	.799
Peak wrist deceleration (mm/s ²)	.140	.959	-.083	.050
Peak wrist velocity (mm/s)	-.182	.900	.067	-.039
Homing-in phase duration (ms)	.227	-.008	.869	.092
Primary submovement length (%)	-.239	-.027	.845	-.070

3.1.3. Principal component analysis

In order to simplify data interpretation, we performed a PCA (with Oblimin rotation) for each condition. For the reach-to-grasp condition four components were selected (Table 2), namely a global descriptor of the reach-to-grasp timing (comprising the total movement time, the reaching time, the grasping time, the time of peak grip aperture and the time of peak wrist deceleration), a reaching kinematics component (the amplitude of peak wrist velocity and the amplitude of peak wrist deceleration showed a positive correlation with the second component), a grasping submovements component (including the primary submovement length and the homing-in phase duration), and a gripping kinematics component (including the amplitude of maximum opening velocity and the amplitude of maximum closing velocity). The four selected components accounted for 78% of the variance (33%, 17%, 14%, 14% respectively). The four components were correlated with each other, ranging from .04 to -.26.

For the reaching condition, three components were selected (Table 3), which accounted for 79% of variance (31%, 27%, 21%, respectively). The first component, comprising the reaching time, the time of maximum peak wrist deceleration, and the time of maximum peak wrist velocity, can be interpreted as a global descriptor of the *reaching timing*. The amplitude of peak wrist velocity and the amplitude of peak wrist deceleration showed a strong correlation with the second component, and can be considered as a *reaching kinematics* component. Finally, the primary submovement length and the homing-in phase duration weighted substantially on the third component, suggesting that it can be interpreted as a *reaching submovements* component. The three components were correlated with each other, ranged from -.02 to .21.

3.1.4. Data analysis

The same approach to data analysis and model comparison adopted for Experiment 1 was used. Outlier removal led to the discarding of ~1.75% and ~0.95% of trials from the reach-to-grasp condition and reaching condition, respectively. Because of technical problem, we removed 22 trials from the reach-to-grasp condition and 9 trials from the reaching condition.

Table 3

Weights of the kinematic parameters for the first three components of the reaching condition.

	Component 1	Component 2	Component 3
Reaching time (ms)	.708	-.039	-.088
Time of maximum peak wrist velocity (ms)	.864	.033	.143
Time of maximum peak wrist deceleration (ms)	.805	-.067	-.100
Peak wrist deceleration (mm/s ²)	.063	.983	-.027
Peak wrist velocity (mm/s)	-.057	-.955	.019
Primary submovement length (%)	.320	-.029	.855
Homing-in phase duration (ms)	-.359	.021	.826

3.2. Results and discussion

3.2.1. Grasping condition

3.2.1.1. Accuracy. The overall error percentage was 21.3%. A GLME analysis, with random intercept for Participants and Blocks, showed that subjects were more accurate following an error (17.7% error-rate) than following a correct response (23.1% error-rate), $z = -3.54$, $p < .001$, $OR = 0.58$.

3.2.1.2. Submovements analysis. The average number of submovements was 2.35 ± 2.12 . A LME analysis, with random intercept for Participants and Blocks (modeling intercepts only), did not revealed any difference between post correct (2.32 ± 2.06) and post error (2.44 ± 2.30) trials in terms of total number of submovements ($\chi^2 = 1.79$, $p = .180$, $BF = 0.09$, $d = 0.05$).

3.2.1.3. Endpoint variability. The mean of the endpoint variability of the reaching movement was $8.03 \text{ mm} \pm 4.52$. A LME analysis, with random intercept for Participants and Blocks (modeling intercepts only), did not show any difference between post correct ($8.02 \text{ mm} \pm 4.38$) and post error ($8.05 \text{ mm} \pm 4.93$) trials in terms of the endpoint variability ($\chi^2 = 0.02$, $p = .885$, $BF = 0.09$, $d = 0.01$).

3.2.1.4. Reaction times. The mean post-correct and post-error RT adjustments are shown in Fig. 6. A LME analysis, with random intercept for Participants and Blocks (modeling intercepts only), revealed a significant difference between post-correct and post-error adjustments $\chi^2 = 37.16$, $p < .001$, $BF > 100$, $d = 0.45$. Contrast analysis showed that when an error was committed, subjects showed a significant post-error slowing ($PES_{\text{robust}} = 103.55 \text{ ms} \pm 28.21$), t

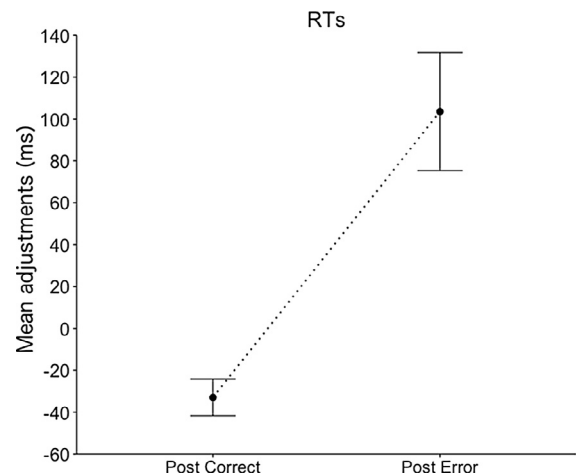


Fig. 6. Mean post-correct and post-error adjustments in RTs. Vertical bars indicate standard error of the mean. Positive values indicate a slowing down.

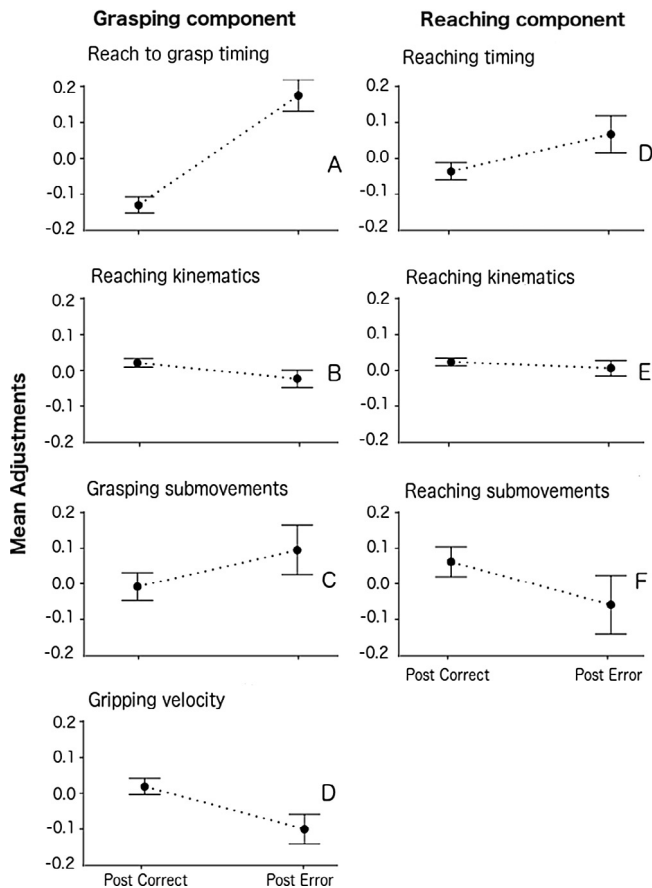


Fig. 7. Mean post-correct and post-error adjustments for the kinematic components of the grasping (left panel) and the reaching (right panel) condition. Vertical bars represent standard error of the mean.

(246) = 3.67, $p < .001$, $BF = 93.39$, $d = 0.23$. After a correct response, subjects showed a post-correct speeding ($-32.93 \text{ ms} \pm 8.7$), $t(774) = -3.76$, $p < .001$, $BF = 89.18$, $d = 0.13$.

3.2.1.5. Reach-to-grasp timing. The mean of post-correct and post-error adjustments of the Reach-to-grasp timing are shown in Fig. 7A. A LME analysis, with random intercept for Participants and Blocks (modeling intercepts only), revealed a significant difference between post-correct and post-error adjustments, $\chi^2 = 41.18$, $p < .001$, $BF > 100$, $d = 0.48$. After an error, subjects showed a significant post-error slowing ($\text{PES}_{\text{robust}} = 0.175 \pm 0.044$, $t(235) = 3.95$, $p < .001$, $BF = 259.44$, $d = 0.25$), whereas after a correct trial a post-correct speeding was present (-0.130 ± 0.022), $t(769) = -5.80$, $p < .001$, $BF > 100$, $d = 0.20$.

3.2.1.6. Reaching kinematics. The mean of post-correct and post-error adjustments for the Reaching kinematics component are shown in Fig. 7B. A LME analysis, with random intercept for Participants and Blocks (modeling intercepts only) did not show any difference between post-correct and post-error adjustments, $\chi^2 = 3.10$, $p = .077$, $BF = 0.35$, $d = 0.12$. Neither a significant post-error slowing ($\text{PES}_{\text{robust}} = -0.023 \pm 0.024$, $t(243) = -0.96$, $p = .334$, $BF = 0.03$, $d = 0.06$) nor a post-correct adjustment (0.020 ± 0.011 , $t(775) = -1.76$, $p = .078$, $BF = 0.01$, $d = 0.06$) were found.

3.2.1.7. Grasping submovements. The mean of post-correct and post-error adjustments of the Grasping submovements component are shown in Fig. 7C. A LME analysis, with random intercept for Participants and

Blocks (modeling intercepts only), did not show any difference between post-correct and post-error adjustments $\chi^2 = 1.63$, $p = .201$, $BF = 0.29$, $d = 0.09$. Contrast analysis did not show any evidence of post-error slowing ($\text{PES}_{\text{robust}} = 0.094 \pm 0.068$), $t(245) = 1.37$, $p = .169$, $BF = 0.03$, $d = 0.08$), or post-correct speeding (-0.007 ± 0.039), $t(769) = -0.19$, $p = .841$, $BF = 0.04$, $d = 0.007$).

3.2.1.8. Gripping velocity. The mean of post-correct and post-error adjustments of the Gripping velocity is shown in Fig. 7D. A LME analysis, with random intercept for Participants and Blocks (modeling intercepts only), revealed a significant difference between post-correct and post-error adjustments, $\chi^2 = 6.49$, $p = .010$, $BF = 3.12$, $d = 0.19$. After an error, subjects showed a significant reduction of gripping velocity ($\text{PES}_{\text{robust}} = -0.100 \pm 0.041$), $t(244) = -2.41$, $p = .016$, $BF = 2.44$, $d = 0.16$. No evidence of post-correct adjustments (0.018 ± 0.023) was found, $t(766) = 0.81$, $p = .413$, $BF = 0.02$, $d = 0.03$.

In summary, these findings mirror those obtained for Experiment 1, in the sense that the failure to reach out and grasp an object slows down the temporal aspects of the subsequent action with specific reference to the grasping component, without affecting the reaching component. Such results strengthen our argument that error-reactivity effects extend to motor execution, but seem to be limited to the grasping component.

3.2.2. Reaching condition

3.2.2.1. Accuracy. The overall error percentage was 21.5%. A GLME analysis, with random intercept for Participants and Blocks, showed no significant difference of post-error (21% error-rate) and post-correct (19.5% error-rate) accuracy, $z = -0.20$, $p = .840$, $OR = 0.97$.

3.2.2.2. Submovements analysis. The average number of submovements was 3.08 ± 3.02 . A LME analysis, with random intercept for Participants and Blocks (modeling intercepts only), did not reveal any difference between post correct (3.01 ± 2.80) and post error (2.97 ± 2.76) trials in terms of total number of submovements ($\chi^2 = 0.31$, $p = .572$, $BF = 0.04$, $d = 0.01$).

3.2.2.3. Endpoint variability. The mean of the endpoint variability of the reaching movement was $8.82 \text{ mm} \pm 13.03$. A LME analysis, with random intercept for Participants and Blocks (modeling intercepts only), did not show any difference between post correct ($10.75 \text{ mm} \pm 6.01$) and post error ($10.10 \text{ mm} \pm 6.64$) trials in terms of the endpoint variability ($\chi^2 = 2.49$, $p = .114$, $BF = 0.36$, $d = 0.12$).

3.2.2.4. Reaction times. The mean post-correct and post-error RT adjustments are shown in Fig. 8. A LME analysis, with random intercept for Participants (modeling both slopes and intercepts) and Blocks (modeling intercepts only), revealed a significant difference between post-correct and post-error adjustments, $\chi^2 = 6.61$, $p = .010$, $BF > 100$, $d = 0.41$. Contrast analysis showed a significant post-error slowing ($\text{PES}_{\text{robust}} = 43.11 \text{ ms} \pm 11.88$), $t(191) = 3.62$, $p < .001$, $BF = 85.46$, $d = 0.26$. After a correct response, a post-correct speeding ($-13.72 \text{ ms} \pm 4.60$) was present, $t(838) = -2.95$, $p = .003$, $BF = 5.95$, $d = 0.10$.

3.2.2.5. Reaching timing. The mean of post-correct and post-error adjustments of the Reaching timing component are shown in Fig. 7D. A LME analysis, with random intercept for Participants and Blocks (modeling intercepts only), did not show any difference between post-correct and post-error adjustments, $\chi^2 = 3.34$, $p = .067$, $BF = 0.44$, $d = 0.14$. Contrast analysis did not show any evidence of post-error ($\text{PES}_{\text{robust}} = 0.066 \pm 0.052$, $t(195) = 1.27$, $p = .204$, $BF = 0.31$, $d = 0.09$) or post-correct adjustment (0.036 ± 0.024 , $t(836) = -1.48$, $p = .136$, $BF = 0.21$, $d = 0.05$).

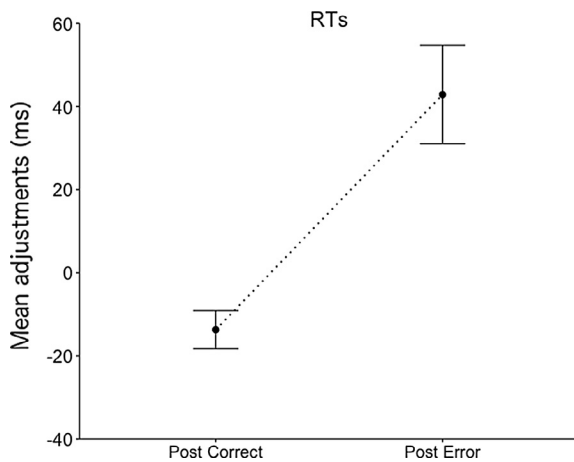


Fig. 8. Mean post-correct and post-error adjustments in RTs. Vertical bars indicate standard error of the mean. Positive values indicate a slowing down.

3.2.2.6. Reaching kinematics. The mean of post-correct and post-error adjustments of the Reaching kinematics component are shown in Fig. 7E. A LME analysis, with random intercept for Participants and Blocks (modeling intercepts only), did not show any difference between post-correct and post-error adjustments $\chi^2 = 0.50$, $p = .475$, $BF = 0.11$, $d = 0.05$. Contrast analysis did not show any evidence of post-error slowing ($PES_{\text{robust}} = 0.006 \pm 0.021$), $t(197) = 0.28$, $p = .778$, $BF = 0.10$, $d = 0.02$), whereas a post-correct speeding was present (0.023 ± 0.010), $t(842) = -2.19$, $p = .028$, $BF = 0.01$, $d = 0.07$).

3.2.2.7. Reaching submovements. The mean of post-correct and post-error adjustments of the Reaching submovements component are shown in Fig. 7F. A LME analysis, with random intercept for Participants and Blocks (modeling intercepts only), did not show any difference between post-correct and post-error adjustments $\chi^2 = 1.60$, $p = .205$, $BF = 0.18$, $d = 0.10$. Contrast analysis did not show any evidence of post-error slowing ($PES_{\text{robust}} = -0.059 \pm 0.082$), $t(195) = -0.72$, $p = .472$, $BF = 0.15$, $d = 0.05$), or post-correct speeding (0.061 ± 0.042), $t(836) = 1.46$, $p = .142$, $BF = 0.21$, $d = 0.05$).

In sum, these results confirm that reaching movements are impermeable to error-reactivity processes. These statement is supported by error rates, endpoint variability and submovements analyses. The differences found for reaching and reach-to-grasp may stem from a differential error coding according to the type of motor action performed by subjects. In other words, error information impact differently on motor organization depending on the type of motor response. We shall elaborate on this issue below.

4. General discussion

The aim of the present study was twofold. Firstly, we investigated error-reactivity in the context of goal-directed actions, in order to examine the extent to which PES effects impact on realistic and complex movements. Secondly, we assessed the influence of error-reactivity on motor execution. We crucially extend previous literature by demonstrating for the first time that error reactivity processes are detectable during motor execution but not in a generalized manner. Reaching seems to be impermeable to PES effects. When reach-to-grasp is the task, however, PES effects influences in a targeted manner the temporal aspects of the grasping component kinematical parameterization.

4.1. The motor preparation phase

In line with the previous literature, RTs analysis showed that error

commission led to a slowdown during the motor preparation phase. This result occurred despite we adopted a ITI (from 6500 to 8500 ms) longer than those the one typically used to investigate error reactivity (from 200 to 5000 ms; e.g., Caudek, Ceccarini, & Sica, 2015; Danielmeier & Ullsperger, 2011; Hajcak, McDonald, & Simons, 2003; King, Korb, von Cramon, & Ullsperger, 2010; Marco-Pallarés et al., 2008). Given that we used very long ITIs, our results seem to be driven by a strategic planning phase, in which the strategic influences of error reactivity are more evident. However, only the grasping component seems to benefit of the adaptive component of error reactivity, in terms of accuracy. Conversely, for the reaching component, no evidence of post error improvements of accuracy was found. In fact, we did not find any difference between post error and post correct trial with respect to error-rates, number of submovements and endpoint variability, which suggests that the reaching accuracy regulation is not influenced by error-reactivity effects.

For the grasping condition of Experiment 2 we found a larger PES in RT than in Experiment 1. This result may depend on the fact that Experiment 2 lasted much longer than Experiment 1, and besides, grasping conditions and reaching conditions were interleaved. A variety of studies have reported that PES is influenced by the control demands of the task (e.g., Hogan, Vargha-Khadem, Kirkham, & Baldeweg, 2005; Schroder, Moran, Infantolino, & Moser, 2013; Regev & Meiran, 2014). For instance, Schroder et al. (2013) manipulated cognitive demands in a flanker task by reversing stimulus-response mappings between blocks. They found a larger PES in the more-demanding S-R reversal blocks than in nonreversal blocks. Our results are in line with previous literature suggesting that task demands play an important role in PES emergence.

4.2. The motor execution phase

The present data showed that error reactivity effects also extend to motor execution, albeit in a selective manner. In fact, we found that PES effects are confined to the reach-to-grasp timing and to the parameterization of the grasping component, whereas no effects were found for the reaching component. Our preferred idea is that PES works in a time based strategic manner depending on task. When the task involves grasping, a slowing in movement duration after the occurrence of an error arises. This might reflect advanced planning, which strategically prolongs the duration of the movement so that reach-to-grasp kinematics is scaled within this allotted time. Indeed, the motor control system relies on visual and proprioceptive feedback loops, and thus, the more time in which these loops can operate, the greater the influence control will exert (Glover, 2004). This type of programming keeps the timing of the commands independent from the spatial parameters of the movement. In other words, selection of the motor plan needing to be activated to carry out a given task keeping into account previous errors can be modified within a centrally generated temporal template that determines the co-ordination of a given action. This might be the easiest and most readily chosen organizational option of the neural system to compensate for the error.

In this connection, the reduction of gripping velocity may serve to lengthen the time window within which contact points can be established more precisely and firmly. Several studies have investigated the effect of object properties and context on the planning of digit placement upon an object (Fu, Zhang, & Santello, 2010; Lukos, Ansuini, & Santello, 2007; Sartori, Straulino, & Castiello, 2011; Zhang, Gordon, Fu, & Santello, 2010). In these studies, subjects grasped and lifted an object with the aim to prevent object tilt. For example, to do so when an object's center of mass is shifted to the right (resulting in a clockwise tilt if uncompensated), a compensatory counter-clockwise moment was required at object lift onset. Subjects created a compensatory moment by placing the thumb lower than the index finger (Lukos et al., 2007). In this example, digit placement is modulated to ensure successful completion of the task. Our finding of a post error reduction in grip

velocity might signify that after an error it is necessary to apply changes related to finger positioning in order to avoid the falling of the target. To do this, participants need a slower closing of the finger during the honing phase as to adjust contact points and possibly the applied forces.

The finding of adaptation of fingers' closing velocity following an error extends to error coding the evidence that subjects' grasping is anticipatory. Anticipatory planning implies that objects are grasped in such a way that allows for movement flexibility. In our task, such flexibility allows to keep into account errors when performing the subsequent movement. Thus, fingers' movement trajectory was dependent on the outcome of the previous trial. In other words, the slowing of the reach-to-grasp timing after an error seems to reflect advanced planning related to the need to increase the control and avoid future errors. This explanation is in line with the most commonly accepted functional explanation for post-error slowing, that is the control hypothesis based on the conflict monitoring theory (Botvinick et al., 2001). It postulates that people continuously monitor their performance and that control levels are flexibly adjusted to environmental demands in order to optimize performance. Specifically, making an error results in the concurrent activation of both the correct and an incorrect response (i.e., response conflict), and the detection of this response conflict leads to increased response thresholds—and thus to more accurate yet slower performance to reduce the likelihood of committing another error. In our circumstances, the correct and incorrect response would be concerned with the determination of fingers' trajectories.

It remains to be explained why the reaching component is impermeable to PES effects. Jeannerod (1981, 1984) proposed that the visuomotor mechanisms responsible for prehension are structured in a modular way. The “reaching channel” extracts from the visual world information on the spatial location of the objects and activates those muscles, which are relevant to carry the hand to the object location. The “grasping channel” extracts information concerning the size and shape of the object and transforms it in the activation of distal muscles relevant to grasping the object. Furthermore, it has been suggested (Jeannerod, 1981, 1984) that the beginning of hand closure (which occurs immediately after maximal hand aperture) starts after the peak velocity of the transport movement.

A point worth noting is that the strict dichotomy between reaching and grasping components has been occasionally questioned. It has been revealed that the component controlling proximal movements can access information about stimulus size and accordingly can modify peak velocity and acceleration (e.g., Gentilucci et al. 1991; Jakobson & Goodale, 1991; Smeets & Brenner, 1999). This weakened the proposal of two independent channels, one responsible for the computation of the stimulus location and arm transport, and the other responsible for the computation of stimulus intrinsic properties and the organization of manipulation. However, the very fact that in our study changes in the organization of the reach-to-grasp movements due to error commission are only evident at the level of the grasping component speaks in favor of the possibility that the two components can be dissociated. In particular, our findings suggest that the impermeability of the reaching component to errors might be strategic, simplifying the processes underlying the reorganization of the movement sequence following an error. This proposal is corroborated by studies indicating that events have confirmed the observation that hand closure initiates during the deceleration phase, but the precise moment of the closure did not have any specific counterpart in the velocity profiles of the reaching component (Gentilucci et al., 1991; Jakobson & Goodale, 1991).

Another interesting aspect that should be noted is that our results are inconsistent with the idea that the hysteresis effect is elicited by erroneous movements. In fact, if errors had produced a hysteresis effect, the motor system would have perseverated in implementing a different movement kinematics on the following trial, increasing the probability of new errors. However, we did not find any evidence of a post error decrease of accuracy. This may suggest that error reactivity processes

lead to an updating of action plan which overwrites any detrimental effect of preceding motor events.

4.3. Nesting kinematics in PES theories

According to functional accounts, PES is related to cognitive control mechanisms which are implemented after the commission of errors (Botvinick et al., 2001). Non-functional accounts, instead, suggest that PES might occur because error processing has a detrimental effect on subsequent information processing. However, both functional and non-functional accounts consider error reactivity as a domain-general effect, consisting in an unspecific slowing of movement. One finding that stands out from the present research is that error reactivity has a different impact on the components of the movement, and it does not always produce slowing down in motor execution. In fact, our results showed that error reactivity effects are confined to the grasping component, and no post-error effects were found at the level of the reaching component. This result may suggest that error reactivity is a flexible process, whose effects on behavior depend on the specific demands of the task as well as on the motor components involved in the action.

Previous studies on error reactivity have tested functional accounts considering the post-error accuracy. However, the implementation of a more conservative strategy does not necessarily imply an improvement in accuracy. In particular, when participants commit too many errors, or when the error rate is too low, there is a reduced chance to improve the performance after an error, regardless of the adoption of a more cautious response criterion (Danielmeier & Ullsperger, 2011). In these situations, post-accuracy is a misleading measure. A potential solution to this problem is the use of kinematical analysis. By investigating how errors influence kinematics parameters it might be possible to directly investigate the strategy adopted after an error, without necessarily considering the final outcome of the action, in terms of accuracy.

5. Conclusions

The present study contributes to the existing literature on post-error slowing by testing post-error slowing with respect to a reach-to-grasp action. Overall, the current study for the first time demonstrated post-error slowing at the action execution level (as opposed to single RT level). We observed that an action is executed slower following an error in a preceding movement as compared to following a correctly executed movement. For our participants, post-error slowing seems to be primarily the result of strategically increased control to prevent future errors (i.e., functional slowing). Yet, non-functional attentional distraction resulting from an orienting response to the error cannot be excluded. Another important aspect emerging from our study is that the reaching component is immune to post-error adjustments. However, it must be noted that this result may be related to the particular demands of the tasks we employed, and thus, further research with realistic and ecological tasks is needed to better clarify this issue.

Supplementary material

All relevant data and R scripts are available at <https://osf.io/a457y/>.

Acknowledgements

This work was supported by a grant from the Progetto Strategico, Università di Padova (grant number 2010XPMFW4).

References

- Anguera, J. A., Seidler, R. D., & Gehring, W. J. (2009). Changes in performance monitoring during sensorimotor adaptation. *Journal of Neurophysiology*, 102(3), 1868–1879.

- Baayen, R. H., Davidson, D. J., & Bates, D. M. (2008). Mixed-effects modeling with crossed random effects for subjects and items. *Journal of Memory and Language*, 59(4), 390–412.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). lme4: Linear mixed-effects models using Eigen and S4 (R package Version 1.1-8). Retrieved from <http://CRAN.R-project.org/package=lme4>.
- Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S., & Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychological Review*, 108(3), 624.
- Botvinick, M., Nystrom, L. E., Fissell, K., Carter, C. S., & Cohen, J. D. (1999). Conflict monitoring versus selection-for-action in anterior cingulate cortex. *Nature*, 402(6758), 179.
- Castiello, U. (2005). The neuroscience of grasping. *Nature Reviews Neuroscience*, 6(9), 726–736.
- Caudek, C., Ceccarini, F., & Sica, C. (2015). Posterror speeding after threat-detection failure. *Journal of Experimental Psychology: Human Perception and Performance*, 41(2), 324.
- Clavijo-Baquet, S., Boher, F., Ziegler, L., Martel, S. I., Estay, S. A., & Bozinovic, F. (2014). Differential responses to thermal variation between fitness metrics. *Scientific reports*, 4.
- Cohen, J. (1988). The effect size. Statistical power analysis for the behavioral sciences. pp. 77–83.
- Critchley, H. D., Tang, J., Glaser, D., Butterworth, B., & Dolan, R. J. (2005). Anterior cingulate activity during error and autonomic response. *Neuroimage*, 27(4), 885–895.
- D'Amico, M., & Ferrigno, G. (1990). Technique for the evaluation of derivatives from noisy biomechanical displacement data using a model-based bandwidth-selection procedure. *Medical and Biological Engineering and Computing*, 28(5), 407–415.
- D'Amico, M., & Ferrigno, G. (1992). Comparison between the more recent techniques for smoothing and derivative assessment in biomechanics. *Medical and Biological Engineering and Computing*, 30(2), 193–204.
- Danev, S. G., & Winter, C. R. (1971). Heart rate deceleration after erroneous responses. *Psychological Research*, 35(1), 27–34.
- Danielmeier, C., & Ullsperger, M. (2011). Post-error adjustments. *Frontiers in Psychology*, 2, 233.
- Darling, W. G., & Gilchrist, L. (1991). Is there a preferred coordinate system for perception of hand orientation in three-dimensional space? *Experimental Brain Research*, 85(2), 405–416.
- Dixon, P., & Glover, S. (2009). Perseveration and contrast effects in grasping. *Neuropsychologia*, 47(6), 1578–1584.
- Dixon, P., McAnish, S., & Read, L. (2012). Repetition effects in grasping. *Canadian Journal of Experimental Psychology/Revue Canadienne de Psychologie Expérimentale*, 66(1), 1.
- Dutilh, G., van Ravenzwaaij, D., Nieuwenhuis, S., van der Maas, H. L., Forstmann, B. U., & Wagenmakers, E. J. (2012a). How to measure post-error slowing: A confound and a simple solution. *Journal of Mathematical Psychology*, 56(3), 208–216.
- Dutilh, G., Vandekerckhove, J., Forstmann, B. U., Keuleers, E., Brysbaert, M., & Wagenmakers, E. J. (2012b). Testing theories of post-error slowing. *Attention, Perception, & Psychophysics*, 74(2), 454–465.
- Eliasson, A. C., Rösblad, B., & Forssberg, H. (2004). Disturbances in programming goal-directed arm movements in children with ADHD. *Developmental Medicine and Child Neurology*, 46(1), 19–27.
- Elliott, D., Helsen, W. F., & Chua, R. (2001). A century later: Woodworth's (1899) two-component model of goal-directed aiming. *Psychological Bulletin*, 127(3), 342.
- Erdfeiler, E., Faul, F., & Buchner, A. (1996). GPOWER: A general power analysis program. *Behavior Research Methods, Instruments, & Computers*, 28(1), 1–11.
- Erlhagen, W., & Schöner, G. (2002). Dynamic field theory of movement preparation. *Psychological Review*, 109(3), 545.
- Fan, J., Flombaum, J. I., McCandless, B. D., Thomas, K. M., & Posner, M. I. (2003). Cognitive and brain consequences of conflict. *Neuroimage*, 18(1), 42–57.
- Fradet, L., Lee, G., & Dounskaia, N. (2008). Origins of submovements in movements of elderly adults. *Journal of Neuroengineering and Rehabilitation*, 5(1), 28.
- Fu, Q., Zhang, W., & Santello, M. (2010). Anticipatory planning and control of grasp positions and forces for dexterous two-digit manipulation. *Journal of Neuroscience*, 30(27), 9117–9126.
- Gehring, W. J., & Fencsik, D. E. (2001). Functions of the medial frontal cortex in the processing of conflict and errors. *Journal of Neuroscience*, 21(23), 9430–9437.
- Gehring, W. J., Liu, Y., Orr, J. M., & Carp, J. (2011). *The error-related negativity (ERN/Ne)*. Oxford, UK: University Press 231–291.
- Gelman, A., & Hill, J. (2007). *Data analysis using regression and multi-level/hierarchical models*. Cambridge, UK: Cambridge University Press.
- Gentilucci, M., Castiello, U., Corradini, M. L., Scarpa, M., Umiltà, C., & Rizzolatti, G. (1991). Influence of different types of grasping on the transport component of prehension movements. *Neuropsychologia*, 29(5), 361–378.
- Glover, S. (2004). Separate visual representations in the planning and control of action. *Behavioral and Brain Sciences*, 27, 3–78.
- Glover, S., & Dixon, P. (2013). Perseveration effects in reaching and grasping rely on motor priming and not perception. *Experimental Brain Research*, 226(1), 53–61.
- Gordon, J., Ghilardi, M. F., Cooper, S. E., & Ghez, C. (1994). Accuracy of planar reaching movements. *Experimental Brain Research*, 99(1), 112–130.
- Grafton, S. T. (2010). The cognitive neuroscience of prehension: Recent developments. *Experimental Brain Research*, 204(4), 475–491.
- Haith, A. M., Pakpoor, J., & Krakauer, J. W. (2016). Independence of movement preparation and movement initiation. *Journal of Neuroscience*, 36(10), 3007–3015.
- Hajcak, G., McDonald, N., & Simons, R. F. (2003). To err is autonomic: Error-related brain potentials, ANS activity, and post-error compensatory behavior. *Psychophysiology*, 40(6), 895–903.
- Hogan, A. M., Vargha-Khadem, F., Kirkham, F. J., & Baldeweg, T. (2005). Maturation of action monitoring from adolescence to adulthood: An ERP study. *Developmental Science*, 8(6), 525–534.
- Holroyd, C. B., & Coles, M. G. (2002). The neural basis of human error processing: Reinforcement learning, dopamine, and the error-related negativity. *Psychological Review*, 109(4), 679.
- Houk, J. C., Bastianen, C., Fansler, D., Fishbach, A., Fraser, D., Reber, P. J., ... Simo, L. S. (2007). Action selection and refinement in subcortical loops through basal ganglia and cerebellum. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1485), 1573–1583.
- Houtman, F., & Notebaert, W. (2013). Blinded by an error. *Cognition*, 128(2), 228–236.
- Jakobson, L. S., & Goodale, M. A. (1991). Factors affecting higher-order movement planning: A kinematic analysis of human prehension. *Experimental Brain Research*, 86(1), 199–208.
- Jax, S. A., & Rosenbaum, D. A. (2007). Hand path priming in manual obstacle avoidance: Evidence that the dorsal stream does not only control visually guided actions in real time. *Journal of Experimental Psychology: Human Perception and Performance*, 33(2), 425.
- Jeannerod, M. (1981). Specialized channels for cognitive responses. *Cognition*, 10(1), 135–137.
- Jeannerod, M. (1984). The timing of natural prehension movements. *Journal of Motor Behavior*, 16(3), 235–254.
- Jeffreys, H. (1961). *Theory of probability*. Oxford, UK: Oxford University Press.
- Jentzsch, I., & Dudschig, C. (2009). Why do we slow down after an error? Mechanisms underlying the effects of posterror slowing. *The Quarterly Journal of Experimental Psychology*, 62(2), 209–218.
- Jentzsch, I., & Leuthold, H. (2006). Control over speeded actions: A common processing locus for micro- and macro-trade-offs? *The Quarterly Journal of Experimental Psychology*, 59(8), 1329–1337.
- Jones, A. D., Cho, R. Y., Nystrom, L. E., Cohen, J. D., & Braver, T. S. (2002). A computational model of anterior cingulate function in speeded response tasks: Effects of frequency, sequence, and conflict. *Cognitive, Affective, & Behavioral Neuroscience*, 2(4), 300–317.
- Kaiser, H. F. (1960). The application of electronic computers to factor analysis. *Educational and Psychological Measurement*, 20(1), 141–151.
- Kelso, J. A. S., Buchanan, J. J., & Murata, T. (1994). Multifunctionality and switching in the coordination dynamics of reaching and grasping. *Human Movement Science*, 13(1), 63–94.
- Kent, S. W., Wilson, A. D., Plumb, M. S., Williams, J. H., & Mon-Williams, M. (2009). Immediate movement history influences reach-to-grasp action selection in children and adults. *Journal of Motor Behavior*, 41(1), 10–15.
- Khan, M. A., & Franks, I. M. (2003). Online versus offline processing of visual feedback in the production of component submovements. *Journal of Motor Behavior*, 35(3), 285–295.
- King, J. A., Korb, F. M., von Cramon, D. Y., & Ullsperger, M. (2010). Post-error behavioral adjustments are facilitated by activation and suppression of task-relevant and task-irrelevant information processing. *Journal of Neuroscience*, 30(38), 12759–12769.
- Krigolson, O. E., & Holroyd, C. B. (2006). Evidence for hierarchical error processing in the human brain. *Neuroscience*, 137(1), 13–17.
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2013). lmerTest: Tests for random and fixed effects for linear mixed effect models (R package Version, 2.0-25). Retrieved from <http://cran.r-project.org/web/packages/lmerTest/>.
- Lukos, J., Ansuini, C., & Santello, M. (2007). Choice of contact points during multidigit grasping: Effect of predictability of object center of mass location. *Journal of Neuroscience*, 27(14), 3894–3903.
- Marco-Pallarés, J., Camara, E., Münte, T. F., & Rodríguez-Fornells, A. (2008). Neural mechanisms underlying adaptive actions after slips. *Journal of Cognitive Neuroscience*, 20(9), 1595–1610.
- Meyer, D. E., Abrams, R. A., Kornblum, S., Wright, C. E., & Keith Smith, J. E. (1988). Optimality in human motor performance: Ideal control of rapid aimed movements. *Psychological Review*, 95(3), 340.
- Morey, D., Rouder, J. N., & Jamil, T. (2014). Bayes factor: Computation of Bayes factors for common designs (R package version 0.9.8). Retrieved from <http://CRAN.R-project.org/package=BayesFactor>.
- Neubert, F. X., Mars, R. B., Buch, E. R., Olivier, E., & Rushworth, M. F. (2010). Cortical and subcortical interactions during action reprogramming and their related white matter pathways. *Proceedings of the National Academy of Sciences*, 107(30), 13240–13245.
- Notebaert, W., Houtman, F., Van Opstal, F., Gevers, W., Fias, W., & Verguts, T. (2009). Post-error slowing: An orienting account. *Cognition*, 111(2), 275–279.
- Novak, K. E., Miller, L. E., & Houk, J. C. (2002). The use of overlapping submovements in the control of rapid hand movements. *Experimental Brain Research*, 144(3), 351–364.
- O'Connell, R. G., Dockree, P. M., Bellgrove, M. A., Kelly, S. P., Hester, R., Garavan, H., ... Foxe, J. J. (2007). The role of cingulate cortex in the detection of errors with and without awareness: A high-density electrical mapping study. *European Journal of Neuroscience*, 25(8), 2571–2579.
- Pinheiro, J. C., & Bates, D. M. (2000). Mixed-effects models in S and S-PLUS. In J. Chambers, W. Eddy, W. Hardle, S. Sheather, & L. Tierney (Eds.). *Statistics and computing* (pp. 57–96). New York, NY: Springer-Verlag.
- R Core Team (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Regev, S., & Meiran, N. (2014). Post-error slowing is influenced by cognitive control demand. *Acta Psychologica*, 152, 10–18.
- Revelle, W. (2012). psych: Procedures for Psychological, Psychometric, and Personality Research (Version 1.2.1). Retrieved from <http://cran.r-project.org/web/packages/psych/index.html>.
- Ridderinkhof, R. K. (2002). Micro- and macro-adjustments of task set: Activation and suppression in conflict tasks. *Psychological Research*, 66(4), 312–323.

- Rossetti, Y. (1998). Implicit short-lived motor representations of space in brain damaged and healthy subjects. *Consciousness and Cognition*, 7(3), 520–558.
- Rouder, J. N., Morey, R. D., Speckman, P. L., & Province, J. M. (2012). Default Bayes factors for ANOVA designs. *Journal of Mathematical Psychology*, 56(5), 356–374.
- Sartori, L., Straulino, E., & Castiello, U. (2011). How objects are grasped: the interplay between affordances and end-goals. *PLoS One*, 6(9), e25203.
- Schroder, H. S., Moran, T. P., Infantolino, Z. P., & Moser, J. S. (2013). The relationship between depressive symptoms and error monitoring during response switching. *Cognitive, Affective, & Behavioral Neuroscience*, 13(4), 790–802.
- Smeets, J. B., & Brenner, E. (1999). A new view on grasping. *Motor Control*, 3(3), 237–271.
- Stojic, H. (2015). Useful functions for cognitive modeling <https://rdr.io/github/hstojic/cogmod/>.
- Szumilas, M. (2010). Explaining odds ratios. *Journal of the Canadian Academy of Child and Adolescent Psychiatry*, 19(3), 227.
- Vocat, R., Pourtois, G., & Vuilleumier, P. (2011). Parametric modulation of error-related ERP components by the magnitude of visuo-motor mismatch. *Neuropsychologia*, 49(3), 360–367.
- Wagenmakers, E. J., & Farrell, S. (2004). AIC model selection using Akaike weights. *Psychonomic Bulletin & Review*, 11(1), 192–196.
- White, C. N., Ratcliff, R., Vasey, M. W., & McKoon, G. (2010). Using diffusion models to understand clinical disorders. *Journal of Mathematical Psychology*, 54(1), 39–52.
- Wong, A. L., Haith, A. M., & Krakauer, J. W. (2015). Motor planning. *The Neuroscientist*, 21(4), 385–398.
- Zhang, W., Gordon, A. M., Fu, Q., & Santello, M. (2010). Manipulation after object rotation reveals independent sensorimotor memory representations of digit positions and forces. *Journal of Neurophysiology*, 103(6), 2953–2964.