Article

Controlling the trajectory of a moving object substantially shortens the latency of motor responses to visual stimuli

slower responses

faster responses !

Choice RT
Pressing the button launches the ball

Control
Pressing the button alters the ball trajectory

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Highlights

Button-press responses occur faster when controlling a moving object than for choice RTs

These shorter latencies probably result from faster sensorimotor processing (LATER model)

Controlling a moving object also reduces the variability of response times

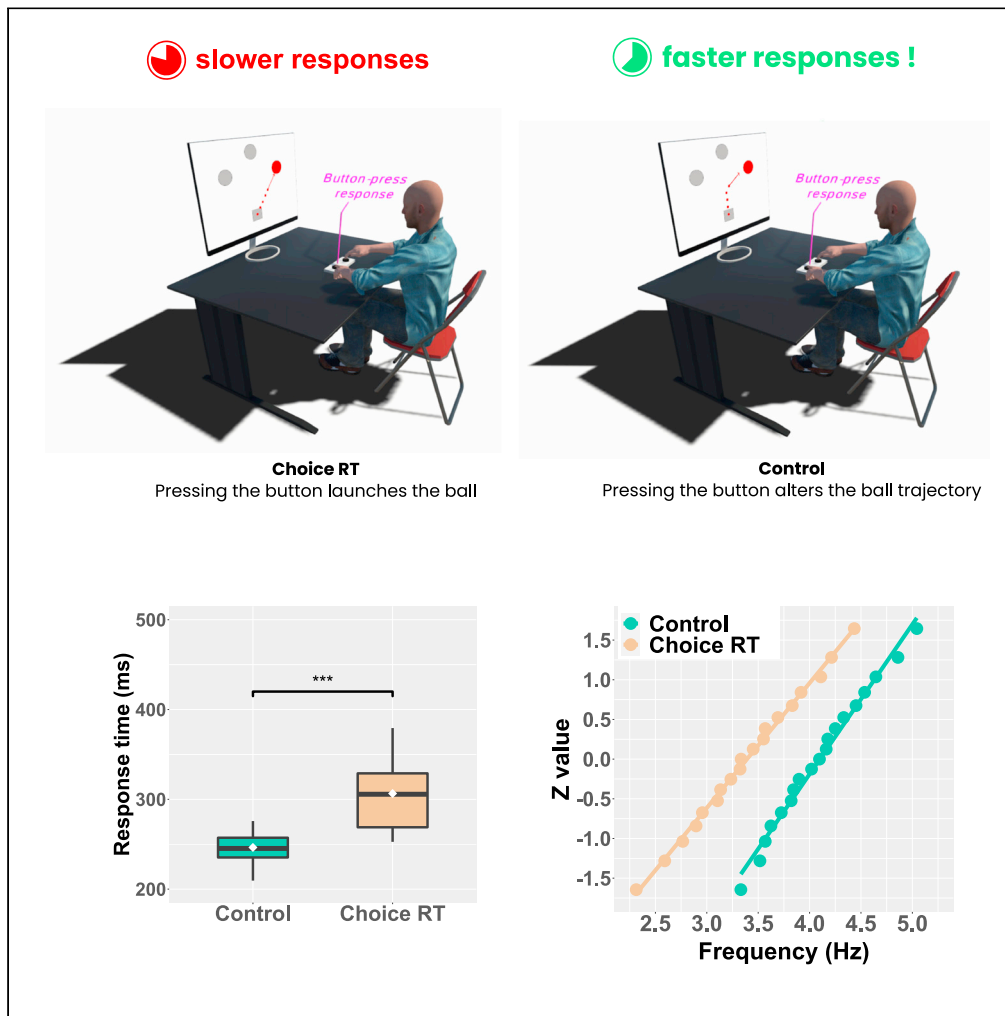These faster and less variable responses cannot be attributed to forward models

Article

Controlling the trajectory of a moving object substantially shortens the latency of motor responses to visual stimuli

Thibaut Le Naour,[1,2] Michael Papinutto,[3] Muriel Lobier,[4] and Jean-Pierre Bresciani[1,5,6,*]

SUMMARY

Motor responses to visual stimuli have shorter latencies for controlling than for initiating movement. The shorter latencies observed for movement control are notably believed to reflect the involvement of forward models when controlling moving limbs. We assessed whether controlling a moving limb is a "requisite" to observe shortened response latencies. The latency of button-press responses to a visual stimulus was compared between conditions involving or not involving the control of a moving object, but never involving any actual control of a body segment. When the motor response controlled a moving object, response latencies were significantly shorter and less variable, probably reflecting a faster sensorimotor processing (as assessed fitting a LATER model to our data). These results suggest that when the task at hand entails a control component, the sensorimotor processing of visual information is hastened, and this even if the task does not require to actually control a moving limb.

INTRODUCTION

For over a century, response latency has been extensively used to investigate the mechanisms underlying information processing, motor planning, and motor control. In most paradigms, response latency corresponds to the time that elapses between the presentation of a stimulus and the first detectable motor response to this stimulus. Several factors have been shown to affect response latency. For simple reaction times, response latency depends on intra-individual factors, such as the age and gender of the probed person,[1] his/her level of fatigue, attention or arousal,[1] as well as the influence of substances, such as alcohol[2] or caffeine.[3] Response latency also depends on the type,[1] intensity,[4] and duration of the stimulus,[5] as well as on the number of stimulus-response alternatives.[6] Last but not least, response latency can be strongly affected by task-related factors, such as the complexity[7,8] or the nature and consequences of the required motor response.[9–12] In particular, for the same level of motor complexity, as for instance simple reaching movements performed with the arm, response latency to a visual stimulus is usually much shorter when the task entails a control component, such as adjusting the trajectory of an ongoing movement (i.e., online control), than when it consists in initiating the reaching movement.[12–15]

The short response latencies usually observed in control tasks are hardly compatible with the time required to process visual information in reaction-time tasks.[16] As a matter of fact, the feedback loops controlling ongoing movements have been shown to be very fast[14,17–23] and automatic.[19–21,24–26] To account for these characteristics, several authors have suggested that during movement execution, motor control likely relies on the internal models using efference copy to predict the consequences of motor commands.[16,21,27,28] Specifically, throughout movement execution, sensory information about the current position of the effector relative to the target would be continuously compared to its predicted/desired position, the latter being "computed" by a forward model (see[16] for a detailed description). Any detected difference between the actual and the predicted position of the effector would trigger modifications of the motor command, which in turn would modify the trajectory of the effector. Functionally, forward models would thereby contribute to compensate the delays inherent to sensory feedback, which would explain the shorter response times usually observed in motor control tasks/during movement execution. In other words, when controlling an ongoing movement, information processing would be different from and more efficient than the "purely" feedback-based processing occurring before movement initiation. Along that line, a very elegant study performed by Day and Brown[14] with a split-brain patient (i.e., a patient who

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underwent a surgical resection of the callosal fibers) suggests that the neural structures underlying online control might be distinct, at least partially, from those involved in the preparation of the action.

In the current study, we investigated whether the shorter response latency usually observed in control tasks is exclusively imputable to the reliance on internal models and feedforward mechanisms, or whether there might be more to it. More specifically, control tasks are usually characterized by important time constraints, which have to be met to ensure the success of the action. We reasoned that to cope with these time constraints, sensorimotor processing might be hastened when the task at hand entails a control component and this even if the task does not require to control the trajectory of a limb. If this is the case, then motor responses could be triggered faster when associated with a control task, and this irrespective of whether actual motor control is required. Such faster motor responses would be somewhat similar, though probably not identical, to the shortening of saccade reaction times observed under certain task conditions. For instance, saccade reaction time is substantially shorter when a perceptive or discrimination task must be performed at the saccade landing location than for "simple" target-elicited saccades.[10,29,30] Shorter saccade reaction times are also observed when an arm movement is performed simultaneously to the saccade.[31] We speculated that a similar latency reduction might be observed for manual responses when the task entails a control component. To address this question, we assessed whether a control task exempt of any actual motor control of a moving limb might give rise to shorter response latencies than a choice reaction time task. For that, we used a control task in which participants could alter the trajectory of a moving object by simply pressing on a button. In this task, no actual control of the arm trajectory was required, and the motor output was strictly identical to that of a choice reaction time task to which it was compared. Importantly, the control performed in the control task was not "continuous". Specifically, a single and unique button press allowed participants to redirect the moving object, but after this button press, participants did not have any further control on the trajectory of the object until the end of the trial.

RESULTS

The participants were seating in a dark room in front of a monitor with their head resting on a chin and forehead rest. Their eye movements were recorded using an infrared eye-tracking system. Their motor responses to the stimuli consisted in pressing with the left and right index fingers on the left and right buttons of a response box. The visual scene displayed on the monitor consisted of a starting area at the bottom center of the scene, and of three targets arranged on the arc of a circle (−25 to 25°, see Figure 1) in the middle/upper part of the screen. At the beginning of each trial, the participants had to fixate the central target. If and when this target "jumped" to the left or right target location, which occurred in a random two-thirds of the trials (i.e., one-third on each side), the participants had to press as fast as possible the response button corresponding to the side of the target jump, i.e., left button for a left jump and right button for a right jump. For trials without any target jump, i.e., a third of the trials, participants had to refrain from pressing any button.

In the first experiment, response latency was measured in two different conditions which were manipulated within-subject and presented in blocks in counterbalanced order. In the choice reaction time (CRT) condition, pressing one of the response buttons launched a red disc representing a ball in the direction of the target located on the side of the pressed button, i.e., left target for a left button press, right target for a right button press. The ball was launched from the starting area (see Figure 1). When no response button was pressed, the ball was launched toward the central target after a given delay (see the STAR Methods section for details). In the controlled ball (CB) condition, the red ball was launched toward the central target before any target jump occurred. If and when a response button was pressed, the already moving ball deviated toward the target located on the side of the pressed button. When no response button was pressed, the ball pursued its straight path toward the central target. The difference between the two response conditions was that in the CRT condition, the participant's response affected the direction in which the ball was launched, whereas in the CB condition, the participant's response controlled the direction of the ball while it was already moving. Figure 1A illustrates the time course of a trial with rightwards target jump in the CB condition.

The response condition significantly affected response latency (χ^2 (1) = 41.14, p < 0.001). On average, participants responded 60 ms earlier when the response altered the ball trajectory than when it did not (mean response latency = 246.43 ms in the CB condition vs. 306.50 ms in the CRT condition, see Figure 2A). The difference between the two conditions explained 51% of the variance of response latency (marginal
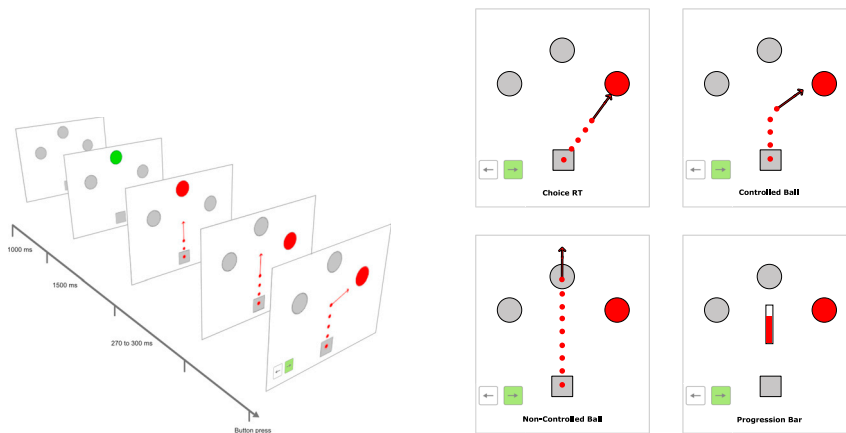
Figure 1. Procedure and conditions

(A) Time course of a trial with a target jump to the right in the controlled ball condition (Exp. 1 & 2). After the participant fixated the central target for 1000 ms, it turns green for 1500 ms. The central target then turns red and the red ball is simultaneously launched from the starting area toward the central target. A random 270 to 330 ms after the central target turned red, the central target jumps to the right. When the target jumps to the right, the participant presses as fast as possible the right response button, which redirects the red ball toward the right target. Note that changing the color of the central target from green to red 270 to 330 ms before a potential jump provided the participant with the same time-related pre-cue in all response conditions.

(B) Visual scene after a target jump to the right and a right button press for the four different conditions (Exp. 1 & 2). In the choice RT condition (top left quadrant), pressing the right response button in response to a right target jump launched the red ball from the starting area toward the right target. In the controlled ball condition (top right quadrant), the red ball was already moving upward toward the central target before the target jump, and pressing the right response button in response to a right target jump redirected the ball toward the right target. In the non-controlled ball condition (bottom left quadrant), the red ball was already moving upward toward the central target and pressing the right response button did not have any effect on the ball trajectory. In the progression bar condition (bottom right quadrant), the red progression bar started moving upward before the target jump and pressing on the response button did not have any effect on the visual scene.

$R^2 = 0.51$), and its significance was confirmed by a paired comparison between the two levels ($p < 0.001$, $R = 0.88$). On the other hand, the required direction of the response did not have any effect on response latency, which was almost the same for left and right responses (276.33 ms vs. 276.60 ms, $\chi^2 (1) = 0.002$, $p = 0.97$, marginal $R^2 = 0.00001$). There was no interaction between the two main factors ($\chi^2 (1) = 0.28$, $p = 0.60$). We also assessed whether the two factors affected the intra-individual variability of response latency. As for average response latencies, the response condition significantly affected the intra-subject variability of response latency ($\chi^2 (1) = 16.14$, $p < 0.001$). Specifically, participants' response latency was almost twice as variable in the CRT than in the CB condition (mean variability of response latency = 47.70 ms vs. 29.98 ms, see Figure 2B). This difference explained 24% of the measured variance (marginal $R^2 = 0.24$), and its significance was confirmed by a paired comparison between the two conditions ($p < 0.001$, $R = 0.67$). The direction of the response did not affect response latency variability (50.86 ms vs. 52.61 ms for responses to the left and to the right, respectively, $\chi^2 (1) = 0.40$, $p = 0.53$, marginal $R^2 = 0.005$, see Figure S1), and there was no interaction between the two factors ($\chi^2 (1) = 1.10$, $p = 0.29$).

The results of the first experiment clearly show that when the motor response altered the trajectory of an already moving object rather than setting it in motion/launching it in a given direction, response latencies were much shorter and much less variable. Importantly, these shorter and less variable response latencies cannot be attributed to differences in the programming/reprogramming of the motor output, because the required motor command was identical in both response conditions, namely pressing a button. In accordance with our initial hypotheses, these results suggest that when involved in the control rather than the initiation of movement, the sensorimotor loops processing sensory information and triggering motor responses are more "efficient", at least regarding response latency. However, one might argue that the moving ball provided some kind of "urgency" signal that was not present in the CRT condition. Specifically, the progression of the ball toward the central target provided time-related information, and this feedback might have "urged" participants to react faster because of time pressure. A second experiment was
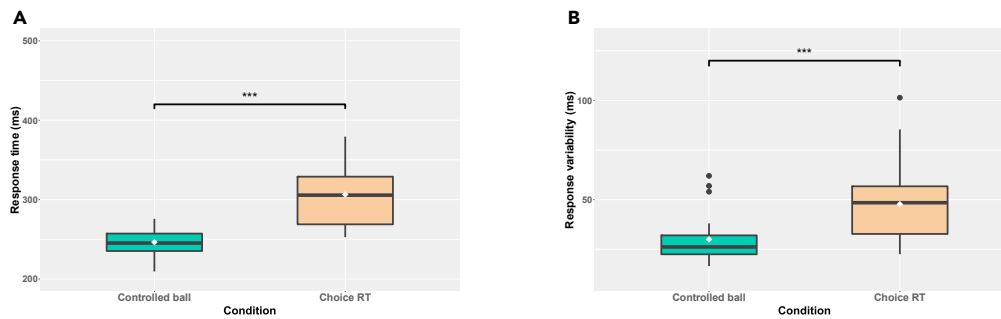
Figure 2. Effect of the response condition on response time and variability in Exp. 1
(A) Participants responded significantly faster when controlling the trajectory of the ball (green box) than when launching the ball in the choice RT condition (beige box) [Wilcoxon signed-rank test, p < 0.001, R = 0.88, i.e., large effect size].
(B) Intra-subject variability of response time was significantly larger when the task consisted in launching the ball in the choice RT condition (beige box) than when it consisted in controlling the ball trajectory (green box) [Wilcoxon signed-rank test, p < 0.001, R = 0.67, i.e., large effect size].

designed to assess whether the reduced response time observed in experiment 1 could indeed trivially result from time-related information. Experiment 2 consisted of three conditions. The CB condition was identical to that of experiment 1. The non-controlled ball condition was similar to the CB condition except for the fact that when the participant pressed a button, it did not have any effect on the ball, which merely pursued its straight path toward the central target, went through it, and left the scene by the top of the screen. In the progression bar condition, no ball was launched but a progression bar was displayed between the starting area and the central target. This bar provided the same time-related information as the ball, so as to standardize between conditions any time pressure induced by the moving stimuli. As in experiment 1, for each condition and in each trial, there were three possible responses, namely press left, press right, or not press. For each of the four conditions presented in experiments 1 and 2, Figure 1B illustrates the consequences of pressing the right button in response to a rightwards target jump.

As in the first experiment, response latency was significantly affected by the response condition (χ^2 (2) = 27.73, p < 0.001), which explained 18% of the measured variance (marginal R^2 = 0.18). In particular, Bonferroni-corrected paired comparisons indicated that response latency was significantly faster in the CB (mean = 261.19 ms) than in the non-controlled ball (mean = 295.42 ms, p < 0.01, R = 0.68) and in the progression bar conditions (309.52 ms, p < 0.001, R = 0.88). The latter two conditions were not significantly different from one another. There was no main effect of the response direction (mean = 288.00 vs. 289.41 ms, χ^2 (1) = 0.04, p = 0.84, marginal R^2 = 0.0002) and no interaction between the two factors (χ^2 (2) = 0.02, p = 0.99). Figure 3A summarizes the differences between the three conditions. Regarding the intra-subject variability of response latencies, the pattern of results was almost identical to that observed for the average response latency. Specifically, there was a main effect of the response condition on the intra-subject variability of response latency (χ^2 (2) = 28.65, p < 0.001), this effect explaining 28% of the variance (marginal R^2 = 0.28). The variability of response latencies was significantly smaller in the CB (mean = 27.35 ms) than in the non-controlled ball (mean = 34.58, p < 0.01, R = 0.59) and in the progression bar conditions (43.63 ms, p < 0.001, R = 0.86, see Figure 3B). The variability of response latencies was also significantly smaller in the non-controlled ball condition than in the progression bar condition (p < 0.05, R = 0.57). There was no main effect of the direction of the response (34.92 vs. 35.45 ms, χ^2 (1) = 0.06, p = 0.81, marginal R^2 = 0.0004, see Figure S2) and no interaction between the main factors (χ^2 (2) = 3.13, p = 0.21).

The results of experiment 2 suggest that the faster and less variable response latencies observed when the motor response controlled the ball trajectory are not imputable to a sense of urgency provided by the moving object. Specifically, in experiment 2, all three response conditions provided the same "putative" urgency signal, yet response latencies were significantly faster and less variable in the CB condition than in the other two conditions. To further assess whether the moving ball and the progression bar actually provided any urgency signal which might reduce response latencies, we directly compared the mean response latency measured in those two conditions with that measured in the CRT condition of experiment 1. For that, two separate Wilcoxon rank sum tests for independent groups were performed. Both tests were non-significant, with p values larger than 0.70. Even though the measured p values were far from the
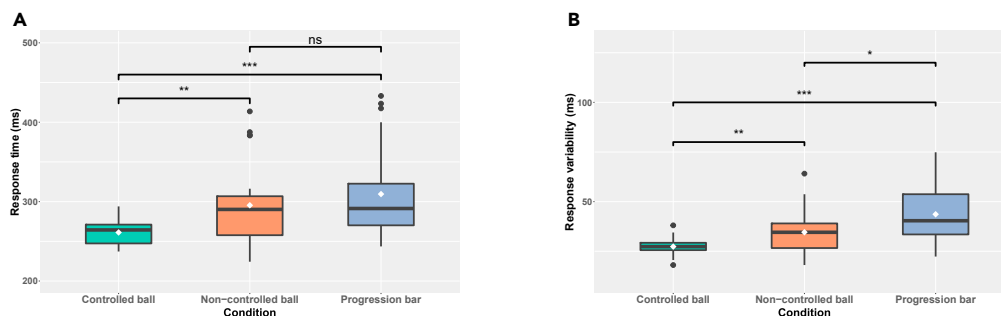
Figure 3. Effect of the response condition on response time and variability in Exp. 2

(A) Participants responded significantly faster when controlling the ball trajectory (green box) than when their response had no effect on the ball trajectory (non-controlled ball, orange box) ($p < 0.01$, R = 0.68, i.e., large effect size) and when a progression bar was displayed (purple box) ($p < 0.001$, R = 0.88, i.e., large effect size). The latter two conditions were not different from one another ($p = 0.27$, R = 0.35, i.e., medium effect size). All paired comparisons were performed using Wilcoxon signed-rank test and p values were Bonferroni-corrected.

(B) Intra-subject variability of response time was significantly smaller when participants controlled the ball trajectory (green box) than when their response had no effect on the ball trajectory (non-controlled ball, orange box) ($p < 0.01$, R = 0.59, i.e., large effect size) and when a progression bar was displayed (purple box) ($p < 0.001$, R = 0.86, i.e., large effect size). In addition, the variability of response time was significantly smaller in the non-controlled ball condition than in the progression bar condition ($p < 0.05$, R = 0.57, i.e., large effect size). All paired comparisons were performed using Wilcoxon signed-rank test and p values were Bonferroni-corrected.

significance threshold, failing to find a significant difference does not mean that there is no difference between the compared means. In particular, because "classical" statistical tests based on p values have been "developed" to decide whether to reject or not the null hypothesis, those tests are asymmetrical by nature. Indeed, they do not quantify the evidence in favor of the null hypothesis, and failing to reject the null hypothesis can only be interpreted as a current lack of evidence in favor of the alternative hypothesis. In other words, when failing to reject the null hypothesis, one can only conclude that the observed data are insufficient to show that there is a difference between the compared means. Here, we wanted to go further and evaluate the likelihood of the compared means to be similar. Therefore, for each comparison, we computed the Bayes factor, which corresponds to the ratio of the likelihood of the observed data under two (competing) hypotheses, so that it can be used not only to quantify the evidence against, but also in favor of a hypothesis, in this case the null hypothesis. The computed Bayes factors was 0.43 for the choice RT vs. non-controlled ball comparison, and 0.38 when comparing choice RT vs. progression bar. Those values both indicate a weak evidence in favor of the null hypothesis, i.e., no difference between the compared means, thereby extending the results of the Wilcoxon tests. The exact same tests were run on intra-individual variability values. Here again, the two Wilcoxon rank sum tests failed to find any significant difference between the choice RT condition on the one hand, and the non-controlled ball and progression bar condition on the other hand. The computed Bayes factors indicated a weak evidence in favor of the null hypothesis for the choice RT vs. progression bar comparison (BF = 0.51), and a weak evidence in favor of the alternative hypothesis for the choice RT vs. non-controlled ball comparison (BF = 2.90).

Though reaction times are useful indicators to make inferences about information processing, they do not constitute a perfect measure of the stimulus-response relationship. This is notably because information processing is noisy, and some portion of the observed variance is random/unexplained. In line with this, we complemented our analysis by fitting a LATER model to our data. The LATER model (Linear Approach to Threshold with Ergodic Rate) is a quasi-Bayesian model that has been developed to compare iRTs (i.e., inverse of reaction times) distributions in order to make inferences about the underlying decision processes.[32] Figure 4 shows the cumulative distribution of the iRTs for the different response conditions. In experiment 1, the Bayes factor (comparison of the two distributions) was larger than 10^5, providing a very strong evidence that responses were faster in the CB (mu = 4.27 ± 0.11, sigma = 2.45 ± 0.08) than in the choice RT condition (mu = 3.39 ± 0.03, sigma = 0.63 ± 0.02). Regarding experiment 2, the computed Bayes factors provide a very strong evidence (BF > 10^5) that responses were faster in the CB (mu = 3.89 ± 0.02, sigma = 0.48 ± 0.02) than in the progression bar (mu = 3.38 ± 0.03, sigma = 0.68 ± 0.02) and non-controlled ball conditions (mu = 3.52 ± 0.03, sigma = 0.67 ± 0.02). They also provide strong evidence (BF > 10^3) that responses were faster
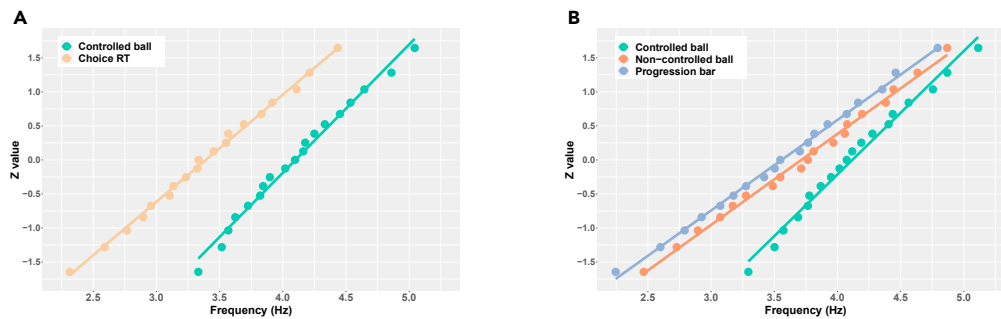
Figure 4. Cumulative distribution of the reciprocal of the latency (i.e., frequency in Hz) on a probit scale (i.e., reciprobit plot)

For all conditions, the data almost perfectly fits a straight line, so that the latencies can be assumed to follow a Gaussian distribution, as predicted by the LATER model.

(A) Experiment 1. The lines are parallel, so that we can deduce that the frequencies of the controlled ball condition (green) are drawn from a Gaussian distribution with a higher mean value than that of the choice RT condition (beige). This indicates that the controlled ball condition is characterized by faster reaction times.

(B) Experiment 2. The blue (progression bar condition) and orange (non-controlled ball condition) lines are almost identical. The green line (controlled ball condition) intersects Z = 0 at a higher frequency, indicating that the mean value of the controlled ball distribution is higher and that reaction times are faster in this condition. In addition, the slope of the controlled ball condition is steeper, indicating a lower variability in this condition.

in the non-controlled ball than in the progression bar condition. Overall, the results of this additional analysis confirmed those reported previously with more "traditional" RT analysis.

DISCUSSION

Motor responses taking place during movement execution, i.e., in the control phase of the movement, are usually characterized by very short latencies.[14,17–23] Because such short latencies are hardly compatible with the processing of visual information taking place before movement onset,[16,33,34] it has been suggested that in the control phase of the movement, visual information might be processed differently, at least partially, as when programming a movement to come. In particular, the feedback loops underlying movement control would rely on forward/internal models using efference copy to predict the consequences of motor commands.[16,21,27,28] By partially compensating the delay of sensory feedback, forward models would contribute to shorten the latency of motor responses occurring during movement execution. Our results confirm that the response latency to visual stimuli is much shorter when the outcome of the motor response has a control component than when it does not. However, and importantly, our results show for the first time that such short-latency responses take place even without any actual motor control of a moving limb. Specifically, all previous experiments reporting shorter response latencies in control tasks were based on reaching tasks in which participants controlled the trajectory of an ongoing reaching movement. As opposed to that, the control task used in our experiment did not entail any motor control because the arm and hand were static at the time of the motor response. Yet, on average and depending on the condition, participants responded 35 to 60 ms faster to the visual stimuli when the motor response affected the trajectory of a moving object. These values correspond to a gross latency reduction of 12–20%, and this latency reduction can hardly be attributed to forward models based on efference copy. Indeed, the motor response was "circumscribed" to a button press, and this motor response was the exact same in all conditions. Please note that we do not challenge the view that forward models play an important role in the control of ongoing movements. Rather, our results show that even without actual motor control and the associated involvement of forward models, motor responses take place with shorter latencies when the outcome of the response has a control component. This is an important result, because it suggests that if required by the constraints of the task at hand, sensory information can be processed faster and motor responses can be triggered earlier. In line with this, the absence of difference between the choice RT condition and both the non-controlled ball and the progression bar conditions suggests that the time-related information provided in these latter two conditions did not alter the perceived time constraint of the task. As opposed to that, being able to modify the trajectory of the moving ball likely increased the perceived time constraint. This might indicate that a certain level of visuomotor binding[35] or agency[36,37] is required for the perceived time constraint of the task to be altered.

The hypothesis that the sensorimotor processing of visual information might be more efficient when the task entails a control component seems further supported by the pattern of intra-individual response variability. Specifically, in both experiments, the intra-individual variability of the measured response latency was significantly smaller when the response had a control component, i.e., when pressing the button altered the trajectory of a moving object. In most cases, the intra-individual variability was almost twice smaller in the control than in the "no-control" conditions. In previous studies, an increased variability of motor response latency has been associated with aging,[38–40] neurobiological disturbance,[41–43] neurodegenerative disorders,[44] and ADHD.[45] These works highlight the fact that the intra-individual variability of response latency constitutes a marker of the efficiency of sensorimotor processing. In that respect, the reduced variability of intra-individual response latency measured in our experiment is an important result that further hints at an enhanced efficiency of the sensorimotor processing of visual information when the task entails a control component.

Previous studies have shown that under specific circumstances, the sensorimotor processing of visual information can unfold faster. This is notably the case for saccades, for which shorter reaction times have been observed when an arm movement is performed simultaneously to the saccade,[31] or when a perceptive or discrimination task has to be performed at the saccade landing location.[10,29,30] Initially conceived by Roger Carpenter, the LATER model (Linear Approach to Threshold with Ergodic Rate, see[32] for a recent review) "accounts" for these observations by appraising and quantifying the relationship between some experimental conditions and measured reaction times. More specifically, in many settings, RTs can be shown to follow a recinormal distribution, which means that the inverse of the RTs (iRT) closely follows a Gaussian law.[46] This characteristic led to the development of the LATER model, a parametric model in which the iRT are assumed to follow a normal distribution. The LATER model has the advantage that its parameters, namely the average and standard deviation of the normal distribution, have been shown to be correlated with experimental conditions, such as urgency[47] or stimulus visibility.[48] While the LATER model was originally designed for saccadic reaction times, more recent studies have shown that it can also be applied to manual responses.[49] In line with this, we fitted a LATER model to the iRTs collected in our experiments. The results of this additional analysis are in line with the other results reported in this study, as the mean value mu changed significantly between distributions, resulting in a lateral shift of the reciprobit. According to previous studies on the LATER model, this finding suggests that the shorter RTs observed in the CB condition might well result from a faster sensorimotor processing.[32]

As mentioned previously, the feedback loops underlying the online control of reaching movements have been investigated in several studies. And these studies notably highlighted the fact that during movement execution, sensory information is probably processed differently than it is before movement initiation. Interestingly though, very few studies directly compared the latency of reaction times preceding movement initiation with that of online responses to perturbations occurring during movement execution. And for methodological reasons, across-studies comparisons are difficult. In particular, manual reaction times to a stimulus are often measured using button-press responses, whereas the latency of online responses usually corresponds to the first detectable modification of the hand trajectory. To our knowledge, only two studies directly compared the latency of choice reaction times to that of online responses. In a study performed by Day and Brown in 2001,[14] motor responses occurred on average 114 ms earlier in the online control task than in the CRT task (137 ms vs. 251 ms). Note that in this study, response latency was measured using different methods for the two tasks, namely using a touch-plate for reaction times and computing kinematic deviations of the hand trajectory for reach adjustments. A very similar difference in response latency between online responses (about 100 ms) and choice reaction times (about 200 ms) was observed by Reichenbach and colleagues.[12] In this latter study, the method used to measure response latency was the same for the online control and the choice RT task, namely the first detectable electromyographic burst. Importantly; however, in both aforementioned studies, the type of motor response differed between the online control task and the choice RT task. Specifically, choice RT latencies corresponded to the delay between stimulus presentation and hand movement initiation, whereas online response latencies corresponded to the delay between stimulus presentation and the first measurable deviation of the hand trajectory. Put differently, when the visual stimulus was presented, the arm and hand were static in the choice RT task, whereas they were already in motion in the online control task. In our study, there was no such "bias", as the motor response was exactly the same in all conditions, whether they entailed a control component or not. And as mentioned previously because the motor response was a single button press, the measured latency difference between "control" and "no control" conditions cannot be imputed

to forward models. Interestingly though, in experiment 1 (in which the compared conditions were the most similar to those of Day and Brown[14] and Reichenbach et al.[12]), response latency was on average 60 ms shorter in the control task than in the RT task. This corresponds to more than half the amplitude of the latency difference reported by Day and Brown[14] and Reichenbach et al.[12] This suggests that less than half of the latency reduction observed in motor control tasks (as compared to RT tasks) might actually be imputable to forward models. The remaining and larger "share" of the reduction might well derive from a hastened sensorimotor processing triggered by (perceived) tighter time constraints associated with the task.

As a final remark, one might wonder to which extent the results reported in this study might be somehow related to some sampling bias or to particularly slow reaction times. In the literature, the reported latency for simple reaction times to visual stimuli usually ranges between 230 and 330 ms.[14,50–52] The latencies measured in our study fall within this range, with values ranging from 246 ms for the "fastest" condition (CB, experiment 1) to 309 ms for the "slowest" condition (progression bar, experiment 2). Importantly, all latencies measured in our study were choice response times, which for button-press/manual responses are known to be longer than simple reaction times.[6] Taken together, these elements indicate that the large latency differences that we measured between the condition in which pressing the button controlled the ball and the other conditions cannot be merely attributed to some sampling bias or to particularly slow reaction times.

Limitations of the study

The main limitation of our study lies in the use of the LATER model to "interpret" the response times measured in the different conditions. Specifically, the LATER model has initially been developed to try to specify the relationship between the distribution of saccadic reaction times and the underlying decision processes. Though reaction time is the time separating stimulus presentation and movement onset, and this irrespective of the effector, eye movements and manual responses are somehow different. In particular, saccades are highly automatic and "overlearned" motor responses, which as opposed to manual responses remain unaffected by stimulus-response uncertainty.[53,54] Therefore, the sensorimotor processing preceding saccade onset is likely different in nature, at least partially, from that preceding button-press responses. In that context, one should be more cautious when interpreting the fitting of a LATER model to manual responses, even though some authors have suggested that it can validly be used to model the decision process of manual responses.[49]

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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Supplemental information can be found online at https://doi.org/10.1016/j.isci.2023.106838.

REFERENCES

1. Welford, A.T. (1980). Choice reaction time: basic concepts. In Reaction Times, A.T. Welford, ed. (Academic Press), pp. 73–128.

2. Hernández, O.H., Vogel-Sprott, M., and Ke-Aznar, V.I. (2007). Alcohol impairs the cognitive component of reaction time to an omitted stimulus: a replication and an extension. J. Stud. Alcohol Drugs *68*, 276–281. https://doi.org/10.15288/jsad.2007. 68.276.

3. Durlac, P.J., Edmunds, R., Howard, L., and Tipper, S.P. (2002). A rapid effect of caffeinated beverages on two choice reaction time tasks. Nutr. Neurosci. *5*, 433–442.

4. Luce, R.D. (1986). Response Times: Their Role in Inferring Elementary Mental Organization (Oxford University Press).

5. Froeberg, S. (1907). The relation between the magnitude of stimulus and the time of reaction. Arch. Psychol. *8*.

6. Hick, W.E. (1952). On the rate of gain of information. Q. J. Exp. Psychol. *4*, 11–26.

7. Henry, F.M., and Rogers, D.E. (1960). Increased response latency for complicated movements and a memory drum theory of neuromotor reaction. The Research Quaterly *31*, 448–458.

8. Gálvez-García, G., Albayay, J., Rehbein, L., Bascour-Sandoval, C., and Michael, G.A. (2018). Response inhibition as a function of movement complexity and movement type selection. Front. Psychol. *9*, 2290. https://doi. org/10.3389/fpsyg.2018.02290.

9. Bieg, H.J., Bresciani, J.P., Bülthoff, H.H., and Chuang, L.L. (2013). Saccade reaction time asymmetries during task-switching in pursuit tracking. Exp. Brain Res. *230*, 271–281. https://doi.org/10.1007/s00221-013-3651-9.

10. Bieg, H.J., Bresciani, J.P., Bülthoff, H.H., and Chuang, L.L. (2012). Looking for discriminating is different from looking for looking's sake. PLoS One 7, e45445. https:// doi.org/10.1371/journal.pone.0045445.

11. Bieg, H.J., Chuang, L.L., Bülthoff, H.H., and Bresciani, J.P. (2015). Asymmetric saccade reaction times to smooth pursuit. Exp. Brain Res. *233*, 2527–2538. https://doi.org/10.1007/ s00221-015-4323-8.

12. Reichenbach, A., Thielscher, A., Peer, A., Bülthoff, H.H., and Bresciani, J.P. (2009). Seeing the hand while reaching speeds up on-line responses to a sudden change in target position. J. Physiol. *587*, 4605–4616. https://doi.org/10.1113/jphysiol.2009. 176362.

13. Evarts, E.V., Teräväinen, H., and Calne, D.B. (1981). Reaction time in Parkinson's disease. Brain *104*, 167–186. https://doi.org/10.1093/ brain/104.1.167.

14. Day, B.L., and Brown, P. (2001). Evidence for subcortical involvement in the visual control of human reaching. Brain *124*, 1832–1840. https://doi.org/10.1093/brain/124.9.1832.

15. Jaśkowski, P., and Sobieralska, K. (2004). Effect of stimulus intensity on manual and saccadic reaction time. Percept. Psychophys. *66*, 535–544. https://doi.org/10.3758/ bf03194899.

16. Desmurget, M., and Grafton, S. (2000). Forward modeling allows feedback control for fast reaching movements. Trends Cognit. Sci. *4*, 423–431. https://doi.org/10.1016/ s1364-6613(00)01537-0.

17. Carlton, L.G. (1981). Processing visual feedback information for movement control. J. Exp. Psychol. Hum. Percept. Perform. *7*, 1019–1030. https://doi.org/10.1037//0096-1523.7.5.1019.

18. Soechting, J.F., and Lacquaniti, F. (1983). Modification of trajectory of a pointing movement in response to a change in target location. J. Neurophysiol. *49*, 548–564. https://doi.org/10.1152/jn.1983.49.2.548.

19. Prablanc, C., and Martin, O. (1992). Automatic control during hand reaching at undetected two-dimensional target displacements. J. Neurophysiol. *67*, 455–469. https://doi.org/ 10.1152/jn.1992.67.2.455.

20. Day, B.L., and Lyon, I.N. (2000). Voluntary modification of automatic arm movements evoked by motion of a visual target. Exp. Brain Res. *130*, 159–168. https://doi.org/10. 1007/s002219900218.

21. Gritsenko, V., and Kalaska, J.F. (2010). Rapid online correction is selectively suppressed during movement with a visuomotor transformation. J. Neurophysiol. *104*, 3084–3104. https://doi.org/10.1152/jn.00909.2009.

22. Gritsenko, V., Yakovenko, S., and Kalaska, J.F. (2009). Integration of predictive feedforward and sensory feedback signals for online control of visually guided movement. J. Neurophysiol. *102*, 914–930. https://doi. org/10.1152/jn.91324.2008.

23. Wijdenes, L.O., Brenner, E., and Smeets, J.B.J. (2013). Comparing online adjustments to distance and direction in fast pointing movements. J. Mot. Behav. *45*, 395–404. https://doi.org/10.1080/00222895.2013. 815150.

24. Goodale, M.A., Pelisson, D., and Prablanc, C. (1986). Large adjustments in visually guided reaching do not depend on vision of the hand or perception of target displacement. Nature *320*, 748–750. https://doi.org/10.1038/ 320748a0.

25. Sarlegna, F., Blouin, J., Bresciani, J.P., Bourdin, C., Vercher, J.L., and Gauthier, G.M. (2003). Target and hand position information in the online control of goal-directed arm movements. Exp. Brain Res. *151*, 524–535. https://doi.org/10.1007/s00221-003-1504-7.

26. Pisella, L., Gréa, H., Tilikete, C., Vighetto, A., Desmurget, M., Rode, G., Boisson, D., and Rossetti, Y. (2000). An 'automatic pilot' for the hand in human posterior parietal cortex: toward reinterpreting optic ataxia. Nat.

Neurosci. *3*, 729–736. https://doi.org/10.1038/76694.

27. Bridgeman, B. (1995). A review of the role of efference copy in sensory and oculomotor control systems. Ann. Biomed. Eng. *23*, 409–422. https://doi.org/10.1007/BF02584441.

28. Miall, R.C., Weir, D.J., Wolpert, D.M., and Stein, J.F. (1993). Is the cerebellum a smith predictor? J. Mot. Behav. *25*, 203–216. https://doi.org/10.1080/00222895.1993.9942050.

29. Montagnini, A., and Chelazzi, L. (2005). The urgency to look: prompt saccades to the benefit of perception. Vis. Res. *45*, 3391–3401. https://doi.org/10.1016/j.visres.2005.07.013.

30. Trottier, L., and Pratt, J. (2005). Visual processing of targets can reduce saccadic latencies. Vis. Res. *45*, 1349–1354. https://doi.org/10.1016/j.visres.2004.12.007.

31. Lünenburger, L., Kutz, D.F., and Hoffmann, K.P. (2000). Influence of arm movements on saccades in humans. Eur. J. Neurosci. *12*, 4107–4116. https://doi.org/10.1046/j.1460-9568.2000.00298.x.

32. Noorani, I., and Carpenter, R.H.S. (2016). The LATER model of reaction time and decision. Neurosci. Biobehav. Rev. *64*, 229–251. https://doi.org/10.1016/j.neubiorev.2016.02.018.

33. Hollerbach, M.J., and Flash, T. (1982). Dynamic interactions between limb segments during planar arm movement. Biol. Cybern. *44*, 67–77. https://doi.org/10.1007/BF00353957.

34. Gerdes, V.G., and Happee, R. (1994). The use of internal representation in fast gold-directed movements: a modeling approach. Biol. Cybern. *70*, 513–524. https://doi.org/10.1007/BF00198804.

35. Reichenbach, A., Urgen, B.M., Apostolakis, S., Michlin, L., and Diedrichsen, J. (2022). Factors governing the assignment of visual consequence to the corresponding action. J. Neurophysiol. *127*, 756–766. https://doi.org/10.1152/jn.00450.2021.

36. Haggard, P. (2017). Sense of agency in the human brain. Nat. Rev. Neurosci. *18*, 196–207. https://doi.org/10.1038/nrn.2017.14.

37. Welniarz, Q., Worbe, Y., and Gallea, C. (2021). The forward model: a unifying theory for the role of the cerebellum in motor control and sense of agency. Front. Syst. Neurosci. *15*, 644059. https://doi.org/10.3389/fnsys.2021.644059.

38. Hale, S., Myerson, J., Smith, G.A., and Poon, L.W. (1988). Age, variability, and speed: between-subjects diversity. Psychol. Aging *3*, 407–410. https://doi.org/10.1037//0882-7974.3.4.407.

39. Morse, C.K. (1993). Does variability increase with age? An archival study of cognitive measures. Psychol. Aging *8*, 156–164. https://doi.org/10.1037/0882-7974.8.2.156.

40. Shammi, P., Bosman, E., and Stuss, D.T. (1998). Aging and variability in performance. Aging Neuropsychol. Cognit. *5*, 1–13.

41. Hendrickson, A.E. (1982). The biological basis of intelligence. Part I: Theory. In A model for intelligence, Eysenck (Springer-Verlag), pp. 151–196.

42. Hultsch, D.F., MacDonald, S.W.S., and Dixon, R.A. (2002). Variability in reaction time performance of younger and older adults. J. Gerontol.: Psychol. Sci. *57*, 101–115.

43. Li, S.C., and Lindenberger, U. (1999). Cross-level unification: a computational exploration of the link between deterioration of neurotransmitter systems and dedifferentiation of cognitive abilities in old age. In Cognitive Neuroscience and Memory, N. Markowitsch, ed. (Hogrefe & Huber), pp. 103–146.

44. de Frias, C.M., Dixon, R.A., Fisher, N., and Camicioli, R. (2007). Intraindividual variability in neurocognitive speed: a comparison of Parkinson's disease and normal older adults. Neuropsychologia *45*, 2499–2507. https://doi.org/10.1016/j.neuropsychologia.2007.03.022.

45. Kofler, M.J., Rapport, M.D., Sarver, D.E., Raiker, J.S., Orban, S.A., Friedman, L.M., and Kolomeyer, E.G. (2013). Reaction time variability in ADHD: a meta-analytic review of 319 studies. Clin. Psychol. Rev. *33*, 795–811. https://doi.org/10.1016/j.cpr.2013.06.001.

46. Carpenter, R.H., and Williams, M.L. (1995). Neural computation of log likelihood in control of saccadic eye movements. Nature *377*, 59–62. https://doi.org/10.1038/377059a0.

47. Reddi, B.A., and Carpenter, R.H. (2000). The influence of urgency on decision time. Nat. Neurosci. *3*, 827–830. https://doi.org/10.1038/77739.

48. Carpenter, R.H.S. (2004). Contrast, probability, and saccadic latency; evidence for independence of detection and decision. Curr. Biol. *14*, 1576–1580. https://doi.org/10.1016/j.cub.2004.08.058.

49. Antoniades, C.A., Ober, J., Hicks, S., Siuda, G., Carpenter, R.H.S., Kennard, C., and Nemeth, A.H. (2012). Statistical characteristics of finger-tapping data in Huntington's disease. Med. Biol. Eng. Comput. *50*, 341–346. https://doi.org/10.1007/s11517-012-0863-2.

50. Jain, A., Bansal, R., Kumar, A., and Singh, K.D. (2015). A comparative study of visual and auditory reaction times on the basis of gender and physical activity levels of medical first year students. Int. J. Appl. Basic Med. Res. *5*, 124–127. https://doi.org/10.4103/2229-516X.157168.

51. Nissan, J., Liewald, D., and Deary, I.J. (2013). Reaction time and intelligence: comparing associations based on two response modes. Intelligence *41*, 622–630.

52. Cole, W.R., Gregory, E., Arrieux, J.P., and Haran, F.J. (2018). Intraindividual cognitive variability: an examination of ANAM4 TBI-MIL simple reaction time data from service members with and without mild traumatic brain injury. J. Int. Neuropsychol. Soc. *24*, 156–162. https://doi.org/10.1017/S1355617717001187.

53. Kveraga, K., Boucher, L., and Hughes, H.C. (2002). Saccades operate in violation of Hick's law. Exp. Brain Res. *146*, 307–314. https://doi.org/10.1007/s00221-002-1168-8.

54. Lawrence, B.M., St John, A., Abrams, R.A., and Snyder, L.H. (2008). An anti-Hick's effect in monkey and human saccade reaction times. J. Vis. *8*, 26.1–26.7. https://doi.org/10.1167/8.3.26.

55. Hakeloh, U., and Hojsgaard, S. (2014). A kenward-roger approximation and parametric bootstrap methods for tests in linear mixed models – the R package pbkrtest. J. Stat. Software *59*, 1–32.

56. Nakagawa, S., and Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol. Evol. *4*, 133–142.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Original human experimental data and analysis code (R)	Mendeley	https://data.mendeley.com/datasets/6pd2xbjdx4/1
Software and algorithms		
R	https://cran.r-project.org/	Version 4.0.2

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Jean-Pierre Bresciani (jean-pierre.bresciani@unifr.ch).

Material availability

This study did not generate new unique reagents or other materials.

Data and code availability

- Raw human experimental data have been deposited at (Mendeley Data: https://data.mendeley.com/datasets/6pd2xbjdx4/1) and are publicly available as of the date of publication. DOI are listed in the key resources table.

- All original code (R analysis scripts) have been deposited at (Mendeley Data: https://data.mendeley.com/datasets/6pd2xbjdx4/1) and is publicly available as of the date of publication. DOI are listed in the key resources table.

EXPERIMENTAL MODEL AND SUBJECTS DETAILS

Participants

Twelve participants (8 females, aged 18–28 years, mean = 23.5 years, 12 right-handed) were included in Experiment 1 and twelve different participants (10 females, aged 20–32 years, mean = 22.92 years, 11 right-handed) in Experiment 2. All were able-bodied with normal or corrected-to-normal vision, and they were naive as to the purpose of the research. The study was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and approved by the Ethics Committee of the University of Fribourg. Participants had the option to withdraw from the study at any time without penalty and without having to give a reason.

METHODS DETAILS

Materials

The participants sat in an adjustable chair in front of a 23.6 inch TFT monitor (VIEWPixx 3D Lite, 1920*1080 pixel, 120 Hz refresh rate, VPixx Technologies Inc., QC, Canada) in an otherwise dark room. Their head rested on a chin and forehead rest at a viewing distance of 57 cm of the monitor. An optical infrared eye-tracking system was used to record eye movements at a sampling rate of 1000 Hz (SR Research Desktop-Mount Eyelink 1000, average gaze position error of about 0.25° and spatial resolution of 0.01°). Response times were measured using a handheld response box (RESPONSEPixx, VPixx Technologies Inc., QC, Canada) positioned on the table in front of the participant. The participants had their left and right index fingers positioned on the left and right buttons of the response box, respectively.

Experimental procedures

The visual scene consisted of a square starting area (2.3*2.3 degrees of visual angle) and three circular targets (2.4° in diameter) arranged on an arc of a circle at equal distance (26°) of the starting area. The starting area and the central target were located at the middle of the scene. The left and right targets were located

25 degrees of arc to the left (CCW) and right (CW) of the central target, respectively, that is at a horizontal distance of about 11 degrees of visual angle (see Figure 1). The background was light gray (RGB 200 200 200). The starting area and the three targets were medium dark gray (RGB (225 225 225)).

At the beginning of each trial, the participant had to gaze at the central target and keep fixating it. After the participant fixated the central target for 1000 ms, it turned green (RGB 43 216 0) for 1500 ms before turning red (RGB 255 0 0). A random 270 to 330 ms after it turned red, the central target either 'jumped' to the left, to the right, or remained central (a third of the trials in each case). Target jumps were produced by turning the central target from red to medium dark gray while simultaneously turning one of the lateral targets from medium dark gray to red. Trials with and without jumps were presented in random order. When the target jumped, the participant was instructed to press as fast as possible the response button corresponding to the direction of the jump, i.e., left button for a left jump and right button for a right jump. When the target remained central, the participant was instructed not to press any button. In other words, the participant always had three possible responses, namely pressing left, pressing right, or not pressing. This was the case for all subsequently presented conditions.

Experiment 1 consisted of two response conditions. In the CRT condition, when the participant pressed one of the response buttons, a red disc (1.2° in diameter, RGB 255 0 0) representing a ball was launched from the starting area at a speed of 37.5 cm/s (i.e., 37.5 degrees of visual angle per second) in the direction of the left or right target, depending on whether the participant pressed the left or the right button. When no button was pressed, the ball was launched toward the central target between 270 and 330 ms after the central target turned red. In the Controlled Ball (CB) condition, the red ball was launched toward the central target when this latter turned red, i.e., 270 to 330 ms before a potential target jump. When the participant pressed a button after a target jump, the already moving ball deviated toward the target located on the side of the pressed button. When no response button was pressed, the ball pursued its straight path toward the central target. The difference between the two response conditions was that in the CRT condition, the participant's response affected the direction in which the ball was launched, whereas in the CB condition, the participant's response controlled the direction of the ball while it was already moving. Note that changing the color of the central target from green to red 270 to 330 ms before a potential jump provided the participant with the same time-related pre-cue in the two response conditions. Figure 1A illustrates the time course of a trial with rightwards target jump in the CB condition.

Experiment 2 consisted of three response conditions. The CB condition was identical to that of experiment 1. The Non-controlled Ball condition was similar to the CB condition, but pressing a button did not affect the ball trajectory. Specifically, irrespective of whether a button was pressed or not, the ball pursued a straight path toward the central target, went through it, and left the scene by the top of the screen. In the Progression Bar condition, no ball was launched but a progression bar was displayed between the starting area and the central target. The bar provided the same time-related information as the ball. The Non-controlled Ball and Progression Bar conditions allowed us to assess whether the moving stimuli induced some kind of time pressure which might affect response time. For each of the four conditions presented in experiments 1 and 2, Figure 1B illustrates the consequences of pressing the right button in response to a rightwards target jump.

Design

For both experiments, response time was the main dependent variable, which we measured and compared between conditions. Response time was defined as the time elapsed between presentation of the response-triggering stimulus and button press. We also computed intra-individual response time variability, which corresponded to the standard deviation of response time as measured for each participant and each combination of the factors. As for response time, response time variability was compared between conditions. There were two main factors (i.e., independent variables), namely the Condition and the Direction of the required response. As mentioned above, the response Condition factor consisted of two levels in the first experiment (CRT vs. CB) and three levels in the second experiment (CB vs. Non-controlled Ball vs. Progression Bar). For both experiments, the Direction of the required response consisted of two levels, namely left vs. right. For both experiments, the levels of the two factors were manipulated within participants, i.e., we used a repeated measures design. Condition levels were presented in different blocks, namely one block per level. For both experiments, the order of presentation of the blocks/levels was fully counterbalanced across participants. Within each block, the Direction of the required response

varied randomly across trials. Specifically, there were as many trials with left and right required responses, and the order of presentation of these trials was fully random. Each participant performed 20 trials for each combination of response condition and response direction, for a grand total of 120 trials per participant in Experiment 1, and 180 trials per participant in Experiment 2. This grand total includes the trials in which no response was required, namely 20 trials per response condition per participant. Note however that only trials in which a target jump occurred were considered for the analysis. This is because those were the trials in which a response was required. Note also that the trials in which the response was incorrect or faster than 150 ms (i.e., the participant anticipated) were discarded and repeated later in the course of the block. In total, less than 2% of the trials were discarded and repeated. For both experiments, participants performed 20 familiarization trials per condition before starting the main experiment. The total duration of the experiment (i.e., including instructions, familiarization, break(s) and experimental blocks) was about 25 min for Experiment 1 and 35 min for Experiment 2.

QUANTIFICATION AND STATISTICAL ANALYSIS

Statistical analyses

The effect of the two factors and of their interaction on the dependent variable was assessed using a linear mixed-effects modeling approach. Specifically, for both experiments, the two main factors were entered into the model as fixed effects, whereas the intercepts for the participants were entered as random effects. For each experiment, four models were fitted, namely, 1. A model including only the intercept, 2. A model including the intercept and the Condition factor as predictor, 3. A model including the intercept and both the Condition and Direction factors as predictors, and 4. A model including the intercept, the two factors as predictors and an interaction term. The four models were then compared and p values were obtained using likelihood ratio tests. The degrees of freedom were approximated using the Kenward-Roger method.[55] Note that we also fitted three models including random slopes, but these more complex models only slightly lowered the Akaike and Bayesian information criteria (i.e., AIC and BIC), and the results pattern remained exactly the same. For this reason, we only reported the results obtained with the 'less complex' random intercept models. The effect size of each factor was computed using the marginal R squared, which indicates the proportion of variance explained by the fixed effects in the model.[56]

Further direct comparisons between means and intra-individual variability values were performed using non-parametric tests. Paired comparisons were performed using Wilcoxon signed-rank tests when measures were repeated within participant, and Wilcoxon rank sum tests when the compared groups were independent (i.e., for comparisons between the two experiments). P-values were Bonferroni-corrected when multiple comparisons were performed, and R was computed as indicator of the effect size. When the result of the Wilcoxon test was non-significant, and when relevant, we additionally computed the Bayes Factor to estimate the likelihood that the Null Hypothesis be true.