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Variance in exposed perturbations impairs retention of visuomotor adaptation

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Sensorimotor control requires an accurate estimate of the state of the body. The brain optimizes state estimation by combining sensory signals with predictions of the sensory consequences of motor commands using a forward model. Given that both sensory signals and predictions are uncertain (i.e., noisy), the brain optimally weights the relative reliance on each source of information during adaptation. In support, it is known that uncer-tainty in the sensory predictions influences the rate and generalization of visuomotor adaptation. We investigated whether uncertainty in the sensory predictions affects the retention of a new visuomotor rela-tionship. This was done by exposing three separate groups to a visuomotor rotation whose mean was common at 15° counterclock-wise but whose variance around the mean differed (i.e., SD of 0°, 3.2°, or 4.5°). Retention was assessed by measuring the persistence of the adapted behavior in a no-vision phase. Results revealed that mean reach direction late in adaptation was similar across groups, suggest-ing it depended mainly on the mean of exposed rotations and was robust to differences in variance. However, retention differed across groups, with higher levels of variance being associated with a more rapid reversion toward nonadapted behavior. A control experiment ruled out the possibility that differences in retention were accounted for by differences in success rates. Exposure to variable rotations may have increased the uncertainty in sensory predictions, making the adapted forward model more labile and susceptible to change or decay.

NEW & NOTEWORTHY The brain predicts the sensory conse-quences of motor commands through a forward model. These predic-tions are subject to uncertainty. We use visuomotor adaptation and modulate uncertainty in the sensory predictions by manipulating the variance in exposed rotations. Results reveal that variance does not influence the final extent of adaptation but selectively impairs the retention of motor memories. These results suggest that a more uncertain forward model is more susceptible to change or decay.

sensorimotor adaptation; visuomotor rotation; uncertainty; retention; arm reaching movement

EFFICIENT MOTOR CONTROL requires an accurate estimate of the state of the body in real time, which is conveyed through sensory reafferent signals. The brain optimizes state estimation by combining these sensory signals with predictions concern-ing the sensory consequences of descending motor commands using a forward model (Wolpert et al. 1995). Considerable work has shown that these predictions are under adaptive control throughout development and aging, underlying our capacity to interact accurately with the world despite changing sensorimotor contexts. Adaptation has been demonstrated across a wide range of tasks (Krakauer et al. 1999; Martin et al. 1996; Morton and Bastian 2004; Shadmehr and Mussa-Ivaldi 1994) and is thought to be driven by sensory prediction errors, which arise whenever a discrepancy is detected (consciously or not) between the predicted and actual sensory consequences of the movement (Izawa and Shadmehr 2011; Mazzoni and Krakauer 2006; Miall and Wolpert 1996; Wolpert et al. 1995).

Because sensory feedback and predictions are both inher-ently noisy and thus uncertain (Wei and Körding 2010), prob-abilistic Bayesian theory has provided a fruitful framework to study sensorimotor control. Seminal work has shown that for the control of reaching movements, the relative reliance on sensory predictions (i.e., the prior) and sensory feedback (i.e., the evidence) depends on their uncertainty (Körding and Wol-pert 2004). This framework has been extended to sensorimotor adaptation, with greater uncertainty in the prior being associ-ated with a greater tendency to update motor behaviors given new sensory evidence. In support, Wei and Körding (2010) investigated the influence of uncertainty in the prior on the rate of adaptation to randomly changing perturbations. To manip-ulate uncertainty, they initially submitted participants to con-ditioning blocks in which they either reached with veridical visual feedback of the hand (low prior uncertainty), with no visual feedback of the hand (moderate prior uncertainty), or sat idle (high prior uncertainty). Afterward, participants performed reaches in a condition in which the cursor could be veridical or perturbed laterally by ±2 cm. The authors found that the more uncertain the prior, the greater the trial-by-trial rate of adapta-tion to these random perturbations. A similar finding was reported by Turnham et al. (2012), who assessed adaptation to +30° or −30° visuomotor rotations after participants had undergone a conditioning phase in which they were either provided with veridical visual feedback of the hand (low prior uncertainty) or submitted to random perturbations between −60° and 60° (high prior uncertainty). They found that adap-tation to +30° or −30° rotation was significantly faster for the random feedback group compared with the veridical feedback group.

A separate line of work has investigated the influence of uncertainty in the prior on the generalization of visuomotor adaptation (Fernandes et al. 2014). These authors manipulated

uncertainty by exposing participants to visuomotor rotations whose variance around the mean was varied parametrically across groups. They then measured the extent to which adaptation generalized from a learned reaching direction toward new directions. Interestingly, they found that the mean of the prior and the uncertainty in the prior presented different patterns of generalization. Indeed, although generalization of adaptation was local in the sense that it was greatest around the mean of the trained reaching direction (i.e., width of ~30°), uncertainty in the prior had a much more global effect, influencing movements in all directions. The authors argued that the internal representation of the mean of a prior may be distinct from the representation of its uncertainty (see also Fernandes et al. 2012).

In light of these findings showing an influence of prior uncertainty on the rate and generalization of visuomotor adaptation, it is possible that variance in exposed rotations also influences the retention of a newly formed memory. In the present study we address this issue by parametrically manipulating the variance in exposed rotations, but not the mean, during an adaptation phase, and assessing retention through the persistence of the adapted behavior in a no-vision phase immediately following adaptation (Bernier et al. 2005; Galea et al. 2015; 2011; Krakauer et al. 1999). It was hypothesized that training under a more variable perturbation schedule would increase the uncertainty of the adapted forward model and lead to weaker retention.

METHODS

Participants. A total of 55 healthy right-handed participants (22 men, 19–37 yr old, mean age 22.2 ± 2.5 yr) took part in the main ($n = 32$) and control ($n = 23$) experiments. They were all naive as to the purpose of the experiment. All participants read and signed consent forms approved by the ethical committee of the Centre Hospitalier de l'Université de Sherbrooke. They were encouraged to ask any question relative to the consent form if it was unclear.

Apparatus. The experimental setup consisted of a table supporting a computer monitor that projected visual stimuli on a semireflective mirror, preventing participants from seeing their hand (Fig. 1A). The monitor (20-in. Dell P1130; resolution 1,024 × 768; refresh rate 150 Hz) was mounted face down 29 cm above the horizontal mirror. The mirror itself was mounted 29 cm above the table. With this setup the visual stimuli appeared to be projected directly onto the surface of the table on the same plane as the hand. Participants were instructed to rest their chin on a self-made cushion fixed above the mirror to prevent head motion during the experiment.

Participants performed reaching movements using a two-joint planar manipulandum placed on the table that they held with their right hand via a stylus located at its mobile end. The manipulandum was custom-built with two lightweight metal rods (48 and 45 cm, respectively), with the fixed end attached to the upper left of the table. A thin sheet of smooth plastic was put on the table surface, and foam pads were installed under the hinges, allowing the manipulandum to be moved anywhere on the table with minimal inertia and friction. Two potentiometers positioned in the joints of the manipulandum allowed us to measure the angle of each segment, from which the kinematics of the stylus were estimated in the *X* (left, right) and *Y* (near, far) dimensions. This information was then used to project a cursor corresponding to participants' hands in real time on the mirror. During recording, raw kinematic data were spatially corrected with a Kalman filter to estimate hand position in real time. With this procedure, the total time necessary to collect the *X* and *Y* coordinates of the hand and present the corresponding visual cursor was estimated to be ~7–9 ms. The sampling rate of the manipulandum was 1,000 Hz.

Task. Participants were instructed to make center-out reaching movements with the right hand, bringing the visual cursor (green circle; 6 mm in diameter) toward the visual targets. There were 8 targets (white circles, 15 mm in diameter, or 6°) displayed in a circular array 10 cm away from a starting point. The target array was offset counterclockwise (CCW) by 22.5° from the *x*-axis (see Fig. 1B). The starting point was located at the center of the workspace and consisted of a circle (gray; 11 mm in diameter). Each target was presented once every eight trials in a pseudorandom order, forming a cycle. Participants were instructed to make accurate movements toward the targets in a prescribed movement time of 150 ms. They were instructed not to stop on the targets but to "strike" through the targets with a single movement impulse and to complete their movements ~5 cm beyond the target radius. There was no physical element stopping their movements. Fast, straight, and ballistic movements were emphasized so that movement end points would reflect mainly the planning of the movement rather than visually guided online corrections (Elliott et al. 2001; Khan et al. 2003, 2006; Woodworth 1899). Visual inspection of the data revealed that trajectories were very straight.

Figure 1B illustrates the sequence of events for a single trial. Participants brought the cursor into the starting point to begin a trial. After a 1,500-ms resting period, a target was presented, prompting participants to perform the fast reaching movement. The end of the movement was defined as the time when the cursor crossed the target radius, 10 cm away from the starting point. Binary feedback regarding task success was provided immediately at movement end, i.e., at the crossing of the target radius, hence while in motion. The target turned green if participants successfully achieved the target or turned red if they missed it (see "*Success rate*" for more details). Visual feedback of the cursor was provided throughout the entire trial, except during the no-vision phase (see below). At the end of the trial, participants were instructed to stay still until the target disappeared (500 ms after movement end), at which point they could return to the starting point to initiate the next trial. Visual feedback of the cursor was removed for the return phase.

Main experiment. Before the experiment, participants practiced the task for 80 trials to get acquainted with the timing of the movement. They then took part in the main experiment. In the baseline phase, participants performed 80 trials with veridical (nonrotated) feedback of the cursor. In the adaptation phase, participants were exposed to a new visuomotor relationship for 240 trials. This was done through a cursor rotation, which generates a mismatch between the predicted visual feedback and the actual visual reafferent feedback, i.e., sensory prediction error. Participants were divided into three groups according to the variance in cursor rotations they experienced during the adaptation phase. Figure 1C shows the distribution of cursor rotations in each group. In the constant (C) group ($n = 10$; 4 men; mean age 23.3 ± 5.0 yr), the cursor rotations were constant at 15° CCW throughout the adaptation phase. In the low-variance (LV) group ($n = 11$; 3 men; mean age 21.8 ± 1.5 yr), the cursor rotations pseudorandomly varied between 10° (20% of trials), 15° (60% of trials), and 20° CCW (20% of trials) throughout the adaptation phase. This corresponds to a standard deviation (SD) of 3.2°. In the high-variance (HV) group ($n = 11$; 3 men; mean age 21.9 ± 1.8 yr), the cursor rotations pseudorandomly varied between 10° (40% of trials), 15° (20% of trials), and 20° CCW (40% of trials) throughout the adaptation phase. This corresponds to a SD of 4.5°. Importantly, the mean of exposed cursor rotations (15°) was identical across groups. An important aspect of the chosen rotations, which was validated by pilot testing, is that although participants would consciously perceive the presence of visuomotor rotations, they would perceive neither their different levels (10°, 15°, or 20°) nor that they could vary on a trial-by-trial basis. Also, because random rotations directly impact the end-point error between the cursor and the target, the target sizes were specifically chosen to allow maximal control over success rates across the three groups. Indeed, pilot testing allowed us to adjust the target size so that if participants fully compensated for the cursor rotation (i.e.,
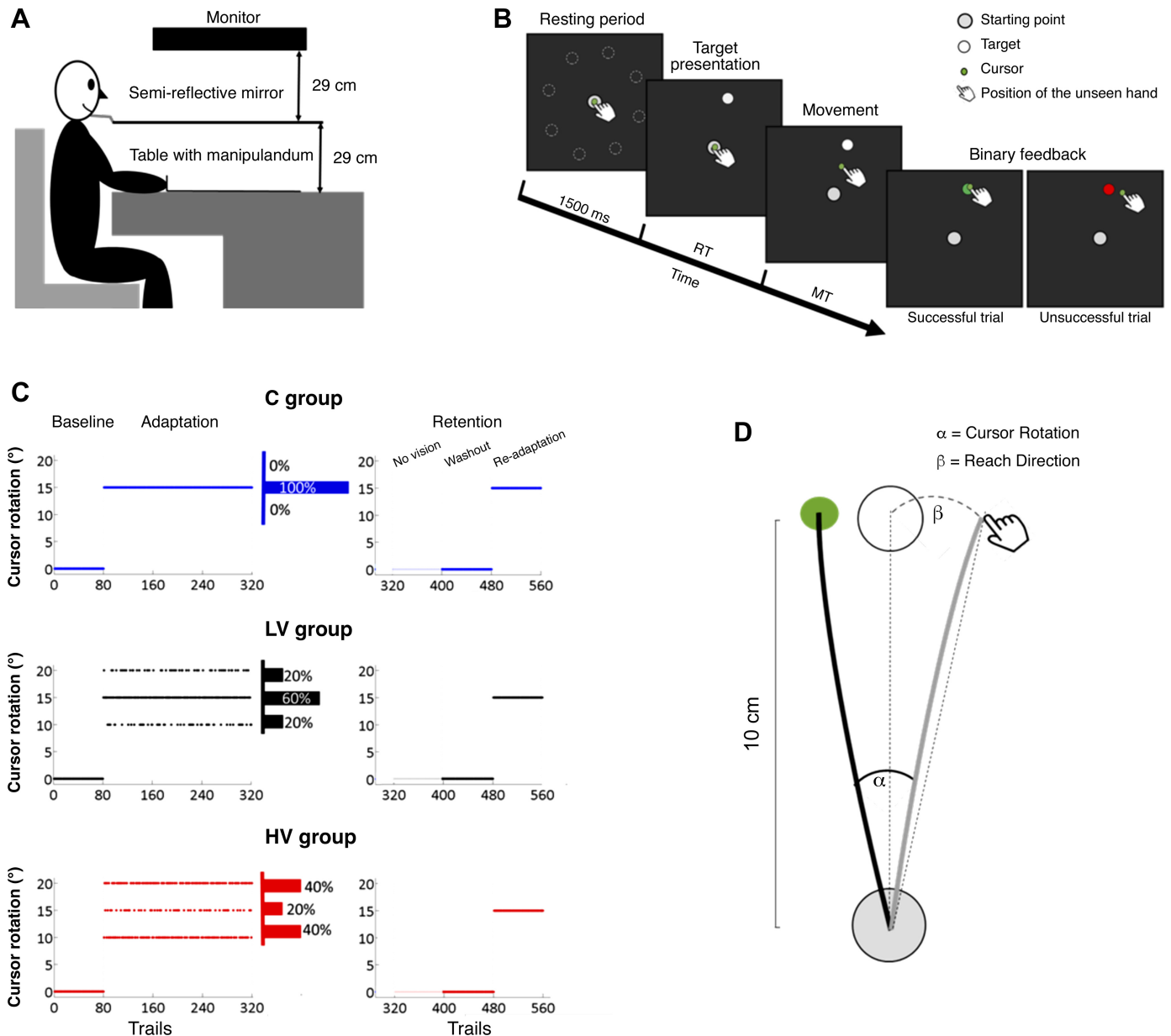
Fig. 1. Apparatus and experimental procedures. *A*: side view of the apparatus. *B*: time sequence of a typical trial. *C*: experimental protocol. *D*: schematic of cursor (black trace) and unseen hand (gray trace) trajectories. Cursor rotation consisted of the angular difference between the trajectories of the cursor and the unseen hand (α). Reach direction was calculated as the angular difference between the unseen hand and the target at target radius (β). Figure not to scale.

reaching 15° CW with respect to the targets), then cursor rotations of 15° CCW would lead to hitting the target, whereas cursor rotations of 10° and 20° CCW would be associated with missing the target. This was done so that the three groups would present reliable (and thus experimentally tractable) differences in success rates during adaptation.

Immediately after the adaptation phase, participants took part in a no-vision phase, a washout phase, and a readaptation phase. These allowed us to assess retention and savings of the newly acquired visuomotor relationship (Galea et al. 2011, 2015; Smith et al. 2006; Taylor et al. 2014). All three phases consisted of 80 trials and were identical for the three groups. In the no-vision phase, the cursor was not provided and there was no binary feedback regarding task success. Participants were simply instructed to reach to the targets as accurately as possible. In the washout phase, veridical (nonrotated) feedback of the cursor was provided. Finally, in the readaptation phase, all

participants were submitted to a constant 15° CCW cursor rotation. Breaks of ~1 min were given between each phase. Overall, the experiment comprised 560 trials and lasted ~55 min.

Reaction time. Reaction time (RT) was calculated as the time between target onset and movement onset, which was defined as the moment when the distance between the manipulandum and the starting point exceeded 2 mm. In a first rejection phase, trials for which RT was smaller than 100 ms or larger than 1,000 ms were discarded. In a second phase, trials were rejected on a per-participant basis. Specifically, trials for which RT was beyond ± 3 SD from a participant's mean were rejected. This corresponded to 1.6% of the data across participants (492 trials).

Movement time. Movement time (MT) was calculated as the time between movement onset and movement end, which corresponded to the moment the cursor crossed the 10-cm target radius. In a first rejection phase, trials for which MT was smaller than 50 ms or larger

than 500 ms were discarded. In a second rejection phase, trials were rejected on a per-participant basis. Specifically, trials for which MT was beyond ±3 SD from a participant's mean were rejected. This corresponded to 2.0% of the data across participants (607 trials).

Reach direction. Reach direction was defined as the angular difference between the physical location of the unseen hand at movement end and the target. This was done by subtracting the angle subtended by the X and Y coordinates of the hand at movement end from that of the target (Fig. 1D). Trials for which reach directions were beyond ±100° were considered abnormal and were rejected. This corresponded to 0.5% of the data across participants (146 trials). Overall, a total of 4.1% of the data were rejected.

Variability in reach direction. It was hypothesized that uncertainty of the forward (i.e., inverse) model would be influenced by variance in exposed rotations. As a proxy for uncertainty, the variability in reach directions was measured, because it reflects the level of noise in motor commands (Bays and Wolpert 2007; Harris and Wolpert 1998; Izawa and Shadmehr 2011). Specifically, the SD of reach directions was computed over the last 40 trials of the baseline phase (*cycles 6–10*), providing a baseline assessment of variability, and over the last 40 trials of the adaptation phase (i.e., *cycles 36–40*), when participants were adapted to the visual perturbation.

Success rate. To provide feedback regarding task success, the angular difference between the cursor and the target at movement end was computed. Specifically, a successful trial was defined as a trial for which the angular difference was less than that subtended by the radii of the cursor and the target (i.e., there was physical overlap between the cursor and the target). Note that the position of the cursor is the product of both the physical location of the unseen hand and the experimentally induced visuomotor rotation, which could vary on a trial-by-trial basis. Success rates were assessed by calculating the percentage of successful trials over the last 40 trials of the baseline phase (i.e., *cycles 6–10*), providing a baseline assessment of success rates, and over the last 40 trials of the adaptation phase (i.e., *cycles 36–40*), when participants were adapted to the visual perturbation.

Statistical analyses. A preliminary analysis sought to confirm that RT and MT did not differ across groups over the course of the experiment. This was done by conducting a three-group (C, LV, HV) × five-phase (baseline, adaptation, no vision, washout, readaptation) mixed-effects analysis of variance (ANOVA).

Another analysis sought to confirm that movements did not differ across groups during baseline. To do so, reach directions, variability in reach directions and success rates were measured over the last 40 trials of the baseline phase (i.e., *cycles 6–10*). These data were submitted to separate three-group (C, LV, HV) one-way ANOVAs.

The next analysis sought to evaluate the influence of variance in exposed rotations on the initial rate of adaptation to the new visuomotor relationship. This was calculated in two ways. First, adaptation rates were measured for each participant by fitting an exponential function over all trials of the adaptation phase (Huang et al. 2011; Morehead et al. 2015). The function had the following form:

$$y = a - b * e^{x*c}$$

Parameter fitting was implemented using the MATLAB function fminbnd to minimize squared error (y). The asymptotic performance parameter, *a*, was set to the mean of the last five cycles of the adaptation phase (i.e., *cycles 36–40*). The parameter corresponding to the total amount of adaptation, *b*, was taken as the difference between the mean of the last five cycles of the adaptation phase and the mean of the last five cycles of the baseline phase. The variable *x* refers to the trial number, and *c* is the adaptation rate constant, which was the only free parameter in the equation (Huang et al. 2011).

This analysis was supplemented by a model-free analysis in which mean reach direction over the first five cycles of the adaptation phase (i.e., *cycles 11–15*) was compared across groups. This form of analysis has been shown to reliably capture initial adaptation in similar paradigms (Galea et al. 2011; Krakauer et al. 2005; Morehead et al.

2015). This window of trials was chosen because it captured the bulk of the changes in reach direction up to the point where participants reached asymptotic levels. To control for inter-individual differences in baseline performance, mean reach direction in the last 5 cycles of the Baseline phase was subtracted for each participant (see Morehead et al. 2015). Separate 3 Groups (C, LV, HV) one-way ANOVAs were conducted on the adaptation rate and mean reach direction data.

The final extent of adaptation was assessed by comparing mean reach direction between groups over the last five cycles of the adaptation phase (i.e., *cycles 36–40*). To do so, the mean reach direction data were submitted to a three-groups (C, LV, HV) one-way ANOVA. To evaluate whether exposure to different levels of variance in rotations influenced the variability in reach directions as well as success rates, these data were measured over the last five cycles of the adaptation phase (i.e., *cycles 36–40*) and submitted to separate three-group (C, LV, HV) one-way ANOVAs.

Finally, a last set of analyses assessed the influence of variance in exposed rotations on the retention of the new visuomotor relationship. The main test of retention consisted of the no-vision phase, which immediately followed adaptation. Indeed, in the absence of corrective feedback, the persistence of the adapted behavior can be taken as evidence for retention (Galea et al. 2011, 2015). Some participants did not present a reliable drift in reach directions during no vision. As a result, not every participant's data were well fit by an exponential function such that a "decay rate" analysis was not used. Rather, reach directions were averaged over the first five cycles (i.e., *cycles 41–45*; early no vision) and the last five cycles of the no-vision phase (i.e., *cycles 46–50*; late no vision). This allowed us to capture possible changes over the course of the no-vision phase (Galea et al. 2011). These data were then submitted to a three-group (C, LV, HV) × two-epoch (early no vision, late no vision) mixed-effects ANOVA. To evaluate a possible direction dependency associated with the use of multiple targets during this critical phase, a three-group (C, LV, HV) × eight-target repeated-measures ANOVA with target as a within-participant factor was also conducted on the reach direction data from that phase (Hadipour-Niktarash et al. 2007).

As for the washout and readaptation phases, the deadaptation rates (i.e., during washout) and readaptation rates (i.e., during readaptation) were assessed. In both cases, parameter *a* was set to the last cycle of each phase, and parameter *b* was taken as the difference between the last cycle of each phase and the last cycle of the previous phase. These analyses were supplemented by a three-group (C, LV, HV) × two-epoch (early, late) mixed-effects ANOVA conducted on the reach direction data. Finally, to assess savings (i.e., more rapid adaptation on second exposure to the perturbation compared with the first), the adaptation rates were compared with the readaptation rates using a three-group (C, LV, HV) × two-phase (adaptation, readaptation) mixed-effects ANOVA.

It should be noted that the potential influence of variance in exposed rotations was expected to attenuate over the washout and readaptation phases, because variance was not manipulated across groups anymore. Hence, although the readaptation phase allowed us to assess savings, it did not constitute the key condition on which differences in retention would be assessed across conditions. All effects were deemed significant at $P < 0.05$, and Tukey's test was used for post hoc comparisons.

RESULTS

Verbal debriefing with participants after the experiment confirmed that although they did perceive the suddenly introduced visuomotor rotations, they neither perceived their different levels (10°, 15°, or 20°) nor that they could vary on a trial-by-trial basis.

Before we assessed whether variance in exposed rotations influenced the acquisition and retention of the new visuomotor

relationship, the RT and MT data were compared to ensure that they did not differ across groups. This was confirmed. Indeed, the ANOVA conducted on the RT data only revealed a main effect of phase [$F_{(4, 116)} = 8.4$; $P < 0.001$; $\eta_p^2 = 0.22$], with RTs tending to increase over the course of the experiment. However, it revealed neither a main effect of group (448 ± 17, 406 ± 16, and 426 ± 16 ms for C, LV, and HV, respectively; $P = 0.24$; $\eta_p^2 = 0.09$) nor an interaction ($P = 0.53$; $\eta_p^2 = 0.06$). Similarly, the ANOVA conducted on the MT data also revealed only a main effect of phase [$F_{(4, 116)} = 5.7$; $P < 0.001$; $\eta_p^2 = 0.17$], with MTs being slightly higher in the baseline phase compared with the other phases. Most importantly, it revealed neither a main effect of group (151 ± 5, 152 ± 5, and 151 ± 5 ms for C, LV, and HV, respectively; $P = 0.98$; $\eta_p^2 = 0.001$) nor an interaction ($P = 0.72$; $\eta_p^2 = 0.04$).

Adaptation. The mean reach directions in the three groups across each cycle of the adaptation phase are presented in Fig. 2*A*. As can be seen, the three groups did not differ significantly during baseline. Indeed, the ANOVA carried out on the baseline phase data revealed no significant difference in mean reach direction [−0.1 ± 0.1°; $F_{(2, 29)} = 1.1$; $P = 0.35$; $\eta_p^2 = 0.07$] or variability in reach directions [2.7 ± 0.1°; $F_{(2, 29)} = 2.1$; $P = 0.14$; $\eta_p^2 = 0.13$], as well as success rates [89.0 ± 1.5%; $F_{(2, 29)} = 0.02$; $P = 0.98$; $\eta_p^2 = 0.001$].

Figure 2*A* also shows that the three groups adapted to the new visuomotor relationship rapidly, reaching near-asymptotic levels within approximately five cycles. As shown in Fig. 2*B*, adaptation rates were similar across groups, with the C, LV, and HV groups presenting values of 0.05 ± 0.01, 0.04 ± 0.003, and 0.05 ± 0.01, respectively. This was confirmed by the ANOVA, which revealed no significant difference across

groups [$F_{(2, 29)} = 1.2$; $P = 0.32$; $\eta_p^2 = 0.08$]. The same conclusion emerged from the analysis of the mean reach direction over the first five cycles of the adaptation phase [8.3 ± 0.5°; $F_{(2, 29)} = 1.1$; $P = 0.34$; $\eta_p^2 = 0.07$]. Overall, these data suggest that the initial rate of adaptation was unaffected by variance in exposed rotations.

As also shown in Fig. 2*A*, the three groups tended to plateau at a similar level of performance (~14°) late in adaptation, compensating near fully for the mean rotation of 15° CCW to which they were exposed. To assess the final extent of adaptation, mean reach direction over the last five cycles of the adaptation phase was compared across groups. As shown in Fig. 2*C*, there was minimal difference across groups, with the C, LV, and HV groups presenting mean reach directions of 13.9 ± 0.1°, 13.7 ± 0.2°, and 13.6 ± 0.2°, respectively. Accordingly, the ANOVA revealed no significant difference across groups [$F_{(2, 29)} = 0.55$; $P = 0.6$; $\eta_p^2 = 0.04$]. This indicates that variance in exposed rotations did not affect the final extent of adaptation.

Retention. Reach directions in each cycle of the no-vision, washout, and readaptation phases are presented in Fig. 2*D*. As can be seen, movements were still biased toward the adapted reach direction in the no-vision phase, demonstrating retention. However, reach directions tended to drift over that phase, going from ~14° to ~6°. Retention of the newly acquired visuomotor relationship was primarily assessed through reach directions in the no-vision phase, which are presented in Fig. 2*E*. Critically, mean reach direction during that phase tended to be graded across groups, with the C group showing the highest mean reach direction during no vision (i.e., better retention). This was confirmed by the ANOVA, which revealed a signif-
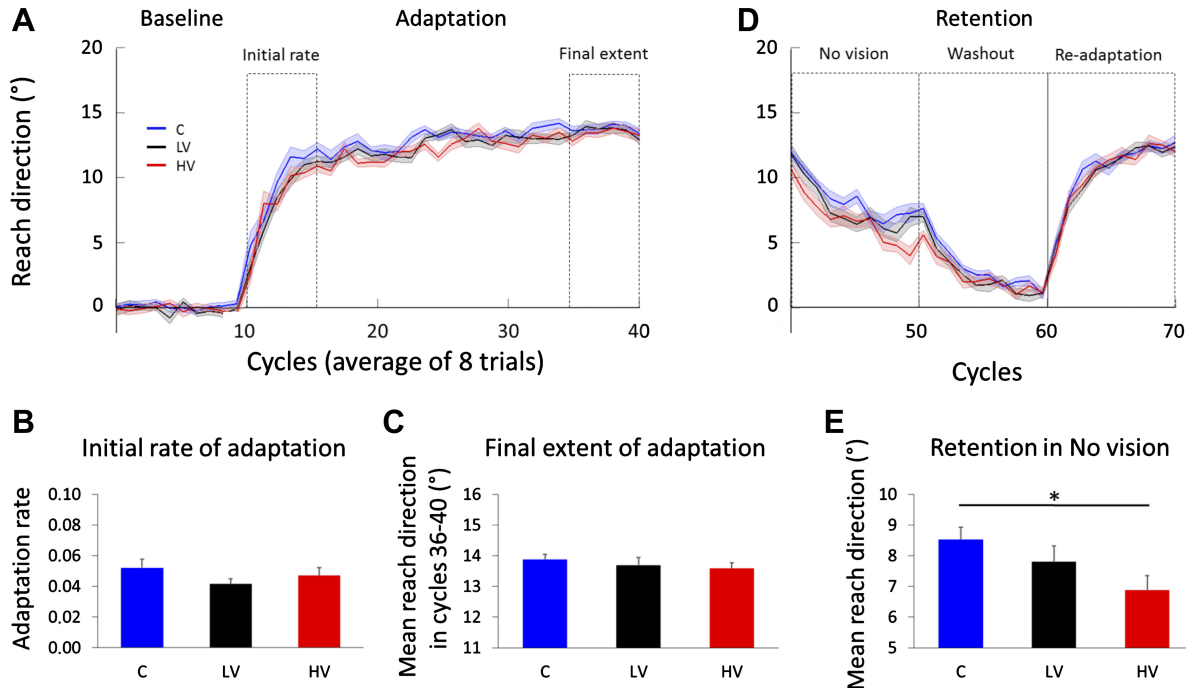

Fig. 2. Main experiment results. *A*: time course of reach directions for each group during adaptation, with data binned in cycles (8 trials). *B*: initial rate of adaptation, as measured by fitting an exponential function over all trials of the adaptation phase. Variance in exposed rotations did not influence the initial rate of adaptation. *C*: final extent of adaptation, as measured by mean reach direction over the last 5 cycles of the adaptation phase (i.e., *cycles 36–40*). Variance in exposed rotations did not influence the final extent of adaptation. *D*: time course of reach directions for each group during retention. *E*: retention of the new visuomotor relationship, as measured by mean reach direction in the no-vision phase. Higher variance in exposed rotations was associated with lower retention. Error bars represent SE. *$P < 0.05$.

icant main effect of group [$F_{(2, 29)} = 3.4$; $P = 0.04$; $\eta_p^2 = 0.19$]. Post hoc comparisons revealed that mean reach direction in the C group ($8.5 \pm 0.5°$) was significantly greater than in the HV group ($6.8 \pm 0.5°$; $P = 0.04$). The LV group was intermediate ($7.8 \pm 0.5°$) but did not differ significantly from that in the two other groups (both $P > 0.1$). There was also a significant main effect of epoch [$F_{(1, 29)} = 181.6$; $P < 0.001$; $\eta_p^2 = 0.86$], with reach directions decreasing significantly between early no vision (*cycles 41–45*; $9.0 \pm 0.3°$) and late no vision (*cycles 46–50*; $6.4 \pm 0.3°$). Importantly, there was no group × epoch interaction [$F_{(2, 29)} = 0.2$; $P = 0.8$; $\eta_p^2 = 0.01$], suggesting that the differences across groups were maintained throughout the no-vision phase. In sum, these data indicate that as variance in exposed rotations increased, retention decreased.

To evaluate a possible direction dependency during the critical no-vision phase, reach directions were also compared across targets. The ANOVA again revealed a main effect of group [$F_{(2, 29)} = 3.5$; $P = 0.04$; $\eta_p^2 = 0.19$], with the C group again presenting significantly better retention than the HV group ($P = 0.03$). The LV group was intermediate but did not differ significantly from the two other groups (both $P > 0.2$). There was also a main effect of target [$F_{(7, 203)} = 14.4$; $P < 0.001$; $\eta_p^2 = 0.33$], with reach directions differing across targets, possibly attributable to biomechanical constraints. Critically, however, there was no group × target interaction [$F_{(14, 203)} = 0.9$; $P = 0.6$; $\eta_p^2 = 0.06$].

Reach directions gradually reverted back from ~6° to ~1° during the washout phase. This was confirmed by the ANOVA, which revealed a significant main effect of epoch [$F_{(1, 29)} = 385.2$; $P < 0.001$; $\eta_p^2 = 0.93$]. Although mean reach direction tended to be slightly graded across groups during this phase ($3.2 \pm 0.3°$, $2.6 \pm 0.3°$, and $2.5 \pm 0.3°$ for C, LV, and HV,

respectively), there was no significant main effect of group [$F_{(2, 29)} = 1.8$; $P = 0.19$; $\eta_p^2 = 0.11$]. Similarly, the ANOVA carried out on the deadaptation rates did not show a significant main effect of group [0.05 ± 0.01; $F_{(2, 28)} = 1.2$; $P = 0.31$; $\eta_p^2 = 0.08$].

As for the readaptation phase, participants rapidly reacquired the new relationship, with reach directions going from ~1° to ~14°. The ANOVA carried out on the reach direction data revealed a significant main effect of epoch [$F_{(1, 29)} = 308.5$; $P < 0.001$; $\eta_p^2 = 0.91$]. However, there was no significant main effect of group [$10.8 \pm 0.3°$, $10.5 \pm 0.3°$, and $10.5 \pm 0.3°$ for C, LV, and HV, respectively; $F_{(2, 29)} = 0.35$; $P = 0.7$; $\eta_p^2 = 0.02$]. Similarly, the ANOVA carried out on the readaptation rates did not show a significant main effect of group [0.08 ± 0.01; $F_{(2, 28)} = 0.27$; $P = 0.76$; $\eta_p^2 = 0.02$]. Even though readaptation was similar across groups, there was evidence for savings, because the readaptation rates (0.08 ± 0.01) were significantly greater than the initial adaptation rates [0.05 ± 0.005; $F_{(1, 26)} = 28.9$; $P < 0.001$; $\eta_p^2 = 0.53$]. This suggests a persistent memory representation of the adapted forward model in all three groups (Smith et al. 2006).

Variability in reach directions and success rates. Although participants' mean reach direction did not differ across groups late in the adaptation phase, they may have presented different levels of variability in reach directions. To visually represent this, the distributions of reach directions of all trials in the last five cycles of the adaptation phase were averaged across participants and are presented in Fig. 3*A*. As can be seen, the three groups presented unimodal distributions with a mean at ~14°. This is consistent with the finding that the three groups adapted their mean reach direction similarly. Interestingly, however, there was a tendency for the variance groups (LV and
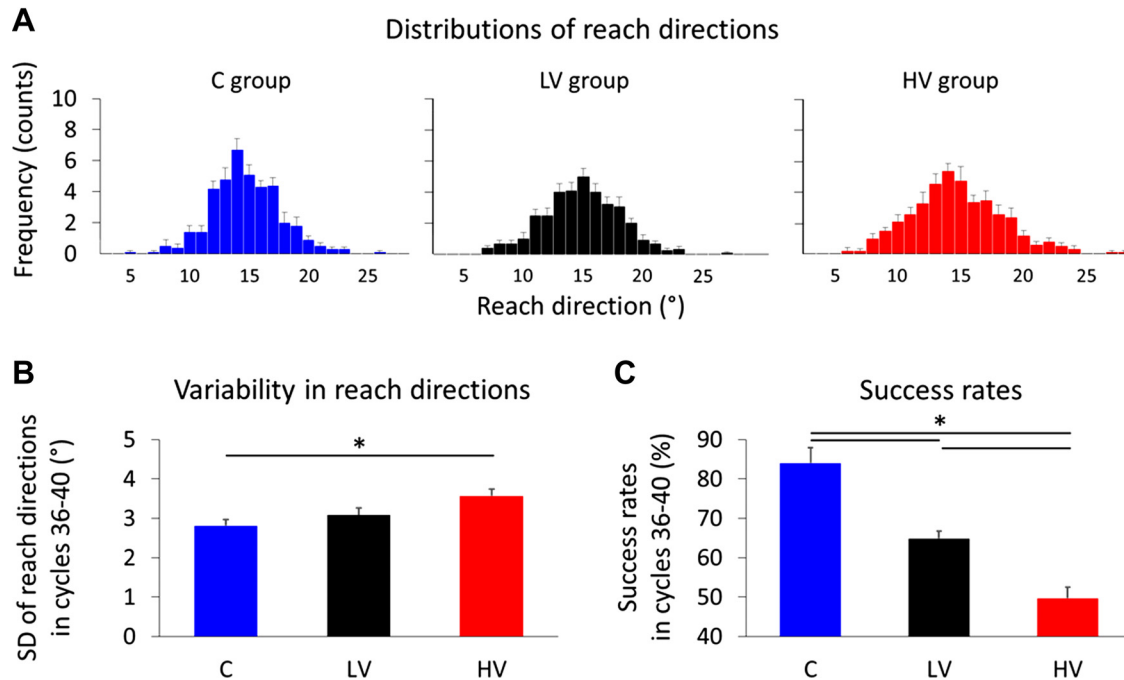

Fig. 3. Main experiment results. *A*: distributions of reach directions of all trials in the last 5 cycles of the adaptation phase (i.e., *cycles 36–40*), averaged across participants and presented for each group. *B*: mean variability in reach directions for each group, assessed by calculating the SD of reach directions over the last 5 cycles of the adaptation phase (i.e., *cycles 36–40*). Higher variance in exposed rotations was associated with higher variability in reach directions. *C*: mean success rates for each group over the last 5 cycles of the adaptation phase (i.e., *cycles 36–40*). Higher variance in exposed rotations was associated with lower success rates. Error bars represent SE. *$P < 0.05$.

HV) to be associated with broader distributions (i.e., more variability in reach directions). This was confirmed by the ANOVA conducted on the SD of reach directions in the last five cycles of the adaptation phase, which revealed a significant main effect of group [$F_{(2,29)} = 4.9$; $P = 0.02$; $\eta_p^2 = 0.25$; see Fig. 3B]. Post hoc comparisons revealed that SD in the C group ($2.8 \pm 0.2°$) was significantly smaller than in HV group ($3.6 \pm 0.2°$; $P = 0.01$), whereas that in the LV group ($3.1 \pm 0.2°$) was intermediate but did not differ significantly from that of the other groups (both $P > 0.1$).

Success rates in the last five cycles of the adaptation phase were also compared across groups and are presented in Fig. 3C. The ANOVA again revealed a significant main effect of group [$F_{(2,29)} = 33.8$; $P < 0.001$; $\eta_p^2 = 0.7$], with the highest success rates for the C group ($84.0 \pm 4.0\%$), followed by the LV group ($64.9 \pm 1.8\%$) and the HV group ($50.0 \pm 2.7\%$). Post hoc comparisons revealed that all three groups differed significantly from each other (all $P < 0.005$). This was expected, given that participants' mean reach direction was ~14° in all three groups, hence leading to target hits whenever the cursor rotation was 15° CCW, but misses whenever the rotation was 10° or 20° CCW.

Control experiment. Results from the main experiment revealed that retention of the new visuomotor relationship differed across groups in the no-vision phase (Fig. 2E). Although this suggests that variance in exposed rotations was the key factor influencing retention, a possible confound is the fact that the three groups also differed in terms of overall success rates (see Fig. 3C). In light of recent work showing that rewards impact the retention of a new visuomotor relationship (Galea et al. 2015), it was important to confirm that the observed group differences in retention were not merely accounted for by differences in success rates. To do so, two additional groups were created (C-control; $n = 11$; 6 men, mean age 22.1 ± 1.1 yr, and HV-control; $n = 12$; 6 men, mean age 22.2 ± 1.2 yr), for which the size of the targets was manipulated to modulate success rates. Identically to the C group, the C-control group had no variance in exposed rotations (i.e., constant 15° CCW) but was presented with smaller targets (10 mm in diameter),

thereby decreasing success rates. This target size was chosen so that the success rates would approximate those of the HV group late in adaptation (i.e., 50%). On the other hand, the HV-control group was submitted to the same high-variance perturbation schedule as the HV group but was provided with larger targets (24 mm in diameter), thereby increasing success rates. This target size was chosen so that the success rates would approximate those of the C group late in adaptation (i.e., 84%). All other features of the control experiment were identical to the main experiment. If the C-control group still presented better retention than the HV-control group, then it would rule out that the differences in retention observed in the main experiment were merely accounted for by differences in success rates.

Success rates were first assessed to confirm the effectiveness of the target size manipulation. This was the case, because an independent-samples *t*-test conducted on the success rates late in the adaptation phase revealed that the C-control group presented significantly lower success rates than the HV-control group [$43.0 \pm 2.1\%$ and $86.0 \pm 2.3\%$, respectively; $t_{(21)} = 13.6$; $P < 0.001$].

The mean reach directions across each cycle of the adaptation phase are presented in Fig. 4A. The two groups did not differ significantly during baseline in any of the dependent variables (all $P > 0.4$). As shown in Fig. 4B, the initial rate of adaptation was similar across groups. This was confirmed by independent-samples *t*-tests, which revealed no significant difference across groups both for the adaptation rates (0.06 ± 0.02; $P = 0.8$) and the mean reach direction over the first five cycles of the adaptation phase ($8.8 \pm 0.7°$; $P = 0.9$).

The final extent of adaptation was also similar across groups (Fig. 4C). Indeed, the *t*-test conducted on the mean reach direction over the last five cycles of the adaptation phase revealed no significant difference across groups ($13.7 \pm 0.1°$; $P = 0.6$). As for variability in reach directions late in the adaptation phase, the HV-control group presented higher variability compared with the C-control group ($3.6 \pm 0.2°$ and $3.2 \pm 0.1°$, respectively), although this did not reach statistically significant levels ($P = 0.4$).
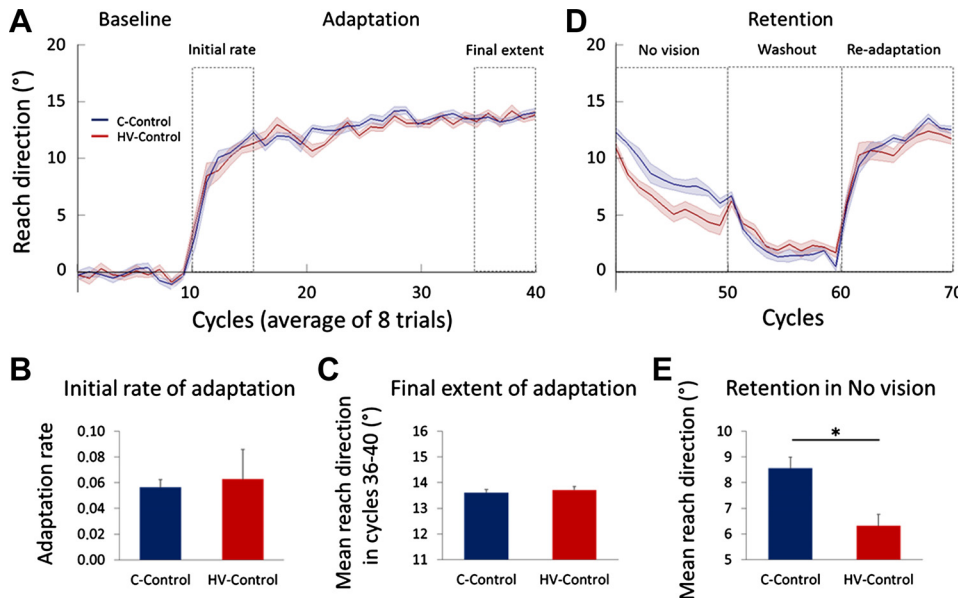

Fig. 4. Control experiment results. *A*: time course of reach directions for each group during adaptation, with data binned in cycles (8 trials). *B*: initial rate of adaptation, as measured by fitting an exponential function over all trials of the adaptation phase. Variance in exposed rotations did not influence the initial rate of adaptation. *C*: final extent of adaptation, as measured by mean reach direction over the last 5 cycles of the adaptation phase (i.e., *cycles 36–40*). Variance in exposed rotations did not influence the final extent of adaptation. *D*: time course of reach directions for each group during retention. *E*: retention of the new visuomotor relationship, as measured by mean reach direction in the no-vision phase. Higher variance in exposed rotations was associated with lower retention. Error bars represent SE. *$P < 0.05$.

Figure 4, *D* and *E*, presents the mean reach direction in the no-vision phase, used to assess retention. Critically, retention was better in the C-control group than in the HV-control group (8.6 ± 0.4° and 6.3 ± 0.4°, respectively), as confirmed by the ANOVA, which revealed a significant main effect of group [$F_{(1, 21)}$ = 13.0; P = 0.002; η_p^2 = 0.38]. There was also a significant main effect of epoch [$F_{(1, 21)}$ = 113.8; $P <$ 0.001; η_p^2 = 0.84], with reach directions decreasing between early no vision (9.0 ± 0.5°) and late no vision (6.0 ± 0.6°). Again, there was no group × epoch interaction [$F_{(1, 21)}$ = 0.1; $P =$ 0.7; η_p^2 = 0.01], indicating that the group differences were maintained across the no-vision phase. There were no differences across groups during the washout and the readaptation phases, in either the mean reach direction analyses or the rate analyses (all $P >$ 0.2).

In sum, using independent data sets, the control experiment replicates the findings of the main experiment in that variance in exposed rotations did not influence adaptation but selectively impaired retention of the new visuomotor relationship. Importantly, it confirms that in the present context, retention was mainly influenced by variance in exposed rotation and not by different success rates.

DISCUSSION

The present study investigated the influence of uncertainty in the sensory predictions on the retention of a new visuomotor relationship. This was done by parametrically manipulating the variance in exposed rotations, but not the mean during visuomotor adaptation, and then measuring the persistence of the adapted behavior in a no-vision phase. Results revealed that mean reach direction was similar across groups late in adaptation. Interestingly, however, retention differed across groups, with increased variance being associated with a more rapid reversion toward nonadapted behavior, i.e., weaker retention. A control experiment confirmed that differences in retention were not attributable to differences in success rates during adaptation. These results suggest that exposure to more variable rotations increased the uncertainty of the adapted forward model, making it more labile and susceptible to change or decay.

Variance in exposed rotations does not influence the mean of the adapted forward model, but rather its uncertainty. Results revealed that the initial rate of adaptation and the final extent of adaptation were not influenced by variance in exposed rotations. This supports previous work from Burge et al. (2008) and Scheidt et al. (2001), who also found that random variability in exposed perturbations had no effect on adaptation in humans. However, this is in contrast to Fernandes et al. (2012), who reported slower and less complete adaptation under high-variance conditions. It is possible that the difference between the present results and those of Fernandes et al. (2012) is attributable to the fact that the variances used in the present study (SDs of 0°, 3.2°, 4.5°) were much smaller than theirs (SDs of 0°, 4° and 12°). In this regard, it should be reiterated that the present goal was for participants not to consciously perceive the induced variance in rotations, which was indeed the case. The fact that mean reach direction was similar across groups late in training thus suggests that adaptation was robust to differences in variance (at least in the range tested in this

study) and was rather dependent on the mean of exposed perturbations.

Interestingly, even though the three groups similarly adjusted their mean reach direction toward 15° during adaptation, exposure to higher levels of variance impacted the trial-to-trial variability of those movements. Indeed, variability (SD) in reach directions significantly differed across groups late in adaptation, being largest in the HV group, intermediate in the LV group, and smallest in the C group (see Fig. 3*B*). This suggests a more uncertain estimate of the adapted forward model on exposure to variance, because more variable movements are thought to underline a more uncertain forward (and inverse) model (Bays and Wolpert 2007). The increased variability in reach directions is unlikely to have reflected a strategy of offsetting the perturbations by aiming at 10° or 20°, or the separate adaptation to three independent rotations, because the distributions of reach directions were clearly unimodal with a peak near 15° in all three groups (Fig. 3*A*). This is especially striking for the HV group, whose schedule of perturbations was bimodal, suggesting that participants adapted to the mean and not to the most likely rotation [see also Scheidt et al. (2001) for similar observation]. Overall this result points to variability in reach directions as truly reflecting uncertainty around the mean. This is consistent with previous work showing that adding variance around a perturbation acts to increase the uncertainty of the adapted forward model (Fernandes et al. 2012, 2014; Tan et al. 2016).

Together, these findings indicate that the rate and extent to which the adapted forward model "shifted" from 0° to 15° depended on the mean evidence sampled over the course of the adaptation phase. In contrast, variance in exposed rotations acted to increase the uncertainty (i.e., noise) around this new mean.

Variance in exposed rotations influences the retention of the adapted forward model. The main finding of the present work is that despite the fact that the three groups presented similar mean reach directions late in adaptation, variance in exposed rotations influenced the retention of the new visuomotor relationship. This effect was specific to the no-vision phase. Indeed, although there was significant savings on reexposure to the rotation in the readaptation phase, there was no difference across groups in that phase. A similar finding was recently reported by Maeda et al. (2017), who also found no difference in the relearning of a visually guided walking task between groups that had trained under a constant vs. noisy visuomotor mapping. Still, it is possible that the absence of group effect during readaptation is simply attributable to the fact that the influence of variance in exposed rotations had washed away during the washout phase.

In light of the preceding evidence for differences in uncertainty, a first possibility accounting for the differential retention during no vision derives from the Bayesian framework, which suggests that greater uncertainty in the prior is associated with a greater tendency to adjust motor behaviors given new sensory evidence (Wei and Körding 2010). Indeed, the present adaptation phase could be considered as a conditioning phase, effectively modulating uncertainty of the adapted forward model. The retention phase, in turn, would reflect participants' tendency to change their behavior given new sensory evidence. Whereas a no-vision condition is generally considered as providing no feedback, and thus no "new sensory

evidence" with which to adjust behavior, participants could still rely on proprioceptive information to plan, control, and evaluate the outcome of their movements. Interestingly, it is well documented that visuomotor adaptation is accompanied by proprioception recalibration (Cressman and Henriques 2009; Simani et al. 2007), and a recent study showed that variance in exposed rotations tends to reduce the degree of proprioceptive recalibration (Saijo and Gomi 2012). Specifically, the authors investigated proprioceptively guided online control by using probe trials in which vision was unpredictably removed. They found that reaches during probe trials were more biased toward the actual (i.e., nonrotated) target location when variance in exposed rotations was high, suggesting that proprioceptive recalibration was reduced by variance. In this light, the drift toward baseline during the present no-vision phase may have been attributable to a proprioceptively driven task error (i.e., the comparison between final hand position and target position), and the different rate at which this occurred across groups may have been a result of differences in proprioceptive recalibration. In this framework, given that variance in exposed rotations *1*) makes the sensorimotor system rely less on the prior and more on new sensory evidence (Wei and Körding 2010) and *2*) reduces the degree of proprioceptive recalibration (Saijo and Gomi 2012), it would follow that higher levels of variance in exposed rotations led to a faster reversion toward nonadapted behavior.

Alternatively, it is possible that the differences observed in the no-vision phase were due to a competition between two visuomotor memories: the adapted forward model at 15° CCW and the "original" forward model at 0°. In support, Shmuelof et al. (2012) proposed that the drift toward baseline observed in no-vision or error-clamp conditions is the reflection of a gradual reversion toward the original well-learned forward model. In this light, increased uncertainty in the adapted prior may have led the sensorimotor system to attribute a greater weight to the original prior, thus explaining the more rapid drift.

Another possibility is that the different retention across groups reflected differences in the stability of the new motor memory (Vaswani and Shadmehr 2013), perhaps driven by different rates of forgetting of the adapted forward models. Specifically, variance in exposed rotations may have influenced the relative contribution of the fast and slow components of adaptation across groups, which show differential adaptation rates and capacity for retention (Joiner and Smith 2008; Shadmehr et al. 2010; Smith et al. 2006). Namely, the fast component shows high adaptation rates but poor retention, whereas the slow component shows low adaptation rates but high retention. A key element is that uncertainty in the prior has previously been associated with faster adaptation rates (Turnham et al. 2012; Wei and Körding 2010), a sign that the fast component is exacerbated in this context. In turn, higher variance may have been associated with a proportionally lesser contribution of the slow component to adaptation, accounting for the weaker retention of the adapted forward model in this context.

Finally, the differences in retention may have been partly attributable to the fact that movements were more repetitive (smaller SD) in the C group than the in LV and HV groups (see Fig. 3*B*), leading to use-dependent plasticity (UDP). Indeed, the repetition of movements in a given direction fosters the formation of a stronger memory trace by the creation and strengthening of neural connections through Hebbian processes (Diedrichsen et al. 2010; Huang et al. 2011; Kantak et al. 2013; Rroji et al. 2015; Verstynen and Sabes 2011). Although UDP is a possibility, it has been shown to contribute to retention mainly in contexts in which a single or few targets are used. To our knowledge it remains to be demonstrated whether UDP plays a significant role when there is inherent variability in motor commands across trials given the large number of targets.

Retention was not modulated by task success. In the main experiment, variance in exposed rotations covaried with success rates, making it possible that the graded retention was attributable to differences in rewards across groups (Galea et al. 2015). However, a control experiment in which success rates were independently manipulated by changing target size confirmed that differences in retention were uniquely attributable to variance in exposed rotations. These results demonstrate that in the present context, behavioral success did not have a significant bearing on the retention of the new visuomotor relationship. In support of the present results, a recent study tested how external reward feedback affects sensorimotor adaptation (Nikooyan and Ahmed 2015). They found that although it is possible to learn from reward feedback alone, it does not lead to a remapping of the visuomotor relationship, which is necessary to drive aftereffects and retention (see also van der Kooij and Overvliet 2016). Similarly, Izawa and Shadmehr (2011) reported that, whereas sensory and reward prediction errors can both lead to changes in motor commands during adaptation, only sensory prediction errors alter the predicted consequences of motor commands and cause sensory remapping. These interpretations are in line with the present results in that feedback about task success was not the defining factor of retention.

Conclusion. The present study suggests a dissociation between the influence of variance in exposed rotations on the mean reach direction late in adaptation vs. the retention of a new visuomotor relationship. This extends previous work suggesting differential internal representations of the mean and uncertainty of priors (Fernandes et al. 2014). These results may have implications in rehabilitation settings involving virtual reality, where visual reafferent feedback can be manipulated. Efforts should focus on developing interfaces that minimize variability in the feedback being delivered to patients, hence fostering the long-term storage of motor memories.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

C.A.C., F.B., and P.-M.B. conceived and designed research; C.A.C. performed experiments; C.A.C. and P.-M.B. analyzed data; C.A.C., F.B., and P.-M.B. interpreted results of experiments; C.A.C. and P.-M.B. prepared figures; C.A.C. and P.-M.B. drafted manuscript; C.A.C., F.D., F.B., and P.-M.B. edited and revised manuscript; C.A.C., F.D., F.B., and P.-M.B. approved final version of manuscript.

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