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1 **Reliability of Online Visual and Proprioceptive**
2 **Feedback: Impact on Learning and Sensorimotor**
3 **Coding**

4
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1 **Abstract**

2 Multisensory integration is essential for learning and sensorimotor coding, facilitating learners'
3 adaptation to environmental changes. Recent findings confirm that introducing unreliability
4 into visual feedback enhances the use of motor coding, probably because proprioceptive cues
5 are given greater weight. The present study was designed to test this hypothesis and, more
6 generally, to explore the impact of visual versus proprioceptive cue reliability on learning
7 processes. Participants performed a 12-target pointing sequence 100 times with different
8 combinations of visual and proprioceptive feedback: reliable versus unreliable. Retention tests
9 and intermanual transfer tests were administered 24 hours later. Results showed that learning
10 and sensorimotor coding were both affected by the different combinations of visual and
11 proprioceptive cue reliability. Fully reliable feedback allowed for the best retention, while fully
12 unreliable feedback resulted in the worst retention. Visual reliability alone mediated the level
13 of visuospatial coding performance in visuospatial transfer, regardless of the level of
14 proprioceptive reliability, and conversely, reliable proprioception combined with unreliable
15 vision provided the optimum sensory environment for motor coding in the motor transfer test.
16 Overall, our study highlighted the essential role of both visual cue reliability and proprioceptive
17 cue reliability -and their interactions- in motor learning and its generalization.

1 *Statements and Declarations*

2 No conflicts of interest, financial or otherwise, are declared by the authors. The authors have
3 full control of all primary data and agree to allow the journal to review their data if requested.

4

5 *Keywords:* sensorimotor learning, sensorimotor coding, feedback reliability, sequential task,
6 tendon vibration

7

1 **Introduction**

2 The integration of sensory information is key to efficient sequence motor learning,
3 allowing learners to quickly and fluidly adapt to environmental changes (for a review, see Shea
4 et al., 2011). More precisely, motor learning and transfer capabilities rely on internal
5 representations of motor skills constructed using different coordinates or coding systems
6 (Coello et al., 1996; Criscimagna-Hemminger et al., 2003; Lange et al., 2004). Two coding
7 systems have been identified: visuospatial and motor (Hikosaka et al., 1999, 2002; Jordan &
8 Wolpert, 1999; Park & Shea, 2005) based on dissociated neural loop circuits between: the
9 fronto-parietal cortex and the basal and cerebellar associative areas (*visuospatial coding*), the
10 motor cortex and the basal and cerebellar motor areas (*motor coding*; see Doyon et al., 2003;
11 Hikosaka et al., 2002). Visuospatial coding involves the conscious use of relevant visuospatial
12 (i.e., extrinsic) coordinates, such as spatial limb and stimulus locations. *Motor coding* involves
13 the unconscious (i.e., intrinsic) coding of muscle activation and joint angle patterns, and relies
14 more on proprioceptive cues. A harmonious development of both coding systems (i.e., mixed
15 coding) improves specific sensorimotor skills but also their generalization, allowing individuals
16 to engage in adaptive behaviors (see Shea et al., 2011). However, several studies have
17 confirmed the dominance of visuospatial coding over motor coding in the sensorimotor learning
18 of visuomanual tasks (e.g., Boutin et al., 2010, 2012; Kovacs et al., 2009; Park & Shea, 2002,
19 2005), even after extended periods of practice (e.g., 12 days of practice; Kovacs et al., 2009).
20 This dominance of visuospatial coding comes from the overuse of visual cues relative to the
21 other available sensory cues, and has negative consequences: the more motor learning is to one
22 sensory modality, the more dependent it becomes on this modality (specificity of practice
23 hypothesis; Tremblay & Proteau, 1998). Developing the motor coding would lead to a more
24 stable and durable learning as, contrary to the visuospatial coding, motor coordinates rely on
25 implicit knowledge and do not require attention or working memory (Shea et al., 2011). Thus,

1 one of the remaining challenges is to understand the mechanisms for integrating different
2 sensory modalities in order to reduce reliance on visual cues and therefore the dominance of
3 visuospatial coding. Based on recent literature (Bernardo et al., 2023a, 2023b; Hewitson et al.,
4 2018; Körding & Wolpert, 2004), here we specifically address this issue by varying visual
5 and/or proprioceptive reliability. Uncovering these mechanisms and the most favorable
6 conditions for learning and transfer should enable to characterize the role of sensory
7 information in the representation of actions.

8 Several potential solutions to the visual dominance of the motor learning process have
9 been explored through the manipulation of proprioceptive cues, signals that refer to the position
10 and movement of our body segments, as well as the sense of effort, force, and heaviness (Proske
11 & Gandevia, 2012). For instance, some authors have artificially enhanced proprioceptive inputs
12 by attaching weights to the effector limb (Toussaint et al., 2017), while others have reduced the
13 reliability of the visual feedback (Bernardo et al., 2023a, 2023b; Hewitson et al., 2018; Körding
14 & Wolpert, 2004). Bernardo et al. (2023a, 2023b) recently showed that decreasing visual
15 feedback reliability during the acquisition phase of a visuomanual task promotes motor coding,
16 as assessed with intermanual transfer tests. Although this result strongly suggests that
17 individuals resort to proprioception to overcome visual unreliability and develop an intrinsic
18 representation of the task (i.e., motor coding), the lack of a direct manipulation of the
19 proprioceptive modality prevented the authors from confirming this hypothesis.

20 As motor learning involves developing and optimizing internal representations of the
21 motor task, the processing of proprioceptive information should be essential. The involvement
22 of proprioception in sensorimotor processes has been widely referenced in research among
23 deafferented people (e.g., Cole & Katifi, 1991; Miall et al., 2018; Sarlegna et al., 2010) and in
24 studies where a temporary proprioceptive deficit has been artificially created (e.g., anesthesia:
25 Paqueron et al., 2004; short-term immobilization: Scotto et al., 2020). As an alternative to

1 reducing or suppressing proprioceptive inputs, tendon vibration can be used to induce either
2 illusory muscle lengthening or proprioceptive noise (e.g., Cordo et al., 1995; Goodman &
3 Tremblay, 2018). External mechanical vibrations applied to a single tendon increase discharges
4 of muscle spindle afferents from the vibrated muscle, and therefore create an illusory sensation
5 of lengthening (Capaday & Cooke, 1981; Goodwin et al., 1972) that can affect the movements
6 spatial outcome (Redon et al., 1991). Simultaneous stimulation of agonist/antagonist muscles
7 (e.g., biceps and triceps brachii at the same time and frequency) produces contradictory
8 activation stimuli in the muscle sensory channels, cancelling the lengthening illusion but still
9 increasing proprioceptive noise (Cordo et al., 1995; Goodman et al., 2018). This simultaneous
10 stimulation therefore offers interesting perspectives as a tool for manipulating the reliability of
11 proprioceptive inputs in motor learning.

12 To our knowledge, only one study has so far manipulated both vision and proprioception
13 reliability in a motor sequence learning task (Vidoni & Boyd, 2008). To create visual
14 unreliability, the authors gradually reduced the visibility of a cursor for 200 ms every 2 s (i.e.,
15 fading across blocks of practice). To create proprioceptive unreliability, they applied external
16 mechanical vibration to the tendons of the shoulder muscles (i.e., biceps and triceps brachii and
17 deltoids). Despite reduced visual feedback and altered proprioceptive feedback during practice,
18 participants displayed motor learning. However, several studies have shown that visual
19 unreliability alone has negative effects (Bernardo et al., 2023a, 2023b; Hewitson et al., 2018;
20 Körding & Wolpert, 2004). Additionally, the vibration had no specific effect on retention
21 performance, even when vision was unreliable, suggesting that proprioceptive feedback may
22 *not* have contributed to the learning process. However, studies have already shown that the use
23 of proprioceptive feedback is more important when vision is unreliable (e.g., Goodman &
24 Tremblay, 2018; Touzalin-Chretien et al., 2010). For Vidoni and Boyd (2008), proprioceptive
25 unreliability may have been compensated by greater attention being paid to the task in the

1 unreliable condition. Here we specifically assessed the effect of visuo-proprioceptive reliability
2 on the overall learning process, including the content of task representations (i.e.,
3 visuospatial/motor coding).

4 The purpose of the present study was to characterize the learning and sensorimotor
5 coding of a continuous arm movement toward visual targets (see Bernardo et al., 2023a, 2023b;
6 Boutin et al., 2010; Kovacs et al., 2009 for similar protocols), according to the reliability of
7 visual and proprioceptive feedback. We used a typical learning protocol featuring three
8 experimental phases: acquisition, retention, and transfer (e.g., Bernardo et al., 2023a; Boutin et
9 al., 2010; Park & Shea, 2005). During acquisition, one group practiced with reliable visual and
10 proprioceptive feedback (VrPr), a second with reliable visual and unreliable proprioceptive
11 feedback (VrPu), a third with unreliable visual and reliable proprioceptive feedback (VuPr),
12 and a fourth with unreliable visual and proprioceptive feedback (VuPu). After 24 hours, all
13 participants returned to perform the retention tests, together with visuospatial transfer (TVS)
14 and motor transfer (TM) tests with reliable feedback to test visuospatial and motor coding. In
15 these classic transfer tasks (for a review see Shea et al., 2011), participants performed the
16 sequence with their nondominant hand and either the same sequence used in acquisition (same
17 visuospatial configuration to maintain visuospatial coding; TVS) or a mirror sequence (same
18 motor configuration to maintain motor coding; TM). First, we expected a negative impact of
19 visual reliability on motor learning, with an additional effect of proprioceptive reliability with
20 regard to the dominance of vision in the visuomotor tasks (Tremblay & Proteau, 1998). We also
21 expected a greater impact of visual reliability on visuospatial coding, and a greater impact of
22 proprioceptive reliability on motor coding. In addition, we hypothesized that reliable visual
23 cues would favor *visuospatial coding* development because it involves the use of relevant
24 visuospatial coordinates (Hikosaka et al., 2002). We also hypothesized that reliable
25 proprioceptive cues would favor *motor coding* development because it involves the use of

1 muscle activation and joint angle patterns (Hikosaka et al., 2002). Finally, according to the
2 model of Hikosaka et al. (2002), participants would develop a visuospatial coding *or* a motor
3 coding. Here, we rather expected that both coding could be developed (i.e., *mixed coding*; for a
4 review, see Krakauer & Mazzoni, 2011), depending on the combination of reliable/unreliable
5 visual and proprioceptive cues (see also Bernardo et al., 2023b for experimental evidence of
6 mixed coding).

7

8 **Methods**

9 **Participants**

10 We recruited 59 students self-identified as right-handed at Poitiers University (mean age
11 \pm SD = 19.0 \pm 1.0 years; 26 women and 33 men). Participants received compensation (i.e.,
12 course credit) for taking part. Each participant signed an informed consent form prior to the
13 experiment, which was approved by the local institutional review board (GLPI #0000192).
14 Participants reported no history of neurological or sensorimotor disorders, and normal or
15 corrected-to-normal eyesight. We randomly divided the participants into four equivalent
16 groups: VrPr (7 women, 8 men; 19.0 \pm 0.3 years), VrPu (8 women, 6 men; 19.1 \pm 0.4 years), VuPr
17 (5 women, 10 men; 18.7 \pm 0.2 years) and VuPu (6 women, 9 men; mean age = 19.1 \pm 0.2 years).
18 An a priori power analysis for F tests was conducted with G*Power 3.1 (Faul et al., 2007) for
19 a power of 0.95 and an effect size of $\eta^2_p = 0.84$, based on the between participants (4 groups)
20 and within-participants (retention test and the two transfer tests) interactions in Bernardo et al.
21 (2023a). Results indicated that the inclusion of 14 participants in each group would be sufficient
22 for the tested parameters.

23 **Apparatus and Stimuli**

24 A Dell computer (Intel® Xeon® W-2123 CPU @3.60 GHz; Windows 10 professional)
25 was combined with a high-definition screen (Acer ROG PG278QR, 2560 x 1440 pixels, 165

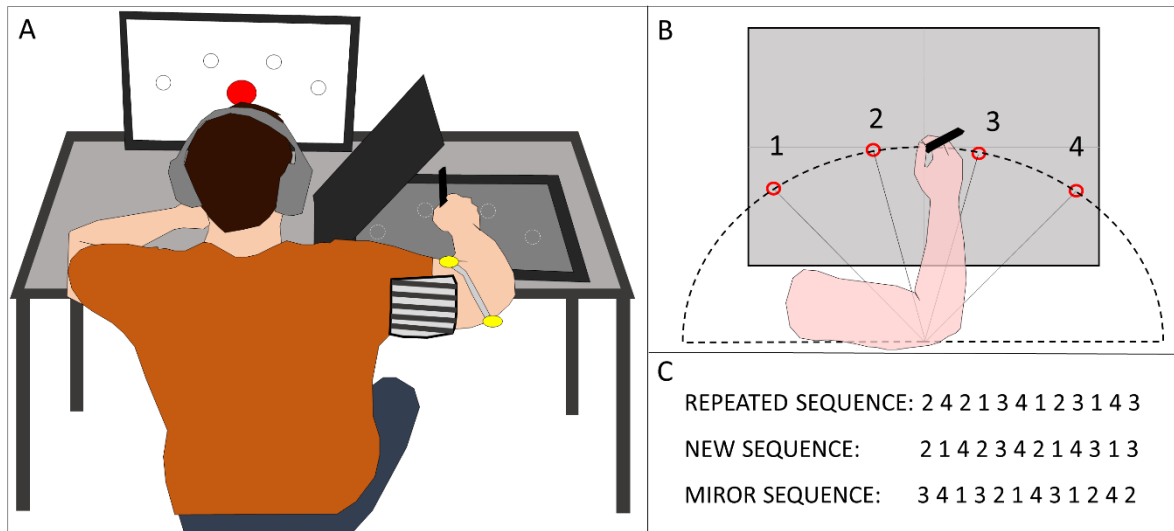
1 Hz refresh rate, NVIDIA GeForce GTX 1080 graphic card) to display the visual stimuli and
2 feedback during a task featuring a 12-target pointing sequence. Participants navigated via the
3 screen of a WACOM high-definition graphics tablet (Intuos4 XL, 1240-d version 2.0,
4 resolution: 5080 lines per inch–0.005 mm per point, sensitive area: 493 x 304 mm, 200 Hz
5 refresh rate) with a digital stylus. The cursor was only displayed on the computer screen when
6 the stylus was in contact with the tablet. The position of the stylus on the tablet was processed
7 by a custom-built application written in C++ using Qt. We used absolute mapping between the
8 tablet and screen, with a gain value of 1 (i.e., what was seen on the screen corresponded to what
9 was done on the tablet). The calibration of the tablet and screen was synchronized so that the
10 centerpoint of the tablet was the centerpoint of the computer screen. We used two types of
11 cursor to manipulate the reliability of the visual feedback (Bernardo et al., 2023a, 2023b;
12 Körding & Wolpert, 2004). The reliable visual cursor took the form of a single black dot ($\varnothing =$
13 1 mm), and the unreliable visual cursor a sparse cloud made of 25 black dots ($\varnothing = 1$ mm,
14 transparency rate = 40%, with a two-dimensional Gaussian distribution: $SD = 20$ mm). Five
15 different clouds with the same characteristics were generated, and were alternated between
16 blocks (i.e., 10 repetitions of pointing sequence), in a pseudorandom and counterbalanced order.

17 Two inertial mechanical vibrators (Techno-Concept® VB115 Vibrasens©, 40-115 Hz)
18 were attached to the right arm of each participant to generate proprioceptive noise on the biceps
19 and triceps brachii muscle spindle afferents (Fig. 1A). In order to limit adaptation (Roll &
20 Vedel, 1982), we used three different vibration frequencies (60 Hz, 70 Hz, and 80 Hz), changing
21 the vibration frequency for each block. Muscle tendons were always vibrated simultaneously
22 and at the same frequency, to minimize illusory sensations of joint rotation (Cordo et al., 1995;
23 Goodman & Tremblay, 2018). Vibrators were attached to the arm with an elastic band, to reduce
24 the propagation of the vibrations to other muscle tendons. They were fitted on all the
25 participants (i.e., including nonvibrated ones). The groups who did not receive any vibration

1 were deemed to have reliable proprioceptive feedback. To ensure that everyone received the
2 same auditory feedback, participants wore earplugs as well as soundproof headphones
3 (Sennheiser, HD 206) playing pink noise. Finally, an armrest was used to maintain the arm in
4 the standard position and reduce fatigue, and a mask was used to prevent participants from
5 looking at their right arm during the task (Fig. 1).

6 The setup was designed to restrict the pointing movement to a purely horizontal elbow
7 flexion-extension movement using the biceps and triceps brachii muscle pair. On the screen,
8 four targets ($\varnothing = 10$ mm each) were displayed equidistantly on an arc, with the center of the arc
9 located below the elbow's axis of rotation. The radius of the arc corresponded to the mean
10 length of an adult forearm (i.e., 36.4 cm for all genders; Casadei & Kiel, 2023; de Leva, 1996).
11 We used the same radius for all participants, as the difference in radius between a small and a
12 large forearm would have had only a minor impact on the target coordinates. The outlines of
13 the targets remained visible throughout the task (Fig. 1). Participants were placed in front of a
14 screen positioned at a distance of 40 cm. The desk was raised until it reached the level of the
15 xiphisternum, and the tablet was positioned in width and depth so that the center corresponded
16 to the stylus drop point with the arm in the standard experimental position (i.e., right shoulder
17 abducted at 90° , and right elbow flexed at 90° ; Fig. 1B). The arm rest and vibrators were then
18 positioned. The standard participant position and set-up organization was reproduced for the
19 second session on Day 2, with a mirror configuration for the transfer tests (i.e., TVS and TM)
20 carried out with the left arm.

21



1

2 **Figure 1. A. Set-up.** Participants sat in front of a screen with their right arm supported by an
3 armrest fixed to the desk. They pointed to visual targets using a tablet positioned on their right
4 side. The tablet was hidden by its lid. The vibrators (depicted in yellow) remained in place
5 throughout the experiment and for all groups, including the two nonvibrated groups. **B. Arm's**
6 **standard position and virtual positions of four targets.** The targets were placed on an arc
7 whose radius corresponded to the mean length of the adult forearm. Reaching toward a target
8 therefore induced a pure flexion-extension movement of the elbow. **C. Design of three**
9 **sequences of visual targets.** The repeated sequence was the one to learn, used in Blocks
10 R0-R10, RETc, RET, and TVS. The new sequence was different from the repeated sequence,
11 but had the same characteristics, and was used in Blocks N1 and N2. The mirror sequence
12 (mirror of repeated sequence) was used in Block TM.

13

14 **Task and Procedure**

15 The task consisted in making arm-pointing movements toward the active targets, which
16 were displayed in an ordered sequence. Participants were instructed to point as fast as possible
17 throughout the trials. When a target was activated (i.e., when participants had to point it), it
18 turned red. Otherwise, only its circular outline remained visible. To start a block of trials,
19 participants had to point to a red calibration target ($\varnothing = 60$ mm; see Fig. 1A), which disappeared
20 immediately afterwards. The first target then turned red and participants had to move the stylus
21 across the tablet as quickly as possible, to validate each target. They did not have to stop the
22 cursor *in* the target: they just needed to cross the circle perimeter. As soon as a target was























1 reached, the color disappeared and only the circular outline remained. The next target then
2 turned red, and so on and so forth until the 12-target sequence was completed. There were 10
3 blocks of 10 sequences (i.e., 120 successive targets). At the end of each block of the acquisition
4 session, participants were informed about their performance (i.e., block duration) and
5 encouraged to do better. This information was not provided at the end of the other blocks
6 dedicated to learning (i.e., retention and transfer tests). Between blocks, participants could take
7 a quick break before starting the next one. Participants were instructed not to lift the stylus from
8 the tablet, otherwise the cursor would disappear. During the acquisition phase (i.e., Day 1), the
9 movement time (MT) for the whole block was displayed on the screen at the end of each block,
10 so that participants could use this feedback to improve their performance on subsequent blocks.
11 Three different sequences, each composed of 12 targets (Fig. 1C), were used in the course of
12 the experiment, in accordance with Boutin et al. (2014). The *repeated sequence* (targets: 2 4 2
13 1 3 4 1 2 3 1 4 3) was the sequence to learn and was used in the acquisition phase (except for
14 Blocks N1 and N2). It had to be reproduced in the retention phase and was used for the TVS
15 test. The *new sequence* (targets: 2 1 4 2 3 4 2 1 4 3 1 3) was an unpracticed sequence with the
16 same characteristics as the repeated sequence, and was used for N1 and N2. Finally, the *mirror*
17 *sequence* (targets: 3 4 1 3 2 1 4 3 1 2 4 2) was used for the TM test (see “Procedure” subsection
18 for more details).

19 Figure 2 summarizes the experimental conditions and procedure. The experiment was
20 spread over 2 consecutive days and carried out in three phases. On Day 1, participants
21 performed the *acquisition phase*. This began with an initial block (i.e., R0) featuring the
22 repeated sequence, with reliable feedback whatever the group. This initial block was used to
23 establish participants’ baseline level and compare it with their performance in the retention
24 phase. We used the classic method of including a new sequence N (e.g., Boutin et al., 2014;
25 Park & Shea, 2005) to differentiate between the general improvement (i.e., generalization of

1 practice) and sequence-specific practice (for a review, see Abrahamce et al., 2010). Participants
2 therefore performed a block with the new sequence (N1) before starting the 10 training blocks
3 featuring the repeated sequence (i.e., Blocks R1-R10), where they were exposed to sensory
4 feedback consistent with their group. After the fifth block, participants took a 10-minute break,
5 when they could remove the vibrators and rest their arm. After the 10th block, they performed
6 a block with the new sequence (N2). The *retention* and *transfer* phases took place 24 hours after
7 the acquisition phase, and were used to assess the persistence and transfer of learning (e.g.,
8 (Blandin et al., 2008; Dean et al., 2008; Lai & Shea, 1998; Panzer et al., 2009; for a similar
9 procedure). Contrary to the acquisition session which refers to practice performance that might
10 vanish over time, this procedure refers to longer-term modifications (see Soderstrom & Bjork,
11 2015).

12 One retention block was performed with reliable visual and proprioceptive feedback (i.e.,
13 retention control, RETc), and another in the feedback condition used during the acquisition
14 phase (i.e., retention, RET). Both retention blocks featured the repeated sequence. The RETc
15 block served to compare learning performances between groups, while the RET block served
16 to ascertain whether the performance observed in the acquisition phase was maintained. Finally,
17 all participants performed two intermanual transfer tests with reliable visual and proprioceptive
18 feedback, and holding the stylus in their left hand, to judge the generalization of learning
19 (Boutin et al., 2010, 2012, 2014; Kovacs et al., 2009; Park & Shea, 2005). More specifically,
20 these transfer tests were used to measure the extent to which the repeated sequence had been
21 stored and coded. The TVS test featured the repeated sequence, while the TM test featured the
22 mirror sequence (Fig. 1C). The order of presentation of the two retention blocks, as well as the
23 two transfer blocks, was counterbalanced within each group.

24

| | Blocks | DAY 1 | | | | DAY 2 | | | |
|------------------|-------------------------------|---|-------------------|---|-------------------|---|-------------------|---|---|
| | | Acquisition phase | | | | Retention phase | | Transfer phase | |
| | | R0 | N1 | R1 to R10 | N2 | RET | RETc | TVS | TM |
| Type of sequence | Repeated sequence | New sequence | Repeated sequence | New sequence | Repeated sequence | Repeated sequence | Repeated sequence | Mirror sequence | |
| GROUPS | V _R P _R | | |   | | | | | |
| | V _R P _U |   | |   | |   | |   |   |
| | V _U P _R | | |   | | | | | |
| | V _U P _U | | |   | |   | |   |   |

1

2 **Figure 2. Experimental groups and procedure.** Four groups performed the experiment on
3 two consecutive days with different combinations of reliable and unreliable visual and
4 proprioceptive feedback. Reliable vision: single dot cursor. Unreliable vision: cloud of 25
5 sparse dots. Reliable proprioception: no vibration (NV). Unreliable proprioception: arm tendon
6 vibration. A blue frame indicates reliable cues, and an orange frame indicates unreliable cues.
7 VrPr: reliable vision–reliable proprioception; VrPu: reliable vision–unreliable proprioception;
8 VuPr: unreliable vision–reliable proprioception; VuPu: unreliable vision–unreliable
9 proprioception. Day 1. Acquisition phase. R0: initial block with repeated sequence and reliable
10 feedback for all groups. N1: pretest block with new sequence. R1-R10: training blocks with
11 repeated sequence. N2: posttest block with new sequence. Day 2. Retention phase. RET:
12 retention block with repeated sequence. RETc: retention block with repeated sequence and
13 reliable feedback for all groups. Transfer phase. TVS: visuospatial transfer block with repeated
14 sequence, reliable feedback, and left hand. TM: motor transfer block with mirror sequence,
15 reliable feedback, and left hand.

16

17 Data Processing

18 We used MATLAB (version r2020b; Mathworks, Natick, MA) to process the data.
19 Position data from the tablet were low-pass filtered with a dual-pass, no-lag Butterworth filter
20 (cutoff frequency: 10 Hz; order: 2). These data were used to compute MT per target in each
21 block. MT corresponded to the mean time (in ms) between the validation of the first and 12th

1 targets in the sequence (i.e., 11 pointing movements). Outlier values (median \pm 2.5 *SDs*) were
2 removed from the analysis (Leys et al., 2013). These represented 2.7% of the data.

3 **Statistics**

4 We used JASP version 0.14.1 to run planned comparisons on MT according to our
5 hypotheses (indicated in each Results subsection) as well as mixed analysis of variance
6 (ANOVA) on the acquisition blocks to describe the learning process. The level of significance
7 was set at .05, and the effect size was reported for all significant effects (partial eta-squared,
8 η^2_p for ANOVA and Cohen's *d* value for planned comparison). When necessary, we applied
9 the Greenhouse-Geisser correction, and reported the corrected degree of freedom. The Shapiro–
10 Wilk test was used to assess normality hypothesis which was respected in all analyses.

11 **Transparency and Openness**

12 We reported all data exclusions, all manipulations, and all measures in the study (see
13 “Data processing” subsection), and followed JARS (Kazak, 2018). All data, together with the
14 MATLAB code, are available at [<https://osf.io/qvxpz/>]. The study design and data analysis were
15 not preregistered.

16

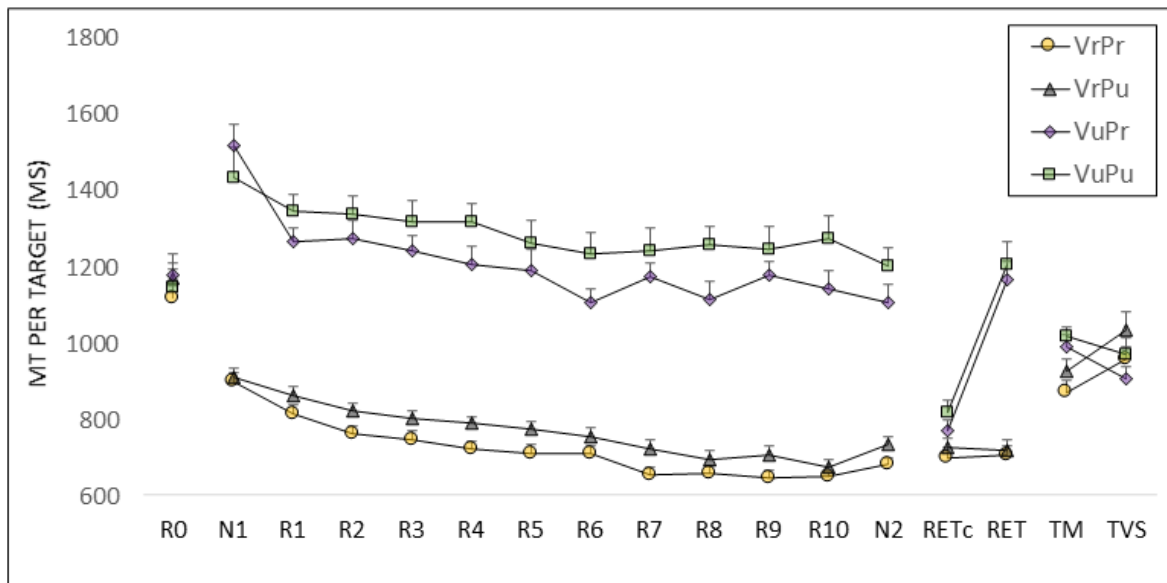
17 **Results**

18 **Effect of Feedback Reliability on Acquisition Performance**

19 Fig 3 depicts MT per target in each of the three phases of the experiment (i.e.,
20 acquisition, retention, and transfer) for each of the four groups (i.e., VrPr, VrPu, VuPr, and
21 VuPu). At R0, the performance appeared similar across groups as the ANOVA 4 (Group: VrPr,
22 VrPu, VuPr, VuPu) failed to reach significance $F(3,47) = 0.4, p = .77$. When the acquisition
23 phase began (i.e., R1), the performance of participant groups varied, depending on the feedback
24 reliability. MT was higher for VuPr and VuPu (Fig 3) than for VrPr and VrPu (Fig 3). By
25 contrast, all groups showed a MT reduction over practice (i.e., R1-R10). These observations
26 were statistically confirmed through a 4 (Group: VrPr, VrPu, VuPr, VuPu) x 10 (Block:
27 R1-R10) two-way mixed ANOVA. Analysis revealed main effects of both *Group*, $F(3,51) =$

1 88.8, $p < .001$, $\eta^2p = .84$, and *Block*, $F(9,459) = 30.9$, $p < .001$, $\eta^2p = .38$, and no *Block x Group*
 2 interaction, $F(27,459) = 1.2$, $p = .21$. MT per target therefore decreased across the successive
 3 blocks (e.g., $R_{10} < R_1$, $p < .001$). In addition, VuPr and VuPu differed from VrPr and VuPu (p
 4 $< .001$ for the four comparisons).

5



6

7 Figure 3. Movement time (MT) per target in the acquisition, retention and transfer phases.
 8 R0-R10: repeated blocks; N1 and N2: new blocks; RET: retention with group feedback; RETc:
 9 retention with reliable (control) feedback; TM: motor transfer; TVS: visuospatial transfer; VrPr:
 10 reliable vision–reliable proprioception; VrPu: reliable vision–unreliable proprioception; VuPr:
 11 unreliable vision–reliable proprioception; VuPu: unreliable vision–unreliable proprioception.
 12 Error bars denote standard error. Contrast analyzes indicated that VrPr and VrPu $<$ VuPr and
 13 VuPu ($p < .001$), VrPr $<$ VuPr ($p < .001$), and VrPu $<$ VuPu ($p < .001$).

14

15 Sequence-Specific Practice

16 To test participants' sequence-specific practice, we calculated a rate of change between
 17 the last acquisition block featuring the repeated sequence (i.e., R10) and the new sequence (i.e.,
 18 N2): $[MT \text{ for } R_{10} - MT \text{ for } N_2] / N_2$ (Fig. 4). A negative value would indicate better
 19 performance (i.e., shorter MT) for the repeated sequence after acquisition (i.e., R10) compared
 20 with the new, unpracticed sequence (i.e., N2). We predicted that groups that received reliable

1 visual feedback (i.e., VrPr and VrPu) would exhibit better sequence-specific practice than
2 groups that received unreliable visual feedback (i.e., VuPr and VuPu), in line with previous
3 studies (Bernardo et al., 2023a, 2023b). The planned comparison on the mean of reliable versus
4 unreliable visual groups confirmed our hypothesis, $b = -0.23$, $t(51) = -4.61$, $p < .001$, $d = 1.07$.
5 More specifically, sequence-specific practice was statistically better for VrPr than for VuPr, b
6 $= 0.09$, $t(51) = 2.51$, $p < .05$, $d = 0.92$, and better for VrPu than for VuPu, $b = 0.14$, $t(51) = 4.00$,
7 $p < .001$, $d = 1.19$. By contrast, no difference emerged between the groups that received reliable
8 proprioception (VrPr and VuPr) versus unreliable proprioception (VrPu and VuPr), $b = 0.003$,
9 $t(51) = 0.06$, $p = .96$. In addition, no differences were detected between VrPr and VrPu, $b =$
10 0.03 , $t(51) = 0.81$, $p = .42$, and between VuPr and VuPu, $b = 0.03$, $t(51) = 0.74$, $p = .46$.

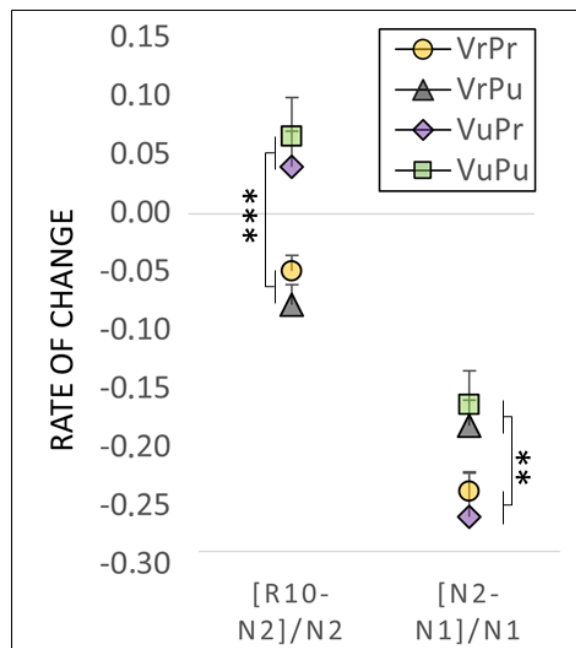
11 We also assessed whether the rates of change were statistically different from zero
12 through one-sample t tests. The results of these tests indicated significant differences from 0 for
13 VrPr, $t(13) = -3.73$, $p < .01$, $d = 1.02$, and VrPu, $t(12) = -4.56$, $p < .001$, $d = 1.31$. Rates of
14 change were not however, statistically different from 0 for VuPu, $t(13) = 1.98$, $p = 0.07$, and
15 VuPr, $t(13) = 1.28$, $p = .22$. Thus, only the groups that received reliable visual feedback
16 exhibited sequence-specific practice.

17 **Generalized Practice Effect**

18 We also expected to observe a generalized practice effect (i.e., MT reduction partly due
19 to practice per se), and therefore calculated a rate of change between N2 and N1 (i.e., $[MT \text{ for}$
20 $N2 - MT \text{ for } N1] / N1$; Fig 4). A negative value would indicate a generalized practice effect,
21 with better performance on N2 than on N1. We predicted that groups that received reliable
22 proprioceptive feedback (i.e., VrPr and VuPr) would display a generalized practice effect,
23 compared with groups that received unreliable proprioceptive feedback (i.e., VrPu and VuPu),
24 owing to sensorimotor difficulty induced by the vibrators. The planned comparisons showed
25 that groups that received reliable proprioceptive feedback (mean of VrPr and VuPr) exhibited

1 a greater generalized practice effect than groups that received unreliable proprioceptive
 2 feedback (mean of VrPu and VuPr), $b = -0.15$, $t(52) = -2.80$, $p < .01$, $d = 0.72$. More specifically,
 3 VuPr exhibited a greater generalized practice effect than VuPu, $b = 0.10$, $t(52) = 2.51$, $p < .05$,
 4 $d = 0.74$, but this difference disappeared when the visual feedback was reliable, such that VrPr
 5 did not differ from VrPu, $b = 0.06$, $t(52) = 1.46$, $p = .15$. No differences were observed between
 6 groups with reliable versus unreliable visual feedback: $b = -0.003$, $t(52) = -0.06$, $p = .95$ for
 7 VrPr and VrPu versus VuPr and VuPu; $b = -0.02$, $t(52) = -0.58$, $p = .57$ for VrPr versus VuPr;
 8 and $b = 0.02$, $t(52) = 0.47$, $p = .64$ for VrPu versus VuPu.

9 We also compared the rates of change relative to 0 with one-sample t tests. Results
 10 indicated a generalized practice effect for all groups: VrPu, $t(12) = -8.38$, $p < .001$, $d = 2.21$;
 11 VuPu, $t(13) = -5.73$, $p < .001$, $d = 1.59$; VuPr, $t(13) = -6.91$, $p < .001$, $d = 1.91$; and VrPr, $t(14)$
 12 $= -14.38$, $p < .001$, $d = 2.12$. Overall, a generalized practice effect appeared for all groups, and
 13 even more for groups that received reliable proprioceptive feedback.



14

1 Figure 4. Rates of change for R10 compared with N2, and for N2 compared with N1. $[R10 -$
2 $N2] / N2$ corresponds to $[MT \text{ for } R10 - MT \text{ for } N2] / MT \text{ for } N2$. $[N2 - N1] / N1$ corresponds
3 to $[MT \text{ for } N2 - MT \text{ for } N1] / MT \text{ for } N1$. VrPu: reliable vision–unreliable proprioception;
4 VuPu: unreliable vision–unreliable proprioception; VuPr: unreliable vision–reliable
5 proprioception; VrPr: reliable vision–reliable proprioception. Error bars denote standard error.
6 ** $p < .01$, *** $p < .001$

8 Retention

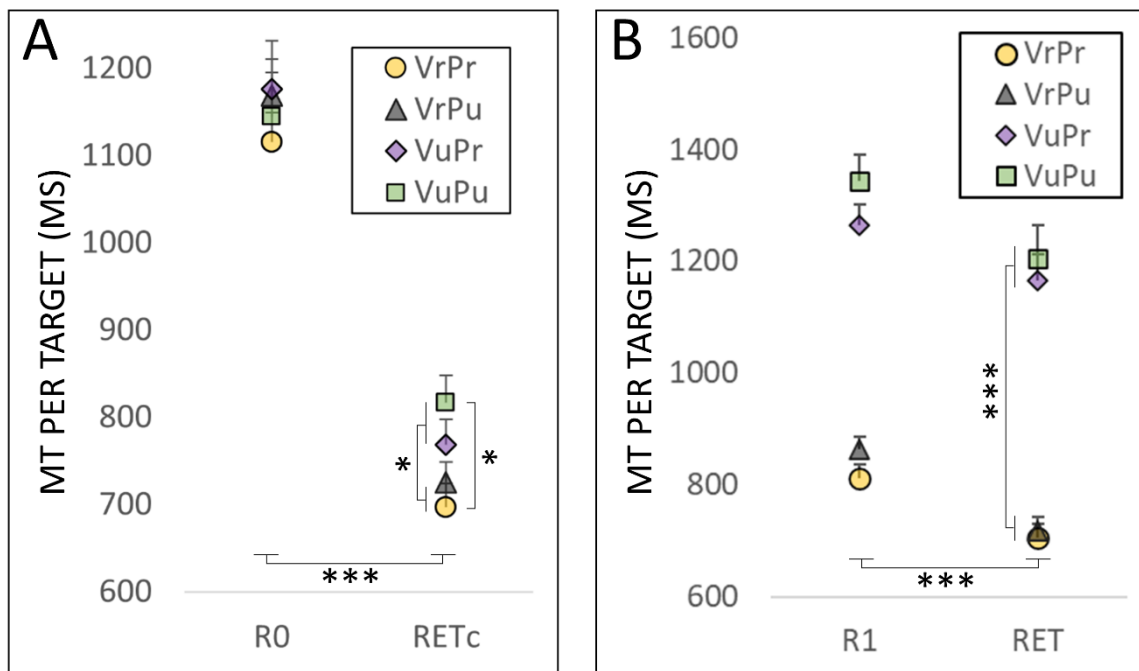
9 With our experimental design, retention can be assessed in two complementary ways by
10 comparing the groups' performances i) with control feedbacks (i.e., reliable visual and
11 proprioceptive feedback), and ii) with acquisition feedbacks (i.e., depending of the group). For
12 the first comparison (R0 vs. RETc; Fig. 5A), we conducted the planned comparisons in line
13 with our hypothesis predicting that MT would be longer at the start of the acquisition phase
14 (i.e., R0) than in the retention phase (i.e., RETc) for all participants. The planned comparison
15 confirmed our hypothesis, $b = -4664.71$, $t(584.61) = -62.62$, $p < .001$, $d = 1.62$. More
16 importantly, we predicted that the two groups that received reliable visual feedback (VrPr and
17 VrPu) would exhibit better retention than the two groups that received unreliable visual
18 feedback (VuPu and VuPr). This was confirmed by the planned comparison on the mean of
19 reliable versus unreliable visual groups, $b = 151.46$, $t(84.26) = 2.02$, $p < .05$, $d = 0.24$. The
20 comparison between VuPr and VrPr was not significant, $b = 71.18$, $t(84.26) = 1.40$, $p = .16$, and
21 nor was that between VuPu and VrPu, $b = 80.28$, $t(84.26) = 1.46$, $p = .15$. No specific difference
22 was detected between groups, except that VrPr exhibited better retention than VuPu: $b = 108.35$,
23 $t(84.26) = 1.97$, $p < .05$, $d = 0.65$. Thus, the groups that received reliable visual and
24 proprioceptive feedback exhibited better retention.

25 For the second comparison (R1 vs. RET, see Fig.5B), we predicted longer MT at the
26 onset of the acquisition phase (i.e., R1) than in the retention phase (i.e., RET) for all participants.
27 The planned comparison confirmed our hypothesis, $b = 537.6$, $t(584.61) = 7.58$, $p < .001$, $d =$

1 1.52. Furthermore, we predicted that the two groups that received reliable visual feedback (VrPr
 2 and VrPu) would exhibit better retention than the two groups that received unreliable visual
 3 feedback (VuPu and VuPr). This prediction was confirmed by the planned comparison on the
 4 mean of reliable versus unreliable visual groups, $b = 897.9$, $t(82.4) = 12.2$, $p < .001$, $d = 0.36$.
 5 As each group started with different performance at R1 due to different feedbacks reliability,
 6 we computed the rate of change between R1 and RET (RET-R1/R1). Planned comparisons
 7 between groups did not reveal any significant difference ($ps > .05$): all groups appeared to learn
 8 equally despite a different initial level of performance at the start of the acquisition (i.e., R1).

9 Overall, the analyzes indicated that all the groups displayed significant learning from
 10 the beginning of practice (R0 or R1) to retention (RETC or RET). In addition, the groups that
 11 received reliable visual and proprioceptive feedback exhibited better retention in the control
 12 condition (R0-RETC).

13
 14



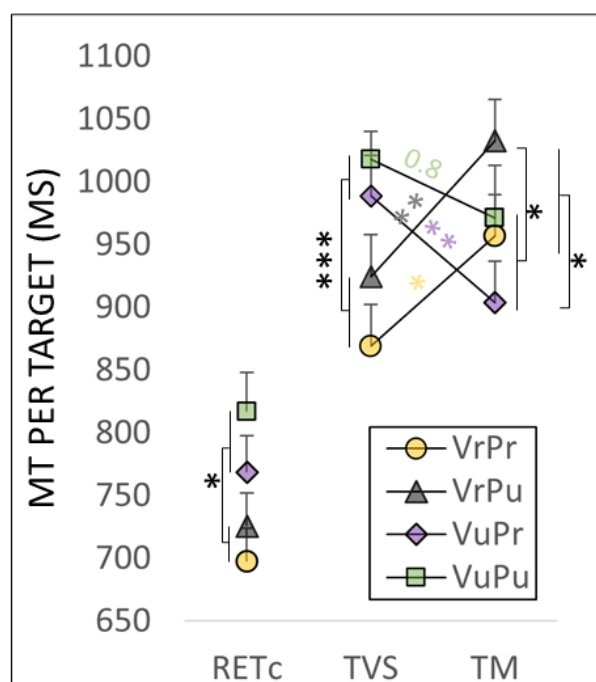
15

1 Figure 5. Movement time (MT) per target indicating the learning effect (retention) **A**) with
 2 control feedbacks (i.e., reliable vision and reliable proprioception; R0-RETc) and **B**) with the
 3 acquisition feedbacks (i.e., R1-RET). **A**) R0: initial repeated block; RETc: retention with
 4 control feedback; **B**) R1: initial acquisition block with the group's feedback conditions RET:
 5 retention with the group's feedback conditions. VrPr: reliable vision–reliable proprioception;
 6 VrPu: reliable vision–unreliable proprioception; VuPr: unreliable vision–reliable
 7 proprioception; VuPu: unreliable vision–unreliable proprioception. These blocks were
 8 performed with control (i.e., reliable) feedback. Error bars denote standard error. * $p < .05$, ***
 9 $p < .001$.

10

11 Sensorimotor Coding

12 We assessed the nature of the coding following practice by analyzing performances on
 13 the TVS and TM tests. The retention block was used specifically to compare the efficiency of
 14 coding (Boutin et al., 2010, 2014; Park & Shea, 2005). We ran planned comparisons to
 15 characterize the coding according to our hypotheses (Fig. 6). The planned comparison between
 16 the transfer (i.e., TVS and TM) and retention (i.e., RETc) tests indicated shorter MT for RETc
 17 than for TVS and TM, $b = 1638.63$, $t(98) = 15.30$, $p < .001$, $d = 0.85$. The following analyses
 18 specifically assessed the influence of feedback reliability on the two intermanual transfer tests
 19 involving visuospatial versus motor coding.



20

1 Figure 6. Movement time (MT) per target for the four groups for transfer versus retention.
2 RETc: retention with reliable (control) feedback; TVS: visuospatial transfer; TM: motor
3 transfer; VrPr: reliable vision–reliable proprioception; VrPu: reliable vision-unreliable
4 proprioception; VuPr: unreliable vision–reliable proprioception; VuPu: unreliable vision–
5 unreliable proprioception. TVS was performed with the left hand and the repeated sequence.
6 TM was performed with the left hand and the mirror sequence (see Fig. 1). Both blocks were
7 performed with reliable feedback. Error bars denote standard error. * $p < .05$. ** $p < .01$. *** p
8 $< .001$

9
10 To test our prediction that the modality of reliable feedback (i.e., visual or
11 proprioceptive) would have an effect on TVS, we conducted planned between-group
12 comparisons. As expected, MT was longer for groups with unreliable vision than for groups
13 with reliable vision (i.e., mean of reliable versus unreliable visual groups differed) $b = 225.42$,
14 $t(88.1) = 3.35$, $p < .001$, $d = 0.85$. More specifically, MT was longer for VuPr than for VrPr, b
15 $= 121.36$, $t(88.1) = 2.64$, $p < .05$, $d = 0.92$, and longer for VuPu than for VrPu, $b = 104.07$,
16 $t(88.1) = 2.12$, $p < .05$, $d = 0.83$. No differences were found between groups with unreliable
17 proprioception versus groups with reliable proprioception, $b = 96.42$, $t(88.1) = 1.43$, $p = .16$.
18 Nor were differences observed between VrPr and VrPu, $b = 56.86$, $t(88.1) = 1.24$, $p = .22$, and
19 between VuPr and VuPu, $b = 39.57$, $t(88.1) = 0.81$, $p = .42$.

20 When we ran the same analyses on TM performance, no differences emerged regarding
21 visual reliability (VrPr and VrPu vs. VuPr and VuPu; VuPr vs. VrPr, and VuPu vs. VrPu).
22 Regarding proprioceptive reliability, comparisons revealed a difference between VrPr and VuPr
23 versus VrPu and VuPu, $b = 139.10$, $t(88.1) = 2.07$, $p < .05$, $d = 0.48$. Interestingly, analyses
24 revealed a longer MT for VrPu than for the other groups, $b = -269.61$, $t(88.1) = -2.36$, $p < .05$,
25 $d = 0.59$, and a shorter MT for VuPr than for the other groups, $b = 258.68$, $t(88.1) = 2.27$, $p <$
26 $.05$, $d = 0.55$. Reliable visual feedback associated with unreliable proprioceptive feedback
27 constituted the worst condition for TM, while unreliable visual feedback associated with
28 reliable proprioceptive feedback constituted the best condition. Finally, no differences were

1 detected between VrPr and VrPu, $b = 72.29$, $t(88,1) = 1.57$, $p = .12$, and between VuPr and
2 VuPu, $b = 66.82$, $t(88,1) = 1.36$, $p = .18$.

3 In addition, we ran planned within-group comparisons to observe the general coding
4 patterns according to feedback reliability. Results revealed shorter MT for TVS than for TM in
5 VrPr, $b = 93.07$, $t(98) = 3.11$, $p < .01$, $d = 0.67$, and VrPu, $b = 108.50$, $t(98) = 3.63$, $p < .001$, d
6 $= 0.69$. They also revealed shorter MT for TM than for TVS in VuPr, $b = -88.07$, $t(98) = -2.95$,
7 $p < .01$, $d = 0.38$, and a trend toward a shorter MT for TM than for TVS in VuPu, $b = -60.82$,
8 $t(98) = -1.80$, $p = .075$, $d = 0.67$. These within-group comparisons suggested that MT was lower
9 for TM than for TVS when the proprioceptive feedback was unreliable, with the opposite being
10 the case when the visual feedback was unreliable.

11 **Discussion**

12 The main objective of the present study was to characterize the learning and
13 sensorimotor coding of a continuous arm movement according to the reliability of visual and
14 proprioceptive feedback. Both acquisition performance (R10) and sequence-specific practice
15 were found to depend solely on visual feedback reliability. Retention, by contrast, depended on
16 the reliability on both vision and proprioception: the more reliable these two sensory sources,
17 the stronger the retention. Interestingly, results for coding differed from learning, because MT
18 varied according to a combination between visual and proprioceptive reliability. For TVS, the
19 two groups that received unreliable visual feedback (VuPu and VuPr) performed more poorly
20 than the two groups that received reliable visual feedback (VrPr and VrPu). For TM, the
21 optimum sensory combination was reliable proprioception associated with unreliable vision
22 (VuPr), and the least propitious combination was unreliable proprioception associated with
23 reliable vision (VrPu). These results are discussed relative to the learning processes (i.e., from
24 training to generalization).

25

1 *Vision dominates during acquisition but proprioception matters in retention*

2 We observed that reliable visual feedback and reliable proprioceptive feedback affected
3 the various aspects of learning in different ways. The degree of visual reliability was decisive,
4 as only reliable visual feedback permitted to increase sequence-specific practice: the rate of
5 change between the final training block (R10) and the new block (N₂) was higher when vision
6 was reliable, regardless of proprioceptive reliability (see Figure 4). Several studies have already
7 shown that unreliable visual feedback impairs sequence-specific practice (Bernardo et al.,
8 2023a, 2023b; Hewitson et al., 2018; Körding & Wolpert, 2004), the present results further
9 show that the reliability of proprioceptive feedback does not modify this effect. We could
10 conclude that individuals do not lend as much weight to proprioception as they do to vision, as
11 visuomotor learning tasks are mainly driven by visual cues (for reviews, see Krakauer et al.,
12 2019; Sigrist et al., 2013), especially when the visual information is reliable (e.g., Adams, 1977;
13 Ernst & Banks, 2002; Ernst & Bühlhoff, 2004). In the present study, the relative visual
14 dominance we observed for sequence-specific practice concerned the whole acquisition phase
15 (i.e., training blocks R1-R10) as well as the two new blocks (N1 and N2; generalized practice
16 effect), where MT depended mainly on visual reliability. One may argue that the noise induced
17 by the vibrations of agonist/antagonist muscles was not sufficient to alter proprioception,
18 potentially due to the partial adaptation of muscle spindles to the constant vibration within the
19 block duration (i.e., mean block duration = 106.0 ± 0.1 s). This adaptation typically begins
20 within seconds and can lead to a significant reduction in spindle response after several minutes
21 of continuous stimulation (Hagbarth & Eklund, 1966).

22 However, several results of the present study demonstrated that the unreliability of
23 proprioception due to vibrations induced performance changes, notably in the long-term, that
24 suggested a latent learning (see Soderstrom & Bjork, 2015). Previous studies already showed a
25 short-term impact of agonist/antagonist vibration on force production (Bock et al., 2005),

1 postural control (Vuillerme et al., 2002), adaptation to mechanical distortions (Pipereit et al.,
2 2006), as well as limb matching task (Bock et al., 2007). Besides, proprioception can even
3 dominate in visuomotor tasks, notably when the visual feedback about the hand (or the cursor)
4 is not available and/or biased (Block & Sexton, 2020; Liu et al., 2018; Mon-Williams et al.,
5 1997; van Beers et al., 1996, 1999, 2002; Wali et al., 2023). Therefore, matching the position
6 of a visual target conveyed more errors than a proprioceptive target without visual feedback of
7 the hand.

8 Interestingly, here we showed that proprioception impacted long-term performance: the
9 best delayed retention (+ 24 hours) performances were observed when both modalities were
10 reliable (i.e., VrPr) and the worst performances when both were unreliable (i.e., VuPu).
11 Contrary to Vidoni and Boyd (2008), our results showed that visual reliability and
12 proprioceptive reliability both have a significant impact on motor learning. Moreover,
13 proprioceptive reliability was essential both to optimize retention performance (i.e., when
14 vision was reliable) and to avoid the significant deterioration in learning observed when both
15 modalities were unreliable. The motor aspects of a task are better integrated by learners after a
16 rest phase (Cuppone et al., 2018). We can assume that reliable proprioceptive feedback
17 available during the acquisition phase allows for better consolidation and retrieval of the motor
18 sequence. This hypothesis is supported by the role of proprioception during the acquisition
19 phase on the generalized practice effect observable through the rate of change between the new
20 block prior to training (N1) and the new block after training (N2). The vibrated groups (i.e.,
21 VrPu and VuPu) familiarized themselves less quickly with the parameters of the task than the
22 nonvibrated groups (i.e., VrPr and VuPr). In other words, visuomotor adaptation was even more
23 difficult with unreliable proprioception than with unreliable vision. This result is in line with
24 studies of visuomotor adaptation to prisms, which have revealed faster proprioceptive and
25 motor adaptation relative to visual adaptation (e.g., Hay & Pick, 1966; for a review, see Redding

1 et al., 2005). Modification of limb position sense and muscle patterns involved in the
2 task -mainly based on proprioception- preceded apparent visual changes in effector position
3 relative to the target. Proprioceptive calibration would also be more robust as recently shown
4 by Wali et al. (2023) who investigated the retention of visual and proprioceptive recalibration
5 in response to a visuomotor mismatch. After 24 hours of delay, participants exhibited offline
6 gains in proprioceptive recalibration while they forget visual recalibration. Taken together, our
7 results revealed that the combination of reliable or unreliable visual and proprioceptive
8 feedback has a decisive impact on the generalized practice effect, sequence-specific practice,
9 and retention.

10

11 *Specific influence of visual and proprioceptive reliability for learning generalization*

12 Learning generalization was assessed through transfer tests performed with the left
13 hand. The two groups that received reliable visual feedback (i.e., VrPr and VrPu) performed
14 better on the TVS test than the two groups that received unreliable visual feedback, regardless
15 of proprioceptive reliability. This development of visuospatial coding had previously been
16 observed with reliable visual and proprioceptive feedback (Bernardo et al., 2023a, 2023b;
17 Robin et al., 2004; Toussaint et al., 2017). Therefore, when the visual information is reliable,
18 the beneficial impact on visuospatial stems from the acquisition itself (see subsection below):
19 the central nervous system stores and develops the repertoire of extrinsic representations so that
20 the learning becomes specific to the visual modality. This result is in line with the specificity
21 of practice hypothesis (Tremblay & Proteau, 1998). The development of extrinsic
22 representations (i.e., visuospatial coding) for reliable visual information is often accompanied
23 by the underdevelopment of intrinsic representations (i.e., motor coding), as resources are
24 concentrated on the dominant modality (Bernardo et al., 2023a, 2023b; Boutin et al., 2010,
25 2012; Kovacs et al., 2009). Furthermore, in the present study, the unreliability of the

1 proprioceptive feedback owing to the vibrations had no effect, probably because this type of
2 sensory information is not primarily used to construct extrinsic representations.

3 The reliability of the visual feedback also affected motor coding, as we observed better
4 performance for TM than for TVS in the two groups with unreliable vision. Here, the
5 unreliability of the visual feedback favored the development of intrinsic representations (i.e.,
6 motor coding), suggesting that proprioception played a major role in this process. The most
7 important contribution of the present study is that it provides tangible evidence of the role of
8 proprioceptive inputs in sensorimotor coding. We observed that the development of motor
9 coding depended on the combination of visual *and* proprioceptive reliability, with the optimum
10 combination being reliable proprioception and unreliable vision (VuPr). The opposite
11 combination (i.e., unreliable proprioception and reliable vision, VrPu), had a negative impact
12 on motor coding. These results provide evidence of differential activations in visual and
13 somatosensory areas based on sensory cue reliability: enhanced activation was observed in
14 regions associated with reliable cues compared to unreliable ones (Mizelle et al., 2016).
15 Specifically, enhanced activation of the cerebelloparieto-frontal network was found with
16 reduced visual reliability and increased occipital activation was found with reduced
17 somatosensory reliability. Proprioception has been described as essential for transforming the
18 planned kinematics of reaching movements (mainly defined through vision) into motor
19 commands (for a review, see Sarlegna & Sainburg, 2009). Proprioception is also used to update
20 the internal model of the arm relative to the environment, according to Sainburg et al. (1995),
21 who conducted studies of proprioceptive deprivation among deafferented patients and normal
22 individuals with short-term arm immobilization. We can therefore assume that in the present
23 study, the tendon vibration that reduced the reliability of proprioceptive cues prevented the
24 central nervous system from updating the internal model of the arm, and consequently inhibited
25 the development of intrinsic representations (i.e., motor coding). The group that received

1 reliable visual feedback (i.e., VrPu) tended to develop extrinsic representations (i.e.,
2 visuospatial). We can make the opposite assumption for VuPr (i.e., unreliable vision and
3 reliable proprioception), namely that motor coding was promoted rather than visuospatial
4 coding. The optimized development of motor coding in the VuPr group highlighted an
5 important issue in the literature: visual dominance in visuomotor tasks.

6 *Limitations*

7 Despite the significant findings of the present study, several limitations should be
8 acknowledged to provide a more comprehensive understanding of the results and guide future
9 research. One limitation is that sensory reliability is graded rather than binary. For instance,
10 increasing the blur of the visual cursor further decreases reliability and affects learning
11 (Bernardo et al., 2023a). Varying the level of each sensory modality in future research would
12 allow a broader comprehension of the learning processes as reliability is not “on/off”. In
13 addition, while we used blurred visual stimuli that have been previously tested (e.g., Bernardo
14 et al., 2023a, 2023b; Hewitson et al., 2018; Körding & Wolpert, 2004) and blurred
15 proprioceptive stimuli through vibrations (e.g., Cordo et al., 1995; Goodman et al., 2018), it is
16 difficult to assess the relative correspondence between each sensory level of noise. Up to now,
17 it is unclear whether the amount of visual unreliability in the tasks is equivalent to the one
18 introduced to proprioception. Further research may integrate or compare other paradigms
19 affecting proprioceptive reliability, such as arm immobilization (e.g., Meugnot & Toussaint,
20 2015; Scotto et al., 2020), cold application (e.g., Heus et al., 1995; Scotto et al., 2024) or the
21 involvement of deafferented patient (e.g. Cole & Paillard, 1995; Miall et al., 2018). Finally, the
22 study should be replicated with a broader age population, from young to older adults, to improve
23 the generalizability of the findings.

24

1 **Conclusion**

2 To reduce reliance on visual feedback in learning a visuomotor task, it is important to
3 develop both visuospatial and motor coding (i.e., *mixed coding*; for a review, see Krakauer &
4 Mazzoni, 2011). Like a virtuous circle, this mixed coding feeds and maintains a larger repertoire
5 of sensorimotor representations that in turn allow individuals to switch between coding systems,
6 depending on task demands (Ghafouri et al., 2002). An important finding is that the sensory
7 conditions that favored motor coding (i.e., unreliable vision, reliable proprioception) were not
8 the same as the sensory conditions that favored retention (i.e., reliable vision, reliable
9 proprioception). They were also different from the sensory conditions that favored visuospatial
10 coding (i.e., reliable vision, regardless of proprioceptive reliability). Varying the reliability of
11 these two sensory sources during the acquisition phase may be the best compromise when it
12 comes to preserving retention and generalization, as Bernardo et al. (2023b) recently showed
13 that providing first reliable visual feedback then unreliable feedback during acquisition favors
14 both retention and transfer.

15

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- 13
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1 **Compliance with Ethical Standards**

2 No funding was received for conducting this study. No conflicts of interest, financial or
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4 (no. 201965) with the ethical standards laid down in the 1964 Declaration of Helsinki and its
5 later amendments. All participants gave written informed consent prior to the study.

6

7 **Author Contributions**

8 C.S. and Y.B. conceived and designed the research; C.S., M.B., G.C. and R.T. set up
9 the experiment; M.B. performed the experiments; C.S., M.B., and Y.B. analyzed the data; C.S.
10 interpreted the results of the experiments; C.S. and M.B. prepared the figures; C.S. and M.B.
11 drafted the manuscript; C.S., Y.B. and R.T. edited and revised the manuscript.

12

13 **Data transparency**

14 Dataset, code, and methods are available at <https://osf.io/xknh4/>.

15