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Visual awareness of stimulus features shapes motor control through action end-state comfort

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Within the dorsal stream account of visuomotor control, the role of visual awareness in guiding action remains controversial. We argue that addressing this question requires considering how action demands influence the processing of task-relevant visual information. Accordingly, we conducted two experiments in which participants performed a reaching movement to match their hand orientation to that of a briefly presented Gabor patch. Action biomechanical demands were modulated by varying the end-state comfort of hand rotations (i.e., amplitudes and directions). Experiment 1 tested clockwise rotations at small and large amplitudes, whereas Experiment 2 included both clockwise and counterclockwise rotations, each at two amplitudes. Visual awareness was manipulated by presenting Gabor orientations at the perceptual threshold, enabling comparisons of performance between aware and unaware trials. We analysed three parameters indexing distinct aspects of the action's underlying processes: hand rotation accuracy, rotation onset, and rotation smoothness. We found that visual information not consciously available could partially guide movement selection, but only when the movement was comfortable. Conversely, visual awareness was critical for uncomfortable movements, as performance dropped substantially when orientations were not consciously perceived. In addition, visual awareness produced different effects across phases of movement control: facilitated movement preparation (higher accuracy, earlier onset) but restrained execution (reduced smoothness). Our findings offer new insights into perception–action coupling and help clarify conflicting results in the literature concerning the role of visual awareness in motor control: whether visual awareness is necessary for motor control may depend on the biomechanical demands of the planned action.

Keywords Action-perception, Two streams hypothesis, Visual awareness, Motor control, Active inference

According to the idea that cognition is grounded in sensorimotor coupling, the two visual streams hypothesis[1] postulates that the visual control of actions is mediated by a specialised network projecting from early visual areas to the posterior parietal cortex (i.e., the dorsal stream). By contrast, the transformation of the visual input into a coherent conscious representation of the external world is mediated by the visual network projecting to the inferotemporal cortex (i.e., the ventral stream). Recent advances in neuroimaging and analysis techniques have revealed that the dorsal–ventral stream segregation extends into the prefrontal cortex (PFC)[2,3]. Distinct PFC subregions, in particular the frontal eye field (FEF) and the inferior frontal junction (IFJ), exhibit dissociative connectivity profiles, aligning with dorsal (spatially oriented) and ventral (object-feature oriented) visual streams[4]. A central assumption of this model is that the dorsal stream is mainly responsible for action preparation and real-time control, operating independently of visual awareness. The independence of the dorsal stream from visual awareness is referred to as 'dorsal bias'[5]. Several studies using different methods to disrupt conscious perception have shown that action-relevant features can still be processed without visual awareness[6–14]. However, other findings have failed to support this independence[15–19], for example, by reporting no advantage in action control under disrupted conscious perception[20], leaving the existence of a dorsal bias an open question[5]. In general, evidence suggests that consciousness is a global cognitive function[21–24]: the relationship between brain activity and visual awareness is graded[25–27], conscious experience emerges from the integrated activity of several areas, including temporal, occipital, and parietal cortices[28–31], and the same structures are implicated in the processing and brief maintenance of unconscious information[21,32]. Similarly, the conscious perception of visual stimuli is context-dependent and dynamically modulated[33–35]. For example, prior expectations play

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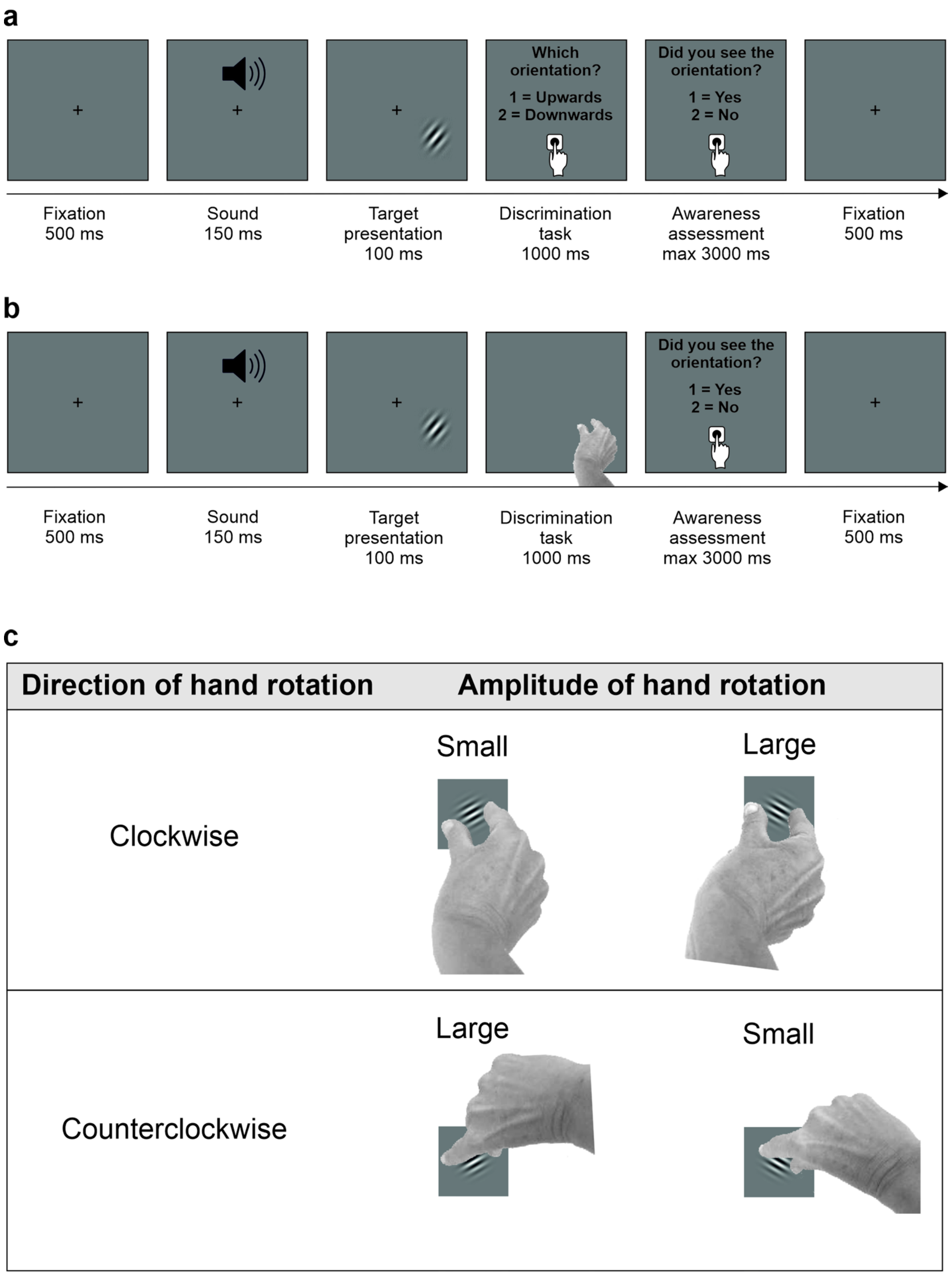

FIG.1: Trial procedure and experimental conditions

a fundamental role in determining the content of visual consciousness[36–42], and the fate of the visual input, whether it becomes conscious or not, may depend on what will happen later[43–46]. Taken together, these findings indicate that how visual information is processed and whether it becomes consciously available depend on dynamic interactions with higher-order cognitive processes. From this perspective, the existence of the dorsal bias, meaning the independence of the dorsal stream from visual awareness, may not be absolute but instead contingent on specific contexts or conditions.

From the ecological perspective, the coupling between action and perception is rooted in the concept of affordances. Affordances are defined as the action possibilities that an object or environment provides to a user, based on the object's physical characteristics and the user's abilities[47,48]. Accordingly, what we perceive is not an accurate representation of reality but reflects our ability to act on objects in our environment[47,49–51]. The role of actions in shaping perception has been recognised in various domains, from language processing[52] to vision[53–55] and touch[56]. Individual motor ability modulates perception within various dimensions and multiple actions[57–59],

◀**Fig. 1**. Trial procedure and experimental conditions. (**a**) Threshold assessment. A two-alternative forced-choice discrimination task was used to determine the optimal stimulus orientations for the experiment. Gabor patches were presented at different orientations, and on each trial, participants first indicated the orientation (discrimination task) and then reported whether the orientation was consciously perceived (perceptual awareness assessment). (**b**) Experimental task. At stimulus onset, participants reached toward the target, mimicking a precision grip (i.e., with the thumb and index fingers). When they perceived a non-horizontal stimulus orientation, they were required to adjust the alignment of their fingers to match the stimulus as quickly and accurately as possible. When no tilt was perceived, participants were instructed to select either an upward or downward orientation at random. Participants then reported whether they had perceived the stimulus orientation. (**c**) Experimental conditions. The experimental design for the first (upper panel) and second experiments (both panels). In Experiment 1, clockwise hand rotation was considered at two amplitudes (small and large); in Experiment 2, both clock and counterclockwise hand rotations were considered, each at small and large amplitudes. The upper panel shows the hand rotation required for clockwise direction, while the lower panel it for counterclockwise direction.

with the reach-to-grasp movement receiving particular attention due to its fundamental role in perception–action coupling within the environment[60,61]. Goal-directed movement preparation involves the selective, action-specific extraction of motor-relevant information from the visual scene. Attention is distributed across multiple relevant locations, forming an 'attentional landscape' that closely reflects the requirements of the planned action, such as temporal instancy, required accuracy, and difficulty[62]. Hence, preparing a reach-to-grasp act can improve the visual processing of action-relevant features[63–65,65–69]. Neural activity in early sensory cortices encodes effector-specific information and movement goals (e.g., reaching, grasping) before execution[70–73], while parietal cortex additionally represents complex, sequential actions[74]. These representations are likely mediated by reentrant signals from higher-order regions[71,75–80]. Specifically, functional and effective connectivity reveal that spatial and non-spatial selection depend on FEF and IFJ interactions with posterior regions[2,3]. Consistent with the dual-stream framework, FEF acts as a spatial priority map, whereas IFJ dynamically modulates non-spatial processing to allocate attention flexibly according to task demands[4].

Adopting an affordance-based framework offers a possible explanation of the inconsistencies observed in the literature on the dorsal bias. Specifically, because task demands elicit specific performance requirements (i.e., affordances), action-relevant visual features may or may not afford an action outside conscious perception, depending on the 'affordance' relationship (i.e., task demands and user's abilities). In other words, because perception and movement initiation are closely aligned from the early phases of motor planning[81], creating action-specific 'attentional landscapes'[62], the selection of relevant visual information likely overlaps with the anticipation of the biomechanical demands (e.g., difficulty or comfort) of the forthcoming action[4,82–84]. Based on this framework, this study aimed to reveal the impact of non-conscious visual information on reaching movements and how it interacts with the biomechanical demands of the action. Non-conscious visual information was operationalised using near-threshold presentation, in which the target feature was presented at the perceptual threshold, and thus barely detectable. Action biomechanical demands were modulated by varying the level of end-state comfort associated with the intended action (i.e., hand rotation amplitude and direction). Specifically, we tested two hypotheses: (i) Unconscious visual information might guide reaching movements accurately[8]; (ii) If access to visual information is regulated by top-down processes based on the biomechanical demands of planned actions (i.e., end-state comfort), then the effect of visual awareness should depend on those demands. More precisely, we expected visual awareness to be critical for movements ending in uncomfortable positions, whereas comfortable end-state actions might be successfully performed even in the absence of visual awareness.

Results

We conducted two experiments to explore the perception–action relationship in the presence of different levels of visual awareness of stimulus features (aware, unaware) and various levels of action end-state comfort (small and large amplitudes of rotation, and clockwise and counterclockwise directions of rotation). Participants performed a reaching movement in response to the brief presentation of a Gabor patch, directing their hand toward the 2D stimulus as if grasping it, adjusting hand orientation to align with the stimulus features (Fig. 1). The Gabor was slightly tilted upward or downward relative to the horizontal axis. The optimal stimulus orientation was previously determined with an individual threshold assessment (Fig. 1a). The movement required to align the index and thumb fingers to reproduce the exact orientation of the stimulus as precisely and as quickly as possible. Moving toward the 'upward' or the 'downward' Gabor could be performed by rotating the hand clockwise or counterclockwise with different rotation amplitudes (Fig. 1c). For each trial, participants reported whether they had consciously perceived Gabor's orientation. To assess the impact of movement end-state comfort, movements were categorised by direction and hand rotation amplitude. In Experiment 1, the clockwise direction of rotation was considered with two amplitudes (small and large); in Experiment 2, both clock and counterclockwise rotations were considered, each with small and large amplitude (Fig. 1c). To assess the impact of perceptual awareness, we sorted the trials into either 'aware' or 'unaware' according to the subjective report of the participants. We analysed three key parameters to characterise the response action based on its most salient features: hand rotation accuracy, rotation onset, and rotation smoothness. Each parameter captures a distinct aspect of the underlying cognitive and motor processes. Hand rotation accuracy reflects the ability to select the correct movement across conditions and serves as the primary measure of whether visual information is sufficient for accurate task execution. Hand rotation onset indexes the rapidity of pre-movement cognitive processing, including perceptual analysis, decision-making, and motor specification[85]. Finally, hand rotation smoothness reflects the integration of preplanning[86] with online control processes, characterised by continuous adjustments during movement execution[87–89].

The interplay between perceptual awareness and action end-state comfort (Experiment 1)

In Experiment 1, participants were instructed to match the stimulus's orientation by rotating the hand clockwise (Fig. 1c, upper panel). Participants reported being aware of the stimulus orientation 65% of the time. Movement onset is reported as cube-root-transformed milliseconds, and movement smoothness is reported using SPARC metric, a dimensionless measure.

Hand rotation accuracy

Accuracy for unaware trials (M = 64.45%, SD = 17.41%) was significantly above the chance level (t(19) = 16.55, $p < 0.001$), indicating that participants could use information not consciously available to lead the movement in the right direction. There was a significant main effect of amplitude of rotation ($\chi^2\,(1) = 396.55, p < .001$) and awareness ($\chi^2\,(1) = 1317.41, p < .001$), indicating that accuracy was greater for small amplitudes (M = 90.91%, SD = 14.17%) compared to large amplitudes (M = 75.78%, SD = 18.68%), and for aware trials (M = 93.48%, SD = 11.25%) compared to unaware trials (M = 64.45%, SD = 17.41%). The interaction amplitude of rotation x awareness was also significant ($\chi^2\,(1) = 7.34, p = .007$). Post hoc comparisons confirmed that accuracy was greater in aware trials than in unaware trials across all rotation amplitudes. However, the effect was lower for small amplitudes (log OR = −3.01, z = −17.73, 95% CI[−3–34,−2.67], $p < 0.001$, M = 98.16%, SD = 11.93%, and M = 78.75%, SD = 18.89% for aware and unaware respectively) compared to large amplitudes (log OR = −2.50, 95% CI[−2.68, −2.32], z = −27.52, $p < 0.001$, M = 89.85%, SD = 12.54%, and M = 51.85%, SD = 19.20% for aware and unaware respectively). Performance dropped at the chance level for unaware trials in the uncomfortable condition (large amplitude of rotation, Fig. 2a). This decline is evident in the rotation angle distribution through a markedly attenuated peak and broader dispersion (Fig. 2b).

Hand rotation onset

There was a significant main effect of amplitude of rotation ($\chi^2\,(1) = 45.09, p < .001$) and awareness ($\chi^2\,(1) = 7.16, p = .01$), indicating that the hand rotation began earlier for small amplitudes (M = 6.92 cube-root ms, SD = 0.73) compared to large amplitudes (M = 7.10 cube-root ms, SD = 0.73, Fig. 3a), and for aware trials (M = 7.00 cube-root ms, SD = 0.73) compared to unaware trials (M = 7.07 cube-root ms, SD = 0.77, Fig. 3b).

Rotation smoothness

There was a significant main effect of amplitude of rotation ($\chi^2\,(1) = 211.61, p < .001$) and awareness ($\chi^2\,(1) = 18.49, p < .001$) indicating that small hand rotations (M = −1.14, SD = 0.01, SPARC) were smoother than large hand rotations (M = −1.15, SD = 0.02, SPARC) and that aware trials (M = −1.14, SD = 0.01, SPARC) were smoother than unaware trials (M = −1.15, SD = 0.02, SPARC). The interaction amplitude of rotation x awareness was also significant ($\chi^2\,(1) = 5.01, p = .025$). Post hoc comparisons showed that aware trials (M = −1.14, SD = 0.01, SPARC) did not significantly differ from unaware trials (M = −1.14, SD = 0.01, SPARC) in the small amplitude condition ($b = -0.0015$, [−0.0033, 0.0004], $t(7875) = -1.52$, $p = 0.130$). However, aware trials (M = −1.14, SD = 0.01, SPARC) were smoother than unaware trials (M = −1.15, SD = 0.01, SPARC) in the large amplitude condition ($b = -0.0046$, 95% CI [−0.0066, −0.0026], $t(7868) = -4.46$, $p < 0.001$; Fig. 3c).

Experiment 1 revealed that accuracy and kinematic parameters were all affected by both comfort and awareness. Aware movements presented greater accuracy, were initiated earlier, and were performed more smoothly than unaware movements. Crucially, when subjects were unaware of the stimulus orientation, they nevertheless selected the correct action and moved smoothly. However, this was only the case for comfortable actions; for large amplitudes, accuracy dropped (Fig. 2a, b), and smoothness decreased substantially (Fig. 3c). In other words, visual awareness played a minor role in easy movements but was necessary to accomplish difficult ones. Cognitive processing preceding movement initiation (as indexed by rotation onset) was slightly facilitated by conscious perception regardless of action end-state comfort (Fig. 3b). To clarify this pattern of results better, experiment 2 introduced an additional action constraint (direction) by asking participants to perform a counter-clockwise movement, presenting small and large amplitudes.

The effect of different levels of action end-state comfort (Experiment 2)

In Experiment 2, we replicated the conditions of Experiment 1 and added a new condition in which participants performed counterclockwise hand rotations (Fig. 1c, lower panel). Participants reported being aware of the stimulus orientation 68% of the time. Movement onset is reported as cube-root-transformed milliseconds, and movement smoothness is reported using SPARC metric, a dimensionless measure.

Hand rotation accuracy

Accuracy for unaware trials (M = 56.58%, SD = 7.58%) was significantly above the chance level (t(18) = 32.55, $p < 0.001$). There was a significant main effect of amplitude of rotation ($\chi^2\,(1) = 701.77, p < .001$), direction of rotation ($\chi^2\,(1) = 144.15, p < .001$), and awareness ($\chi^2\,(1) = 3306.32, p < .001$) indicating that accuracy was greater for small amplitudes (M = 88.45%, SD = 7.85%) compared to large amplitudes (M = 71.25%, SD = 10.97%), for the clockwise direction (M = 84.37%, SD = 6.63%) compared to the counterclockwise direction (M = 75.57%, SD = 9.9%), and for aware trials (M = 91.60%, SD = 8.02%) compared to unaware trials (M = 56.58%, SD = 7.58%). The interactions amplitude of rotation x direction of rotation ($\chi^2\,(1) = 29.89, p < .001$), amplitude of rotation x awareness ($\chi^2\,(1) = 113.85, p < .001$), and direction of rotation x awareness ($\chi^2\,(1) = 131.24, p < .001$) were also significant. The three-way interaction was significant ($\chi^2\,(1) = 5.43, p = .020$). Post hoc comparisons

FIG.2: Hand rotation accuracy for experiment 1

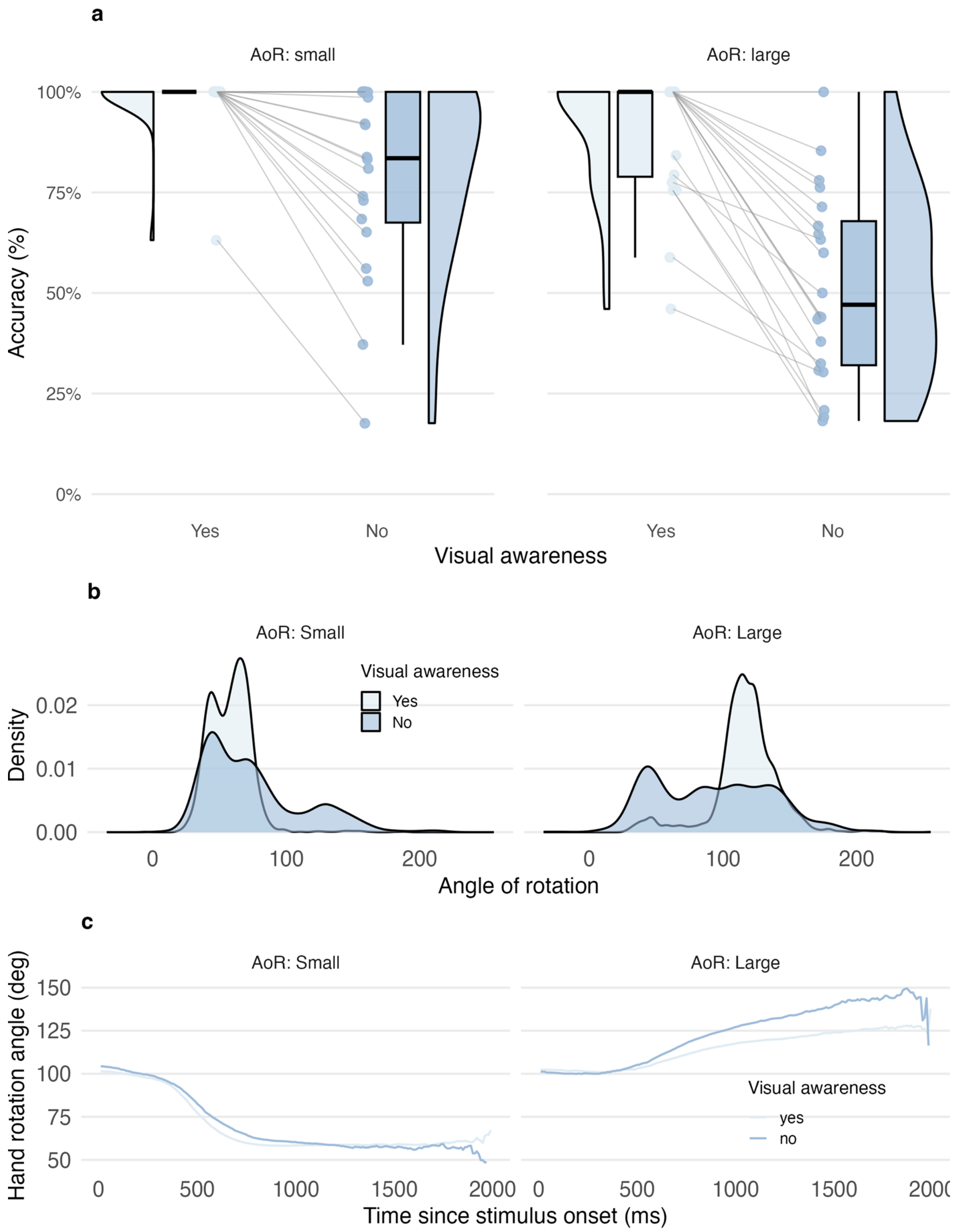

Fig. 2. (**a**) Raincloud plot showing the effect of amplitude of rotation and awareness in hand rotation accuracy for experiment 1. The right half (violin-shaped density plot) illustrates the data distribution, the middle (boxplot) displays the median (central line), interquartile range (box), and 95% confidence intervals (whiskers), while the left half (individual points) shows raw data points. Accuracy was always significantly greater for aware trials compared to unaware trials, but the effect was lower for small amplitudes compared to large amplitudes. Performance dropped at the chance level for unaware trials in the uncomfortable condition (large amplitude of rotation). (**b**) Kernel density estimates depict the probability distribution of rotation angles for each condition, highlighting preferred angles (peaks) and variability (spread). (**c**) Time changes of the hand rotation angle averaged across subjects for the different conditions.

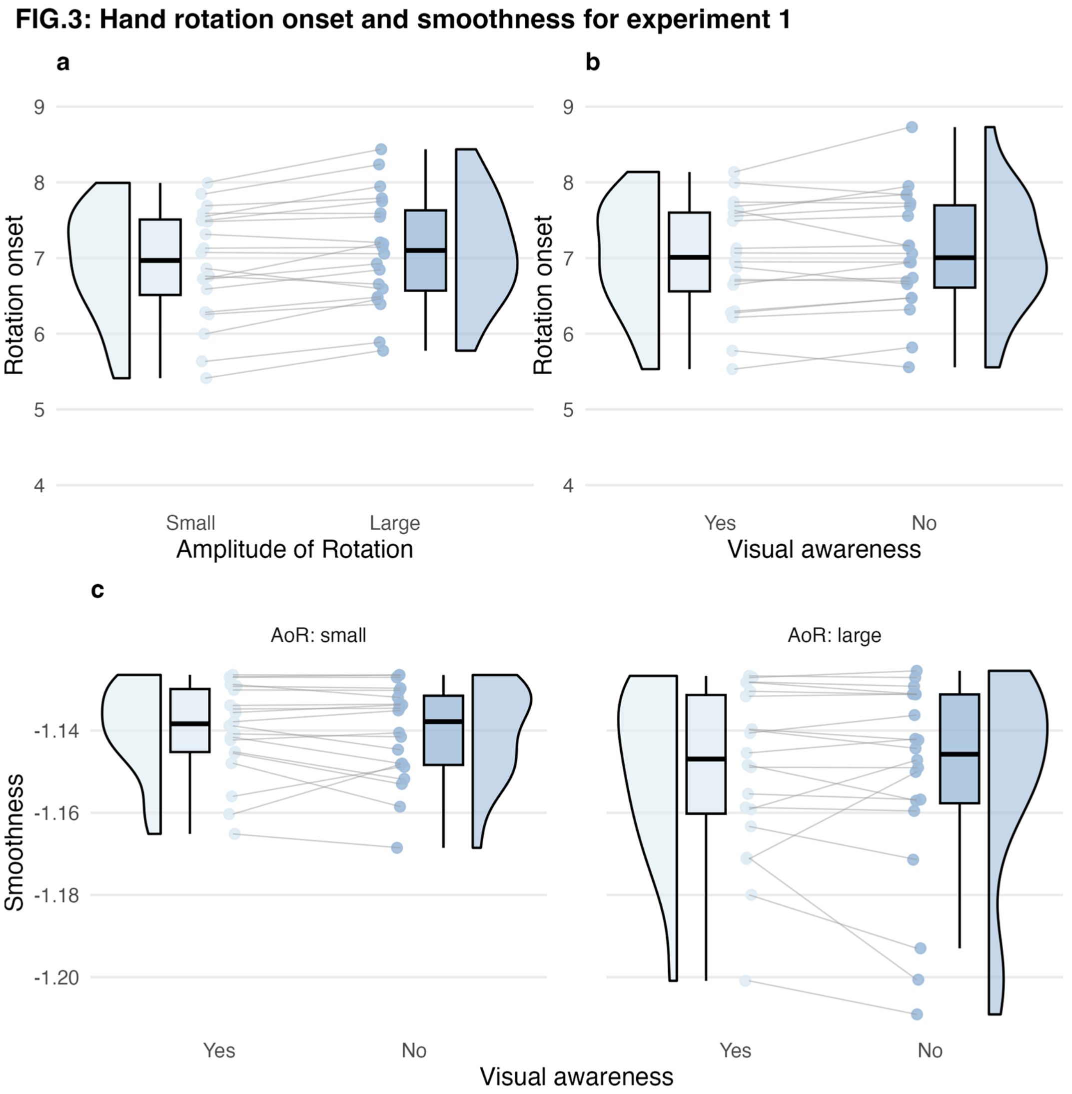

Fig. 3. (**a**) Raincloud plot showing the effect of amplitude of rotation for rotation onset (cube root transformed) for experiment 1. Hand rotation began earlier for small amplitudes compared to large amplitudes (**b**) Raincloud plot showing the effect of awareness for rotation onset (cube root transformed) for experiment 1. Hand rotation began earlier for aware trials compared to unaware trials. (**c**) Raincloud plot showing the effect of amplitude of rotation and awareness in hand rotation smoothness for experiment 1. Aware trials did not significantly differ from unaware trials for the small amplitude condition while aware trials were smoother than unaware trials for the large amplitude condition. Variability in movement smoothness increased significantly during uncomfortable movements, indicating greater inter-subject differences.

confirmed significantly higher accuracy in aware trials compared to unaware trials across all conditions (all $p<0.001$), with varying effect magnitudes. The accuracy difference between aware and unaware was 34.3% (OR = 0.015, 95% CI [0.010, 0.023], $z=-19.37$) for small/clockwise, 44.7% (OR = 0.041 [0.033, 0.051], $z=-29.83$) for large/clockwise, 29.5% (OR = 0.048 [0.037, 0.062], $z=-22.30$) for small/counterclockwise, 30.8% (OR = 0.264 [0.232, 0.301], $z=-19.94$) for large/counterclockwise (see Table 1 for descriptive statistics, and Fig. 4). The rotation angle distribution shows a bimodal trend (i.e., two equally probable peaks, Fig. 4b), confirming chance-level performance for unaware/uncomfortable trials (large amplitude of rotation).

Hand rotation onset
There was a significant main effect of amplitude of rotation ($\chi^2\,(1) = 18.92, p < .001$), direction of rotation ($\chi^2\,(1) = 539.59, p < .001$) and awareness ($\chi^2\,(1) = 34.21, p < .001$), indicating that hand rotations began earlier for large amplitudes (M = 6.77 cube-root ms, SD = 0.71) compared to small amplitudes (M = 6.90 cube-root ms, SD = 0.71), for the clockwise direction (M = 6.61 cube-root ms, SD = 0.64) compared to the counterclockwise direction (M = 7.02 cube-root ms, SD = 0.89), and for aware trials (M = 6.82 cube-root ms, SD = 0.68) compared to unaware trials (M = 6.94 cube-root ms, SD = 0.76). The interaction amplitude of rotation x awareness was significant ($\chi^2\,(1) = 6.87, p = .01$). Post hoc comparisons showed significant

DoR	AoR	Awareness	Mean (%)	SD (%)
Clockwise	Small	Yes	98.96	5.29
Clockwise	Small	No	64.94	15.38
Clockwise	Large	Yes	96.13	9.20
Clockwise	Large	No	51.39	12.05
Counterclockwise	Small	Yes	98.06	4.61
Counterclockwise	Small	No	68.61	18.00
Counterclockwise	Large	Yes	72.97	16.76
Counterclockwise	Large	No	42.18	16.77

Table 1. Descriptive statistics for hand configuration accuracy in Experiment 2.

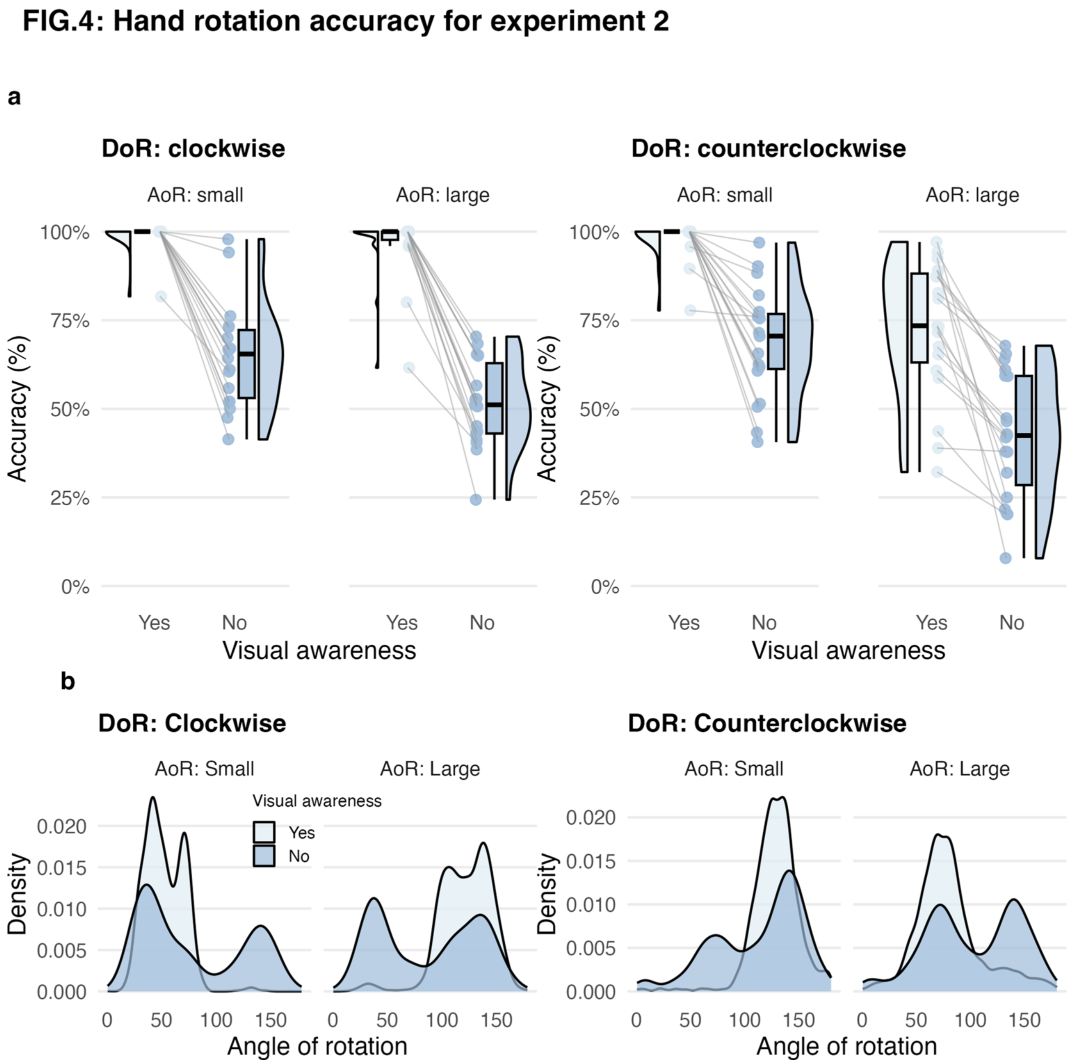

Fig. 4. (**a**) Raincloud plot showing the effect of amplitude of rotation, direction of rotation and awareness in rotation accuracy for experiment 2. Accuracy was always significantly greater for aware trials than for unaware trials. Still, the effect was greater when the movement was large and/or in the counterclockwise direction (i.e., less comfortable; see Table 1 for descriptive statistics). Data distribution shows higher variability for the uncomfortable conditions. (**b**) Kernel density estimates depict the probability distribution of rotation angles for each condition, highlighting preferred angles (peaks) and variability (spread).

earlier onsets in aware versus unaware trials, with amplitude-dependent effect sizes. The aware-unaware delay difference was smaller for small amplitudes (8.44, corresponding to 14.7 ms, $b = 0.062$, 95% CI [0.0125, 0.112], t(11,735) = 2.451, $p < 0.029$) compared to large amplitudes (21.8, corresponding to 37.0 ms, $b = 0.166$, 95% CI [0.1067, 0.221], t(11,735) = 5.636, $p < 0.0001$, Fig. 5a). The interaction direction of rotation x awareness was significant (χ^2 (1) $= 9.51, p < .001$). Post hoc comparisons showed that hand rotations began earlier for aware trials (M = 6.56 cube-root ms, SD = 0.35) compared to unaware trials (M = 6.73 cube-root ms, SD = 0.23) for the clockwise direction ($b = 0.172$, 95% CI [0.119, 0.226], $t(11{,}734) = 6.31$, $p < 0.0001$). By contrast, aware trials (M = 7.02 cube-root ms, SD = 0.30) did not differ from unaware trials (M = 7.06 cube-root ms, SD = 0.29) for the counterclockwise direction ($b = 0.054$, 95% CI [0.00, 0.107], $t(11{,}734) = 1.98$, $p = 0.09$), Fig. 5b).

Rotation smoothness

There was a significant main effect of amplitude of rotation (χ^2 (1) $= 305.61, p < .001$) and direction of rotation (χ^2 (1) $= 1267.25, p < .001$) indicating that small hand rotations (M = −1.15, SD = 0.01, SPARC) were smoother than large hand rotations (M = −1.16, SD = 0.01, SPARC) and that clockwise rotations (M = −1.14, SD = 0.01, SPARC) were smoother than counterclockwise rotations (M = −1.17, SD = 0.02, SPARC). The

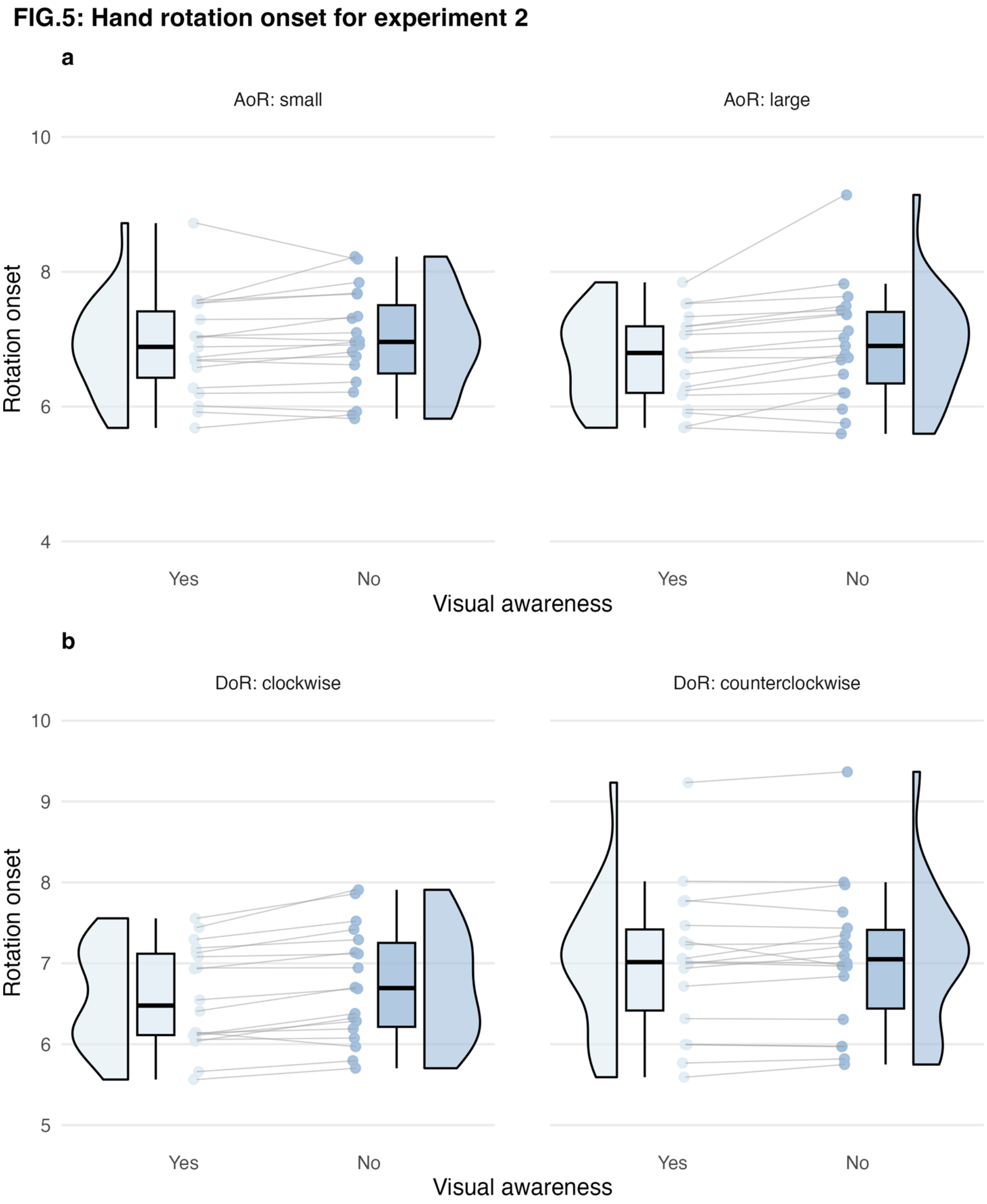

Fig. 5. (**a**) Raincloud plot showing the effect of amplitude of rotation and awareness in rotation onset (cube root transformed) for experiment 2. Hand rotations began earlier for aware trials compared to unaware trials, and the effect was lower for small amplitudes compared to large amplitudes. (**b**) Raincloud plot showing the effect of direction of rotation and awareness in rotation onset (cube root transformed) for experiment 2. Hand rotations began earlier for aware trials compared to unaware trials for the clockwise direction. By contrast, aware trials did not differ from unaware trials for the counterclockwise direction.

FIG.6: Hand rotation smoothness for experiment 2

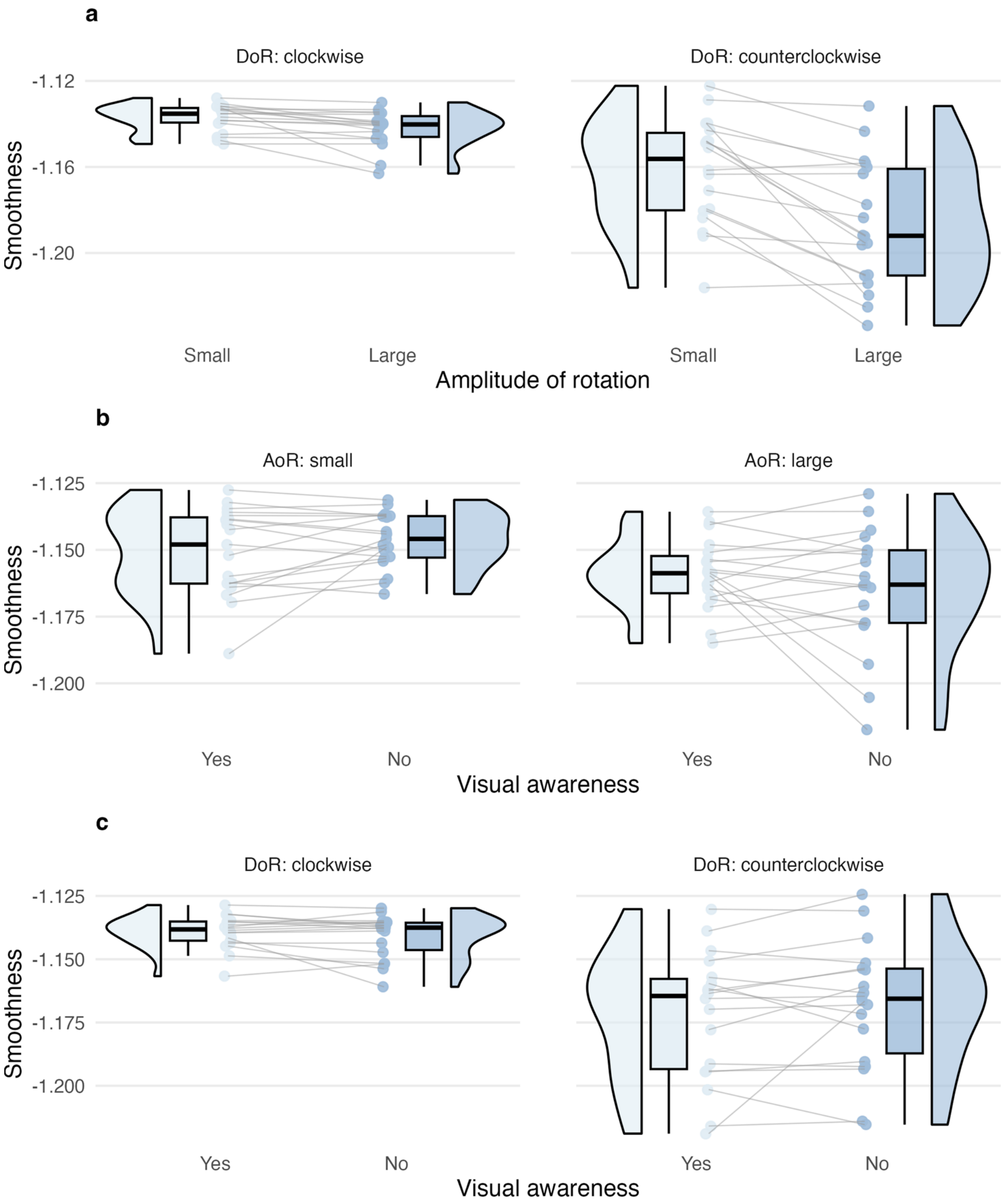

Fig. 6. (**a**) Raincloud plot showing effect of amplitude and direction of rotation in rotation smoothness for experiment 2. Small amplitudes were smoother than large amplitudes for both the clockwise direction and the counterclockwise direction. Still, the effect was larger for the counterclockwise direction. (**b**) Raincloud plot showing the effect of amplitude of rotation and awareness in rotation smoothness for experiment 2. Aware trials were less smooth than unaware trials for small amplitudes. By contrast, aware trials did not significantly differ from unaware trials for large amplitudes. (**c**) Raincloud plot showing the effect of direction of rotation and awareness in rotation smoothness for experiment 2. Aware trials did not significantly differ from unaware trials for the clockwise direction. By contrast, aware trials were less smooth than unaware trials for the counterclockwise direction.

interaction amplitude of rotation x direction of rotation was significant ($\chi^2\ (1) = 118.18, p < .001$). Post hoc comparisons showed significantly greater movement smoothness in small versus large trials for both rotation directions (both ps < 0.0001). However, the effect was weaker for clockwise direction (b = 0.006, 95% CI [0.004, 0.009], z = 4.78) compared to the counterclockwise direction (b = 0.026, 95% CI [0.0237, 0.0289], z = 19.939, Fig. 6a). The interaction amplitude of rotation x awareness was significant ($\chi^2\ (1) = 10.62, p = .001$). Post hoc comparisons revealed that aware trials (M = -1.151, SD = 0.01, SPARC) were less smooth than unaware trials (M =–1.146, SD = 0.01, SPARC) for small amplitudes ($b = 0.00435$, 95% CI [0.00193, 0.00677], $z = 3.527$, $p < 0.001$). By contrast, aware trials (M = −1.159, SD = 0.01, SPARC) did not significantly differ from unaware trials (M = −1.165, SD = 0.01, SPARC) for large amplitudes ($b = -0.0017$, 95% CI [−0.00441, 0.00102], $z = -1.224$, $p = 0.442$, Fig. 6b). The interaction direction of rotation x awareness was significant ($\chi^2\ (1) = 7.41, p = .006$). Post hoc comparisons indicated that aware trials (M = −1.140, SD = 0.01, SPARC) did not significantly differ from unaware trials (M = 1.141, SD = 0.02, SPARC) for the clockwise direction ($b = -0.00118$, 95% CI [−0.00372, 0.00135], $z = -0.914$, $p = 0.722$). By contrast, aware trials (M = −1.172, SD = 0.02, SPARC) were less smooth than unaware trials (M = −1.168, SD = 0.02, SPARC) for the counterclockwise direction ($b = 0.00384$, 95% CI [0.00125, 0.00643], $z = 2.906$, $p = 0.0073$, Fig. 6c).

Experiment 2 replicated the effect of action end-state comfort but revealed an interesting dissociation in the impact of awareness across movement phases[87]. Similar to experiment 1, visual awareness facilitated motor planning, as demonstrated by improved accuracy (Fig. 4) and earlier onset (Fig. 5), particularly in the case of uncomfortable movements. That is, awareness was necessary to select the correct movement when it was uncomfortable, with less impact on comfortable movements. Conversely to experiment 1, visual awareness had either no significant effects on movement smoothness or was associated with reduced smoothness (Fig. 6b, c). Movement smoothness reflects the integration of pre-planning[86] with online control, which involves continuous adjustments[87,89,90]. The greater difficulty in the counterclockwise direction likely led to increased action control in aware trials[91–93].

Discussion

This study investigated the effects of non-conscious visual information on reaching movements. We addressed two fundamental research questions: (I) If the dorsal stream operates independently of visual awareness during action preparation and online control (i.e., the dorsal bias), accurate reaching movements should be possible even without visual awareness of stimulus features, relying on unconscious visual information; (II) However, if the role of visual awareness in guiding the action is modulated by top-down processes related to the biomechanical demands of planned actions (i.e., end-state comfort), the effect of visual awareness should depend on those demands. As predicted, results revealed significantly above-chance performance in movement selection even when participants reported no conscious perception of the stimulus orientation. That is, visual awareness supported comfortable movements but was not strictly necessary for their successful execution. By contrast, uncomfortable movements depended critically on conscious visual perception. These findings confirm that the online control of action can operate at least partially independently of visual awareness. At the same time, they also reveal a critical constraint: this partial independence, the dorsal bias, is modulated by the demands of the task at hand.

To address whether conscious perception is necessary for accurate reaching, participants performed reaching movements that matched their hand orientation to that of a briefly presented Gabor patch. The Gabor orientation was individually calibrated to each participant's threshold of awareness, resulting in conscious perceptions on approximately half of the trials. Perceptual stability emerges from iterative feedforward and feedback interactions across brain regions[94–96], persisting beyond stimulus presentation[97,98] and modulated by task demands[99]. Sensory evidence accumulation favouring one of the alternatives[100–102] is a noisy and time-varying process[34,103–106], resulting in variable confidence about feature representations[107,108]. When near-threshold stimuli are presented, the same feature can either become conscious or not[109–111]. Accordingly, our participants reported being aware of the stimulus orientation about 65% of the time. Concerning our first question, when participants consciously perceived the stimulus orientation, performance showed higher hand rotation accuracy, earlier rotation onset and smoother movements. However, when participants reported being unaware of the stimulus orientation, the correct hand rotation was selected less frequently, but performance remained clearly above the chance level (Fig. 2a). Partially consistent with previous findings supporting a dorsal bias, our results indicate that visual awareness contributes to performance without being a strict prerequisite for successful action[6–14], providing further evidence for the complementary functions of ventral and dorsal visual streams[1,51].

Motor tasks require solving kinematic redundancy—selecting among infinite possible joint/muscle combinations (equifinality[112]). Typically, subjects prefer the most comfortable solution: mid-range joint amplitudes that minimise effort and avoid extreme positions[113–115]. In our paradigm, reaching the target required a combination of a modest or substantial hand amplitude rotation (small and large conditions) while moving in a clockwise or counterclockwise direction. Consistent with expectations, our data showed that actions characterised by greater end-state comfort (small amplitude of rotation, clockwise direction, i.e., fewer degrees of freedom) resulted in higher accuracy, earlier onset and smoother execution. By contrast, the most extreme range position (large amplitude, counterclockwise direction) exhibited the worst performance (Fig. 3a, and Fig. 6a). Building on this, the second objective of this study was to address whether the end-state comfort[113] mediates the effect of visual awareness. The results showed that only more comfortable end-state actions (presenting fewer degrees of freedom redundancy[112]) took advantage of information not consciously perceived. Conversely, performance dropped substantially when the movement was uncomfortable (presenting greater degrees of freedom redundancy[112], Fig. 2a, and Fig. 4a, Table 1). Similarly, participants delayed the start of the hand rotation when unaware of the stimulus orientation (Fig. 3b). When the range of end-state comfort levels was large enough (experiment 2), delays were longer in the uncomfortable conditions (Fig. 5b, c). Therefore, conscious perception of stimulus orientation was crucial for selecting the correct action and initiating the movement promptly when the end-state was biomechanically uncomfortable. By contrast, conscious perception had reduced significance for action in which the end-state was closer to the middle range of movement amplitude (i.e., more comfortable). In other words, unconscious visual information was occasionally sufficient to bias the selection among competing actions toward the correct movement, but exclusively for comfortable end-state actions[82,83].

Interestingly, awareness of stimulus orientation appeared to exert distinct, seemingly inconsistent effects during movement execution rather than during the planning phase[87]. As a benchmark indicator for assessing movement control during the execution phase, we analysed the movement smoothness[116]. In Experiment 1, smoothness analysis replicated the accuracy and rotation onset results, consistent with a role for perceptual awareness of stimulus features in anticipating future action states[117]. In Experiment 2, which included more challenging movements, this pattern partially reversed (Fig. 6b, c): conscious access to stimulus features was associated with reduced smoothness during counterclockwise movements. Because of the increased difficulty of the uncomfortable condition, participants might have monitored the action closely for aware trials[93]. Research showed that closely monitoring step-by-step performance may disrupt the execution of overlearned motor skills[92,118,119]. This interference effect is attributed to online motor control relying on highly automatic processes[87,120,121], and to conscious focus on movement, which disrupts these efficient, unconscious motor control mechanisms[91]. By contrast, not interfering with these automatic processes results in superior performance[91,93,122]. Accordingly, movements were smoother in unaware trials, during which participants performed at chance level (i.e., the action was executed automatically). In addition, inspecting individual performance[123] reveals substantial variability (Fig. 6c), potentially reflecting subjective differences in coping with uncertainty.

Our findings have several theoretical implications. A primary implication concerns the computational mechanism driving these effects. Motor preparation involves the parallel specification of available actions before sensory evidence integration is completed[51,124–128]. The perceptual decision-making process (upward vs. downward orientation discrimination) thus entailed the concurrent specification of all biomechanically relevant action parameters (hand rotation amplitude and direction) critical for task performance[129]. As a consequence of extensive practice, comfortable end-state actions likely had lower activation thresholds, such that even unconscious visual input could bias selection toward these effortless movements.

Crucially, motor preparation involves forming an ‘attentional landscape’ that reflects the requirements of the planned action and weights visual input accordingly[4,62]. Under a predictive coding scheme[130–132], comfortable, well-practised actions might have generated stronger top-down predictions, selectively enhancing motor-relevant visual processing at lower hierarchical levels (i.e., active inference,[133];[134];[135]). This explanation aligns with theories of consciousness as emerging from globally integrated representations[24], which are selectively modulated by task-dependent top-down signals[33]. However, further studies are needed to distinguish the contributions of feedforward and feedback mechanisms.

Further, our findings can help to explain the conflicting results about the ‘dorsal bias’[5,16,17]. Preventing conscious perception of visual stimuli should selectively disrupt stimulus identification mediated by the ventral pathway, while processing features relevant to action via the dorsal pathway would remain unaffected[136,137]. Our findings suggest that the dorsal bias might be tied to specific contexts or conditions[137–139]. Specifically, while less demanding movements may be executed without conscious access to visual information, this would be necessary to guide difficult actions[33,140]. However, note that in this study, participants reached towards a 2D stimulus presented on a screen, which might differ from a reach-to-grasp movement on a 3D object in more natural conditions[141,142]. Future studies should test whether the observed end-state comfort effect generalises to 3D grasping.

In conclusion, the traditional categorisation of processes as purely perceptual or, conversely, dedicated to motor control is proving increasingly inadequate[143,144]. Action and perception systems are highly interdependent[52,145], and can be more effectively conceptualised as a single active inference machine[129,133]. Consistent with an ecological perspective[47], our results indicate that visual awareness is not a strict prerequisite for movement control, but its role is modulated by biomechanical constraints (end-state comfort). Visual awareness was critical for movements ending in uncomfortable positions, while comfortable movements could occasionally be executed successfully even in the absence of visual awareness. Following Gibson, each task demand requires a specific performance characterised by the task constraints and the body’s degrees of freedom involved, defining the individual ability[47–49,146].

Methods

Participants

Twenty-one students of the University of Verona participated in the first experiment (nine females, mean age = 20.43, SD = 1.75 years), and twenty participated in the second experiment (twelve females, mean age = 21.46, SD = 3.15 years). An a priori simulation (500 iterations, using simr package[147]) indicated that 20 participants completing 100 trials per condition would provide 99.8% power (95% CI: 98.9–100%) to detect a three-way interaction effect of OR = 0.40 using our planned GLMM structure (random intercepts: $\sigma^2 = 0.19$, $\alpha = 0.05$). This corresponds to a medium effect (log-odds = −0.92) based on Brysbaert and Stevens (2018) recommendations for mixed-effects models, aligning with typical effect magnitudes in cognitive psychology research[148]. All participants were naive to the purpose of the experiment, and they had normal or corrected-to-normal vision. Participants gave informed written consent before participating in the experiment. The procedure was approved by the local ethics committee of the University of Verona (protocol n. 28.R1/2024). The experiment was performed in accordance with relevant guidelines and regulations and the Declaration of Helsinki. Participants had to perform the task accurately to be included in the study. Specifically, participants were required to show no systematic bias toward either stimulus orientation in catch trials, in which neither option was correct, and responses should have been random. Those selecting one orientation more than 55% of the time in catch trials were excluded (See Threshold assessment).

Procedure

Experiment 1 consisted of a single session. First, participants completed the individual threshold assessment to determine their optimal stimulus orientations for the experimental task. This assessment identified two stimulus orientations (one upward-oriented and one downward-oriented) that each participant reported seeing approximately 50% of the time. After a 15-min break, participants performed the experimental task during which their individually selected stimuli were presented. In experiment 2, participants completed two sessions on separate days to avoid fatigue. Each session consisted of the individual threshold assessment followed by the experimental task and lasted approximately two hours. One session was identical to experiment 1, while the other employed the reversed response mapping (i.e., hand movement–stimulus association).

Threshold assessment

The individual optimal stimulus orientation was determined using a 2-alternative forced-choice discrimination task (Fig. 1a). The stimuli were Gabor patches (see Methods from Colombari et al.,[31]), which could be oriented either horizontally (- 90° with respect to the vertical axis, clockwise direction—catch trials), upward (< 90°), or downward (> 90°). Orientations spanned 87° to 93.5° in 0.5° increments. Behavioural responses were collected using a customised response box with two vertically arranged buttons. Participants used the same buttons to sequentially perform a discrimination task, followed by a perceptual awareness assessment. This task order minimised potential biases that could arise if participants' judgments about their own perception (as in the perceptual awareness assessment) influenced performance in the discrimination task. In addition, the discrimination task served as a control to verify that participants were performing it correctly, thereby ensuring data reliability. The task started with a 500 ms central fixation cross, followed by a 150 ms auditory cue preceding stimulus onset. The stimulus appeared for 100 ms ± 2 ms in the right lower field (with 2° eccentricity, covering 1° of the visual field). Participants were instructed to indicate stimulus orientation (discrimination task) as quickly as possible: pressing the upper button (middle finger) for upward orientation (< 90°), the lower button (index finger) for downward orientations (> 90°), or either button randomly for horizontal orientations (90°). A response screen appeared, prompting participants to report their perceptual awareness of the stimulus orientation within 3 s: upper button to report a detectable tilt ('oriented') or lower button to report no perceived tilt ('horizontal'). After the participant's response (or after a 3000 ms timeout if no response), a 500 ms central fixation cross was presented, starting the next trial. The final fixation cross provided an additional fixation period. However, because no event intervened between the initial and final fixation crosses, they were perceived as a single continuous 1000 ms fixation. Participants were instructed to maintain gaze on the fixation cross throughout the trial. The threshold assessment session consisted of six experimental blocks of sixty-five trials each (five horizontal, sixty oriented). For each trial, the stimulus orientation was selected randomly, but ensuring that each orientation was represented an equal number of times during the block. For each tilt direction (upward, downward), six critical orientations were tested (87.0°, 87.5°, 88.0°, 88.5°, 89.0°, 89.5° and 91.0°, 91.5°, 92.0°, 92.5°, 93.0°, 93.5°, respectively). Each orientation was presented 10 times per block, for a total of 60 presentations per session. Before starting the session, participants could practice the task, performing at least 2–3 blocks.

Experimental task

The experimental task required participants to perform a reaching movement following the presentation of the stimulus (Fig. 1b). The stimulus was oriented in one of three directions: the individual's optimal 'upward' orientation, optimal 'downward' orientation, or horizontally. The right hand was placed on the table in front of the participant with the index and thumb fingers touching at a marked starting position. At stimulus onset, participants reached toward the target, mimicking a precision grip (i.e., with the thumb and index fingers). When they perceived a non-horizontal stimulus orientation, they were required to adjust their fingers' alignment to match the stimulus as quickly and accurately as possible (Fig. 1c). If no tilt was perceived, participants were instructed to select either an upward or downward orientation randomly. The left hand remained on the response box to report orientation perceptual awareness (as in threshold assessment). The next trial began after a button press.

Matching 'upward' or 'downward' stimulus orientation (< 90° or > 90°, respectively) required distinct hand rotation amplitudes, imposing different biomechanical constraints to the movement (i.e., end-state comfort). In Study 1, participants matched stimulus orientation by rotating the hand clockwise (Fig. 1c, upper panel). Based on the *amplitude of rotation*, we categorised trials requiring < 90° rotation as small (comfortable) and those requiring > 90° rotation as large (uncomfortable). In study 2, the two sessions differed in the stimulus/response mapping (i.e., *direction of movement*). In the clockwise session, the mapping mirrored Study 1. In the counterclockwise session (Fig. 1c, lower panel), participants rotated their hand in the opposite direction. Here, the small (comfortable) condition corresponded to 'downward' stimuli (> 90° stimulus orientation, > 270° hand rotation), while the large (uncomfortable) condition corresponded to 'upward' stimuli (< 90° stimulus orientation, < 270° hand rotation). For each trial, the stimulus orientation was selected randomly but such that each orientation was represented an equal number of times during the block. Study 1 consisted of ten experimental blocks of sixty trials each (ten horizontal and fifty oriented). Study 2 consisted of ten experimental blocks of sixty trials each (ten horizontal and fifty oriented) for each session. For study 2, the order of sessions was counterbalanced among participants. Before starting the session, participants could practice the task, performing at least 2–3 blocks.

Data acquisition and processing

The experiment took place in a dim room. Participants were seated in front of the screen at a distance of 50 cm. The presentation of the stimuli was controlled by a computer running E-Prime software[149]. Stimuli were presented on a 24-in Asus VG248 monitor (resolution: 1920 × 1080 pixels, refresh rate: 60 Hz). The experimental set-up included an optoelectronic motion capture system (MX Ultranet, VICON, Oxfordshire, UK) equipped with retro-reflective markers (14 mm in diameter). Eight infrared-emitting cameras (MX 13, VICON) were placed on a tripod around the movement volume at a height that permitted optimal detection of the entire movement. Five markers were placed on the right arm in the following bony landmarks: the middle of the nail edge of the index finger, the middle of the nail edge of the thumb, the ulnar head, the olecranon, and the acromion. While full kinematic data were recorded to allow comprehensive movement analysis, this study focused specifically on hand rotation, using only index and thumb marker data. The signal was digitised at 100 Hz, low-pass filtered (12 Hz cut-off frequency) using a tenth-order Butterworth filter, segmented into trials, and derived to obtain the standard kinematic descriptions: position and velocity (i.e., time derivative of position). Data preprocessing was performed using Matlab 9.9.0 software[150].

Hand rotation accuracy

Response accuracy was measured by comparing the angle of the hand aperture rotation (APEr) to the stimulus orientation. APEr was calculated at the screen's nearest position as the inverse tangent of the index-thumb distance (degrees) in x and z planes. Correct trials required APEr < 90° for upward stimuli (stimulus orientation < 90°) or APEr > 90° for downward stimuli (stimulus orientation > 90°), for study 1 and session *clockwise* (study 2). Because of the reversed hand response mapping (Fig. 1c), correct trials required APEr < 270° for upward stimuli (stimulus orientation < 90°) or APE > 270° for downward stimuli (stimulus orientation > 90°), for session *counterclockwise* (study 2).

Hand rotation kinematics

We analysed two kinematic measures of hand rotation (APEr): (1) rotation onset was computed from stimulus appearance using an automated movement-parsing algorithm[151] on the time series of the APEr; (2) rotation smoothness was quantified using the spectral arc length[88], a Fourier-based metric of the speed profile that is both more sensitive to behavioural changes and more noise-resistant than alternative measures. The speed profile (angular velocity of the hand aperture) was computed as the sum of vectorial products of distance and velocities divided by the norm squared of the distance:

$$\omega = \frac{d \times v_T + d \times v_I}{|d|^2}$$

ω is the angular velocity; d is the distance between thumb and index; v_T is the thumb velocity; v_I is the index velocity and velocities divided by the norm squared of the distance. Distance and velocity are taken in the coronal plane.

Statistical analysis

The kinematic parameters analysis was performed only on accurate trials. For each parameter, the effects of the amplitude of rotation and awareness for study 1, plus the effect of direction of rotation for study 2 (Fig. 1c), were analysed using mixed-effect multiple regression modelling[152,153]. For study 1, each model included two fixed effects and their interaction: *amplitude of rotation* (AoR, two levels: small, large) and *awareness* (two levels: aware, unaware). For study 2, each model included three fixed effects and their interactions: *amplitude of rotation* (two levels: small, large), *awareness* (two levels: aware, unaware), and *direction of rotation* (DoR, two levels: clockwise, counterclockwise). The random structure of the models included by-subject random intercepts. We selected a parsimonious structure to balance Type I and Type II error control optimally and maintain statistical power while avoiding overfitting[154,155]. We performed a Type III test to assess the significance of the main effects and interactions. For accuracy, because the variable was dichotomous, a generalised multiple regression model with a logistic link function and binomial variance was adopted[156], and p-values were calculated via the likelihood ratio tests. For the kinematic parameters, the data were transformed using the cube root after errors in measurement were removed. We excluded trials with hand rotation onset outside the 100–2000 ms range (9.57% and 12.57% for experiments 1 and 2, respectively) and trials with smoothness values below − 3 (0.24% in Experiment 1 and 1.23% in Experiment 2). The cutoff value of -3 was selected because it lies below the first quartile (− 1.541 to − 1.573) and is physiologically implausible for healthy movement smoothness (SPARC typically ranges from − 2 to 0 in human reaching movements;[88];[157]). Values beyond this threshold likely indicate non-physiological noise or artefacts, such as sensor errors. P-values for multiple comparisons were corrected using Bonferroni procedure[158]. Observations with a standardised residual at a distance greater than 2.5 standard deviations from zero[159] were removed (2.83% and 2.34% for accuracy; 1.78% and 2.04% for rotation onset; 2.50% and 3.95% for rotation smoothness). In addition, participants with an average accuracy 2SD below the mean performance were excluded from the analysis (one participant for each study). Statistical analyses were performed using lme4 package[154], afex package[160], lmerTest package[161], emmeans package[162], and ggrain package[163] in the R environment[164].

Data availability

The experimental data that support the findings of this study are available from OSF with the identifier https://doi.org/10.17605/OSF.IO/UTNVE.

Received: 4 April 2025; Accepted: 6 March 2026

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Acknowledgements

We want to express our gratitude to Matteo Bertucco for his valuable suggestions. We also wish to thank Gianni Finizia, Francesca Nardello, and Matteo Meneghetti for their technical support, and Francesco Longo and Alex Tirapelle for their contributions to data collection.

Author contributions

E.C., S.S., and P.C. conceive the study. V.M., E.C., S.S., and P.C designed the experiment. V.M. and F.P. ran the experiments and analyzed the data. V.M. drafted the manuscript. All authors interpreted and discussed the results and revised the manuscript at all stages.

Funding

Fondazione Cassa di Risparmio di Verona Vicenza Belluno e Ancona, 2018.0861, Ministry of University and Research (MUR), 897 1553 11.10.2022. E.C. was supported by Fondazione Cassa di Risparmio di Verona Vicenza Belluno e Ancona "Ricerca scientifica d'eccellenza 2018" (grant no. 2018.0861). S.S. was supported by NEXTGENERATIONEU (NGEU) and funded by the Ministry of University and Research (MUR), National Recovery and Resilience Plan (NRRP), project MNESYS (PE0000006)—A multiscale integrated approach to the study of the nervous system in health and disease (DN. 897 1553 11.10.2022).

Declarations

Competing interests

The authors declare that they have no competing interests.

Additional information

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