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Mechanisms of proprioceptive realignment in human motor learning

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Adaptation is a form of motor learning that alters movement in response to a predictable perturbation to the body or environment. This process can also realign or bias proprioception of the adapted movement. Here, we discuss recent work on two mechanisms that are suggested to underlie proprioceptive realignment following motor learning: a sensory mechanism that hinges on mismatches between estimates of limb state across sensory modalities, and a motor mechanism driven by the recalibration of sensory predictions of movement. We review work focused on normal behavior, neuroimaging studies and assessments of neurologic patients suggesting that motor systems, such as the cerebellum, and sensory association systems, such as somatosensory and posterior parietal cortices, may play a role in proprioceptive realignment.

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Introduction

Proprioception is a term that broadly encompasses the sense of body position and movement in the absence of vision [1]. It is well established that proprioception is needed for normal movement control and motor learning, both of which are essential for successful interactions with the environment. Here, we discuss the opposite phenomenon — how movement and motor learning affect proprioception. It has long been known that movement can affect proprioception. In particular, the effects of exercise and fatigue on proprioceptive acuity have been well documented [2–5]. Furthermore, a type of motor learning

called 'adaptation' can affect an individual's perception of limb position (e.g. Refs. [6,7]). This review focuses on recent work addressing this latter phenomenon in the context of reaching, walking and how it develops in childhood. We then discuss a recent framework for interpreting and further testing these phenomena, as well as current data on the neural substrates that might be involved.

The term 'proprioceptive realignment' is used here to refer to shifts or biases in the perception of limb position or movement thought to arise from central processing mechanisms. This review will not cover any peripheral manipulations that can bias proprioception, such as muscle vibration, contraction or stimulation [1]. We also will not discuss the body of work that shows the nervous system can re-weight which sensory modality it depends on most, a phenomenon that has been modeled using minimum variance integration [8,9].

Motor adaptation realigns proprioceptive estimation in reaching and walking

Motor adaptation describes the processes of learning to alter movement commands in response to a novel, predictable perturbation to the body or environment [10]. It involves multiple learning processes - some operating across movement types and adaptation conditions, and others exhibited only in specific paradigms. One learning process thought to operate across adaptation types is the recalibration of a forward model, which uses information about a motor command and the current state of the body to generate a prediction of the expected sensory outcome of a movement [11,12]. When movement is first perturbed, the predicted sensory outcome does not match the actual outcome, signaling a sensory prediction error. Sensory prediction errors drive a recalibration of the forward model to account for the perturbation. As the forward model is recalibrated, movement errors are reduced. A hallmark of this process is observed when the perturbation is removed, and movement does not immediately return to the pre-adapted state. Instead, individuals exhibit 'after-effects,' which reflect the newly stored sensorimotor calibration.

Visuomotor adaptation in reaching occurs to account for a visual-proprioceptive mismatch perturbation and has long been known to realign proprioceptive estimates of hand position [6]. Visuomotor adaptation is often induced by asking subjects to reach while wearing laterally shifting prism glasses or in a virtual environment where visual

feedback about their hand position is rotated. The latter is depicted in Figure 1a. In early adaptation, when subjects reach straight ahead to the target (blue), they are shown a cursor whose movement is rotated 45° to the left (black). By late adaptation, subjects learn to rotate their reaching movements rightwards so the cursor successfully reaches the target. This new reaching angle is taken as a measure of motor adaptation. When the visual rotation is removed post-adaptation, subjects continue to reach with a rightwards rotation showing that a recalibrated forward model prediction of rotated visual feedback has been stored. They also realign proprioception such that when asked to reach straight ahead, they actually reach to a rightwards endpoint position that feels straight ahead (post-adaptation perceptual change, purple). The reaching angle produced here is taken as a measure of proprioceptive realignment.

Studies of proprioceptive realignment in visuomotor adaptation tasks have identified some key characteristics. First, the magnitude of proprioceptive realignment is typically less than the magnitude of motor adaptation, making up only 25-45% of the total motor change on average [13–17]. The rate of proprioceptive realignment also tends to lag the rate of motor adaptation [16]. Finally, proprioceptive realignment with visuomotor adaptation is robust to task manipulations such as removing visual feedback during movement [18], removing visual feedback at movement endpoint [19], and increasing explicit awareness of the perturbation [20].

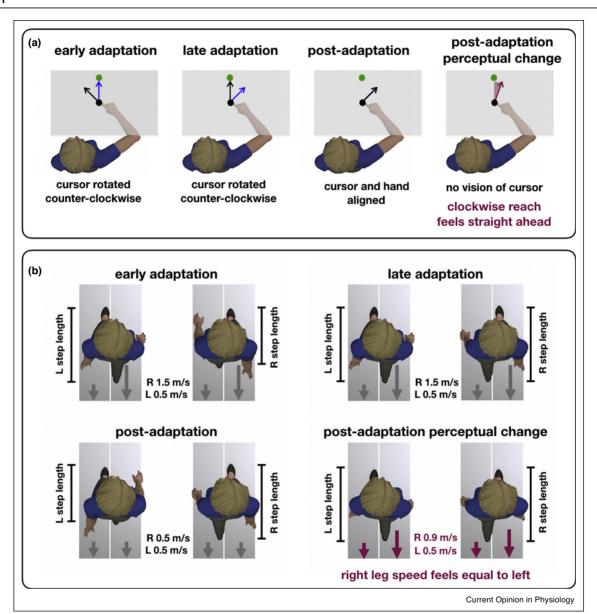
Most work studying proprioceptive realignment with adaptation has examined visual-proprioceptive mismatch perturbations. However, a growing body of literature is showing that proprioceptive realignment also occurs with adaptation paradigms that elicit other types of sensorimotor perturbations. In reaching, adaptation to force-field perturbations can realign proprioceptive estimates of hand position [21-23,24°]. Other work has studied locomotor adaptation, which is driven by a split-belt treadmill and requires individuals to alter their walking pattern to account for a perturbation that forces one leg to move faster than the other. Figure 1b depicts a common locomotor adaptation paradigm where subjects walk with their right leg moving three times faster than their left leg. In early adaptation, when the split-belt perturbation is initially applied, people walk with an asymmetric stepping pattern. That is, they walk with right steps that are shorter than the left steps (R and L step lengths, black lines) and produce a limping gait. Over hundreds of steps, people adapt their step length while walking to re-establish a symmetric stepping pattern. By late adaptation, they exhibit equal step lengths across legs, despite the treadmill moving the legs at different speeds. Post-adaptation, when the split-belt perturbation is removed (and the treadmill moves both legs at the same speed), people exhibit a new asymmetric stepping pattern that is the inverse of the asymmetry shown in early adaptation. They show an after-effect where they walk with right steps that are longer than the left steps. This after-effect shows that the forward model has recalibrated to account for the imposed difference in leg speeds.

Following locomotor adaptation, individuals do not develop a biased perception of foot position during walking, but do realign their perception of leg speed [25] and, as a consequence, the perception of step length [26**]. This proprioceptive realignment has been tested by having participants adjust the speed of the right treadmill belt, until they perceive it to be equal to the speed of the left belt [25]. Hence, participants select walking speeds of the two legs that are perceived as equal. A difference in selected speeds indicates a realignment of leg speed perception. This paradigm has shown that the leg trained on the "fast" treadmill belt is perceived to be moving slower than its true speed. Hence, after adapting to walk with the right leg 3x faster than the left, individuals report a perception that their legs are moving at the same speed when, in reality, the right leg is moving approximately 80% faster than the left leg (Figure 1b, post-adaptation perceptual change). Notably, the realigned perception does not transfer to backwards walking, suggesting that proprioceptive realignment in this case is specific to the movement that was adapted [25].

Locomotor and reaching adaptation are also known to exhibit savings, which is defined as the faster learning and reduced motor after-effects associated with re-exposure to the same perturbation [10,27,28]. For example, after five days of repeated locomotor adaptation, subjects show reduced initial stepping asymmetry upon introduction to the split-belt treadmill perturbation - the initial stepping asymmetry is $\sim 20\%$ of that shown on day one. Furthermore, locomotor after-effects are reduced to a stepping asymmetry that is ~20% of that observed on day one [27,29°]. Recently, Leech et al. [29°] showed that proprioceptive realignment with locomotor adaptation also exhibits savings-like behavior. After one exposure to split-belt walking, subjects perceived their leg speeds to be equal when the right speed was $\sim 80\%$ faster than the left. After 5 exposures to split-belt walking, this difference in leg speeds was reduced to $\sim 30\%$. Thus, after 5 exposures, proprioceptive realignment is reduced to $\sim 40\%$ of that observed in day one, which is different from the reduction in motor after-effects. Therefore, savings-like behavior is seen in the perceptual domain, but to a lesser extent than is seen in the motor domain.

One interpretation of Leech et al.'s results is that the mechanisms for motor adaptation and proprioceptive realignment are partially shared. Additional evidence for a partial sharing of mechanisms between motor adaptation and proprioceptive realignment comes from a study of development. Rossi et al. [30**] showed that the

Figure 1



Proprioceptive realignment following visuomotor and split-belt adaptation. (a) In visuomotor adaptation, participants reach to a visual target while being exposed to a visual-proprioceptive mismatch that artificially rotates visual information of the hand. Early adaptation: the participant reaches straight to the target with their hidden hand (blue), but the cursor representing hand position is rotated 45 degrees counterclockwise from the hand (black). Late adaptation: the participant learns to compensate for the mismatch by reaching 45° clockwise (blue), such that the cursor successfully lands on the target (black). Post-adaptation: the visual rotation is removed (i.e. the cursor now shows veridical hand position), but the subject continues to reach with a clockwise rotation (black), showing that the recalibrated forward model prediction of the rotated visual feedback has been stored. Post-adaptation perceptual change: after adaptation, participant's sense of hand position is biased rightward. The participant feels that they are reaching straight ahead when in reality they are reaching ~20° clockwise (purple). Hand position bias is also measured when a robotic device passively displaces participant's hand. (b) In split-belt treadmill adaptation, participants learn to walk with the belt under one foot moving faster than the belt under the other foot. Early adaptation: the participant walks with the right leg moving 3x faster than the left leg. Initially, this causes the right steps to be shorter than the left steps. Late adaptation: the participant learns to compensate for the difference in leg speeds by adjusting the position and timing of their steps. They still walk with the right leg moving 3x faster than the left, but they exhibit equal step lengths across the legs. Post-adaptation: the legs now move at the same speed, but the participant shows a new asymmetric stepping pattern that is the inverse of the asymmetry shown in early adaptation (they take shorter left steps). This is because the recalibrated forward model prediction of the walking pattern has been stored, and the participant continues to walk with the adapted walking pattern. Post-adaptation perceptual change: the participant's perception of leg speed is biased such that the right leg (which was trained to move faster), now feels slower than its true speed. The participant perceives their legs to move at the same speed, when in reality, their right leg moves 0.4 m/s faster than their left. This reflects what we refer to as a proprioceptive realignment.

learning mechanisms underlying proprioceptive realignment and motor adaptation may develop at a similar age in childhood. Their study examined the development of proprioceptive realignment with locomotor adaptation in children aged 6-8 years. Previous work showed that, in this age range, children become progressively faster at adapting their step length, until some children show adult-like motor adaptation [31,32]. Rossi et al. showed that proprioceptive realignment is also developing in this age range, such that some children show no or reduced realignment of leg speed perception, and others are like adults. The authors interpret this as evidence for the maturation of a new mechanism that is coming online in children. However, across individuals the magnitude of proprioceptive changes did not correlate with either the extent or rate of motor adaptation. Given this result, the authors posit that proprioceptive realignment reflects only one of multiple mechanisms involved in generating the time course of motor adaptation. Alternatively, the motor and perceptual changes that occur with adaptation could reflect co-developing, but independent, processes.

Proprioceptive realignment with adaptation may reflect the output of two mechanisms

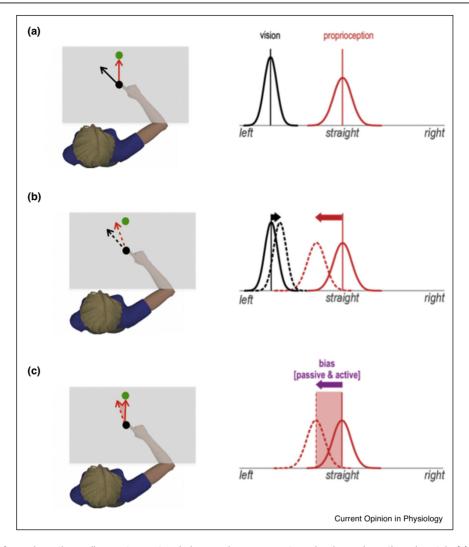
As reviewed in the preceding section, adaptation to different perturbations appears to induce dissociable types of proprioceptive realignment. Adaptation to visual-proprioceptive mismatch perturbations appears to realign the perception of limb position. In contrast, adaptation to split-belt treadmill perturbations does not realign the perception of limb position, but rather realigns perceptions of limb movement (i.e. speed and displacement). Taken together, these results suggest that proprioceptive realignment may stem from the output of two mechanisms whose relative contribution depends on the adaptation paradigm tested. Here, we discuss two mechanisms proposed to contribute to proprioceptive realignment: a sensory mechanism driven by a mismatch between sensory modalities and a motor mechanism driven by a recalibrated forward model.

The sensory mechanism can be engaged when proprioceptive estimates of limb position differ from the estimates of another sensory modality, such as vision. Figure 2 depicts a typical paradigm used to study the sensory mechanism of realignment. A robotic device passively moves participants' right hand straight ahead (Figure 2a). The true hand position is hidden, and participants are instead shown a cursor that is rotated 45° to the left. With sufficient exposure to the sensory mismatch, the proprioceptive estimate is shifted towards the visual estimate (Figure 2b). When vision is removed, the proprioceptive shift persists such that the sense of hand position becomes biased - participants perceive that their hand moves leftwards when, in reality, it moves straight ahead (Figure 2c). Visual estimates are also shifted towards proprioceptive estimates, but to a lesser extent (Figure 2b) [33,34]. Importantly, the sensory mechanism does not require that movement be performed or adapted. The realignment here occurs simply through repeated exposure to the sensory mismatch. Despite this, proprioceptive realignment through the sensory mechanism can influence motor output. While it is not known exactly how this occurs, it is possible that proprioceptive realignment from the sensory mechanism could bias the estimate of current body state, thereby altering motor output without recalibrating forward model predictions per se.

The motor mechanism of proprioceptive realignment is not well understood and has been the subject of recent study. It is hypothesized to be driven by the same sensory prediction error thought to drive motor adaptation. As adaptation recalibrates the forward model in response to sensory prediction errors, perception of body position and motion could also be biased. Indeed, forward model predictions are known to influence proprioceptive estimation [35,36]. The sensory and motor mechanisms could operate independently as well as in combination, depending on the perturbation. Adaptation to a visuomotor perturbation involves both prolonged exposure to a visual-proprioceptive mismatch and a recalibration of the forward model. As a result, both sensory and motor mechanisms are hypothesized to contribute to the proprioceptive realignment seen in these tasks. Conversely, adaptation to split-belt treadmill perturbations involves a mismatch between predicted and actual proprioceptive feedback, which drives a recalibration of the forward model. Split-belt treadmill adaptation is not driven by a mismatch between sensory modalities. Therefore, the proprioceptive realignment observed with locomotor adaptation is hypothesized to reflect only the motor mechanism.

Figure 3 shows how the sensory and motor mechanisms may combine to produce proprioceptive realignment in visuomotor adaptation. Initially, participants reach straight ahead, and both predict and sense their hand to move straight ahead, but the visual cursor moves 45 degrees leftwards (Figure 3a). This generates both visual-proprioceptive mismatches and sensory prediction errors, which respectively drive proprioception and forward model predictions to recalibrate towards vision (Figure 3b). The recalibrated forward model predicts that rightward reaches will be seen as straight ahead, and this prediction, together with biased proprioception, realigns the sense of hand position such that rightward reaches also feel straight (Figure 3c). Figure 4 shows instead how the motor mechanism may alone produce proprioceptive realignment in split-belt locomotor adaptation. Initially, participants walk with motor commands that are predicted to produce equal step lengths, but instead the belt speed difference imposes a step length asymmetry (Figure 4a). This generates sensory prediction errors that drive forward model predictions to recalibrate towards

Figure 2



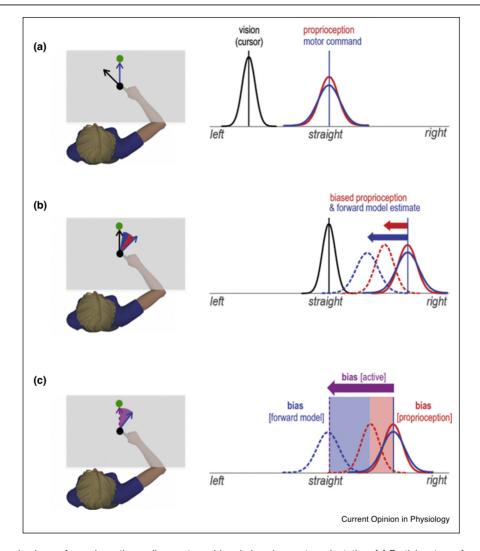
Sensory mechanism of proprioceptive realignment operates during passive exposure to a visual-proprioceptive mismatch. (a) Participants are passively moved through a reach using a robotic device. The true hand position (red) is hidden and the visual cursor representing hand position is rotated 45° to the left of the true hand position (black). This results in a sensory mismatch (i.e. a mismatch between visual and proprioceptive estimates of hand position). (b) With prolonged exposure to the sensory mismatch, vision and proprioception realign (dashed black and dashed red), such that the two estimates are closer to each other and the perceived mismatch is reduced. (c) When visual information is removed, the proprioceptive realignment is maintained. Participants' sense of hand position is now biased so that, when the hand is moved straight ahead (solid red), participants perceive it to the left of its true position (dashed red). This effect is visible in both passive and active (i.e. voluntary) movement of the hand. Adapted from Munoz-Rubke et al. [43] and Petitet et al. [44].

proprioception (Figure 4b). The recalibrated forward model predicts that an asymmetric set of motor commands will produce equal step lengths, and this prediction affects proprioception such that asymmetric step lengths and leg speeds feel equal (Figure 4c). The legends of Figures 3 and 4 describe in detail how sensory predictions from the forward model may combine with proprioception to alter the sense of hand position, step length or leg speed as tested by studies discussed here.

The contribution of motor and sensory mechanisms to proprioceptive realignment can be differentially

measured using either active or passive tests. The sensory mechanism's contribution would be present for both tests. In contrast, the motor mechanism's contribution should only be observed in active tests, because forward model predictions are generated from motor commands. Using this framework, Mostafa et al. [37**] dissected the sensory and motor mechanisms of proprioceptive realignment following visuomotor adaptation to rotated visual feedback in reaching. Proprioceptive realignment was measured by asking participants to report their perceived hand location at the endpoint of a reach. This reach was executed either passively using a robotic device (passive

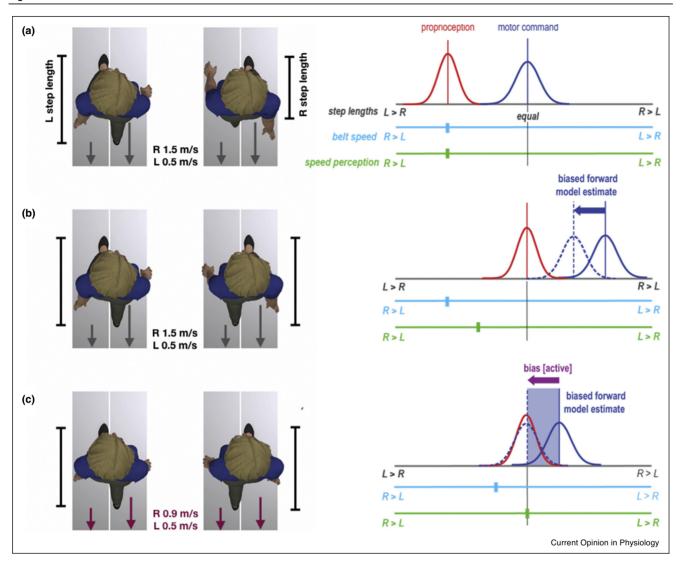
Figure 3



Sensory and motor mechanisms of proprioceptive realignment combine during visuomotor adaptation. (a) Participants perform active reaching movements to a target while their hand is hidden from view (blue). The visual cursor representing hand movement is rotated 45° to the left of the true hand position (black). This causes two types of mismatches. First, a sensory mismatch (i.e. a mismatch between visual and proprioceptive estimates of hand position - black and red). Second, a mismatch between the predicted and actual sensory consequences of movement (blue and black), which generates sensory prediction errors. Specifically, participants predict that when reaching straight ahead, the cursor movement will follow the motor command (blue), but in reality the cursor is seen to move to the left (black). (b) The sensory mismatch drives proprioception to realign towards vision (red arrow), such that the hand position is perceived to be leftwards of its true position (dashed red). Concurrently, sensory prediction errors also drive the forward model prediction to recalibrate (blue arrow), such that the cursor is predicted to move leftwards of the true motor command generated (dashed blue). The forward model recalibration, along with additional motor learning mechanisms, corrects the reaching direction to account for the imposed cursor rotation: the participant reaches 45° rightwards (solid blue) and the cursor is seen to move straight ahead (black). (c) When vision is removed, the realignment of proprioception (dashed red) and of the forward model (dashed blue) are maintained. The forward model predicts that rightward reaches will be seen as straight ahead. It also contributes to proprioceptive realignment such that, when the participant actively reaches rightwards (solid blue), they perceive that their hand has moved straight ahead (dashed blue). The bias in active hand position (purple arrow) is a combination of proprioceptive (red shade) and forward model (blue shade) realignments. Proprioception and forward model estimates may add as shown here, or integrate in a Bayesian manner, or combine in other ways. Instead, when the participant's arm is passively moved rightward by a robot (solid red), the bias in passive hand position only reflects realignment of proprioception and is smaller (dashed red). Adapted from Petitet et al. [44].

proprioceptive test) or actively by the participant (active proprioceptive test). The passive test detected a small bias ($\sim 3^{\circ}$ on average) in participants' sense of hand position in the direction of the rotation perturbation. The active test detected a larger bias in hand position sense (\sim 6°) in the same direction. The authors posited that the passive test reflected only the sensory mechanism of proprioceptive realignment, while the active test reflected the contribution of both the sensory and motor mechanisms.

Figure 4



The motor mechanism of proprioceptive realignment operates during split-belt adaptation. (a) Participants walk on a split-belt treadmill that forces the right leg to move faster than the left leg. They initially adopt the same set of motor commands as they would on a normal treadmill, and predict that this will result in symmetric step lengths (blue). However, the difference in belt speeds imposes a step length asymmetry such that participants walk with left steps that are longer than the right steps. This gait pattern asymmetry is sensed through proprioception (red). The discrepancy between forward model prediction and proprioception generates sensory prediction errors. (b) The sensory prediction errors drive a recalibration of the forward model prediction towards proprioception (dashed blue). Participants use this and other mechanisms to adjust their motor commands (solid blue) to generate equal step lengths (red). Subjects perceive the belt speed difference to be less than it is (green versus cyan). It is not fully understood how the forward model and proprioceptive estimates are combined. (c) After adaptation, the recalibrated forward model prediction is maintained such that an asymmetric set of motor commands (solid blue) is predicted to produce equal step lengths (dashed blue). Recalibrated forward model predictions are then integrated with (unbiased) proprioception, such that the novel set of motor commands feels more symmetric than it really is (purple arrow). This proprioceptive realignment manifests as biased perception of leg speed and step length. The realignment of leg speed perception is tested by having participants actively walk on the treadmill and select belt speeds that feel equal. The belt speeds are perceived to be equal when step lengths are both predicted and sensed to be equal; that is, when both forward model predictions (dashed blue) and proprioception of gait pattern asymmetry (red) are at symmetry. This configuration occurs by selecting a right belt speed that is faster than the left (cyan), accounting for the degree of forward model recalibration (blue shade). The realignment of step length perception is instead tested with participants walking with equal belt speeds and it is not depicted here. In this configuration, the recalibrated gait pattern generates asymmetric steps lengths. The step lengths are predicted to be equal by the forward model, and also feel more equal than they really are. Note that the biases in leg speed and step length perception only reflect the recalibration of the forward model, while proprioception remains unbiased. Therefore, they are only measurable with active voluntary movement.

In a second experiment Mostafa et al. tested whether the motor mechanism of proprioceptive realignment corresponded to the recalibration of forward model predictions driven by motor adaptation. The authors passively exposed participants to the same visual-proprioceptive mismatch as in their first experiment, using a robot to move the arm. As the task involved no motor commands, the authors posited that forward model predictions should not be recalibrated, which would preclude the motor mechanism's contribution to any proprioceptive realignment observed. Following passive exposure to the visual rotation, the authors measured proprioceptive realignment with active and passive tests. In contrast to experiment 1, the measured hand position bias did not differ between the two tests, suggesting that only a sensory but not a motor — mechanism contributed to realignment. This result confirms that a recalibration of forward model predictions (as driven by adaptation) is needed for a motor mechanism of proprioceptive realignment to operate. Together, the results of both experiments confirm that forward model predictions generated during movement are capable of realigning proprioception and suggest they can combine with the realignment that occurs from sensory mismatches.

Work from Sombric et al. [26^{••}] investigated the contribution of a motor mechanism to proprioceptive realignment following locomotor adaptation to a split-belt treadmill. Realignment of step length perception was measured by asking participants to report the perceived distance between their feet. Sombric et al. used both a passive test — where the treadmill relocated participants' feet while they stood still — and an active test — where participants were asked to walk with steps of specific lengths (before adaptation, participants underwent training to ensure they could take steps of the desired length). The passive test showed almost no proprioceptive realignment, suggesting that the sensory mechanism may not contribute to realignment in locomotor adaptation. In contrast, the active test showed substantial realignment of perceived step length. That is, the steps taken by the leg adapted to move faster were perceived to be 10-20% shorter than the true value, and the steps taken by the leg that moved more slowly in adaptation were perceived to be 10–20% longer than the true value. Overall, these results indicate that proprioceptive realignment in locomotor adaptation may stem entirely from a motor mechanism.

Potential neural substrates of proprioceptive realignment

Motor mechanism of proprioceptive realignment

The motor mechanism of proprioceptive realignment appears to be tightly coupled with movement and motor learning. Hence, it is possible that brain regions important for motor control and learning may contribute to proprioceptive realignment. Of particular interest is the cerebellum. Damage to this structure induces deficits in motor adaptation (e.g. Ref. [38]) that are thought to stem from an impairment affecting forward model predictions [39-41]. Furthermore, cerebellar damage has been shown to disrupt proprioceptive acuity in a manner that is consistent with disrupted prediction [35]. The idea that the cerebellum is involved in sensory processing is also informed by the fact that it is substantially interconnected with the sensory systems. It receives direct proprioceptive input via the spinocerebellar tract as well as forming multiple reciprocal loops with sensory areas of the cerebral cortex via the thalamus and pons [42]. Thus, it is plausible that a motor mechanism of proprioceptive realignment, which is driven by the recalibration of forward model predictions, may depend on the cerebellum.

A few studies have shown that cerebellar damage can impair both visuomotor adaptation and proprioceptive realignment [43,44,45]. Block et al. [45] dissociated cerebellar involvement in the motor and sensory mechanisms of realignment by manipulating the availability of sensory prediction error feedback in two visual-proprioceptive mismatch tasks. In both tasks, the authors had cerebellar patients and matched control participants perform voluntary reaches to a single target position that could be specified visually (V-target, as a projected image), proprioceptively (P-target, by the configuration of the contralateral arm), or with both sources of information (VPtarget). Participants' arms were hidden from view throughout. Over successive reaches to the VP-target. Block et al. gradually introduced a visual-proprioceptive mismatch by displacing the V-target relative to the Ptarget. They then tested proprioceptive realignment by measuring the bias exhibited on reaches to the P-target. Importantly, the two tasks differed in whether participants were shown their hand position at reach endpoint on VP-target trials. Showing the hand position as the visual target was gradually displaced provided sensory prediction error information, which could be used to recalibrate forward model predictions of the reach and drive the motor mechanism of proprioceptive realignment. By not showing the hand position, Block et al. removed the input necessary to drive the motor mechanism, leaving only the sensory mechanism to drive proprioceptive realignment. Block et al. found that, relative to control participants, cerebellar patients showed reduced proprioceptive realignment in the task that showed the hand position (control realignment: \sim 28 mm, cerebellar realignment: ~16 mm). However, cerebellar patients showed a comparable degree of proprioceptive realignment to control participants in the task that did not show the hand position (control realignment: \sim 13 mm, cerebellar realignment: \sim 15 mm). Together, these results suggest that cerebellar damage induces a selective impairment affecting the motor mechanism of proprioceptive realignment, but leaves the sensory mechanism intact. Notably, the magnitude of proprioceptive realignment exhibited by cerebellar patients was similar across both tasks, which is in agreement with the results of Mostafa *et al.* showing that actively tested realignment reflects the combined input of both mechanisms.

Support for a cerebellar role in the motor mechanism of proprioceptive realignment also comes from a recent study of locomotor adaptation. As noted above, proprioceptive realignment in this task is thought to stem primarily from the motor mechanism. Statton et al. [46°] had cerebellar patients and healthy controls adapt to a splitbelt treadmill perturbation that forced the right leg to move faster than the left leg. The authors then measured proprioceptive realignment as the difference in leg speeds when participants reported them to be equal. Cerebellar patients showed impaired adaptation relative to controls. Accordingly, while healthy controls showed realigned perception of leg speed, cerebellar patients did not. Specifically, control participants chose a right belt speed that was $\sim 20\%$ faster than the left belt speed. Cerebellar patients chose belt speeds that were not significantly different from each other. Notably, Statton et al. found that individual patients' ability to realign proprioception depended on the severity of cerebellar damage, as measured by their clinical score of motor impairment.

Sensory mechanism of proprioceptive realignment

The sensory mechanism of proprioceptive realignment appears to be driven by a pure sensory mismatch (e.g. between proprioception and vision) and does not hinge upon motor learning. Hence, it is possible that brain regions involved in proprioceptive processing and sensory association may play a role in this mechanism of realignment. Of interest are the primary and secondary somatosensory and parietal cortices, as well as the insula, which have all been shown to process proprioceptive information [47]. Visuomotor adaptation has been associated with changes in activity in the posterior parietal cortex (PPC) [48] and PPC damage has been shown to impair learning in these tasks [49]. Functional connectivity between sensorimotor and insular cortex has also been linked to visuomotor adaptation learning [50]. Yet, work on the role of these systems in proprioceptive realignment remains limited.

Block *et al.* [51] used transcranial magnetic stimulation (TMS) to transiently disrupt a region of the PPC before participants were exposed to a visual-proprioceptive mismatch in reaching using the same paradigm as described above in Ref. [45]. Their task had participants reach with the mismatch, but they were not shown their hand position relative to the visual feedback. This ensured that any proprioceptive realignment observed would reflect only the sensory mechanism. Participants showed similar

magnitudes of proprioceptive realignment regardless of whether they received TMS or Sham stimulation. While this study may suggest that the PPC is not necessary for the sensory mechanism of proprioceptive realignment, further work is needed to elucidate whether this is truly the case.

On the other hand, the sensory mechanism of proprioceptive realignment may also involve motor systems. Motor and sensory areas of the brain are highly interconnected, and as stated above, realignment from the sensory mechanism can alter motor output. Recent work from Munoz-Rubke et al. [52°] suggests that the primary motor cortex (M1) may play a role in proprioceptive realignment from the sensory mechanism. These authors exposed participants to a visual-proprioceptive mismatch using the same paradigm as described above in Refs. [45] and [51]. As in Ref. [51], participants were not shown the position of their hand relative to the visual feedback. Therefore, any biasing of perceived hand position would reflect the sensory mechanism. They measured proprioceptive realignment — that is, the magnitude of hand position bias — as well as changes in M1 activity using TMS. They found that larger proprioceptive realignment was correlated with decreased M1 excitability.

Finally, work from Vahdat et al. [53] used fMRI to investigate changes in resting state connectivity between brain regions that may be involved in proprioceptive realignment of hand position with adaptation. Notably, Vahdat et al. had participants adapt to a force-field perturbation during reaching that pushed the hand trajectory in a curved path. Force-field adaptation is an interesting task to consider here. The perturbation drives an adaptation of reaching movements to account for novel environmental dynamics and return the reach trajectory to a straight path. This kind of adaptation is considered to hinge upon a mismatch between predicted and actual proprioceptive feedback driving a recalibration of forward model predictions. Importantly, visual feedback of hand position is never displaced relative to the proprioceptive estimate of hand position, meaning that no mismatch between sensory modalities is introduced. As a result, one would hypothesize that any proprioceptive realignment seen with this task should reflect the motor mechanism alone. Yet, as noted above, force-field adaptation has been shown to realign proprioceptive estimates of hand position at reach endpoint [21–23], even when a passive test was used [24°] — an effect associated with the sensory mechanism.

Vahdat et al. also tested proprioceptive realignment using a passive test. That is, they measured the bias in perceived hand position at the endpoint of a passive, robotcontrolled, reach. They found that proprioceptive realignment was related to changes in connectivity between somatosensory and premotor cortices, as well as between PPC and the cerebellum. Together, these results suggest that the proprioceptive realignment occurring with forcefield adaptation may reflect both the sensory and motor mechanisms, despite the perturbation only providing direct input to the latter. This is highly interesting and begs further research.

Conclusions and future directions

In this review, we discussed recent studies of proprioceptive realignment - the biasing of perceived limb position or motion that can occur with motor adaptation. It has traditionally been assessed using adaptation to visuomotor perturbations, but recent work has begun to study this phenomenon with locomotor adaptation, which is not considered to hinge on a discrepancy between sensory modalities. This new work is revealing that proprioceptive realignment can arise in two ways: from compensation for visual-proprioceptive mismatches (a sensory mechanism) as well as from a biasing of the forward model predictions associated with adapted movement (a motor mechanism). While these two mechanisms may combine in some adaptation paradigms, it is now clear that an altered sensory prediction of movement from the forward model can drive proprioceptive realignment on its own. Importantly, this framework opens new questions that should drive future research. We do not understand how the contributions of sensory and motor mechanisms may be combined. It is possible that the two are integrated in a Bayesian manner as described in Petitet et al. [54°], or their contributions may be additive [55]. Furthermore, the brain areas responsible for the sensory mechanism may differ from those underlying the motor mechanism, but the precise neural mechanisms involved remain unclear. Finally, while a large body of work has studied proprioceptive realignment with adaptation, it is of interest to know whether the phenomenon also occurs with other forms of motor learning, such as in the case of learning new motor skills.

Conflict of interest statement

Nothing declared.

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This is an example of proprioceptive realignment following force-field adaptation. Using a passive task, the study found that participants' sense of hand position becomes biased. They found that proprioceptive realignment and motor after-effects (i.e. lateral deviation of the hand in reaching) occur in the same direction and their magnitudes across participants are correlated. Interestingly, both of these findings (1. passive proprioceptive realignment in the absence of visual-proprioceptive mismatches, and 2. correlated magnitudes of motor and proprioceptive after-effects) differ from what we observe in visuomotor or split-belt adaptation paradigms.

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This study asked whether perception of step length is modified following locomotor adaptation on a split-belt treadmill. The importance of the study is twofold. First, they showed close-to-none changes in step length perception tested passively. This suggests that proprioceptive realignment may not reflect changes in proprioceptive sense per se (i.e. a sensory mechanism). Second, they showed large changes in step length perception tested actively, such that perception of step length was biased towards the motor after-effect of step length. This suggests that changes in motor efferent signals may contribute to the proprioceptive realignment (i.e. a motor mechanism), potentially through the forward model predictions that they generate.

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This study tests for 'savings' of both locomotor adaptation and realignment of leg speed perception. They demonstrate savings of proprioceptive realignment such that the magnitude of the realignment was reduced after five exposures to split-belt walking, as compared to the first exposure. The extent of savings differed for proprioceptive realignment versus motor adaptation: while motor after-effects were reduced to 20% of their first-exposure magnitude, proprioceptive realignment was only reduced to 40% of its first-exposure magnitude. This suggests that motor adaptation and proprioceptive realignment are partially independent

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This study reports on three important findings. First, it dissects the contributions of sensory and motor mechanisms to proprioceptive realignment in visuomotor adaptation. They find that while a sensory mechanism (in response to visual-proprioceptive mismatch) accounts for most of the proprioceptive realignment, a motor mechanism also contributes significantly. Second, it shows that a motor mechanism of proprioceptive realignment only develops during adaptation, and not during a passive exposure to a visual-proprioceptive mismatch, supporting the idea that this mechanism is driven by recalibrated sensory prediction of movement by a forward model. Third, the study demonstrates that the sensory mechanism of proprioceptive realignment driven by the passive exposure to visual-proprioceptive mismatch- also modifies movement. This suggests that the sensory mechanism of realignment may also play an integral role in motor adaptation.

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