eNeurobiología

Vol. 16 | Núm. 41 | ISSN 2007-3054 | DOI: 10.25009/eb.v16i41.2643
Recibido: 31/01/2025 | Aceptado: 27/03/2025 | Publicado: 16/04/2025

Review article

Prism Adaptation: A Window to behavior and cognition

La adaptación a prismas: una ventana a la conducta y la cognición

J. Eduardo Reynoso-Cruz[1], Victor Galvez[2], Juan Fernandez-Ruiz[1,3*]
[1]Departamento de Fisiología, Facultad de Medicina, Universidad Nacional Autónoma de México.[2]Laboratorio de Neurociencias Cognitivas y Desarrollo, Escuela de Psicología, Universidad Panamericana, Ciudad de México.[3]Instituto de Neuroetología, Universidad Veracruzana, Xalapa, Veracruz, México.

This article can be found at: https://eneurobiologia.uv.mx/index.php/eneurobiologia/article/view/2622

*Correspondence: Dr. Juan Fernandez Ruiz; Circuito Escolar 411A, Copilco Universidad, Coyoacán, 04360, Ciudad de México, México; 2281636942; jfr@unam.mx

Vol. 16 | Núm. 41 | ISSN 2007-3054 | DOI: 10.25009/eb.v16i41.2643
Recibido: 31/01/2025 | Aceptado: 27/03/2025 | Publicado: 16/04/2025

Abstract

Prism adaptation (PA) refers to how individuals adjust their motor and perceptual responses to compensate for visual distortions caused by prism lenses. This experimental paradigm is widely used to investigate sensorimotor and cognitive processes underlying adaptation and learning and the neural substrates and mechanisms that support these processes. Research has shown that PA influences the functioning of the prefrontal cortex and subcortical areas such as the cerebellum and basal ganglia, indicating that PA engages both top-down and bottom-up cognitive mechanisms. This review provides a historical overview of the pioneering experiments by Stratton and Ardigò in the late 19th century, which marked the beginning of PA research. It also discusses key theories, such as the proposal of visual, motor, and proprioceptive mechanisms for PA, and the reafference theory., which suggests that PA results from feedback from self-generated movements that the brain uses to predict events and generate motor responses.

Additionally, we emphasize the importance of research involving individuals with conditions such as Parkinson's and Huntington's diseases, which have been instrumental in clarifying the roles of different brain areas. The final section of the review examines the clinical applications of PA, including its use as a tool to improve the efficiency of surgical procedures for strabismus and to reduce spatial errors in patients with spatial neglect. This review aims to provide readers with a comprehensive overview of the methodologies employed in PA research, the cognitive and neural mechanisms required for adapting behavior to visual disruptions, and the potential for PA to evolve from a basic research paradigm into a practical tool for improving various medical conditions.

Keywords: Prism adaptation; top-down mechanisms; bottom-up mechanisms; cognitive control; strabismus; spatial negligence.

Resumen

La adaptación a prismas (AP) es un paradigma experimental y un área de estudio para comprender el control sensoriomotor, los procesos cognitivos y las áreas anatómicas funcionales del cerebro involucradas en la adaptación visomotora, y que podría aplicarse en diferentes situaciones prácticas. Las investigaciones han revelado que la AP influye en el funcionamiento de la corteza prefrontal y de áreas subcorticales como el cerebelo y los ganglios basales, lo que indica que la AP requiere la participación de mecanismos cognitivos descendentes y ascendentes. Esta revisión ofrece un análisis histórico de los experimentos pioneros de Stratton y Ardigò a finales del siglo XIX, considerados los primeros experimentos de AP. También se discuten teorías que propusieron mecanismos visuales, motores y propioceptivos para la AP, o la teoría de la referencia, que plantea que la AP es el resultado de la retroalimentación de movimientos autogenerados que el cerebro utiliza para predecir eventos y generar una respuesta motora, por mencionar solo dos teorías. Como parte del desarrollo teórico, se describe la importancia de las investigaciones con pacientes o condiciones como las enfermedades de Parkinson y Huntington, que han sido esenciales para describir el papel de diferentes áreas cerebrales. La última parte de la revisión incluye una discusión sobre las aplicaciones clínicas de la AP como herramienta para mejorar la eficiencia de los procedimientos quirúrgicos para el estrabismo o para reducir los errores espaciales en pacientes con negligencia espacial. Así, el lector puede comprender cuán flexible es este paradigma, pero también cuán esencial es la AP para entender cómo funciona y se adapta el cerebro.

Palabras clave: Adaptación a prismas; mecanismos top-down; mecanismos bottom-up; control cognitivo; estrabismo; negligencia espacial.

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1. Introduction

Visuomotor learning involves learning and coordinating their visual perception with motor actions. This type of learning is essential for activities requiring precise hand-eye coordination, such as reaching objects, writing, and playing sports. Various methods are available for studying visuomotor processes, such as visuomotor rotation and force-field adaptation. However, Prism Adaptation (PA) is widely used because of its real-world relevance, robust aftereffects, clinical applications, and ability to reduce error signals. These characteristics make it a valuable tool for research and clinical practice, providing unique insights into sensorimotor learning and adaptation mechanisms.[1,2]

This review aims to provide a comprehensive overview of the current state of research on PA. The paper is structured around the following questions: What is PA, and what are the methodological characteristics of this paradigm? What is the history of PA research, and what are the theoretical proposals to explain it? What are the underlying neural and cognitive mechanisms of PA? And what are the clinical applications of PA?

2. Prism adaptation as an experimental paradigm

In a typical PA experiment, researchers study how people adjust their movements when their visual input is altered. Initially, participants perform a pointing or reaching task without any visual distortion to establish a baseline of their natural hand-eye coordination. Then, they wear special prism glasses that shift their visual field to the left or right (or use other types of visual perturbations), causing the objects to look like they appear in different locations than they are. While wearing prism glasses, participants initially make inaccurate movements, but with repeated attempts, they adjust their movements to compensate for the visual alteration; this behavior is why this paradigm is called prism adaptation. After a period of adaptation, the prism glasses are removed, and participants perform the task again, showing an initial bias in the opposite direction of the prism shift, known as the aftereffect. With continued practice without the prism glasses, participants' movements gradually return to their original baseline accuracy.[1,2]

PA typically is a three-phase paradigm, but additional phases could be added to study other relevant mechanisms. The coming paragraphs describe each methodological characteristic.

Baseline phase. During this phase, participants must perform tasks like throwing objects (balls or sacks) to a target, reaching objects, or touching a spatial position in a touchscreen with the tip of the index or middle finger of the dexterous hand, but only in one movement. This behavior measures the individual's motor performance without any visual distortion. This phase is crucial because it is a control measure that provides a reference point against which the effects of the subsequent phases can be compared.[3]

Exposure phase. During this phase, participants should perform the previous behavior while they wear prism glasses that disturb their visual field, depending on the type of prism introduced. Wedge prism glasses cause an initial misalignment between visual input and motor output, leading to errors in responses and causing the object to be thrown. The reaching or the touching happens far from the real location. Over time, participants adapt their motor responses to deal with the visual perturbations caused by the prisms. The duration of this phase can vary, but it typically continues until the participant's

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performance stabilizes, indicating that adaptation has occurred.[1]

Post-exposure phase. This phase happens after removing the prism glasses and is characterized by aftereffects where the motor responses of the participants are biased in the opposite direction of the prism shift. These aftereffects are a hallmark of PA and indicate that the sensorimotor system has adapted to the altered visual input and needs to readjust to the normal visual environment. The aftereffects gradually diminish as the brain reverts to the original sensorimotor mappings. The magnitude and duration of these aftereffects provide insights into the extent and persistence of the adaptation.[4,5]

Retention phase (optional). This optional phase evaluates how long the adaptation effects last. During this phase, participants undergo testing after a delay to determine if the learned motor responses are still present. This phase helps researchers understand whether the adapted motor responses remain stable over time and whether the recalibrated motor responses persist.[4,6] The persistence of adaptation effects is essential for rehabilitation applications where long-term improvements in motor function are sought.

Transfer phase (optional). In this phase, participants undergo various tasks or are placed in different environments to assess whether the adapted motor responses apply to other situations or conditions beyond the specific ones in the Exposure Phase. This phase aims to evaluate the adaptability and generalizability of the adaptation, offering insights into how the brain utilizes learned adjustments in a range of scenarios.[4] Understanding transfer effects is vital for creating interventions to enhance motor function across different activities and settings.

3. Variables affecting prism adaptation

3.1. The effect of the developmental stage

PA has also been studied to understand the maturation of sensorimotor and cognitive processes across different developmental stages. This section explores the findings from various studies on PA in normal development and children with developmental disorders or concussions.

Integrating visual and motor systems is a complex process does not innate but acquired through experience and learning after birth. When we are born, our visual and motor systems are not fully developed. Infants initially have limited control over their motor actions, and their visual acuity is not fully mature. Over time, through interaction with their environment, infants learn how to coordinate their visual inputs with their motor outputs. For example, they learn to reach for and grasp objects, which requires precise hand-eye coordination. This developmental process is crucial for performing coordinated movements based on visual information and is supported by the plasticity of neural circuits during early childhood.[7]

Research on PA in infants has provided valuable insights into the early development of perceptual and motor coordination. McDonnell and Abraham conducted a seminal study on infants aged 6-10 months, demonstrating that these infants could adapt to laterally displacing prisms. The study found robust aftereffects, particularly in active exposure conditions, indicating that infants possess the capacity for perceptual adaptation even in the second half of the first year of life. This adaptation is crucial in early sensorimotor development.[8] In a longitudinal study, the researchers further investigated PA in infants aged 6-9 months. The study revealed that PA could be observed in young infants,

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with greater aftereffects in younger infants (6-7 months) compared to older ones (8-9 months). However, the study found no evidence that prism exposure led to lasting developmental changes in reaching or visual-motor coordination within the studied age range.[9] These findings highlight that PA is evident in early infancy but does not result in long-term developmental changes.

Other studies have examined visuomotor learning and forgetting rates in children aged 4-12 using a PA paradigm. The study found that while all age groups adapted to the prism condition at the same rate, younger children showed slower forgetting rates compared to older children and adults. This indicates asynchronous maturation of the cognitive processes involved in visuomotor learning and adaptation.[10] This difference was later supported by an interesting sensory integration study showing that young children (5-7 years old) exhibit less flexibility in recalibrating sensory cues compared to older children and adults.[11] These studies suggest that the neural mechanism required for sensory integration and calibration is not fully developed in young children, resulting in perceptual differences between age groups.

PA studies have also been instrumental in understanding sensorimotor impairments in children with developmental disorders. A group of researchers assessed procedural and strategic visuomotor learning deficits in children with Developmental Coordination Disorder (DCD) using PA paradigms. The DCD group showed larger variable errors and smaller adaptation and aftereffect magnitudes, indicating impairments in procedural and strategic visuomotor learning processes. These findings suggest inherent problems within the motor control and learning systems of children with DCD, emphasizing the necessity for specialized attention and support for their development.[12]

In addition to developmental disorders, PA paradigms have been used to assess sensorimotor impairment in youth following concussion. Little et al. used a prism task to evaluate adaptation in young individuals with different concussion histories. The study revealed significant differences in PA measures across groups. This suggests that concussion may affect the brain's ability to adapt to altered sensory input, making the prism task a potential diagnostic instrument for detecting sensorimotor impairments in young individuals following a concussion.[13]

4. The effect of sex differences on prism adaptation

Research has shown that there are significant sex differences in how individuals adapt to visual distortions, indicating distinct underlying mechanisms of motor control and learning between women and men. One key finding is the difference in motor performance and strategic calibration between the sexes. Men generally demonstrate superior throwing accuracy compared to women (less deviation to the target), and this skill remains consistent even when prism lenses introduce visual distortions.[14,15] This suggests men may have an inherent advantage in specific motor skills. However, this advantage does not translate into faster adaptation to the prisms. Both men and women require almost the same number of trials to recalibrate their motor responses and reach baseline levels after using the prisms.[14] These results indicate that the sex difference in the accuracy during the throwing is not due to differences in motor adaptation processes.

Further research has highlighted that women may experience greater disruption from concurrent tasks during PA, suggesting that their adaptation process may be more susceptible to cognitive load.[16] However,

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women exhibit larger aftereffects (larger deviations) once the prisms are removed, indicating a greater reliance on strategic calibration and spatial alignment processes during motor learning.[15] This suggests that women might be using two types of recalibration, spatial and motor, leading to more pronounced aftereffects, while men may rely more on immediate motor adjustments, resulting in shorter deviation during the aftereffects.

5. The effect of visual feedback on prism adaptation

Visual feedback refers to the sensory information received from the visual system that allows individuals to adjust their motor responses to compensate for the visual distortions caused by prism lenses.[17] When individuals are exposed to visual distortions through prism lenses, their initial motor responses are typically inaccurate. One of the key processes influenced by visual feedback is the strategic recalibration of motor commands.[18] Studies have shown that when visual feedback is available, individuals can quickly adjust their motor responses to reduce errors. For instance, continuous visual feedback during movement allows for real-time corrections, leading to more accurate motor performance.[19] This immediate feedback helps fine-tune motor commands to align with the altered visual input.

Another critical process is spatial realignment, which involves adjusting the perceived spatial relationship between the body and the environment.[20] Visual feedback is crucial in this process as it provides information about the difference between expected and actual visual outcomes. Studies have shown that direct visual feedback of the hand and target position can lead to stronger aftereffects, indicating a more robust spatial realignment.[17] This suggests that the visual system uses this feedback to update internal models of the body and environment, resulting in more accurate motor responses over time.

The timing of visual feedback also significantly impacts the adaptation process. Delayed visual feedback has been found to slow the rate and reduce the amount of PA.[21] When visual feedback is delayed, the visuomotor system struggles to integrate the sensory information effectively, leading to less efficient adaptation. This highlights the importance of timely visual feedback in facilitating rapid and accurate adjustments to motor commands. Moreover, the type of visual feedback provided can influence the extent of adaptation. Direct visual feedback, where individuals can see their hands and the target, leads to greater adaptation compared to indirect or abstract feedback.[22] This indicates that the quality and clarity of visual information are crucial for effective recalibration and realignment processes. Visual feedback also plays a role in the decay of prism aftereffects. Studies have shown that aftereffects decay more rapidly when visual feedback is available during the adaptation phase.[23] This suggests that visual reafferent stimulation is necessary to return to normal visuomotor coordination, as it reinforces the newly established motor patterns.

6. Intermanual transfer of prims adaptation

Intermanual transfer refers to the phenomenon where adaptive changes induced in one hand due to exposure to a prismatic shift affect the performance and sensory processing of the other hand.[24,25] This process provides key insights into the lateralization of brain functions and the specificity of motor control.

Hemispheric dominance is crucial to understanding intermanual transfer. Studies indicate that the left hemisphere plays a more significant role in controlling visual-

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spatial information for both hands, whereas the right hemisphere predominantly influences the right hand. This asymmetry suggests that the neural pathways involved in intermanual transfer are not merely mirror images across the hemispheres but are instead governed by a more complex organization of spatial and motor controls.[24]

Another crucial aspect is the specificity of the adaptation process. Research has shown that the transfer of adaptation effects depends not only on the limb used but also on the dynamism of the movements. Previous experiments have demonstrated that adaptations made during fast-reaching movements do not fully transfer to slow movements, indicating that the adaptation is velocity-specific and involves limb-specific neural processes and muscular load during the adaptation process.[26]

The conditions in which the practice takes place also have a significant impact on intermanual transfer. Taub & Goldberg discovered that spaced practice, which involves spreading out sessions over time, tends to enhance more effective transfer compared to massed practice.[25] This suggests that there are differences in how motor memories are stored and recalled in each situation. The process of intermanual transfer also varies with the type of visual distortion experienced. Adaptations to prismatic shifts, which displace visual input, involve more central and encompassing recalibrations, affecting both hands' coordination. In contrast, adaptations to lens-induced distortions, which do not alter proprioceptive feedback, show minimal intermanual transfer, highlighting the role of sensory feedback in shaping the transfer patterns.[27]

Furthermore, the transfer's directionality, whether from the dominant to the non-dominant hand or vice versa, also plays a significant role. A series of studies from different groups have explored how adaptations on one hand can affect the spatial alignment and motor performance of the other hand, revealing directional asymmetry in the transfer process.[6,28]

These findings collectively underscore the complexity of intermanual transfer, illustrating that it is not a straightforward reflection of learning from one hand to another but a dynamic interplay of sensory inputs, motor plans, and cognitive strategies. This intricate process is crucial for developing effective rehabilitation techniques and understanding the fundamental principles of motor control and brain lateralization.

7. Historical context of prism adaptation studies and theorical development

The concept of PA dates to the late 19th century. George M. Stratton is often credited with pioneering this field through his experiments on inverted vision. In his famous 1896 experiment, Stratton wore a monocular inverting lens over his right eye for 8 days, keeping his other eye covered. Initially, he experienced significant disorientation and difficulty in everyday tasks. However, after a few days, Stratton began to adapt to the inverted visual field and could move around more easily. At the end of the experiment, he reported that his visual world had begun to feel normal and upright again, even though he was still wearing the inverting lens. Once the lens was removed, his vision returned to normal after a short readjustment period.[29] Similar results were obtained by Roberto Ardigò a decade before Stratton's findings.[30] Stratton and Ardigò's experiments demonstrated the remarkable adaptability of the human visual system, showing that the brain can adapt to radical changes in visual input over time, and eventually perceive the altered visual world as normal and laid the foundation for later research on PA and perceptual plasticity.

During the 1960s and the 1970s, PA researchers tried to develop theories to

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explain the mechanisms underlying PA. One of the earliest and most influential theories was the proprioceptive change theory. This theory suggests that adaptation involves visual perception, motor control, and proprioception changes. This theory highlighted the complex processes involved in adaptation, including changes in visual localization, muscle coordination, and proprioception.[31,32] Another significant contribution came from a series of studies who developed a technique using prisms to displace the visual image of the hand, showing that participants could adapt to the new relationships between hand and target through repeated trials, reducing their errors.[33] These results are called reafference theory and propose that the brain uses feedback from self-generated movements to update its sensory predictions.

Posterior studies investigated the roles of different types of informational feedback in producing visual adaptation to rearrangement. The findings challenged the reafference theory, which posits that self-induced movement is essential for producing visual adaptation to rearrangement.[34] These findings suggested a more complex interplay of sensory inputs. Posterior research delved deeper into the perceptual and oculomotor changes that occur during PA. The study measured changes in straight-ahead eye position while adapting to wedge prisms, revealing a shift in the perceived position of the visual target. This indicated a change in the judgment of the direction of gaze, emphasizing the intricate interplay between sensory, motor, and cognitive processes in PA.[35] These theories emphasize the importance of visual perception, motor control, proprioception, and nonvisual feedback in PA.

8. Cognitive mechanisms

Posterior the 1970s, researchers focused on revealing the mechanism involved in PA without concentrating on developing a theoretical proposal. To reach this objective, researchers manipulated different parameters of the PA paradigm. The coming paragraphs describe some experiments and their major findings, paying special attention to the mechanism proposed by the researchers.

When wearing laterally displacing or reversing prisms, the visual shift causes a difference between where objects appear and where they are. This often leads to significant errors in motor actions, such as reaching for an object and missing it by a large margin. This initial error is called the prism-induced error.[1] To compensate for the visual distortion, the brain goes through a process of error correction. This involves adjusting the motor commands to match the altered visual input. The adaptation process can be split into two main phases: 1) Immediate Correction. In this phase, individuals make quick, conscious adjustments to their motor actions to minimize errors. Motor performance during this phase varies significantly as the individual learns to compensate for the visual distortion; 2) Long-term adaptation, with continued exposure to the prism glasses, the corrections become more automatic and less conscious. The brain gradually recalibrates the sensorimotor system, producing more accurate and consistent motor actions.[36] This phase involves the creation of new sensorimotor mappings that combine the altered visual input with the appropriate motor responses. These mechanisms are described in more detail below.

Error detection and initial error correction. Error detection is the brain's process of identifying differences between the expected and actual sensory feedback.[37] When a person first wears prism glasses, their visual field shifts, causing them to make errors at pointing or reaching. These

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errors are detected by comparing the intended movement (based on the shifted visual input) with the actual outcome of the movement. Error correction is the process by which the brain adjusts the motor commands to reduce the detected error over time. This process involves updating the internal model of the body and the environment to account for the visual distortion introduced by the prism glasses.[38] The goal is to minimize the error in subsequent movements.

Strategic Adjustment and Recalibration. Two distinct processes contribute to the overall adaptation to visual distortions caused by the prisms. These processes work together to aid individuals in correcting their movements and achieving accurate motor performance despite the altered visual input.[2,38] Strategic adjustment refers to the conscious, deliberate changes in motor behavior that individuals make to compensate for visual distortion.[39] This process involves using cognitive strategies to modify movements based on the perceived error. Strategic adjustments are typically quick and can be implemented immediately after introducing the visual distortion. Recalibration refers to the gradual, unconscious adjustment of the sensorimotor system to visual distortion.[40] This process involves updating the internal model of the body and the environment to account for the altered visual input. Recalibration is slower than strategic adjustment and occurs through repeated practice and feedback.

Motor planning and execution. It involves preparing and organizing the necessary motor commands to achieve a desired movement. This process includes selecting the appropriate muscles, determining the sequence of muscle activations, and predicting the sensory consequences of the movement.[41] In the context of PA, motor planning must adjust for the visual distortion caused by prism glasses, requiring the brain to adapt its predictions and plans to compensate for the shifted visual input. On the other hand, motor execution refers to the actual performance of the planned movement. It involves transmitting motor commands from the brain to the muscles, monitoring the movement in real-time, and making necessary adjustments to ensure accuracy.[42] In PA, motor execution involves adjusting motor plans that compensate for the visual distortion, requiring continuous monitoring and correction to maintain movement accuracy despite the altered visual input.[43]

Sensory-motor integration. It is the coordination of sensory inputs and motor outputs to adapt movements in response to visual distortions. This process involves detecting errors, updating motor plans, executing adjusted movements, and gradually refining motor performance through repeated practice.[44,45] Sensory-motor integration is crucial for successfully adapting to visual distortion caused by wearing prism glasses, allowing individuals to achieve accurate and adaptive motor behavior.

Error sensitivity and adaptation. Error sensitivity is the brain's ability to detect and respond to differences between intended and actual outcomes. This is important in the context of PA, as it helps identify errors caused by the visual shift introduced by prism glasses. When wearing prism glasses for the first time, the visual field shifts, leading to errors at pointing or reaching. The brain detects these errors by comparing the intended target position, based on the shifted visual input, with the actual position reached. The detected error generates a signal indicating the need for adjustment, and the size of this error signal is proportional to the difference between the intended and actual outcomes.[46,47]

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Conscious and nonconscious processes. The processes involved in PA can be classified as either conscious or nonconscious. Conscious processes include cognitive strategies and error awareness, while nonconscious processes involve sensorimotor realignment, proprioceptive recalibration, and automatic error correction. These processes work together to help the brain adapt to visual distortions and maintain accurate motor control.

Cognitive strategies require deliberate conscious efforts to adjust movements based on visual feedback. When individuals first experience the visual distortion caused by prisms, they may consciously aim in the direction of the perceived shift to compensate for the error. This involves higher-order cognitive functions such as planning, attention, and decision-making.[48] Error awareness is the conscious recognition of discrepancies between intended and actual movements, which may lead to implementing cognitive strategies.

During PA, individuals become aware of the errors they make when trying to hit a target by detecting a mismatch between the intended result and the actual result of their actions. This awareness, which usually follows when adapting to large perturbations of the visual field, allows them to consciously adjust their movements to reduce errors in subsequent attempts.[13] Nonconscious processes include sensorimotor realignment, proprioceptive recalibration, and error correction. Sensorimotor realignment is the automatic adjustment of the relationship between sensory inputs (visual and proprioceptive) and motor outputs. The brain automatically recalibrates motor commands to align the perceived visual location with the actual target location. This process occurs without conscious awareness and involves updating the internal model of the body and the environment.[3]

Proprioceptive recalibration automatically adjusts proprioceptive signals to maintain accurate motor control. The brain updates proprioceptive information to align with the new visual input, ensuring that the updated sensory information accurately guides movements. This process occurs without conscious awareness.[3] Similar, error correction is the automatic adjustment of motor commands based on feedback from performance errors. The brain uses feedback from errors to adjust future movements automatically. This process involves the cerebellum and other neural structures that operate without conscious awareness.[49] In PA, when the induced displacement and the resulting initial errors are small, there is minimal conscious involvement, with the correction being driven by more automatic error correction processes.[50]

9. Neural bases of prism adaptation

The possible neural involvement in different processes of PA has also been studied. Four main brain areas have been related, the parietal cortex, the frontal cortex, the cerebellum, and the basal ganglia.

9.1. The parietal cortex

Evidence from studies on patients provides significant insights into the role of the parietal cortex. For example, a patient with damage to both sides of the Posterior Parietal Cortex (PPC) showed a clear difference in their performance on PA tasks, suggesting that different circuits within the PPC are responsible for strategic control and adaptation processes depending on the hand used.[43] Imaging and stimulation studies further support the involvement of the PPC in PA. Repetitive Transcranial Magnetic Stimulation (rTMS) applied to the right PPC has been shown to decrease the magnitude of adaptation aftereffects in proprioceptive and visuo-proprioceptive tasks, highlighting the role of PPC in the

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realignment mechanism.[51] Imaging studies demonstrated changes in activation patterns and functional connectivity within a cerebello-parietal network during the adaptation process.[1,52] Dynamic changes in brain activity during PA revealed a complex interplay between parietal, cerebellar, and temporal regions. The PPC shows significant activation during different phases of prism exposure.[43,51] These findings collectively underscore the PPC's integral role in both the sensory-motor recalibration and cognitive realignment aspects of PA.

9.2. The frontal lobe

Particularly the prefrontal cortex (PFC), and the primary motor cortex (M1) are integral to the process of prism PA. The PFC is involved in the strategic planning and error correction necessary for the initial recalibration phase of PA, where rapid adjustments are made to counteract the visual distortion introduced by the prisms (Exposure phase;). As previously mentioned, this phase is characterized by a fast reduction in terminal error, allowing individuals to adapt their motor responses quickly.[52]

On the other hand, M1 is crucial for the slower sensorimotor adaptation process, involving the update of internal models for accurate reaching and motor memory consolidation.[53] Studies have shown that stimulating M1 can improve the consolidation of sensorimotor aftereffects, indicating that M1 strengthens the temporal synchrony between motor commands and synaptic potentiation.[1] Additionally, PA enhances the activity of intact fronto-parietal areas, including regions within the frontal lobe, in both hemispheres of neglected patients, leading to improved visuospatial performance.[54] This bilateral recruitment of fronto-parietal networks may counteract the pathological changes in these networks caused by unilateral right hemisphere damage. Furthermore, patients with frontal lobe lesions exhibit impaired performance on PA tasks, highlighting the importance of the frontal lobe in visuo-motor learning and adaptation.[55] Additional studies have emphasized the role of the frontal cortex in error detection and correction during PA, emphasizing its role in the dynamic adjustments required for successful adaptation.[56] Overall, integrating the frontal lobe and M1 facilitates the dynamic adjustments and long-term adaptations necessary for successful PA, highlighting their essential roles in visuo-motor plasticity and spatial cognition.

9.3. The cerebellum

The cerebellum plays a pivotal role in recalibrating visuomotor coordination in response to the altered visual input during PA. Studies have demonstrated that cerebellar lesions impair the ability to adapt to prisms, indicating the cerebellum's involvement in error correction and motor learning.[57,58] Specifically, the cerebellum is essential for the recalibration and spatial realignment processes necessary for accurate motor adjustments.[59] Neuroimaging and neurostimulation studies further support the cerebellum's role in PA by demonstrating its interaction with the motor cortex and parietal regions during the adaptation process.[53] Additionally, patients with cerebellar degeneration exhibit increased error sensitivity and impaired learning from abrupt perturbations, highlighting the cerebellum's role in adapting motor commands to gradual changes.[60]

The cerebellum's contribution to PA is also evident in its involvement in short-term sensorimotor memories that facilitate rapid recalibration of limb position when visual input is altered.[58] Furthermore, studies on patients with spinocerebellar ataxia type 2 (SCA2) reveal significant impairments in PA,

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suggesting that cerebellar degeneration disrupts the neural systems involved in spatial realignment.[61] Quantitative evaluations of cerebellar-dependent motor learning through PA tasks have shown that patients with cerebellar diseases have lower adaptability indices than healthy controls, underscoring the cerebellum's critical role in motor learning.[62] Overall, the cerebellum's involvement in PA encompasses error correction, spatial realignment, and the maintenance of sensorimotor memories, making it indispensable for effective visuomotor coordination.

9.4. The basal ganglia

These are a group of subcortical nuclei that play a crucial role in motor control and learning, and their dysfunction is a hallmark of neurodegenerative diseases such as Parkinson's disease (PD) and Huntington's disease (HD).[63] Stern et al. found that a group of PD patients could adapt to the presence of prisms.[64] The only difference noted was a more intense compensatory response when using prisms and aftereffects from the PD patients. Subsequent studies by Fernandez-Ruiz et al. confirmed these findings. They extended them to HD patients.[65] These studies suggest that the basal ganglia are involved in the cognitive processes that support visuomotor learning. In contrast, Swainson et al. found that PD patients adapted to visual perturbation more slowly than healthy controls, but their aftereffects remained intact.[66]

This indicates that the explicit, error-driven processes involved in PA are impaired in PD, while the implicit learning processes remain unaffected. Other studies with patients with HD have also demonstrated that those patients are profoundly impaired in non-error-based learning tasks.[67] This highlights the basal ganglia's critical role in motor learning and adaptation processes that do not rely on direct error correction. On the other hand, Paulsen et al. found that HD patients could not adapt during the prism phase.[68] This inability was related to the severity of their dementia, suggesting again that the impairment in patients with basal ganglia deficits is more related to cognitive processes than to procedural learning. The conflicting results can be reconciled by considering the specific methodologies used in each study to measure the adaptation. Some studies use throwing an object, while others use pointing with the index finger.[65,68] These results suggest that although basal ganglia deficits affect some processes related to procedural learning, their lesion does not prevent the patients from adapting to the prisms.

10. Clinical applications of prism adaptation

Although the PA task seems to be only used for basic research, it has also been used for applied purposes and as part of the rehabilitation process for specific medical conditions, with applications in patients with strabismus and spatial negligence standing out.

10.1. Strabismus

Strabismus is a medical condition in which the eyes are not aligned, causing the person to be unable to focus on stimuli binocularly. Some symptoms include double vision and uncoordinated perception of stimuli.[69] There are different types of strabismus, with the more common ones being esotropia (characterized by one eye moving towards the midline), exotropia (one eye moving laterally towards the opposite direction of esotropia), hypotropia (one eye moving into the inferior portion), and hypertropia (one eye moving to the superior portion of the eye).[69] Prism adaptation (PA) is used to estimate which muscles need to be fixed and how to fix them.[70,71]

10.2. Spatial neglect

Spatial neglect is a neuropsychological condition caused by a lesion, typically in the right hemisphere, but it can also be generated by lesions in the left hemisphere.[72,73] This condition leads to changes in the levels of consciousness, attention, and perception, focusing on the hemifield contralateral to the injury.[74] It was previously believed that spatial neglect was caused by hyperactivity in the non-lesioned hemisphere, but this hypothesis has been proven false.[75,76] Clinical signs of spatial neglect include anosognosia (inability to recognize their illness), spatial disorientation, and motor-intentional issues.[74]

Patients working with a modified version of the PA have shown signs of recovery, especially in body-midline neglect.[77] This indicates that the PA task can help the patients to move their attention focus (top-down) voluntarily but does not help them process the visual field based on stimuli characteristics (bottom-up).[78] A group of researchers from the Czech Republic developed a new version of the PA task for intense rehabilitation programs. The patients in the intensive program showed significant improvement sessions after only 10 sessions, while the group that did not receive the treatment did not improve their spatial neglect.[79]

11. Discussion and future directions

This review presents an overview of research on PA, a phenomenon crucial for understanding sensorimotor integration and neural plasticity. Our review includes the historical context of PA research dating back to the late 19th century, and the basic principles involving a multi-phase process that enables the study of sensorimotor adaptation mechanisms. At the neural level, the parietal cortex, frontal cortex, cerebellum, and basal ganglia play essential roles in cognitive processes like sensory-motor recalibration, strategic control, error correction, and motor learning. Age plays a role in sensorimotor integration, and PA provides insights into the impact of neurodevelopment maturation of sensorimotor and cognitive processes. These previous aspects and many others mentioned in this review demonstrate that PA is a flexible tool for investigating many aspects of sensorimotor integration and the interplay between cognitive and motor processes, and with technical developments for clinical applications.

Future research directions should include exploring dynamic brain region interactions, potential rehabilitation applications besides spatial neglect, and long-term effects of PA, clarifying with more detail the impact of sex and sex differentiation for PA, and leveraging technological advances to elucidate precise molecular mechanisms and their effects in cognitive processes involved in PA. By continuing to explore PA, researchers can continue revealing the intricate machinery of the neural circuits and how these circuits are transformed into behavior and a personal experience; sensorimotor integration requires a more profound understanding to have a comprehensive understanding of human behavior.

12. Conflicts of Interest

The authors declare no conflict of interest. This work received funding from CONAHCYT–Mexico grant no. A1-S-10669 and PAPIIT-UNAM grant no. IN214122 given to Juan Fernandez-Ruiz, and DGAPA-UNAM postdoctoral scholarship program to J. Eduardo Reynoso-Cruz.

13. Contributions

All authors contributed equally to the writing, editing, and proofreading of all the

manuscript versions. We acknowledge using AI tools for spelling and grammar checks in preparing this manuscript. All authors read and approved the final manuscript.

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eNeurobiología
Vol. 16 | Núm. 41 | ISSN 2007-3054 | DOI: 10.25009/eb.v16i41.2643
Recibido: 31/01/2025 | Aceptado: 27/03/2025 | Publicado: 16/04/2025

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