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Trends in
Cognitive Sciences

Review

Functional Use of Eye Movements for an Acting System

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Movements of the eyes assist vision and support hand and body movements in a cooperative way. Despite their strong functional coupling, different types of movements are usually studied independently. We integrate knowledge from behavioral, neurophysiological, and clinical studies on how eye movements are coordinated with goal-directed hand movements and how they facilitate motor learning. Understanding the coordinated control of eye and hand movements can provide important insights into brain functions that are essential for performing or learning daily tasks in health and disease. This knowledge can also inform applications such as robotic manipulation and clinical rehabilitation.

Highlights

Eye movements are tightly coupled with goal-directed hand movements in a variety of tasks.

When reaching for or intercepting an object, humans naturally direct their eyes to the object. Eye movements improve hand-movement accuracy through a combination of visual with efference-copy information.

Eye movements are flexible. They can be suppressed or sped up to optimally support the task.

During skill learning and sensorimotor adaptation, changes to eye and hand movements co-occur, suggesting that eye movements can support motor learning. This provides promising avenues for gaze training in motor learning and clinical rehabilitation.

The information exchange between the eye and hand movement system is bidirectional: execution of a concurrent hand movement can result in improvements in eye movements.

The Supportive Role of Eye Movements in Manual Tasks

Humans and other primates move their eyes continuously to gather visual information and to guide their hands and body toward interesting objects. Despite strong functional coupling of eye and hand movements, research on the control and function of either type of movement has, to a large extent, been carried out in isolation. For example, eye movements are often studied with regard to how they enhance aspects of visual processing, such as spatial resolution [1,2]. Hand movements are considered with regard to how trajectories are optimized to achieve a particular task outcome, such as manipulating an object [3]. Progress toward a better understanding of the control and functionality of these movements can be enhanced by simultaneously assessing both types of movement. We review recent research that is beginning to examine how eye and hand movements are coordinated during motor tasks by integrating behavioral, neurophysiological, and clinical approaches. We focus on the role of eye movements in supporting manual tasks, rather than viewing the eye and hand as two separate effectors. We therefore include studies examining **eye–hand coordination** (see Glossary) in naturalistic tasks, and exclude artificial tasks such as those explicitly requiring participants to simultaneously make an eye and hand movement towards two separate targets. Whereas it has long been known that eye movements accompany and guide hand movements to stationary targets, recent work has provided new insights into the function and flexibility of eye movements in a broad range of motor tasks, including interception of moving targets, making decisions about which actions to perform and when to perform them, **motor skill learning**, and **motor adaptation**. Furthermore, recent research has revealed changes in eye–hand coordination in disease, such as stroke, and this opens up interesting research avenues on the role of eye movements in rehabilitation.

In the first section of this review we discuss the crucial function of eye movements during the performance of goal-directed hand movements, such as reaching for a cup of coffee or catching a ball. In the second section we discuss how eye movements change while learning new goal-directed hand movements, and how eye movements could potentially facilitate such learning and the adaptation of learned movements. We also briefly discuss the somewhat limited knowledge of the neural mechanisms underlying eye–hand coupling and **eye–hand interactions** (Box 1), as well as eye–hand coordination in disease and potential clinical applications (Box 2), and outstanding questions.

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Eye Movements during Goal-Directed Hand Movements

Over the past two decades many studies have demonstrated that eye movements are controlled and organized to support accurate hand and body movements (e.g., [4–7]). We integrate these studies with recent work to first discuss how **fixating** or tracking a target with the eyes improves the accuracy of goal-directed hand movements. We then discuss how eye movements optimize performance by adjusting to task requirements, and how eye movements can be indicators of choices between actions or objects.

Eye Movements Improve Reaching and Interception Performance

When reaching for an object, humans typically make a fast eye movement (**saccade**) to the object before initiating the hand movement, and then keep their gaze aligned with the target (fixation) until around the time the hand arrives [4,5]. Such coupling is demonstrated by the example trajectories in space (top) and time (bottom) of saccadic eye movements and hand movements when reaching toward a visual target in Figure 1A. This coordinated behavior commonly produces correlations between the reaction times of the saccade and the hand movement [8–10].

Foveating the reach goal improves the accuracy of the reach [8], and it does so in multiple ways. First, it allows us to accurately locate the target by combining multiple signals produced by the eye movement: high-resolution visual information from the projection of the target onto the fovea, and non-visual information such as an **efference-copy** signal from the motor command sent to the eye muscles or a **proprioceptive** signal coming from the eye muscles. Manipulation of these non-visual signals causes biases in perceptual judgments and pointing endpoints [11], and saccadic localization errors support the predictions of an optimal integration model of visual, efferent, and proprioceptive signals [12]. Second, foveal visual information is used to guide the hand to the target, as evidenced by improved reach accuracy when visual feedback of the

Box 1. Neural Circuits for the Control of Eye and Hand Movements

Acting to reach, grasp, track, intercept, or catch an object involves a network of sensorimotor areas in the brain that engage the occipital cortex to process visual information, the parietal and frontal cortices to transform visual information into a motor plan [73], and the brainstem projecting to the eye muscles and spinal cord for movement execution. Smooth-pursuit and saccadic eye movements are controlled by partly overlapping circuits [74]. Similarly, different types of hand movements are controlled by partly overlapping circuits that also partly overlap with the saccadic circuit [75,76]. Despite a large body of work on the neural correlates of visual and motor encoding of targets for eye and hand movements, the mechanisms of movement coupling and interaction are unclear. Our limited knowledge on this topic is mostly derived from electrophysiological recordings in monkeys.

One candidate area for eye–hand interactions is the posterior parietal cortex, in particular regions along the **intraparietal sulcus** (**IPS**; Figure I). In monkeys, the **parietal reach region (PRR)** and the **lateral intraparietal area (LIP)** show relative specialization for the encoding of reach and saccade goals, respectively [77]. The mechanisms underlying reach–saccade coupling are unclear. Some studies suggest that LIP coordinates saccades and reaches to the same target [78,79], whereas others propose that coordination of saccades and reaches instead relies on the PRR [80], or that neither of these areas are involved in coordinating eye and hand movements [81,82].

Another candidate for eye–hand integration is the **superior colliculus** (**SC**; Figure I) [83]. In conjunction with its activity related to eye movements, subpopulations of neurons in intermediate and deep SC layers show activation related to the execution of arm movements [84–86]. In addition, electrical stimulation of deep layers elicits short-latency arm movements [87]. Furthermore, fMRI has revealed reach-related activity in human SC [88]. These findings could mean that SC is involved in eye–hand coupling, or, alternatively that SC is more generally involved in target selection for action [89].

Eye–hand coupling in the human brain is inherently difficult to study. The spatial resolution of electroencephalography (EEG) and magnetencephalography (MEG) is insufficient to investigate interactions at the neural level. fMRI studies are challenging because the small space of the scanner limits eye tracking and movement of the arm and hand, and this can also produce head motion and magnetic field artefacts [90]. However, technological advances such as MRI-compatible digitizing tablets [91] or portable MEG [92] may lead to new discoveries concerning the neural mechanisms underlying eye–hand interaction and coupling.

Glossary

Eye–hand coordination: eye and hand movements that are largely synchronous and spatially aligned, without necessarily affecting one another.
Eye–hand interaction: eye and hand movements that affect one another, either unidirectionally or bidirectionally.
Efference copy: an internal copy of a motor command that is sent to sensory brain areas.
Explicit process (of motor adaptation): a strategic learning process driven by the error between the movement endpoint and the target, resulting in a strategic change in movement (e.g., aiming the movement next to the target instead of directly at the target to compensate for rotated movement feedback).
Fixation: period during which a target is kept relatively stable on the fovea and the eyes exhibit only miniature movements (e.g., microsaccades).
Foveate: to direct the eyes such that the target object image falls on or close to the fovea, the part of the retina with the highest photoreceptor (cone) density, resulting in the highest visual resolution.
Implicit process (of motor adaptation): an automatic (i.e., outside voluntary control and awareness) learning process that is driven by the error between the predicted and observed sensory outcome of movement (e.g., the difference between the predicted reach endpoint and the visual feedback of the cursor endpoint), resulting in updating of an internal model which links motor commands and sensory outcomes.
Intraparietal sulcus (IPS): a sulcus located along the lateral surface of the parietal lobe of the macaque and human brain, and that separates the parietal cortex into a superior and inferior lobe.
Lateral intraparietal area (LIP): an area along the lateral wall of the intraparietal sulcus of the macaque brain that is primarily involved in the encoding of saccade targets.
Motor adaptation: the adjustment of movements in response to changes in the body, such as your muscles becoming fatigued, or in the environment, such as when serving a volleyball in a strong wind.
Motor skill learning: the acquisition and improvement of a motor skill

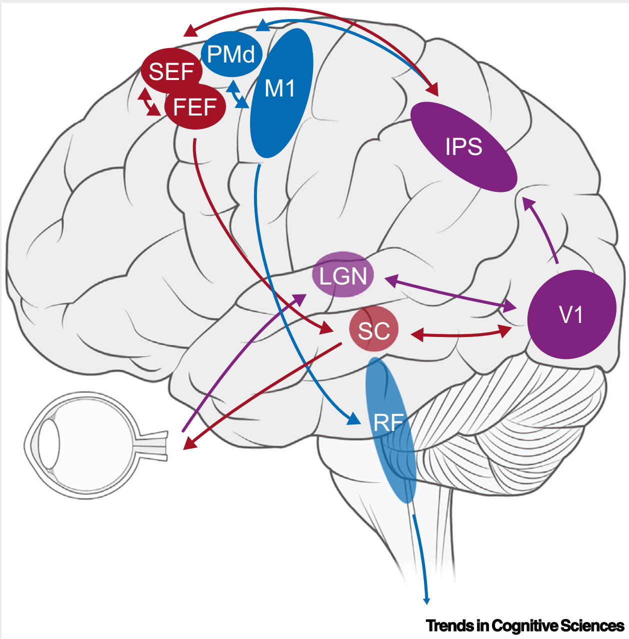

Figure I. Brain Areas Involved in Eye- and Hand-Movement Control. Areas involved in the control of hand movements are shown in blue, areas involved in the control of eye movements in red, and areas involved in the control of both movements in purple. Only primary areas are shown for clarity. Opaque areas are cortical areas, transparent areas are subcortical and brainstem areas. Abbreviations: FEF, frontal eye field; IPS, intraparietal sulcus (includes the human homologs of macaque LIP and PRR); LGN, lateral geniculate nucleus (thalamus); LIP, lateral intraparietal area; M1, primary motor cortex; PMd, dorsal premotor cortex; PRR, parietal reach region; RF, reticular formation; SC, superior colliculus; SEF, supplemental eye field; V1, primary visual cortex.

through practice, such as learning to ride a bicycle.

Parietal reach region (PRR): an area along the medial wall of the intraparietal sulcus of the macaque brain that is primarily involved in the encoding of reach targets.

Proprioception: the sense of the position and movement of our body parts through information from sensors in the muscles, joints, and skin.

Saccade: a fast movement of the eyes to redirect the fovea to a location of interest.

Smooth pursuit: a slow, continuous movement of the eyes elicited by a moving object.

Superior colliculus (SC): a structure in the macaque and human midbrain that is involved in eye-movement control and motor target selection.

Visuomotor gain: the gain of a movement correction in response to a visual perturbation of the movement trajectory.

hand is provided only in the final phase of the movement, compared with when it is provided earlier during the movement [13]. Third, foveating the reach goal enhances monitoring of the trajectory of the hand with peripheral vision. It is known that when the sensorimotor system detects an error in the trajectory of the hand, it produces a rapid (latency ~150 ms), involuntary corrective response [14–16]. We recently showed that the gain of such corrections (often called the **visuomotor gain**) in response to errors detected with peripheral vision is highest when the eyes are directed at the reach target and the direction of gaze is aligned with the direction of movement, compared with when the eyes are directed to nearby fixation locations [17,18]. This suggests that foveating the target facilitates corrections of errors in the movement trajectory.

When intercepting a moving object, humans naturally keep their eyes on the target by tracking it with a combination of low-velocity **smooth pursuit** and fast saccadic eye movements [7]. Figure 1B shows an example of combined smooth and saccadic tracking during interception of a moving target that disappears briefly after its launch. Tracking the target improves the perceptual estimation of its motion and allows the sensorimotor system to continuously update its predictions about the target's future trajectory [19], likely through the combination of visual and efference-copy information [20].

The natural tendency to keep the eyes on a moving target that we intend to catch or hit indicates that eye movements might be beneficial for such tasks. Tracking the target with the eyes improves interception performance as compared with fixating the interception location, and these benefits are likely due to improved high-acuity perceptual estimates of the target's motion

Box 2. Eye–Hand Coordination in Disease

Clinical assessment and rehabilitation of disease typically focuses on primary deficits. For example, the assessment and rehabilitation of motor deficits following acquired brain injury, such as stroke, focuses on upper and lower limb movement. Quantification of diseases that affect the visual system, such as amblyopia or glaucoma, typically focus on visual acuity. Given the close interactions between the visual, oculomotor, and limb-motor systems, deficits in one system could result in related deficits.

The importance of examining both hand and eye function during motor tasks in patients with stroke or neurological disease has been highlighted recently [93]. However, to our knowledge, only two studies have taken this approach. In delayed and memory-guided reaching tasks, chronic stroke patients made predictive saccades with large endpoint errors, and performed more corrective saccades, compared with healthy controls [94]. Whereas stroke patients showed similar reach latencies to controls, their endpoint errors were larger. Singh and colleagues [95] asked chronic stroke patients to perform a digitized trail-making test that involved moving their hand along a sequence of letters and numbers. Patients without visual deficits made more saccades per reach movement (Figure I), performed slower reaches with more trajectory adjustments, and took longer to complete the task, compared with controls. Furthermore, the number of saccades per reach correlated with functional difficulties. Such deficits highlight the potential of enhancing rehabilitation protocols by integrating eye-movement training with motor training [96]. Studies testing such training protocols should include appropriate control conditions, perform detailed analyses, and examine the generalization of results to daily activities.

Deficits in eye and hand movements have also been observed in patients with diseases that impact on visual function. For example, saccade latencies are longer in patients with glaucoma [97] and amblyopia [98,99]. Furthermore, longer hand-reaction times and movement times during goal-directed reaching have been observed in glaucoma [100] and amblyopia patients [101], with a longer interval between the initial saccade to the target and the onset of the hand movement [102]. Together, these observations highlight the interactions among the visual, oculomotor, and limb-motor systems, and argue for a more holistic approach for assessment of function and rehabilitation.

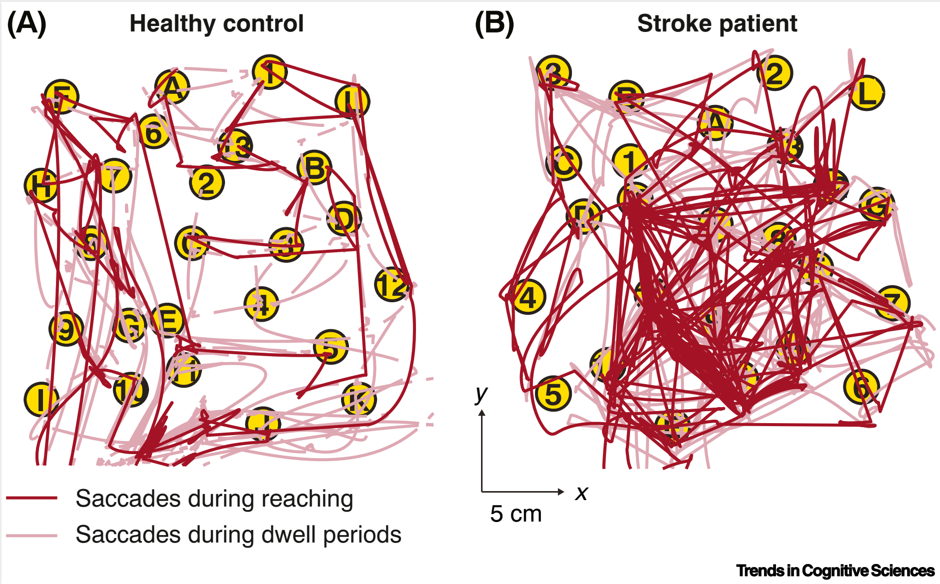

Figure I. Saccades during a Digitized Trail-Making Test. (A) Saccades by a representative control subject. (B) Saccades by a chronic stroke patient. Modified, with permission, from [95].

features when the eyes are aligned with the target [21]. Whereas information about the position and velocity of the hand can be obtained via efferent or proprioceptive signals [22,23], the only way to obtain target information necessary for intercepting it is via visual signals. Congruently, restricting the eyes to a predefined fixation location away from the target, as compared with tracking the target, has been linked to an increase in systematic interception errors [24]. Moreover, interception accuracy is correlated with higher eye-movement quality – fewer corrective saccades [25,26] or lower eye position error [27,28] – as well as with longer pursuit duration

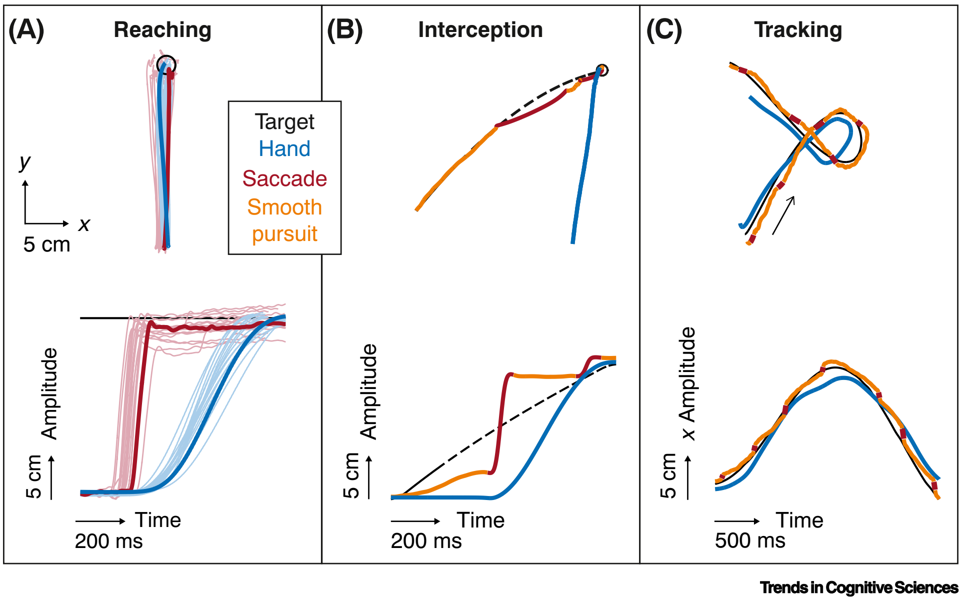

Figure 1. Spatial and Temporal Eye–Hand Coordination. The top row shows spatial coordination, the bottom row shows temporal coordination. (A) During goal-directed reaching to a static visual target, eye movements (in red) and hand movements (in blue) are launched at around the same time, with the eyes arriving ahead of the hand (de Brouwer, A.J. and Spering, M. unpublished data). (B) During interception of a moving target, the eyes follow the target using smooth pursuit (in orange) and saccades (in red), while the hand moves straight to the interception location without first tracking the target. In this example, the moving target became invisible (broken line) after 200 ms (modified, with permission, from [28]). (C) During manual tracking of a moving target, the eyes track the target using pursuit and saccades, while the hand tracks the target smoothly (data from [67]).

[29]. The finding of striking similarities in how eye movements (the direction of a corrective saccade as either forward or backward) affect errors in intercepted and perceived target location [26] further highlights the crucial role of eye movements in contributing to interception via visual perceptual processes. Whereas eye movements are beneficial, they might not always be necessary for accurate interception. For example, when observers were asked to collide their unseen finger (represented by a cursor) with a moving target, they were able to guide interception timing using either foveal or peripheral vision, although large individual differences were noted in this study [30]. Whether accurate eye movements are necessary or merely beneficial might depend on exact task requirements and stimulus environments.

Eye Movements Flexibly Adjust to the Motor Task

Beyond directly impacting hand movement performance via visual processing and efferent or proprioceptive signals, eye movements also adjust to the requirements of the task and to the capacity of the sensorimotor system. For example, corrective saccades during target tracking are generally suppressed around the onset of an interceptive hand movement, presumably to avoid errors in estimating target velocity [7,26]. In some cases it might be beneficial to avoid tracking the target. When intercepting a target with a fully predictable interception location and/or trajectory, participants directed their eyes to the future interception location and monitored the approach of the target with peripheral vision instead of tracking the predictable target [31]. Finally, saccades can be sped up when the task involves a time-critical decision. A reaching and interception task that involved blocks in which participants were required to decide whether to hit or move away from the target, based on the shape of the target, and blocks in which no decision was necessary (i.e., always hit), revealed faster reaction times of the initial saccade and higher saccade peak velocities in decision blocks [32]. Together, these observations suggest that eye movements adjust to the task to optimize hand movement performance.

Congruently, how much observers rely on eye movements appears to determine interception timing. In a task where varsity baseball players intercepted a briefly presented visual target with the simulated motion of a batted baseball (Figure 1B), a tendency to intercept early was best predicted by a combination of tracking error and the memorized ball landing position from previous trials, whereas late interceptions solely relied on accurately tracking the target [28]. A relation between interception timing and baseball experience (higher proportions of late interceptors amongst more senior players) [28] indicates that eye movements can distinguish experts from non-experts in tasks requiring exceptional eye–hand coordination, as also reported for cricket [33] and laparoscopic surgery [34].

Finally, eye movements can indicate decision processes in interception tasks. In a go/no-go task, observers were tasked to track and intercept a briefly presented moving target that either passed through or missed a strike zone shown on a computer monitor. Observers needed to rapidly intercept the target with their finger (go) in pass-trials, and withhold a hand movement (no-go) in miss-trials. Eye movements differed between correct go responses and correct no-go responses, even before the hand started moving [27,35]. Higher initial pursuit velocity was associated with higher go/no-go decision accuracy, whereas high velocity gain during a later time-interval was associated with better timing accuracy [35]. These findings reveal a continuous interaction between eye movements and action decisions.

In summary, vision and eye movements are beneficial, although perhaps not always necessary, for successful interceptive actions. Importantly, eye movements play an integral role in all stages of a task, from initial target localization to accurate movement execution. In the following section we discuss whether eye movements are similarly beneficial when new movement skills are acquired and existing skills are adapted to changing circumstances.

Eye Movements in Motor Learning

Learning a new movement involves extracting and integrating sensory information about the movement target before, during, and after the movement, deciding which movement to make and when and where to move, and adapting appropriately to sensory feedback and error signals [36]. Because eye movements provide crucial information during goal-directed movements, they are probably also involved in movement learning. We discuss below the role of eye movements in two types of learning: motor skill learning and motor adaptation. A better understanding of how learning might potentially be boosted by eye movements could drive advances in clinical rehabilitation (Box 2) or assist training for professionals such as interceptive sport athletes or laparoscopic surgeons [37,38].

Eye Movements Change with the Acquisition of a Motor Skill

A common finding across several studies is that eye movement behavior changes over time as an observer acquires a new skill. In a seminal study, participants were tasked to move a cursor to successively hit visual targets by learning a novel mapping between forces and torques applied to a rigid tool held between the two hands, and cursor motion on a screen [39]. Different stages of learning in this task could be distinguished by hit rate and eye movements. In an exploratory stage, hit rate was low and the eyes most often pursued the cursor with a sequence of saccades and fixations. In a skill-acquisition stage, hit rate improved and eye movements shifted from lagging behind the cursor movement to predictively fixating future cursor locations. In a skill-refinement stage, saccades were primarily made to the target in anticipation of the cursor arriving. Thus, eye-movement behavior changed from reactive to predictive over the course of learning [39].

Other studies have shown changes in the frequency and location of fixations during learning. Generally, participants tend to make fewer fixations but these are to more task-relevant locations with increasing practice of speeded tasks, such as reaching to sequentially presented targets [40,41], bimanual cup stacking [42], and transporting marbles with chopsticks [43]. An example of this can be seen in Figure 2A, which shows the fixations of all nine participants in a bimanual cup-stacking task, during the time-interval between completing the 10-cup pyramid and having rotated the two outer cups to downstack the pyramid, on days 1 and 14 of training. Whereas these studies merely suggest a link between eye movements and skill learning, other studies have revealed a direct impact of eye movements on skill learning by instructing different eye movements. Participants who were allowed to move their eyes freely learned to produce faster movement sequences in a sequential lever-pointing task than participants who were instructed

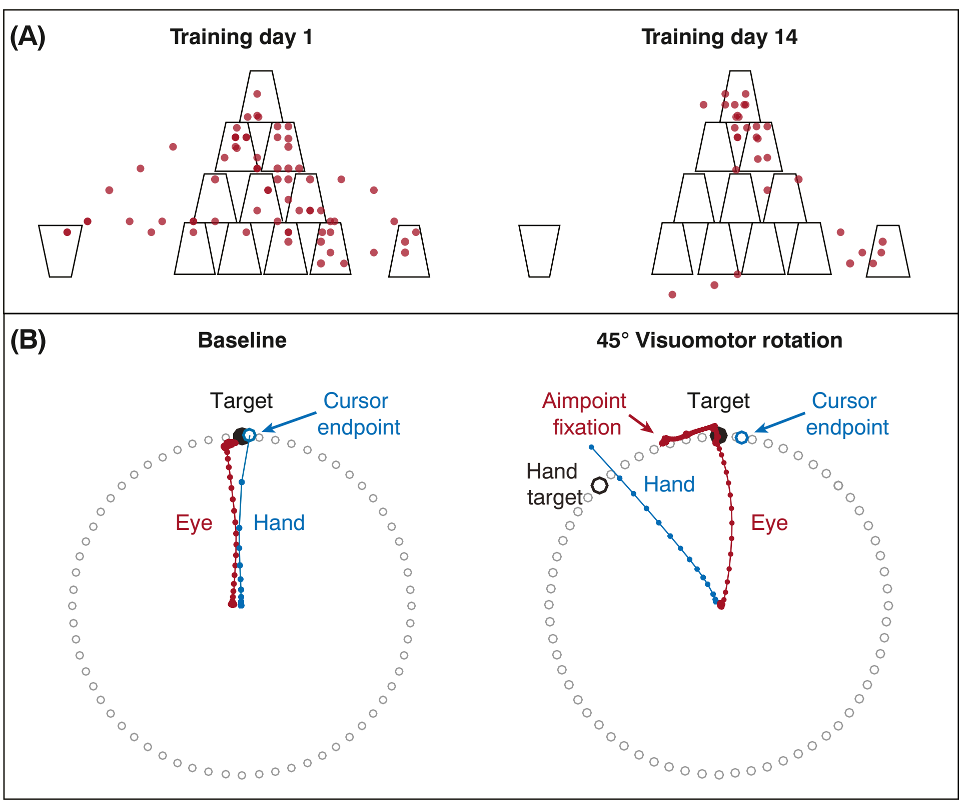

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Figure 2. Eye Movements during Skill Learning and Adaptation. (A) Fixation locations on days 1 and 14 of consecutive training with 45 minutes per day of bimanual speed-stacking practice. As part of a full speed-stacking cycle, observers were tasked to build a 10-cup pyramid and then downstack it into the two outer cups. Each datapoint (in red) shows a fixation for a single time-interval between completing the pyramid and having rotated the outer two cups to downstack the pyramid. Fixations are overlaid for all observers (n = 9). Modified, with permission, from [42]. (B) Eye and hand movements of an example observer in a baseline trial (left) and a trial with a 45° visuomotor rotation (right). The task of the observer was to hit the visual target (in black) with the cursor representing the hand. In the baseline trial, the observer makes a single saccade (in red) to the visual target, followed by a hand movement (in blue) in the same direction. In the rotation trial, the observer makes a series of saccades to a strategic aimpoint (i.e., to compensate for the rotation) following an initial saccade to the visual target. The subsequent hand movement is directed counterclockwise of the aimpoint as a result of the unconscious, implicit component of adaptation. Modified, with permission, from [55].

to fixate [44]. Moreover, participants in the free eye-movement group maintained faster performance in a transfer test 24 h later in which the opposite eye-movement condition was enforced. Whereas the acceleration of learning seemed to be limited to situations in which a larger spatial target range necessitates eye movements, participants who freely moved their eyes performed better in a retention test 24 h later, independently of the target range [45].

The mechanisms underlying the link between eye movements and motor learning are relatively unexplored. Oculomotor brain areas are heavily interconnected with areas controlling hand movements (Box 1) as well as long-term memory [46], and eye movements can facilitate various aspects of working memory performance [47]. One possible mechanism underlying the eye movement-related boost of motor skill learning might be via facilitating the storage and extraction of relevant visual information in long-term memory, mediated by prefrontal cortex [44,48] or hippocampus [46,49]. However, direct evidence for this hypothesis is lacking.

Eye Movements Can Support Motor Adaptation

Once a skill is learned, performance is maintained by adapting it to changes in the body or the environment. Motor adaptation of reaching movements has been extensively studied by distorting the visual field using prism glasses [50] or by applying a visuomotor rotation in which the viewed path of the hand on a computer screen (i.e., as shown by a cursor) is rotated [51]. Adaptation to such visual distortions (i.e., visuomotor adaptation) is thought to involve (at least) two processes: an unconscious or **implicit process** that produces gradual changes in hand movement and a strategic or **explicit process** that drives fast changes in hand movement [52].

Given the tight link between eye and hand movements, and the crucial role of visual feedback when adapting to a distortion, several studies have tried to gain insights into the implicit and explicit processes by examining eye movements during adaptation. These studies have shown that eye movements in a visuomotor rotation task are related to the explicit process [53–56], which involves the implementation of a strategy to aim the hand away from the target to compensate for the rotated visual feedback [57,58]. For example, in a recent study we examined eye movements in a reaching task in which a 45° visuomotor rotation was applied and participants freely moved their eyes [55]. During a short delay following the appearance of the visual target, participants first moved their eyes to this target, as they did in the baseline phase without the rotation (Figure 2B). When the rotation was applied, the majority of participants subsequently moved their eyes to a strategic 'aimpoint', that was rotated away from the visual target, before reaching (Figure 2B), suggesting that fixations can provide a readout of the strategic component during adaptation to a visuomotor rotation (*cf* [54,55]). Although aimpoint fixations were not necessary to implement an aiming strategy, we found that participants with aimpoint fixations showed faster adaptation than did participants who only fixated the visual target [55]. Fixating the aimpoint might speed up adaptation by supporting the successful implementation of a strategy, possibly through facilitating mental rotation of the movement direction [59]. In contrast to the explicit process, the implicit process is not influenced by free or instructed fixation at the visual target or the aimpoint during adaptation to a visuomotor rotation [53,55].

Furthermore, eye movements do not always influence motor adaptation. In a study where participants needed to track a moving target with their hand while visual feedback of the hand cursor path was rotated by 90°, different eye-movement instructions (fixate vs free eye movements) resulted in similar rates and levels of adaptation, despite lower manual tracking accuracy in the fixation group [60]. A possible explanation for the discrepancy between this study and the findings above is that adaptation might benefit from eye movements only in cases where movements are discrete, and where implementing an (aiming) strategy is relatively straightforward. The potential benefit of eye movements for adaptation in discrete motor tasks poses the question whether eye movements could be used as a training tool for motor learning and rehabilitation in healthy and clinical populations (Box 2).

The Influence of Hand Movements on Eye Movements

In the paragraphs earlier we described a wide range of tasks in which hand movements are optimized by eye movements. In addition, improvements in eye movements can occur as a result of concurrent hand movements. Evidence for the effect of hand movements on eye movements comes primarily from studies investigating smooth-pursuit eye movements and hand movements while tracking moving targets. Figure 1C shows an example of the trajectories of the moving target, hand, and smooth-pursuit and saccadic eye movements in a tracking task. In a classic study, Steinbach and Held [61] asked observers to track a target attached to their own fingertip in an active condition, in which the arm was moved by the observer, and in a passive condition, in which the arm was moved by an external force. Pursuit was consistently better with a smaller lag and fewer catch-up saccades in the active condition [61]. Other studies showed that the advantage of self-generated motion over externally generated motion persisted in the presence of a delay between hand and target motion [62], when the mapping between the hand and target motion was reversed [63], or even when the mapping was nonlinear (i.e., a simulated spring) [64]. However, the pursuit benefit was largest when the eyes and hand moved congruently [65]. Synchrony in eye and hand movements (i.e., similarities in phase and position lag) and superior pursuit were also observed when observers were explicitly instructed to concurrently track a target with eye and hand [66–68]. These findings provide evidence that non-visual signals, such as the efference copy of the arm-movement signal, enhance the representation of the target, thereby improving pursuit [68–70]. Coordination through an efference-copy signal is likely mediated upstream of the primary motor cortex [71], possibly by the cerebellum [72]. Together with the evidence presented above, these results show that information exchange between the oculomotor and limb-motor system is bidirectional. The limb-motor system has access to visual, proprioceptive, and/or efference-copy information from the eyes, and the oculomotor system has access to an efference-copy signal from the limb to optimize movement coupling.

Concluding Remarks

Technological advances and the availability of affordable eye- and hand-tracking technology have boosted the quantity and quality of research simultaneously measuring eye and hand movements. These studies have made it clear that, in motor tasks, eye movements are not merely another effector to be investigated but actively guide hand movements (*cf* [5]). This review highlights the flexibility of eye movements in adjusting to the motor task as well as the skill level of the observer. Eye movements improve the accuracy of goal-directed movements and support the learning of new motor skills and the adaptation of familiar movements. Eye movements can also be sensitive indicators of limb-motor processes and performance, and can be influenced by a concurrent hand movement. These findings emphasize the exchange of information and interactions between the visual, oculomotor, and limb-motor systems, and provide interesting avenues for future research on the interaction between eye and hand movements in a broader range of motor as well as cognitive tasks (see Outstanding Questions). At the neural level, eye–hand coupling and interaction are likely mediated by frontoparietal and/or subcortical brain areas, although the exact mechanisms remain to be fully understood. Studying eye movements in conjunction with hand movements is key to understanding the functions of the sensory and motor system. Beyond advancing the field of visual and motor neuroscience, this knowledge has potential implications for improving rehabilitation in patients with motor or visual disabilities,

Outstanding Questions

How do eye and hand movements interact during cognitive events ranging from decision making to object recognition? For example, how are coordinated eye–hand trajectories optimized during choices, trading off factors such as effort, time, and having foveal vision of the target?

How and where in the brain do the populations of neurons involved in controlling eye and hand movements interact?

Are eye movements causally involved in sensorimotor learning? Could gaze training be effective for the improvement of motor skill?

Research in perceptual-cognitive skills in sports has shown differences in eye movements of more skilled versus less skilled athletes. How do eye movements and motor skills codevelop?

How are deficits in the control of eye and hand movements related? How can these deficits be addressed in a more holistic approach for assessing function and for rehabilitation?

training for professionals who require supreme eye–hand coordination (such as laparoscopic surgeons and elite athletes), and the development of robotic devices such as active arm prostheses and brain–computer interfaces.

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Citation Diversity Statement

Recent work in several fields of science has identified a bias in citation practices such that papers from women and other minorities are under-cited relative to the number of such papers in the field [103]. We sought to proactively consider choosing references that reflect the diversity of the field in thought, form of contribution, gender, and other factors. We obtained predicted gender of the first and last author of each reference by using databases that store the probability of a name being carried by a woman [104,105]. By this measure (and excluding self-citations to all authors of our current article), our references contain 10% woman(first)/woman(last), 4% man/woman, 27% woman/man, and 59% man/man categorizations. This method is limited in that (i) names, pronouns, and social media profiles used to construct the databases may not be indicative of gender identity in every case, and (ii) it cannot account for intersex, non-binary, or transgender people. We look forward to future work that could help us to better understand how to support equitable practices in science.

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