

Vision Toolkit Part 1. Neurophysiological Foundations and Experimental Paradigms in Eye-Tracking Research: A Review

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2 ABSTRACT

3 Eye-tracking research offers valuable insights into human gaze behavior by examining the
4 neurophysiological mechanisms that govern eye movements and their dynamic interactions
5 with external stimuli. This review explores the foundational principles of oculomotor control,
6 emphasizing the neural subsystems responsible for gaze stabilization and orientation. Although
7 controlled laboratory studies have significantly advanced our understanding of these mechanisms,
8 their ecological validity remains a critical limitation. However, the emergence of mobile eye tracking
9 technologies has enabled research in naturalistic environments, uncovering the intricate interplay
10 between gaze behavior and inputs from the head, trunk, and sensory systems. Furthermore, rapid
11 technological advancements have broadened the application of eye-tracking across neuroscience,
12 psychology, and related disciplines, resulting in methodological fragmentation that complicates
13 the integration of findings across fields. In response to these challenges, this review underscores
14 the distinctions between head-restrained and naturalistic conditions, emphasizing the importance
15 of bridging neurophysiological insights with experimental paradigms. By addressing these
16 complexities, this work seeks to elucidate the diverse methodologies employed for recording eye
17 movements, providing critical guidance to mitigate potential pitfalls in the selection and design of
18 experimental paradigms.

19 **Keywords:** eye-tracking, experimental settings, review article, human gaze behavior, oculomotor control

1 INTRODUCTION

20 Eye movements are controlled by three pairs of agonist-antagonist extra-ocular muscles. The lateral and
21 medial recti generate horizontal movements, while the superior rectus, inferior rectus, superior oblique, and
22 inferior oblique — collectively known as cyclovertical muscles — work together to produce both vertical
23 and torsional rotations (Leigh and Zee (2015)). Sherrington's law of reciprocal innervation states that the
24 contraction of an ocular muscle is paired with the inhibition of its antagonist, while Hering's law of equal
25 innervation ensures equal neural input to synergistic muscles in both eyes for coordinated movements
26 (Allary (2018)). Human oculomotor control is generally assumed to be governed by five distinct neural
27 subsystems: the vestibulo-ocular reflex (VOR), the optokinetic reflex (OKR), the saccadic system, the
28 smooth pursuit system, and the vergence system (Robinson et al. (1981); Büttner and Büttner-Ennever
29 (1988); Duchowski and Duchowski (2017)).

30 Early research on the neural pathways governing motor neurons of the extraocular muscles led researchers
31 to adopt reductionist approaches in controlled laboratory environments, which limited natural human
32 behavior. However, studies suggest that these artificial constraints, particularly the restriction of head
33 movements, can alter the true functioning of the oculomotor system, leading to biased representations of its
34 behavior in natural contexts (Dorr et al. (2010)). This bias arises not only from isolating neural subsystems
35 with controlled stimuli, but also from the recording methods themselves, which require stabilizing the head
36 with devices such as chin rests and chin bars (Eggert (2007); Wade (2010, 2015)).

37 More recently, the increasing availability of mobile eye trackers has significantly advanced the study of
38 eye movements in natural, or ecological, settings (Kothari et al. (2020)). However, analyzing eye movement
39 data in such conditions remains challenging. Natural gaze exploration involves simultaneous movements
40 of the eyes, head, trunk, and feet, and it has been shown that the properties of eye movements recorded
41 in these contexts differ from those in laboratory settings (Carnahan and Marteniuk (1991); Land (1992,
42 2004); Klein and Ettinger (2019)). While lab experiments typically target specific subsystems, natural eye
43 movements result from the combined action of multiple neural pathways. Indeed, automatic reflexes like
44 the VOR and the OKR, as well as higher-order cognitive processes, motor signals, and sensory inputs,
45 all contribute to ocular motoneuron activity during body movement (Anastasopoulos et al. (2009)). The
46 complexity of eye movement physiology and the limited studies available hinder a full understanding of
47 eye movements in ecological contexts.

48 On the other hand, the growing accessibility of eye movement recording technologies has led to their
49 integration across various research fields, such as neuroscience, marketing, psychology, and medicine,
50 fostering the development of specialized communities. Each discipline has contributed significantly to
51 advancing eye movement research. However, this rapid growth has also caused fragmentation, with insights
52 dispersed across a wide range of literature. Since each field often pursues distinct goals, methodologies and
53 findings are typically field-specific, limiting their applicability across disciplines. This review examines
54 the neurophysiology of eye movements and the experimental paradigms employed in this field, with
55 the aim of synthesizing studies of the oculomotor system across different research communities. Given
56 the extensive scope of the topic, this review is not intended to be exhaustive; rather, it highlights key
57 physiological insights into gaze control mechanisms. The objective is to inform the design of experimental
58 protocols for investigating eye movements, both in controlled environments and in more ecologically valid
59 settings—particularly those without physical constraints on head movements. It is important to note that
60 this brief review focuses solely on the characteristics and description of ocular movements and does not
61 explicitly address visual behavior or the allocation of visual attention.

62 With a primary emphasis on findings from human studies and on the functional aspects of eye movement,
63 the following sections offer an overview of current knowledge on major eye movement types. This work
64 distinguishes findings obtained under controlled laboratory conditions 2 — from those derived in more
65 natural, head-free environments — see Section 3. Finally, building on these neurophysiological insights,
66 we discuss practical considerations to support researchers in designing experimental protocols in Section
67 4.

68 This review stands at the intersection of multiple contributions in the existing literature, providing an
69 overview of eye movements with a clear distinction between findings obtained under controlled laboratory
70 conditions and those from ecological contexts. While aligned with prior works such as Lappi (2016),
71 it is less exhaustive than the comprehensive treatment in Leigh and Zee (2015), which delves into the
72 neurophysiology, neural circuits, and models underlying saccadic and smooth pursuit movements. Our goal
73 is to offer foundational knowledge for researchers interested in integrating eye-tracking methodologies
74 into their studies. The practical section of this review—highlighting methods for recording and analyzing
75 eye-tracking data—distinguishes it from more theoretical works, aligning more closely with reviews
76 focused on practical considerations (Singh and Singh (2012); Lim et al. (2020); Klaib et al. (2021)) or best
77 practices in data acquisition (Carter and Luke (2020)). In summary, this work provides a concise synthesis
78 of key knowledge on the neurophysiology of eye movements with a practical focus. By bridging theoretical
79 insights and practical applications, it aims to help researchers develop robust experimental protocols

2 WHEN THE HEAD IS PHYSICALLY RESTRAINED

80 Most laboratory protocols for studying eye movements are performed with the head constrained. In these
81 conditions, gaze reorientation relies exclusively on eye movements. The following sections outline the
82 canonical components of eye movements under such laboratory settings, *i.e.* saccades, smooth pursuits,
83 fixational eye movements as well as the vestibulo-ocular reflex (VOR) and optokinetic reflex (OKR).

84 2.1 Saccades

85 Saccades are rapid, ballistic eye movements that typically occur at a frequency of 2 – 4 times per second,
86 comprising approximately 10% of total viewing time (Noton and Stark (1971); Klein and Ettinger (2019)).
87 However, this frequency can vary considerably depending on perceptual and cognitive demands (Fischer
88 and Weber (1993a)). The amplitude of saccadic movements generally reaches a maximum of 40–45 degrees,
89 which is somewhat less than the oculomotor range of around 53 degrees (Freedman (2008)). Following each
90 saccade, a refractory period of approximately 120 – 200 milliseconds is commonly observed (Robinson
91 (1968); Zuber et al. (1968)), though Robinson also documented cases where successive saccades occurred
92 within shorter intervals (Robinson (1968)). Fischer and Boch’s pioneering studies in monkeys (Fischer
93 and Boch (1983)) revealed a bimodal distribution of saccadic latency, distinguishing two populations:
94 one with short latencies of 80–120 milliseconds, termed *express saccades*, and another with latencies
95 of 120–200 milliseconds, termed *fast regular saccades*. Similar latency patterns have been observed in
96 humans, though the prevalence of distinct express and regular saccade populations varies among individuals
97 (Wenban-Smith and Findlay (1991); Kingstone and Klein (1993)). Express saccades are more likely to
98 occur with predictable targets and following extensive training.

99 Functionally, saccades can be categorized as either reflexive, also known as *visually guided* (Klein and
100 Ettinger (2019)), or *volitional* in nature (Pierrot-Deseilligny et al. (1995); Patel et al. (2012); Leigh and Zee
101 (2015)). These two saccade types are controlled by parallel subsystems (Patel et al. (2012)): visually guided
102 saccades are primarily driven by external stimuli, while volitional saccades are internally generated, relying

more on cognitive processes like attention, inhibition, and working memory (Seideman et al. (2018); Klein and Ettinger (2019)). Volitional saccades include tasks like predictive saccades, where eye movements anticipate a target's appearance based on learned temporal or spatial patterns, such as tracking a stimulus appearing rhythmically at predictable locations (Leigh and Zee (2015)), and memory-guided saccades, which direct gaze toward a remembered target location without current visual input, engaging working memory to recall the target's position (Seideman et al. (2018)). Similarly, antisaccades require suppressing a reflexive saccade toward a sudden stimulus to instead look at the opposite location, relying on inhibitory control and attention as a measure of cognitive flexibility (Klein and Ettinger (2019)), while saccade sequencing involves planning and executing a series of saccades in a specific order to multiple targets, integrating attention, working memory, and motor planning for precise coordination (Patel et al. (2012)).

These tasks highlight the cognitive demands of volitional saccades, distinguishing them from reflexive saccades while illustrating their interplay along a continuum of saccadic control (Klein and Ettinger (2019)). Earlier work hinted at these mechanisms, with Bahill et al. (1981) observing that intrinsic saccade properties — such as peak velocity, amplitude, and duration — were influenced by higher-order cognitive factors like attention, muscle fatigue, and tiredness. Importantly, the separation between reflexive and volitional saccades should be understood as a continuum rather than a strict dichotomy, as internal cognitive motivations and decision-making processes influence both saccade types (Klein and Ettinger (2019)).

Saccadic eye movements are generated by a distributed network of cortical and subcortical structures. The frontal eye fields (FEF), supplementary eye fields (SEF), and posterior parietal cortex (PPC) initiate voluntary and goal-directed saccades by sending commands to the superior colliculus (SC) and brainstem saccade generators (Leigh and Zee (2015); Pierrot-Deseilligny et al. (2004)). The SC, particularly its intermediate and deep layers, integrates multisensory inputs and contributes to both reflexive and voluntary saccades (Wurtz and Goldberg (1972)). Premotor structures in the brainstem, including the paramedian pontine reticular formation (PPRF) for horizontal saccades and the rostral interstitial nucleus of the medial longitudinal fasciculus (riMLF) for vertical and torsional saccades, generate high-frequency burst activity. These work in conjunction with omnipause neurons in the nucleus raphe interpositus, which inhibit saccade initiation and regulate timing (Scudder et al. (2002)). The cerebellum, especially the fastigial nucleus and dorsal vermis, refines saccadic metrics and mediates motor learning and adaptation (Optican and Robinson (1980); Robinson and Fuchs (2001)). This network operates both hierarchically and in parallel, integrating sensory, cognitive, and motor information to guide rapid eye movements.

Saccade kinematics are typically characterized by a stereotyped, symmetrical velocity profile for movements ranging from 5 to 25 degrees, with larger saccades tending to display a skewed profile, where the deceleration phase is often longer than the acceleration phase. Saccades also exhibit a linear duration-amplitude relationship, with the slope estimated to be between 1.5 and 3 milliseconds per degree, as well as a non-linear relationship between peak velocity and amplitude Bahill et al. (1981); Klein and Ettinger (2019). This latter relationship is commonly referred to as the *main sequence*, a term introduced by Bahill et al. (1975) and borrowed from astronomy, which has since become a major focus of research (Freedman (2008); Gibaldi and Sabatini (2021)). Notably, it has been observed that the peak velocity of a saccade increases as a function of its amplitude, reaching a peak at approximately 20–30 degrees (Bahill et al. (1975); Zuber et al. (1968)), after which it plateaus around 600 degrees per second. Alternative models for the main sequence have been proposed in subsequent studies (Leigh and Zee (2015); Gibaldi and Sabatini (2021)). Nonetheless, the main sequence remains a valuable tool for studying both pathological and non-pathological eye movements in clinical neuroscience (Leigh and Kennard (2004a); Ramat et al. (2006)), for developing and evaluating neural models of saccadic eye movement control (Becker (1989);

147 Robinson et al. (1993); Quaia et al. (1999); Jagadisan and Gandhi (2017)), and for investigating eye
148 movement adaptation (Optican and Robinson (1980)).

149 At the end of a typical saccadic eye movement, just before settling into steady fixation, the pupil signal
150 often shows a damped oscillation, with one or two observable cycles before attenuation (Nyström et al.
151 (2013b); Hooge et al. (2015)). These *post-saccadic oscillations* (PSOs) typically have an amplitude of
152 around 2 degrees, with oscillation periods averaging about 20 milliseconds (Hooge et al. (2015)). The
153 origin of PSOs, long debated, is now believed to be due to dynamic deformations of the iris's inner edge
154 during saccades (Nyström et al. (2013b); Hooge et al. (2016)). Specifically, these oscillations result from
155 movements of the pupil within the eyeball, referred to as *iris wobbling* or the *eye wobbling phenomenon*.
156 It's important to note that PSO characteristics can vary significantly depending on the eye-tracking methods
157 used (Hooge et al. (2016)), the direction of the saccade (Hooge et al. (2015)), and individual differences,
158 such as the observer's age (Mardanbegi et al. (2018)) and pupil size (Nyström et al. (2016)).

159 Saccade metrics were found to be stable within and across trials, thereby making them suitable biometric
160 data for authentication, identification or to reveal differences in perceptual-motor style between individuals
161 (Klein and Ettinger (2019); Vidal and Lacquaniti (2021)). For example, the pioneering work of Holland
162 and Komogortsev (2013) and Rigas and Komogortsev (2016) demonstrated the robustness of individual-
163 specific eye movements characteristics for recognition purposes with different types of visual stimulus.
164 Their approach led to the development of the *complex eye movement extended* biometrics, which consists
165 of several fixation and saccade-related characteristics that together constitute an individual's biometric
166 fingerprint. While these approaches do not yet represent a realistic alternative to existing biometric
167 standards, they represent a promising field of research.

168 In neurological and psychiatric disorders, abnormalities in saccadic eye movements provide insights
169 into impaired motor planning, inhibitory control, and neural circuit dysfunction. In Parkinson's disease
170 (PD), saccades typically exhibit hypometria — reduced amplitude — and prolonged latencies, particularly
171 for volitional saccades. These deficits stem from dysfunction in the basal ganglia, supplementary eye
172 fields, and frontal eye fields (FEF), which impair the generation and execution of planned movements
173 (Terao et al. (2011); Lal and Truong (2019)). Huntington's disease (HD) is associated with increased
174 antisaccade latencies and high error rates, reflecting early degeneration of the striatum and prefrontal
175 cortex, both critical for suppressing automatic responses. Antisaccade errors in HD may precede overt
176 motor symptoms and serve as early markers of cognitive decline (Lal and Truong (2019)). In progressive
177 supranuclear palsy (PSP), vertical saccades — particularly downward — are severely impaired due to
178 degeneration of the rostral interstitial nucleus of the medial longitudinal fasciculus (riMLF) and midbrain
179 structures (Leigh and Zee (2015)). Cerebellar disorders, such as spinocerebellar ataxias, result in dysmetric
180 saccades—overshooting — hypermetria — or undershooting — hypometria — of the target—and poor
181 saccadic adaptation. These effects are attributed to damage in the dorsal vermis and fastigial nucleus, which
182 modulate saccadic accuracy.

183 In schizophrenia, antisaccade errors are markedly increased and latencies highly variable, indicating
184 core deficits in inhibitory control and executive functioning. These deficits are linked to dysfunction in
185 the dorsolateral prefrontal cortex (DLPFC) and its connections with the FEF and basal ganglia. Impaired
186 antisaccade performance is considered a potential endophenotype for schizophrenia (Gooding and Basso
187 (2008)). Similarly, individuals with attention-deficit/hyperactivity disorder (ADHD) demonstrate increased
188 antisaccade error rates and variable reaction times, pointing to immature or dysfunctional prefrontal
189 inhibitory mechanisms (Muñoz et al. (2003)). These deficits reflect challenges in voluntary response
190 suppression and sustained attention. Lastly, saccadic intrusions, such as square-wave jerks — involuntary

191 saccades that briefly displace fixation — are common across neurodegenerative disorders and may interfere
192 with steady gaze. While not volitional, these intrusions further signal brainstem or cerebellar dysfunction
193 (Leigh and Kennard (2004b)).

194 2.2 Smooth Pursuit

195 Ocular pursuit movements are triggered primarily by the continuous motion of a target, causing its image
196 to drift across the retinal surface, and their primary function is to preserve visual acuity by stabilizing the
197 moving image on or near the fovea. The primary input driving these movements is the retinal slip velocity,
198 which refers to the relative motion of the target across the retina (Binder et al. (2009); Klein and Ettinger
199 (2019)). In contrast, saccadic eye movements are typically triggered by discrete positional changes, such as
200 when a target suddenly jumps outside the foveal region, to rapidly recenter the target's image on the fovea.
201 Unlike the saccadic system, which operates in discrete bursts, the smooth pursuit system is continuous and
202 does not exhibit a refractory period (Robinson (1965)). Typical optimal pursuit speeds range from 15 to 30
203 degrees per second (Rashbass (1961); Meyer et al. (1985); Ettinger et al. (2003); Klein and Ettinger (2019)),
204 although efficient tracking of velocities up to 100 degrees per second has been observed for predictable
205 motion patterns. This suggests that pursuit control involves higher-level extra-retinal mechanisms, such as
206 anticipation and predictive processes.

207 Smooth pursuit movements consist of two phases. The initial phase, known as *pursuit initiation*, is driven
208 solely by visual motion information. It is characterized by a latency period — the time required for the
209 eyes to begin tracking the target after it starts moving — which ranges between 120 and 180 milliseconds
210 in healthy individuals, depending on task conditions and experience (Klein and Ettinger (2019)). During
211 the first 100 milliseconds of pursuit initiation, the response is based solely on the initial appearance of the
212 target, unaffected by changes in the retinal image due to eye movement. In this phase, pursuit operates in
213 an *open-loop* manner, relying on target movement without feedback from eye position. This *open-loop*
214 phase can be modified by experience as the system adapts to changes in target velocity, a process known as
215 *pursuit adaptation* (Chou and Lisberger (2004)).

216 The second phase, *pursuit maintenance*, aims to stabilize the target on the fovea. It combines visual
217 feedback with predictions of target velocity to maintain the image within the zone of optimal visual acuity.
218 In this *closed-loop* phase, any deviations from the ideal trajectory are corrected through compensatory eye
219 movements (Thier and Ilg (2005)). Retinal velocity, image acceleration (Lisberger et al. (1987)), and target
220 position relative to the fovea (Blohm et al. (2005)) all serve as error signals guiding pursuit. While pursuit
221 is largely feedback-driven, cognitive factors like experience with target motion and stimulus predictability
222 can modulate its performance (Barnes (2008)).

223 Smooth pursuit eye movements are controlled by an interconnected network of cortical, subcortical,
224 brainstem, and cerebellar structures. The frontal eye fields (FEF), particularly their pursuit-related subregion,
225 initiate and sustain voluntary tracking, while the lateral intraparietal area (LIP) modulates attentional focus
226 and target selection (Tanaka and Lisberger (2002); Thier and Ilg (2005)). Visual motion signals are primarily
227 processed in the middle temporal (MT) and medial superior temporal (MST) areas, which compute retinal
228 slip velocity and convey motion-related input to pursuit pathways (Newsome et al. (1985)). These signals
229 are relayed to the dorsolateral pontine nuclei (DLPN) in the brainstem, which project to the cerebellum to
230 help generate smooth pursuit commands (Mustari et al. (1988)). The cerebellum, especially the flocculus
231 and posterior vermis, refines pursuit accuracy and supports adaptation through motor learning mechanisms
232 (Miles and Fuller (1975); Thier and Ilg (2005)).

233 Due to delays in the visual pathways and the limitations of eye velocity and acceleration, smooth
234 pursuits are often supplemented by corrective or *catch-up* saccades. These rapid saccades are important
235 for maintaining target tracking when smooth pursuit alone cannot compensate for unpredictable target
236 movement or rapidly varying velocities, leading to retinal error accumulation (Haller et al. (2008)). Catch-
237 up saccades are highly controlled and executed without visual feedback, with their precision essential for
238 effective pursuit. Research has shown that their amplitudes are closely aligned with both positional error
239 and retinal slip (De Brouwer et al. (2002)). For a comprehensive discussion of saccade-pursuit interactions,
240 see the recent review by Goettker and Gegenfurtner (2021).

241 Interestingly, studies have demonstrated that the horizontal component of pursuit eye movements is more
242 accurate than the vertical component (Rottach et al. (1996); Grönqvist et al. (2006); Ingster-Moati et al.
243 (2009); Ke et al. (2013)). This increased accuracy in horizontal tracking has been observed not only for
244 targets moving strictly along the horizontal or vertical axes but also for horizontal and vertical components
245 in bidirectional pursuit sequences (Ke et al. (2013)). Moreover, horizontal pursuit mechanisms are found to
246 develop earlier in children, supporting a developmental asymmetry in pursuit capabilities (Grönqvist et al.
247 (2006)). These directional differences align with findings indicating distinct neurophysiological substrates
248 for horizontal and vertical pursuit pathways (Saito and Sugimura (2020); Kettner et al. (1996); Chubb et al.
249 (1984)). The distinct neurophysiological substrates for horizontal and vertical pursuit pathways suggest
250 independent feedback control mechanisms. For instance, Rottach et al. (1996) demonstrated that horizontal
251 smooth pursuit in healthy subjects is more accurate and exhibits lower variability than vertical pursuit, with
252 these differences persisting across horizontal, vertical, and diagonal target trajectories. This asymmetry
253 is further supported by Rottach et al. (1997), who studied Niemann-Pick type C disease and found that
254 horizontal and vertical saccades are independently affected, implying separate neural feedback loops for
255 each axis. These findings suggest that horizontal pursuit relies on more robust control circuits, potentially
256 involving the medial superior temporal area and pontine nuclei, while vertical pursuit engages distinct
257 brainstem and cerebellar pathways, which may be less precise or more susceptible to disruption (Saito
258 and Sugimura (2020); Kettner et al. (1996)). Such independent control underscores the functional and
259 developmental differences observed in pursuit performance.

260 Aberrant smooth pursuit eye movements, characterized by impaired tracking of a moving target, serve
261 as sensitive biomarkers for neurological and psychiatric disorders. In schizophrenia, reduced pursuit gain
262 — eye velocity divided by target velocity — and increased phase lag reflect impaired motion processing
263 in the middle temporal and medial superior temporal areas (MT/MST) and disrupted prefrontal control,
264 particularly in the dorsolateral prefrontal cortex (DLPFC) (Chen et al. (1999); O'Driscoll and Callahan
265 (2008); Lencer et al. (2015)). Cerebellar ataxias, such as spinocerebellar atrophy type 3 (SCA3), exhibit
266 low-gain pursuit, irregular tracking, and frequent catch-up saccades, stemming from floccular and posterior
267 vermal dysfunction that impairs motor learning and predictive pursuit (Miles and Fuller (1975); Buttner
268 et al. (1998)). In Parkinson's disease, pursuit gain is mildly reduced, especially for unpredictable target
269 trajectories, due to basal ganglia deficits disrupting movement initiation and predictive control (Lekwuwa
270 et al. (1999); Frei (2021)). Attention-deficit/hyperactivity disorder (ADHD) patients show fluctuating
271 pursuit gain and elevated velocity errors, linked to frontoparietal attentional control impairments (Karatekin
272 (2007)). Unlike saccadic disorders, which produce discrete spatial errors — e.g. hypometria, square-wave
273 jerks — pursuit dysfunction manifests as continuous tracking inaccuracies, notably altered gain and phase
274 delay, quantifiable via high-resolution eye-tracking (Thier and Ilg (2005)).

275 2.3 Fixational Eye Movements

276 A fixation is defined as a period during which gaze is directed at a specific location, projecting the image
277 onto the high-resolution processing region of the retina, the *fovea centralis*. Despite efforts to maintain a
278 steady gaze, the eyes exhibit continuous, involuntary motion, influencing much of our visual experience.
279 This creates a contradiction in the visual system: while gaze remains fixed on an object, the eyes are never
280 entirely still. The precise roles of fixational eye movements — namely *tremors*, *drifts*, and *microsaccades*
281 (Martinez-Conde et al. (2004); Martinez-Conde (2006)) — in the visual process remain unclear and are
282 the subject of ongoing discussion. It is believed that one function of these movements is to counteract
283 neural adaptation by introducing small, random displacements of the retinal image. This helps ensure
284 continuous stimulation of different photoreceptor cells in the fovea, preventing perceptual fading that would
285 occur if the retinal image remained stationary (Pritchard (1961)). Additionally, fixational eye movements
286 are proposed to play a role in the acquisition and processing of visual information by optimizing retinal
287 sampling and enhancing the fine details of the visual scene (Klein and Ettinger (2019)).

288 2.3.1 Tremors

289 Ocular micro-tremors, sometimes called physiological nystagmus, are tiny, high-frequency, involuntary
290 eye oscillations that occur naturally in healthy eyes. These movements typically vibrate at 70 to 100 cycles
291 per second — though some studies report a broader range of 50 to 200 cycles per second — with amplitudes
292 smaller than 0.01 degrees (Martinez-Conde et al. (2004); Collewijn and Kowler (2008); Klein and Ettinger
293 (2019)). As a normal feature of vision, micro-tremors are not a sign of disease but one of three types of
294 fixational eye movements, alongside slow drifts and microsaccades, which together maintain clear vision
295 during steady gaze. They originate from the rapid, asynchronous firing of fast-twitch motor units in the
296 extraocular muscles, controlled by motor neurons in the brainstem's motor nuclei (Ezenman et al. (1985);
297 Collewijn and Kowler (2008)).

298 The neuroanatomy of micro-tremors centers on the brainstem's extraocular motor nuclei — abducens,
299 oculomotor, and trochlear — which send precise signals to the six extraocular muscles that position the eyes
300 (Leigh and Zee (2015)). These nuclei produce high-frequency firing patterns that create the microscopic
301 oscillations observed in micro-tremors (Ezenman et al. (1985)). The pontine reticular formation, a brainstem
302 region involved in coordinating gaze, likely refines the timing of these signals, contributing to the tremors'
303 rapid frequency (Sparks (2002)). Often described as neural “*noise*” in the ocular motor system, micro-
304 tremors may serve a functional role. One hypothesis suggests they facilitate stochastic resonance, where
305 subtle noise enhances the detection of faint visual signals, such as slight environmental shifts (Simonotto
306 et al. (1997); Hennig et al. (2002)). This idea remains speculative, however, and further research is needed
307 to confirm its significance in visual processing.

308 Early research proposed that micro-tremors in each eye were independent (Riggs and Ratliff (1951);
309 Ditchburn and Ginsborg (1953)). More recent studies, however, have observed partial synchronization,
310 evidenced by peaks in spectral coherence between the two eyes, likely mediated by shared neural pathways
311 like the medial longitudinal fasciculus (Spauschus et al. (1999)). This brainstem structure connects the
312 abducens and oculomotor nuclei, enabling coordinated eye movements. The mechanisms driving this
313 synchronization are not fully understood, highlighting an active area of investigation.

314 Studying micro-tremors is challenging because their high frequency often falls below the noise threshold
315 of standard eye-tracking systems and can overlap with other eye movements, such as drifts or microsaccades
316 (Klein and Ettinger (2019)). Despite these difficulties, advancements in high-precision technologies,
317 including video-based systems, scleral search coils, and specialized devices, have enabled accurate

318 measurements, confirming the tremors' small amplitude and rapid frequency (Collewijn and Kowler
319 (2008); McCamy et al. (2013, 2014)). These movements contribute to retinal image stability, preventing
320 visual fading — known as *Troxler fading* — during fixation (Engbert and Kliegl (2004a)). By introducing
321 subtle motion across the retina, micro-tremors may refresh visual input, supporting sharp, high-resolution
322 vision and potentially aiding tasks requiring fine visual detail.

323 2.3.2 Microsaccades

324 Microsaccades are small-amplitude saccadic eye movements, occurring approximately once or twice per
325 second (Rolfs (2009)). While traditionally considered a type of fixational eye movement, emerging research
326 suggests that microsaccades share neural pathways with larger saccades (Hafed (2011)) and exhibit many
327 similar characteristics (Abadi and Gowen (2004); Otero-Millan et al. (2013)), notably adhering to the main
328 sequence (Zuber et al. (1965)). As such, microsaccades may be viewed as part of the broader continuum of
329 saccadic movements. Interestingly, microsaccades are often regarded as involuntary or unconscious, yet
330 they are regulated by the same endogenous control mechanisms that govern larger saccades (Collewijn
331 and Kowler (2008)). Furthermore, assumption that humans are unaware of their microsaccades requires
332 reconsideration, as individuals can exert a degree of control over them with appropriate training. For
333 example, studies have demonstrated that individuals with experience in laboratory fixation tasks are capable
334 of suppressing their microsaccades for several seconds during tasks requiring high visual acuity (Bridgeman
335 and Palca (1980); Steinman et al. (1967); Winterson and Collewijn (1976)).

336 The neuroanatomy underlying microsaccades involves a distributed network of brain regions that overlaps
337 significantly with the neural circuitry responsible for larger saccadic eye movements. Key structures
338 include the superior colliculus, which integrates sensory and motor signals to initiate microsaccades (Hafed
339 (2011)), and the frontal eye fields, which contribute to their modulation, particularly in voluntary contexts
340 (Tian et al. (2016)). The brainstem, particularly the pontine reticular formation and the oculomotor nuclei,
341 plays a critical role in generating the precise motor commands for these rapid eye movements (Scudder
342 et al. (2002)). Additionally, the cerebellum fine-tunes microsaccade amplitude and timing, ensuring
343 their accuracy during fixation tasks (Otero-Millan et al. (2011)). Neuroimaging and electrophysiological
344 studies suggest that the same cortical and subcortical pathways that govern saccades are recruited for
345 microsaccades, supporting the view that they are part of a continuum of oculomotor behavior (Martinez-
346 Conde et al. (2009)). This shared neural substrate enables the endogenous modulation of microsaccades, as
347 seen in trained individuals who can suppress them to enhance visual acuity in specific tasks (Steinman et al.
348 (1973)).

349 Several studies have examined how anticipation affects microsaccade frequency. Betta and Turatto (2006)
350 demonstrated that anticipating a motor response could reduce the microsaccade rate, while uncertainty
351 about the motor response did not have the same effect (Rolfs (2009)). Similarly, anticipatory responses to
352 sensory events can lead to a phenomenon called *oculomotor freezing*, characterized by a transient reduction
353 in spontaneous microsaccade frequency lasting 100 to 400 milliseconds after the onset of an auditory,
354 tactile, or visual stimulus.

355 The functional role of microsaccades remains a highly debated issue in the literature. Cornsweet (1956a);
356 Krauskopf et al. (1960) hypothesized that microsaccades help counteract the random drift of the eyes,
357 serving a corrective role in both fixation position and binocular disparity — the slight difference between
358 the retinal images of the left and right eyes. Other studies suggested that microsaccades may mitigate
359 retinal adaptation by maintaining motion on the retina with respect to the visual environment (Ditchburn
360 and Ginsborg (1952); Riggs et al. (1953)). Additional research suggests that microsaccades prevent

361 retinal adaptation by promoting super-diffusive dynamics of gaze — where the gaze trajectory during
362 fixation spreads faster than a normal random walk — over short time scales. Over longer time scales,
363 the sub-diffusive dynamics of gaze — characterized by a slower spread of gaze trajectories compared to
364 a normal random walk — mitigate fixation errors and reduce binocular disparity more effectively than
365 an uncorrelated random walk (Engbert and Kliegl (2004b); Moshel et al. (2008); Roberts et al. (2013)).
366 Finally, some authors remain skeptical of the idea that microsaccades serve a unique role in sustaining
367 fixation or preventing retinal adaptation, suggesting that these functions could be adequately fulfilled by
368 smooth pursuit or slow drift movements (Collewijn and Kowler (2008); Kowler (2011); Klein and Ettinger
369 (2019)). In fact, some researchers have even suggested that microsaccades represent an evolutionary enigma
370 (Kowler and Steinman (1980); Martinez-Conde et al. (2004)).

371 Part of the confusion surrounding the functional role of microsaccades stems from ambiguity in their
372 definition. Traditionally, microsaccades are distinguished from regular saccades by amplitude thresholds,
373 with movements below a certain threshold classified as microsaccades. Early studies defined microsaccades
374 as movements ranging from approximately 0.20 to 0.25 degree (Boyce (1967); Cunitz and Steinman (1969);
375 Ditchburn and Foley-Fisher (1967)). Recent studies, however, have expanded the threshold to include
376 movements up to 1 – 2 degrees (Engbert and Kliegl (2004a); Martinez-Conde et al. (2006)). This broader
377 range complicates direct comparisons with earlier literature and raises concerns regarding the functional
378 interpretation of microsaccades.

379 2.3.3 Drifts

380 Ocular drifts are slow, continuous eye movements occurring during inter-saccadic intervals, producing
381 gaze trajectories that approximate a random walk—small, stochastic displacements with varying directions
382 and amplitudes, typically shifting the retinal image by approximately 0.13 degrees at velocities below 0.5
383 degrees per second (Cornsweet (1956b); Engbert and Kliegl (2004a); Collewijn and Kowler (2008); Klein
384 and Ettinger (2019)). While often stochastic, drifts may exhibit subtle directional influences from visual or
385 attentional factors. Neuroanatomically, they stem from tonic activity in the brainstem’s neural integrator,
386 particularly the nucleus prepositus hypoglossi (NPH) and medial vestibular nucleus (MVN), which sustain
387 low-frequency motor neuron firing to extraocular muscles (Cannon and Robinson (1987); Fuchs et al.
388 (1988)). The superior colliculus (SC) modulates fixational stability, while the cerebellar flocculus and
389 vermis fine-tune drift amplitude via feedback (Hafed et al. (2009); Arnstein et al. (2015)). Drifts are
390 involuntary and, alongside microsaccades, help maintain fixation, especially when microsaccades are
391 limited, and contribute to retinal image motion that prevents neural adaptation, supporting continuous
392 perception of visual detail (Engbert and Mergenthaler (2006); Rucci and Victor (2015a)).

393 Research investigating the respective roles of drift and microsaccades in correcting fixation disparity
394 and stabilizing overall fixation position has developed along parallel lines. Early studies suggested that
395 only microsaccades could adjust both binocular disparity and inaccurate fixation positions. However, later
396 findings demonstrated that drifts also contribute to these corrections, particularly in the horizontal direction
397 — for fixation position (Steinman et al. (1967)) and fixation disparity (St.Cyr and Fender (1969)). More
398 recent evidence indicates that both microsaccades and drifts can adjust fixation position on a timescale
399 greater than 100 milliseconds, though only microsaccades appear to be involved in correcting fixation
400 disparity over this relatively extended timescale (Engbert and Kliegl (2004b)). The relative roles of
401 microsaccades and drifts in maintaining stable binocular fixation were further examined by Møller et al.
402 (2006), whose findings suggest that drift-related eye movements — known as *slow control* — primarily
403 maintain the alignment of the visual line of sight within the foveal center during steady fixation.

404 A recent body of research has explored the role of inter-saccadic fixational eye movements — specifically,
405 ocular drifts and tremors — in forming visual spatial representations (Aytekin et al. (2014); Rucci and Poletti
406 (2015); Poletti et al. (2015)). Evidence indicates that the Brownian, or random-like, motion generated by
407 these movements converts the static spatial information of the visual scene into a dynamic spatio-temporal
408 signal on the retina. This movement causes retinal photoreceptors to encounter fluctuating luminance
409 inputs, enhancing high spatial frequencies that emphasize object contours within the environment (Rucci
410 and Victor (2015b)). Thus, inter-saccadic fixational movements contribute to visual processing by encoding
411 spatial information through temporal modulation, aiding in the extraction of features at early stages of
412 visual processing (Rucci and Poletti (2015); Rucci and Victor (2015b)).

413 2.4 Vestibulo-Ocular Reflex

414 The vestibulo-ocular reflex (VOR) stabilizes the retinal image during head movements by producing
415 compensatory eye movements in the direction opposite to head motion. This action maintains visual fixation
416 on a static target in a stationary environment, thus preventing visual blurring. Laboratory research on VOR
417 has been constrained by practical considerations, notably safety considerations that limit the range and
418 intensity of vestibular stimuli for participants. Furthermore, laboratory protocols primarily assess passive
419 head movements in the dark, focusing on controlled conditions in which the head is physically restrained
420 or directly manipulated Büttner and Büttner-Ennever (2006), preventing neck proprioception and visual
421 information to come into play. In healthy humans, passive whole-body motion using a rotating chair —
422 with low-frequency sinusoidal oscillation or persistent rotation in one direction — or passive head rotations
423 using a torque helmet are typically employed Collewijn and Smeets (2000); Bronstein et al. (2015).

424 The vestibulo-ocular reflex (VOR) is initiated when the vestibular system detects head motion, primarily
425 through the semicircular canals and otolith organs of the inner ear. The semicircular canals sense angular
426 acceleration resulting from rotational head movements; fluid displacement within the canals deflects hair
427 cells in the crista ampullaris, transducing head rotation into neural signals that encode direction and
428 velocity (Fernandez and Goldberg (1971)). In contrast, the otolith organs—the utricle and saccule—detect
429 linear acceleration and head tilt by transducing otoconia displacement into hair cell activation, signaling
430 translational motion and orientation relative to gravity (Angelaki and Cullen (2008)). These vestibular
431 signals are conveyed via the vestibular nerve to the vestibular nuclei in the medulla and pons, where input
432 from both ears and other sensory systems is integrated (Cullen (2012)). From there, signals are transmitted
433 through the medial longitudinal fasciculus (MLF) to the oculomotor, trochlear, and abducens nuclei. This
434 pathway drives compensatory, conjugate eye movements in the direction opposite to head motion, thereby
435 stabilizing retinal images during movement (Leigh and Zee (2015)). The cerebellum, particularly the
436 flocculus, nodulus, and posterior vermis, modulates the VOR by calibrating its gain and adapting reflex
437 responses through motor learning. This allows for precise gaze stabilization even under varying head
438 velocities, altered visual feedback, or long-term changes in sensorimotor conditions (Lisberger (1988)).

439 Functionally, the VOR manifests as *vestibular nystagmus*, a rhythmic pattern of compensatory slow
440 phases interrupted by quick phases during sustained head rotations Robinson (1977); Land and Tatler
441 (2009); Chun and Robinson (1978); Barnes (1979). The slow phase counteracts head movement by moving
442 the eyes in the opposite direction, stabilizing the visual field. Ideally, the eye velocity during the slow
443 phase matches the head's velocity in the opposite direction, yielding a gain — eye velocity divided by head
444 velocity — close to 1. The slow phase also demonstrates adaptability in response to visual or vestibular
445 impairment, a process known as *VOR adaptation* or *gain adjustment*. For instance, when altered visual
446 feedback is introduced, the slow phase incrementally adjusts its gain to restore stability, reflecting adaptation

447 under changing conditions Shelhamer et al. (1992). For more details on VOR adaptation mechanisms, see
448 the review from Schubert and Migliaccio (2019).

449 In contrast, the quick phase is a rapid saccadic movement that repositions the eyes centrally after the
450 slow phase, allowing continued compensatory slow phases during sustained head rotation. Eye and head
451 coordination during gaze orientation can follow two strategies, depending on the influence of slow and
452 quick phases of vestibular nystagmus on eye eccentricity Lestienne et al. (1984). The first strategy, seen in
453 highly alert animals, directs the gaze with head motion, known as the "*look where you go*" strategy. In
454 this case, the overall eccentricity of the eye displacement in the orbit — also known as the *beating field*
455 or *schlagfeld* — aligns with the head's movement, as quick phases dominate the slow ones. The second
456 strategy, "*look where you came from*", involves directing the gaze opposite the head's motion. Here, slow
457 phases dominate, causing the beating field to shift contralaterally. These strategies represent the extremes
458 of a spectrum, with intermediate patterns influenced by factors such as the level of alertness, behavioral
459 context, and sensory-motor demands.

460 The VOR consists of rotational and translational components that stabilize vision during head
461 movements. The rotational VOR compensates for angular rotations around the three principal axes,
462 driven by semicircular canals detecting angular acceleration, ensuring near-complete visual stabilization
463 during rapid movements Leigh and Zee (2015). The translational VOR stabilizes gaze during linear
464 displacements—forward, backward, or lateral—via otolith organs, which detect linear acceleration
465 and gravitational forces. However, the translational VOR is subject to limitations due to tilt-translation
466 ambiguity, as the otolith organs respond similarly to both linear acceleration and changes in head tilt relative
467 to gravity Angelaki and Yakusheva (2009). Resolving this ambiguity requires multimodal integration of
468 signals from the semicircular canals, visual inputs, target distance, and image eccentricity Angelaki
469 (1998); Paige and Tomko (1991); Telford et al. (1997). These findings suggest that the VOR is only
470 one contributor to eye stabilization, which is based on multimodal sensory integration, which combines
471 vestibular, visual, and proprioceptive information to optimize both precision and adaptability. Additionally,
472 distinct VOR mechanisms are likely engaged during actively generated head movements, as opposed to
473 passively induced ones Büttner and Büttner-Ennever (2006); Cullen and Roy (2004). These perspectives
474 contrast with previous findings from controlled laboratory settings and will be elaborated in Section 3.1.2.

475 Abrupt head movements, known as *head impulses*, challenge the vestibulo-ocular reflex (VOR) to
476 stabilize vision by producing eye movements that counteract rapid head rotations, typically at velocities of
477 150 to 300 degrees per second. The VOR relies primarily on the inner ear's semicircular canals (Leigh and
478 Zee (2015)). During passive head impulses, such as when a clinician swiftly turns a patient's head, the
479 reflex depends almost entirely on this vestibular input, with little influence from neck muscle feedback
480 or voluntary control. This isolation highlights the VOR's ability to maintain gaze stability, achieving
481 a gain — eye velocity divided by head velocity — close to 1 in healthy individuals, ensuring smooth
482 compensatory eye movements that keep the visual world steady (Halmagyi and Curthoys (1988)). When
483 vestibular disorders like vestibular neuritis disrupt this process, reduced gain causes the eyes to lag behind
484 head motion, leading to retinal slip—blurred vision as the image drifts across the retina—often corrected
485 by saccades to refocus on the target (Strupp and Brandt (2009)).

486 The advent of high-frequency video head impulse testing (vHIT) has transformed how clinicians evaluate
487 VOR performance during these rapid movements. Using high-speed infrared cameras sampling at 250 to
488 500 cycles per second, vHIT captures eye and head movements with high spatial precision. This technology
489 quantifies VOR gain and detects covert saccades — quick, involuntary eye adjustments that compensate
490 for inadequate reflex performance — offering a sensitive measure of vestibular health (MacDougall et al.

491 (2009)) In unilateral vestibular hypofunction, such as in vestibular neuritis, vHIT reveals diminished
492 gain and corrective saccades when the head turns toward the affected side. Bilateral vestibulopathy, often
493 triggered by ototoxic drugs like aminoglycosides, shows severely reduced gain in both directions, resulting
494 in oscillopsia, a disorienting visual motion that disrupts daily activities like walking (Zingler et al. (2007)).
495 Central disorders, particularly those affecting the cerebellum's flocculus and nodulus, impair the brain's
496 ability to fine-tune VOR gain, leading to inconsistent eye responses across head velocities due to disrupted
497 cerebellar modulation (Migliaccio et al. (2004); Kheradmand and Zee (2011)).

498 These impairments underscore the VOR's vulnerability to disruptions in the semicircular canals, brainstem
499 circuits, or cerebellar pathways, all of which can compromise the reflex's ability to stabilize gaze. By
500 pinpointing whether deficits stem from peripheral issues, like inner ear damage, or central causes, such
501 as cerebellar lesions, vHIT provides critical diagnostic clarity, guiding tailored vestibular rehabilitation
502 strategies to restore gaze stability (Tarnutzer et al. (2016); Sulway and Whitney (2019)).

503 2.5 Optokinetic Reflex

504 The optokinetic reflex (OKR) is a visually mediated reflex that engages when a large segment of the
505 visual field moves relative to the eyes, typically triggered when the surrounding environment appears to
506 move while the observer remains stationary Fletcher et al. (1990); Tarnutzer and Straumann (2018); Büttner
507 and Büttner-Ennever (2006). This reflex primarily responds to "*retinal slip*", the relative movement of
508 images across the retina during both environmental and self-induced motion Fletcher et al. (1990). The
509 OKR works synergistically with the vestibulo-ocular reflex (VOR) to process optic flow, responding either
510 to rotational motion around the individual — rotational OKR — or to fronto-parallel translational motion
511 — translational OKR. This synergy is especially important for low-frequency motions below 0.2 Hz, for
512 which the gain of the VOR is low Büttner and Büttner-Ennever (2006); Fletcher et al. (1990); Schweigart
513 et al. (1997); Land and Tatler (2009). Although OKR and VOR share neural substrates, the OKR operates
514 with a longer latency — around 150 milliseconds — due to its reliance on visual input Land and Tatler
515 (2009).

516 The optokinetic reflex (OKR) is driven by a complex neural network involving the retina, brainstem, and
517 cerebellum (Cohen et al. (1977); Leigh and Zee (2015)). Retinal ganglion cells detect large-field visual
518 motion and transmit signals through the accessory optic system, including the nucleus of the optic tract
519 (NOT) and dorsal terminal nucleus, which process directional motion cues (Simpson (1984); Mustari and
520 Fuchs (1990)). These brainstem structures integrate sensory input and collaborate with the vestibular nuclei
521 to produce compensatory eye movements (BuÈttner-Ennever and Horn (2002); Giolli et al. (2006)). The
522 cerebellum, particularly the flocculus and paraflocculus, fine-tunes OKR responses by modulating motor
523 output based on visual feedback and predictive learning, ensuring precise gaze stabilization during head or
524 environmental motion (Waespe et al. (1983); Voogd and Barmack (2006)).

525 Experimentally, the OKR is commonly induced by rotating a striped drum — known as the Bárány
526 nystagmus drum — around the subject, who observes alternating black and white stripes or dot patterns
527 Fletcher et al. (1990); Distler and Hoffmann (2011). This setup typically elicits a reflexive, oscillatory
528 eye movement characterized by an alternating sequence of quick and slow phases Garbutt et al. (2003);
529 Büttner and Büttner-Ennever (2006). Quick phases are fast, ballistic eye movements directed opposite to
530 the direction of the visual flow. These movements share properties with ocular saccades and function to
531 reposition the eyes toward a central orbital position, countering the visual motion stimulus Fletcher et al.
532 (1990); Kaminiarz et al. (2009). In contrast, the slow phases are low-velocity compensatory movements
533 that align with the stimulus motion. The correction, however, is not perfect, as the gain — defined as

534 the ratio of slow-phase velocity to stimulus velocity — is less than one and decreases as stimulus speed
535 increases Fletcher et al. (1990); Land and Tatler (2009).

536 From a computational perspective, three primary models explain the alternation between quick and slow
537 phases in optokinetic nystagmus: (i) the *eye position control hypothesis*, which suggests that quick phases
538 are triggered to keep the eye within a certain orbital position range Ter Braak (1936); (ii) the *internal*
539 *timing hypothesis* — or clocking model — originally proposed by Ohm Ohm (1928), which posits the
540 existence of a central interval generator that times the onset of quick phases; and (iii) the *hybrid position-*
541 *interval generator hypothesis*, which combines elements of both position control and timing regulation.
542 Supporting evidence indicates the presence of a Gaussian-based interval generator — a biological clock —
543 that modulates the timing of quick phases and can be influenced by concurrent cognitive tasks Balaban
544 and Ariel (1992); Balaban and Furman (2017). It's important to note that the timing and amplitude of
545 these phases are highly variable Carpenter (1993); Trillenberg et al. (2002), and the underlying cause of
546 this variability remains not fully understood, despite extensive statistical analysis Waddington and Harris
547 (2012).

548 Studies of the optokinetic reflex (OKR) primarily focus on its slow-phase components, often considered
549 analogous to smooth pursuit Robinson (1968); Klein and Ettinger (2019). The slow phase consists of two
550 components: the direct component, or *ocular following response* Büttner and Kremmyda (2007), and the
551 indirect component, also known as the *velocity-storage mechanism* Raphan et al. (1979); Fletcher et al.
552 (1990); Büttner and Büttner-Ennever (2006). Despite similarities to smooth pursuit, these movements
553 differ in key aspects. The direct component has a much shorter onset latency (60–70 ms) Büttner and
554 Kremmyda (2007), is triggered by motion across a large visual field rather than a single target, and is
555 reflexive rather than volitional. In humans, it accounts for most reflexive OKR movements at velocities up
556 to 120°/s Büttner and Büttner-Ennever (2006); Büttner and Kremmyda (2007). The indirect component, in
557 contrast, develops gradually during sustained stimulation, integrating visual, vestibular, and somatosensory
558 inputs to maintain slow-phase eye velocity Raphan et al. (1979); Fletcher et al. (1990). Although the direct
559 component dominates during initial stimulation Van den Berg and Collewijn (1988), the velocity-storage
560 function of the indirect component is evident in *optokinetic after-nystagmus*, a gradually diminishing
561 nystagmus that continues even after an abrupt transition to complete darkness, reflecting its sustained
562 influence. Magnusson et al. (1985); Büttner and Büttner-Ennever (2006); Tarnutzer and Straumann (2018).

563 Abnormalities in the optokinetic reflex (OKR) are valuable diagnostic markers in a range of neurological
564 and vestibular disorders. In cerebellar ataxias, particularly spinocerebellar ataxia type 1 (SCA1), OKR gain
565 — defined as the ratio of slow-phase eye velocity to stimulus velocity — is typically reduced. The slow
566 phases may appear irregular due to floccular dysfunction, which impairs the *velocity storage mechanism* that
567 sustains the reflex (Leigh and Zee (2015); Lal and Truong (2019)). These abnormalities reflect cerebellar
568 contributions to OKR calibration and integration with vestibular signals. In vestibular neuritis, OKR
569 responses become asymmetrical, with significantly diminished gain toward the side of the lesion. This
570 reflects impaired visual-vestibular integration within the vestibular nuclei, particularly in the absence
571 of peripheral vestibular input (Strupp and Brandt (2009)). Progressive supranuclear palsy (PSP), on the
572 other hand, is associated with profound OKR impairment, especially for vertical motion stimuli, where
573 slow-phase responses are either absent or show severely reduced gain. This is attributed to midbrain
574 degeneration, notably involving the nucleus of the optic tract (NOT) and rostral interstitial nucleus of the
575 medial longitudinal fasciculus (riMLF) (Chen et al. (2010); Leigh and Zee (2015)). OKR dysfunction
576 specifically reflects compromised large-field visual motion processing and its integration with cerebellar
577 and brainstem control systems. OKR gain and slow-phase variability, typically measured using rotating

578 drum setups or full-field optokinetic stimulation, serve as sensitive, non-invasive biomarkers for both
579 central and peripheral pathologies (Büttner and Kremmyda (2007)).

580 2.6 Vergence Eye Movements

581 Vergence eye movements are vital for binocular vision, enabling both eyes to align precisely on objects
582 at varying distances. This alignment produces a single, fused visual image and supports stereoscopic depth
583 perception, essential for activities such as reading, driving, or navigating complex environments (Leigh and
584 Zee (2015)). Unlike saccades, which rapidly shift gaze, or smooth pursuit, which tracks moving objects,
585 vergence involves simultaneous rotation of the eyes in opposite directions. Convergence directs the eyes
586 inward for near objects, while divergence directs them outward for distant ones. These movements depend
587 on four interdependent mechanisms — fusional, accommodative, proximal, and tonic — each responding
588 to distinct visual or perceptual cues (Schor and Ciuffreda (1983)).

589 Fusional vergence, driven by retinal disparity, eliminates image misalignment between the eyes to
590 maintain a single percept, proving vital for dynamic tasks like tracking moving objects (Schor and Ciuffreda
591 (1983)). Accommodative vergence, linked to lens focusing, initiates convergence when ciliary muscles
592 contract to sharpen a blurred image, functioning effectively even in monocular viewing or low-contrast
593 conditions (Fincham and Walton (1957)). Proximal vergence, triggered by perceived object nearness
594 through cues like object size or looming motion, enables rapid eye pre-alignment before disparity or blur
595 cues fully engage, such as when approaching a book to read (Rosenfield and Rosenfield (1997)). Tonic
596 vergence establishes a baseline eye alignment through sustained extraocular muscle tone, maintaining
597 stable posture during rest or minimal visual stimulation (Schor (1985)). These mechanisms work together
598 seamlessly. For instance, during reading, accommodative vergence initiates convergence to focus on text,
599 fusional vergence fine-tunes alignment for single vision, proximal vergence adjusts to the perceived page
600 distance, and tonic vergence ensures stable eye posture (Ciuffreda and Tannen (1995)).

601 A sophisticated neural network coordinates these vergence mechanisms. The midbrain supraoculomotor
602 area, near the oculomotor nucleus, encodes vergence angle and velocity, integrating disparity, blur, and
603 proximity cues to govern fusional, accommodative, and proximal vergence (Mays (1984)). The superior
604 colliculus aligns vergence with saccades for smooth gaze shifts between near and far objects, while the
605 cerebellum, through its vermis and flocculus, calibrates interactions to prevent misalignment (Gamlin
606 (2002)). Cortical regions process complex cues: the visual cortex handles disparity for fusional vergence,
607 the parietal cortex processes depth, and the frontal eye fields integrate vergence with saccades (Cumming
608 and DeAngelis (2001)). The brainstem's pontine reticular formation and pretectal area orchestrate the near
609 triad, linking accommodative vergence to lens accommodation and pupillary constriction (Leigh and Zee
610 (2015)). Disparity-sensitive neurons in the visual cortex drive fusional vergence, blur-sensitive pathways
611 via the Edinger-Westphal nucleus trigger accommodative vergence, the middle temporal area processes
612 motion and depth for proximal vergence, and sustained midbrain motor neuron activity maintains tonic
613 vergence (Gamlin (2002); Cumming and DeAngelis (2001)).

614 Physiologically, vergence relies on extraocular muscles. The medial rectus muscles, controlled by the
615 oculomotor nerve, power convergence, while the lateral rectus muscles, controlled by the abducens nerve,
616 facilitate divergence (Von Noorden (1996)). Vergence operates more slowly than saccades, achieving
617 velocities of 10 to 20 degrees per second with latencies of 160 to 200 milliseconds, relying on visual
618 feedback from disparity and blur (Leigh and Zee (2015)). The near triad integrates accommodative
619 vergence with autonomic processes: accommodation sharpens focus through ciliary muscle contraction,
620 and pupillary constriction enhances depth of field via the sphincter pupillae (Von Noorden (1996)). Fusional

vergence employs fine motor adjustments to align retinal images, proximal vergence initiates broader movements based on perceptual cues, and tonic vergence maintains stability through muscle spindle feedback (Schor (1985)). In young, healthy adults, convergence amplitude typically reaches 25 to 30 prism diopters — a unit measuring eye deviation — while divergence amplitude ranges from 6 to 10 prism diopters, reflecting the greater physiological demand for near vision. These amplitudes may decrease with age or in pathological conditions (Hung et al. (1986)).

Clinical evaluation of vergence is crucial for diagnosing binocular vision disorders. The near point of convergence test measures the closest point at which the eyes maintain single binocular vision, typically 5 to 10 centimeters, assessing fusional and accommodative vergence. A receded near point often indicates convergence insufficiency (Scheiman et al. (2003)). Vergence facility testing evaluates the ability to alternate efficiently between convergence and divergence, reflecting the adaptability of fusional and proximal vergence during prolonged near tasks (Gall et al. (1998)). Prism vergence testing, using base-in and base-out prisms, quantifies the range of fusional vergence, determining the maximum disparity overcome before double vision occurs, critical for assessing compensatory capacity in latent deviations — phorias (Evans (2021)). The cover test, performed unilaterally or alternately, detects phorias and tropias by evaluating alignment under dissociated viewing conditions, revealing deficits in tonic vergence or overall coordination (Von Noorden (1996)).

Common dysfunctions include convergence insufficiency, marked by eye strain, intermittent double vision, headaches, or difficulty sustaining attention during reading or screen use, often due to impaired fusional or accommodative vergence (Scheiman et al. (2003)). Other abnormalities, such as excessive convergence, limited divergence, or vergence paralysis, may stem from midbrain lesions, strabismus, or uncorrected refractive errors (Leigh and Zee (2015)). Management strategies include vision therapy targeting the deficient mechanism, prism lenses to aid compensation, or orthoptic exercises to enhance fusional reserves and vergence facility. These approaches, particularly effective for convergence insufficiency, are supported by clinical evidence (Scheiman et al. (2005); Scheiman and Wick (2008)).

3 ECOLOGICAL CONDITIONS

First and foremost, the term ecological must be nuanced. Rather than striving for ecological validity in its broadest sense — an evolving concept across cognitive sciences and neurophysiology (Holleman et al. (2020)) — the focus here is on experimental paradigms that do not impose physical constraints on the observer's body. Under such conditions, gaze reorientation involves coordinated movements of not only the eyes but also the head, trunk, and feet (Anastasopoulos et al. (2009); Land (2004)). In contrast to tightly controlled environments — particularly experimental settings that involve physical head restraint, where gaze is typically studied in isolation — natural gaze behavior arises from a dynamic system that integrates vestibular, proprioceptive, and visual inputs into task-specific motor outputs.

To investigate eye movements in unconstrained settings, most studies have focused on eye-head coordination, a specific subset of the broader problem (Zangermeister and Stark (1982); Afanador et al. (1986); Fuller (1992); Guitton (1992); Stahl (1999a, 2001); Pelz et al. (2001); Einhäuser et al. (2007); Thumser et al. (2008)). Coordinating gaze shifts with head movements introduces additional complexity, even within this more constrained framework. (Freedman (2008)) posed key questions regarding eye-head coordination: *"Are the eye and head components of gaze shifts tightly linked, or are they dissociable? What factors determine the extent of head involvement? [...] When the head contributes to gaze shifts, it moves concurrently and in the same direction as the eyes, so what role does the vestibulo-ocular reflex (VOR)*

662 play?" While these issues have been extensively explored and numerous hypotheses have been proposed,
663 they remain subjects of active investigation/

664 3.1 Gaze Stabilizing Movements

665 Although maintaining a relatively stable retinal image is crucial for high visual acuity, the human head is
666 almost always in motion. Consequently, tasks that demand fine visual focus, such as reading, would be
667 unfeasible without robust compensatory systems to offset these head movements. Fortunately, a number of
668 mechanisms come into play to provide a stable gaze.

669 3.1.1 Fixational Eye Movements

670 The role — and existence as canonical constituent of eye movements — of microsaccades is even more
671 contentious under natural viewing conditions than when the head is restrained. Some researchers posit
672 that microsaccades contribute to visual attention (Fischer and Weber (1993b)), enhance visual processing
673 (Melloni et al. (2009)), or may indicate levels of concentration Buettner et al. (2019). However, others
674 have observed that microsaccades are exceedingly rare in real-world activities. Malinov et al. (2000), for
675 instance, analyzed eye movements during a naturalistic task and found that only 2 of the 3,375 saccades
676 recorded could be classified as microsaccades. As Collewijn and Kowler (2008) summarize: "*A special role
677 for microsaccades seemed particularly unlikely to emerge under natural conditions, when head movements
678 are permitted during either fixation or during the performance of active visual tasks*".

679 On the other hand, the precise measurement of fine eye movements, including ocular drift and micro-
680 tremor, under natural conditions only became feasible in the 1990s with the development (Edwards et al.
681 (1994)) of the Maryland Revolving-Field Monitor (MRFM). To our knowledge, the MRFM remains the
682 only eye tracker with a precision demonstrated to be sufficient to record these fixational eye movements
683 during normal head movements (Aytekin et al. (2014); Rucci and Poletti (2015)). This field of research thus
684 constitutes somewhat of a niche reserved for a few laboratories with such a set-up. However, a limitation
685 of the MRFM system is the requirement that participants remain within the magnetic field of the device,
686 restricting studies to tasks that involve minimal body movement.

687 Furthermore, during unconstrained fixation, ocular drift appears anticorrelated with involuntary head
688 movements (Aytekin et al. (2014)), effectively compensating — and even anticipating (Poletti et al. (2015))
689 — for the fixational instability of the head (Aytekin et al. (2014)). This compensation, however, is only
690 partial (Poletti et al. (2015)), allowing to maintain retinal image motion close to those experienced when
691 the head is restrained (Poletti et al. (2015)). As a result, the retinal stimulation produced by fixational head
692 and eye movements in natural conditions retains key characteristics of the signal observed in head-fixed
693 ocular drift, including correlated temporal structures and similar spatio-temporal retinal stimulation patterns
694 (Roberts et al. (2013); Rucci and Poletti (2015)).

695 3.1.2 VOR and OKR

696 Introduced in Sections 2.4 and 2.5, respectively, the Vestibulo-Ocular Reflex (VOR) and Optokinetic
697 Reflex (OKR) are two fundamental eye stabilizing mechanisms that act to maintain retinal image stability
698 during body movements. In brief, the VOR counteracts head movements within a stationary environment,
699 while the OKR compensates for movements within the visual field (Robinson (1968)). In practice,
700 both mechanisms operate in tandem to achieve visual stability. Indeed, head movements are inevitably
701 present during natural viewing — the VOR is thus highly active — generating vestibular inputs but also
702 displacement of the visual field (Fletcher et al. (1990)). Therefore, although not predominant compared to

703 VOR (Pelisson et al. (1988)) and with a higher latency (Collewijn and Smeets (2000)), the OKR is at least
704 partly active as well. In sum, VOR and OKR interact naturally through visuovestibular mechanisms (Green
705 (2003)), a phenomenon known as *visually enhanced VOR*, which has garnered substantial clinical interest
706 for its potential applications (Arriaga et al. (2006); Szmulewicz et al. (2014); Rey-Martinez et al. (2018);
707 Halmagyi et al. (2022)).

708 Investigations of VOR and OKR in contexts of free head and body motion have revealed their multi-modal
709 nature, *i.e.* numerous indirect sensory modalities are implicated in the neural circuits underlying these
710 reflexes, suggesting a need for holistic analysis. For instance, primate studies found that neck muscle
711 proprioception, activated during head movement, projects to neurons within the vestibular nuclei (Gdowski
712 and McCrea (2000)). Furthermore, there is evidence that active head movement may lead to partial
713 suppression of vestibular input through extra-retinal mechanisms (Roy and Cullen (2004)). For instance,
714 abrupt head movements — known as head impulses — reveal differences between active — self-generated
715 — and passive — externally applied — responses. In passive head impulses, such as those delivered by a
716 clinician rotating the head, the VOR relies heavily on vestibular input, with minimal contribution from
717 neck proprioception or voluntary control, making it a sensitive measure of vestibular function (Halmagyi
718 and Curthoys (1988)). Active head impulses, where individuals initiate their own rapid head turns, engage
719 additional mechanisms, including pre-programmed motor commands and cervical proprioceptive feedback,
720 which can enhance VOR gain and reduce latency compared to passive conditions (Cullen and Roy (2004)).

721 Beyond vestibular input, active impulses incorporate pre-programmed motor commands from the
722 brain's motor cortex and feedback from cervical proprioceptors, which sense neck muscle activity. These
723 contributions can increase VOR gain and reduce response latency compared to passive conditions, reflecting
724 the brain's ability to predict and optimize eye-head coordination (Cullen and Roy (2004)). For example,
725 during active impulses, healthy individuals may achieve gains slightly above 1, as predictive mechanisms
726 anticipate head motion, ensuring seamless gaze stabilization.

727 Interestingly, during locomotion, studies report distinct compensatory roles for rotational and translational
728 VOR components. Specifically, rotational head movements are fully compensated by the VOR, while
729 translational motion is stabilized only within a fixation plane, such that objects in front of this plane exhibit
730 relative motion opposite to the translation direction (Miles (1998, 1997)). This limitation implies that
731 simultaneous stabilization of near and far objects is not achievable. Subsequent research suggests that,
732 during ambulation, the brain resolves this through an optimized stabilization plane that maximizes visual
733 clarity over distances (Zee et al. (2017)).

734 Furthermore, the incorporation of extra-vestibular information into early vestibular processing enables
735 VOR modulation based on behavioral goals. For instance, the VOR remains robust across a range of
736 velocities and frequencies when gaze stabilization is the primary objective. However, during intentional
737 gaze shifts, an efference copy of the motor command temporarily suppresses the VOR (Laurutis and
738 Robinson (1986); Cullen (2019)). Nonetheless, vestibular feedback remains accessible to the oculomotor
739 system, as demonstrated by the rapid recovery of VOR function following mechanical perturbations of
740 the head during gaze shifts (Freedman (2008); Boulanger et al. (2012)). This dynamic inhibition of the
741 VOR is thought to be a function of the gaze error, defined as the disparity between intended and actual
742 gaze positions (Pelisson et al. (1988); Boulanger et al. (2012)).

743 An intriguing area in the study of nystagmus fast phases is the phenomenon of the *beating field* shift.
744 Specifically, research has shown (Watanabe (2001)) that during optokinetic nystagmus, the average gaze
745 position, or *beating field*, shifts in the direction of the fast phases — meaning it moves opposite to the

746 motion of the visual field. This shift has been observed not only in humans (Abadi et al. (1999); Watanabe
747 (2001)) but also across multiple species (Schweigart (1995); Bähring et al. (1994)). A similar directional
748 shift occurs during vestibular nystagmus, where the mean eye position shifts in the direction of head
749 rotation (Vidal et al. (1982); Chun and Robinson (1978)).

750 Observations in optokinetic and vestibular nystagmus suggest that the *beating field shift* may be a
751 goal-directed involuntary response, acting as a reflexive orienting mechanism toward a *center of interest*
752 (Crommelinck et al. (1982); Vidal et al. (1982); Siegler et al. (1998)). This shift likely helps align gaze with
753 self-motion, enhancing target detection within the moving visual field. Siegler et al. (1998) proposed that
754 cognitive factors influence its magnitude, reflecting an individual's preference for allocentric or egocentric
755 reference frames. Additionally, proprioceptive feedback modulates the beating field by adjusting fast phase
756 amplitude and frequency during nystagmus (Botti et al. (2001)).

757 3.2 Gaze Orienting Movements

758 In this section, we overview the mechanisms that enable foveal reorientation in ecological conditions. As
759 we will discuss, the involvement of head and sometimes hand movements adds complexity to understanding
760 these processes.

761 3.2.1 Gaze Shifts

762 Under natural conditions, while gaze-oriented eye movements can occur without significant head or body
763 segment involvement (Freedman (2008)), head movements frequently accompany gaze shifts (Pelz et al.
764 (2001)), even for small gaze amplitudes, such as those observed during reading tasks (Kowler et al. (1992);
765 Lee (1999)). Importantly, for large-amplitude gaze shifts, coordinated movements between the eyes and
766 head are necessary. Fuller (1992) observed that head movements were essential for horizontal gaze
767 shifts exceeding 40 degrees. Below this threshold, individual differences emerged, with some participants
768 showing a tendency to move their heads with each gaze shift, reflecting an intrinsic behavioral inclination
769 towards head involvement in gaze changes. This variability led to the categorization of individuals as *head*
770 *movers* and *non-head movers* (Fuller (1992); Afanador et al. (1986); Stahl (1999a)).

771 Interestingly, individual predisposition for head movement during gaze shifts was not associated with
772 differences in ocular motor control impairments at high eccentricities (Stahl (2001)). Instead, this tendency
773 to activate the head during gaze shifts appears to be linked to the innate representation of visual space
774 in the central nervous system (Fuller (1992)). Several factors influence the extent of head movement in
775 gaze shifts, including the initial eccentricity of the eyes within their orbits. When the eyes are offset in
776 the same direction as the intended gaze shift, head contribution tends to increase, and the opposite occurs
777 when the offset is in the opposite direction (Freedman (2008)). Furthermore, head dynamics also impact
778 eye movement properties; for instance, ocular saccade amplitude is inversely related to head velocity, with
779 faster head movements resulting in smaller saccades (Guitton and Volle (1987)).

780 It might be hypothesized that the intrinsic properties of saccadic eye movements, such as the *main*
781 *sequence* — the relationship between saccade amplitude, duration, and peak velocity — remain unchanged
782 during combined eye-head gaze shifts. However, evidence reveals significant interactions between saccades
783 and concurrent head movements that modify saccade kinematics, particularly the peak velocity-amplitude
784 relationship. In head-free conditions, the peak velocity of saccades is often reduced compared to head-fixed
785 saccades of the same amplitude, as the vestibulo-ocular reflex (VOR), which stabilizes gaze during head
786 movement, interacts with the saccadic system to coordinate eye and head motion (Freedman and Sparks
787 (1997)). While the main sequence relationship generally holds, the slope or scaling of the velocity-amplitude

788 curve is altered, reflecting modified saccade dynamics influenced by head movement. Additionally, studies
789 show that for horizontal gaze shifts with eyes and head aligned, saccade amplitude increases linearly for
790 small gaze shifts but plateaus as head contribution grows for larger shifts (Guitton and Volle (1987); Stahl
791 (1999a)). While this amplitude saturation could theoretically result from mechanical constraints of the eyes
792 within the orbits, experimental data indicate that recorded saccade amplitudes rarely approach the physical
793 limits of the orbital range (Guitton and Volle (1987); Phillips et al. (1995); Freedman and Sparks (1997)).

794 From a descriptive perspective, eye-head coordination typically begins with a rapid saccadic eye
795 movement toward the object of interest, immediately followed by a head movement in the same direction
796 (Bartz (1966); Barnes (1979); Pelisson et al. (1988); Boulanger et al. (2012)). This coordination results
797 in a characteristic sequence as outlined by Freedman (2008). The gaze shift initiates with a high-velocity
798 saccade — approximately 200–400 degrees per second (Barnes (1979)) — of large amplitude, repositioning
799 the eyes relative to the head. This fast phase generally concludes as the line of sight aligns with the target,
800 at which point the eyes are offset in the orbits by roughly 30 degrees while the head has moved less
801 than 2 degrees. Following this initial saccadic phase, the head continues to rotate for an additional 250
802 milliseconds, covering about 15 more degrees. During this ongoing head movement, the vestibulo-ocular
803 reflex (VOR) compensates by counter-rotating the eyes in the opposite direction, thereby maintaining the
804 gaze on the target. This VOR action minimizes changes in the line of sight, stabilizing the gaze despite the
805 continued head motion.

806 This sequence typically introduces a delay of 25 to 75 milliseconds between eye and head movement
807 onset (Zangermeister and Stark (1981, 1982); Freedman (2008)). This delay is thought to result from the
808 greater visco-inertial load on the neck muscles compared to the lower visco-elastic resistance required for
809 eye movement (Zangermeister and Stark (1981, 1982)). Electromyography (EMG) studies show that neck
810 muscles exhibit an increase in agonist activity and a decrease in antagonist activity about 20 milliseconds
811 before a similar change in eye muscle EMG activity (Bizzi et al. (1972); Zangemeister and Stark (1981)).
812 These findings suggest that neural signals for coordinated eye-head movements are first dispatched to neck
813 muscles, followed shortly by eye muscles (Bizzi et al. (1972)).

814 This raises the question: *Could synchronous eye-head movements be driven by a common, shared motor
815 command?* This idea has intrigued researchers. Lestienne et al. (1984) highlighted the close coupling
816 between saccadic eye and attempted head movements, shown by neck muscle EMG in head-restrained
817 subjects. They suggested that while eye-head coupling may not be mandatory in primates, it likely serves as
818 a mechanism for coordination, particularly involving reticulospinal neurons (Vidal et al. (1983)). Further
819 studies have shown that the covariance of eye and head movement velocities, the timing correlation of
820 latencies, and the linear phase-plane relationship between head acceleration and eye velocity during rapid
821 gaze shifts support the hypothesis of a shared motor command driving both movements (Guitton et al.
822 (1990); Galiana and Guitton (1992))

823 Despite the strong coupling between eye and head movements and the possibility of a shared motor
824 command, numerous studies show that eye and head movements can be initiated separately. The timing of
825 these movements is influenced by factors such as target predictability (Bizzi et al. (1972); Zangemeister and
826 Stark (1982)), gaze shift amplitude (Barnes (1979); Guitton and Volle (1987); Freedman and Sparks (1997)),
827 and individual tendencies for head movement (Stahl (1999b)). For instance, in non-human primates, as
828 gaze shift amplitude increases, the time from saccade onset to head movement onset decreases, eventually
829 reaching synchrony or even showing head movement preceding saccades (Freedman and Sparks (1997)).
830 Similar findings in humans show that head movements can sometimes precede saccades, particularly when
831 the target is predictable (Moschner and Zangemeister (1993)). Moreover, experimentally delaying saccadic

832 onset by stimulating the pontine omnipause neurons does not affect head movement initiation, further
833 supporting the partial independence of eye and head command signals in brainstem structures governing
834 coordinated eye-head actions

835 Yet, despite the relative independence of eye and head command signals, gaze itself — the sum of eye
836 and head contributions — remains tightly controlled, preserving accuracy throughout movement. This
837 precision holds even when the head is subjected to perturbations during its trajectory (Guitton and Volle
838 (1987); Boulanger et al. (2012)). These observations have led some researchers to propose a gaze-feedback
839 model in which VOR-saccade interactions are guided by a gaze-error signal (Guitton and Volle (1987);
840 Boulanger et al. (2012)).

841 Another important factor modulating eye-head coordination is the initial eccentricity of the eyes relative
842 to the head at the start of a gaze shift (Abel et al. (1979); Laurutis and Robinson (1986); Freedman (2008)).
843 The initial eye eccentricity not only affects the head's contribution to the gaze shift but also alters the
844 characteristics of the eye movements. Specifically, when the eyes are offset in the direction of the gaze
845 shift, saccadic velocity decreases compared to when the eyes are centered or offset in the opposite direction
846 (Laurutis and Robinson (1986)). In other words, centrifugal saccades are slower than centripetal ones.
847 Additionally, as the head's role in the gaze shift increases, the saccadic velocity component decreases
848 (Freedman (2008))

849 Similar to eye-head coordination, eye-hand coordination is crucial for interacting with the environment.
850 When humans reach to grasp objects, they typically initiate saccadic eye movements toward the target,
851 followed by guiding the hand to the center of gaze at the moment of grasp (Hayhoe et al. (2002); Johansson
852 et al. (2001)). The eyes usually fixate on the object just before or shortly after the initiation of hand
853 movement, well before the hand reaches the target (Helsen et al. (2000); Starkes et al. (2002)), and maintain
854 fixation until the movement is completed, even during sequential tasks (Neggers and Bekkering (2000,
855 2002)). However, as in eye-head coordination, there is considerable variability in the timing of eye and
856 hand movements during natural tasks (Abrams et al. (1990); Carnahan and Marteniuk (1991); Pelz et al.
857 (2001)).

858 In the broader context of multi-segment coordination, eye-head movement patterns adapt when additional
859 body segments are involved. During reaching and pointing tasks, Carnahan and Marteniuk (1991) found that
860 the timing of eye and head movements varied based on task demands. For rapid pointing, head movement
861 began before the eyes, whereas in precision tasks, the eyes moved first. In trials without hand movements,
862 the eyes consistently initiated movement before the head, suggesting that the involvement of additional
863 body segments and higher-level cognitive factors can modulate eye-head coordination.

864 3.2.2 Gaze pursuits

865 Most studies on ocular pursuit have been conducted under conditions where the head is restrained,
866 allowing only eye movements to track a moving target. However, in real-world scenarios, humans track
867 moving targets through a combination of eye, head, and body movements (Lanman et al. (1978); Ackerley
868 and Barnes (2011b); C. Pallus and G. Freedman (2016)). To date, no studies have fully investigated
869 the mechanisms of visual pursuits under conditions of complete freedom of body movements. Instead,
870 research has typically focused on the more restricted context of eye-head coordination during head-free
871 gaze pursuits, both in humans and non-human primates. Despite this narrower focus, publications on this
872 topic remain limited. As early as 1989, Barnes noted the scarcity of studies on head-free pursuit, citing
873 only six articles from the previous two decades (Barnes and Lawson (1989)). Over 30 years later, this
874 observation still holds true, with only a small number of additional studies contributing to the literature

875 (Collins and Barnes (1999); Dubrovsky and Cullen (2002); Barnes and Collins (2008b,a); Ackerley and
876 Barnes (2011b,a); C. Pallus and G. Freedman (2016); Shanidze and Velisar (2020)).

877 Head-free pursuits differ from head-restrained ones by requiring the integration of visual, vestibular, and
878 neck proprioceptive signals to control both the eyes and the head (Lanman et al. (1978); Dubrovsky and
879 Cullen (2002)). Gaze pursuits involve both retinal and extra-retinal inputs, with their contributions evolving
880 over time. Like head-restrained conditions, head-free gaze pursuits consist of an initiation phase, driven by
881 retinal slip signals during the first 80 – 100 milliseconds, followed by a maintenance phase. In this phase,
882 extra-retinal inputs, including neck proprioception, vestibular signals, attention, expectation, and efferent
883 copies of eye and head movements, are integrated with visual signals to sustain pursuit. Pursuit velocity
884 aligns with the target's velocity, typically reaching equilibrium within 200 to 300 milliseconds (Barnes and
885 Collins (2008a))

886 The role of extra-retinal inputs in maintaining gaze pursuit was demonstrated in extinction paradigms,
887 where removal of the pursuit target shortly after the initiation phase did not immediately disrupt the
888 pursuit. Depending on factors such as the duration of initial target exposure and expectations regarding
889 the target's reappearance, participants could continue pursuing the target with appropriate direction and
890 velocity (Ackerley and Barnes (2011b,a)). These findings suggest that the pursuit system forms an internal
891 representation of the target's motion and velocity, which it uses to continue pursuit even without direct
892 visual feedback. This *memory* of target velocity (Barnes and Collins (2008b)) is likely communicated to the
893 eye and neck motor systems — potentially with different controller parameters to account for the distinct
894 biomechanical properties of the eyes and head — and is thus a key component of eye-head coordination
895 during gaze pursuits (Dubrovsky and Cullen (2002); C. Pallus and G. Freedman (2016)).

896 This close coordination between the eyes and head ensures that gaze characteristics, such as position
897 and velocity, are nearly identical under both head-restrained and head-unrestrained conditions (Ackerley
898 and Barnes (2011b); C. Pallus and G. Freedman (2016)). Pursuit gain — defined as the ratio of gaze
899 displacement to target displacement — remains near unity in both conditions, with the exception of older
900 individuals, who exhibit a slight decrease in pursuit gain when the head is unrestrained (Shanidze and Velisar
901 (2020)). Despite the lack of measurable advantage in terms of accuracy, head movements are consistently
902 coupled with eye movements during pursuit of targets with both predictable and unpredictable trajectories
903 (Lanman et al. (1978); Ackerley and Barnes (2011b)). This is thought to help keep the eyes centered
904 within their orbits, ensuring that any subsequent eye movements toward a secondary point of interest can
905 make use of the full oculomotor range (Dubrovsky and Cullen (2002); C. Pallus and G. Freedman (2016)).
906 For instance, Dubrovsky and Cullen (2002) found that the eyes generally remained within 15 degrees of
907 eccentricity during pursuit in non-human primates .

908 However, this reductionist explanation does not fully capture the considerable variability in strategies
909 used during gaze pursuit (Dubrovsky and Cullen (2002); C. Pallus and G. Freedman (2016)). In some cases,
910 eye and head movements can be entirely uncoupled (C. Pallus and G. Freedman (2016); Collins and Barnes
911 (1999)). In most situations, however, an ocular saccade is first executed toward the target to initiate the
912 pursuit, followed by the recruitment of head movements after a brief delay (Ackerley and Barnes (2011b);
913 Shanidze and Velisar (2020)). This is typically followed by a coordinated but variable combination of
914 eye and head movements to maintain pursuit (C. Pallus and G. Freedman (2016); Shanidze and Velisar
915 (2020)), with the head often accounting for the majority of the gaze displacement, albeit with significant
916 inter-subject variability (Lanman et al. (1978); Ackerley and Barnes (2011a)).

917 During pursuit maintenance, head trajectory or velocity may deliberately diverge from target motion
918 (Collins and Barnes (1999); C. Pallus and G. Freedman (2016)). Variations in head movement are
919 almost immediately compensated by eye movements, minimizing gaze tracking error (Collins and Barnes
920 (1999)). This compensation is thought to arise from an internal gaze-related signal in the central nervous
921 system, incorporating stored information about target velocity (Collins and Barnes (1999); Dubrovsky
922 and Cullen (2002)). While some researchers describe gaze pursuit as a sequence of discrete saccades and
923 smooth pursuits (C. Pallus and G. Freedman (2016); Shanidze and Velisar (2020)), others have identified
924 compensatory mechanisms for head motion within the eye movement trace (Ackerley and Barnes (2011a);
925 Shanidze and Velisar (2020)). These findings suggest that the VOR remains active during gaze pursuit,
926 modulated by visual feedback and extra-retinal signals (Ackerley and Barnes (2011a))

4 PRACTICAL CONSIDERATIONS

927 While the physiological insights discussed thus far highlight the complexity of gaze control, understanding
928 the different methodologies used to record eye and head movements is essential for avoiding potential
929 pitfalls when selecting recording equipment and experimental paradigms.

930 4.1 Eye Movement Measurement

931 In this section, we provide a brief overview of eye movement measurement techniques, highlighting their
932 key characteristics. For more detailed reviews on the history, methods, and techniques of eye tracking,
933 we refer to more comprehensive sources (Young and Sheena (1975); Wade (2007); Hansen and Ji (2009);
934 Holmqvist et al. (2011); Yarbus (2013); Chennamma and Yuan (2013); Cognolato et al. (2018)).

935

936 4.1.1 Electro-Oculography (EOG)

937 Electro-Oculography (EOG) measures electric potential differences using electrodes positioned near the
938 orbital margins, with pairs placed close to the medial and lateral canthi for horizontal movements and above
939 and below the eyes for vertical movements, to track eye movements. By detecting changes in the corneo-
940 retinal standing potential, EOG enables independent monitoring of horizontal and vertical eye movements,
941 making it valuable for clinical applications such as sleep studies where eye closure occurs Barea et al.
942 (2002). Its advantages include affordability, ease of implementation, and the ability to function with closed
943 eyes, which is critical for diagnosing sleep disorders. However, EOG has significant limitations. It is
944 primarily suited for controlled laboratory conditions due to the need for stable electrode contact, which is
945 disrupted by motion, sweat, or skin movement in dynamic environments Bulling et al. (2009). Signal noise
946 from facial muscle activity or external electrical interference reduces accuracy, and frequent recalibration
947 is required due to signal drift Barea et al. (2002). While wearable EOG devices have been explored for
948 monitoring eye movements during daily activities Bulling et al. (2009), their practicality is limited by lower
949 spatial resolution compared to other methods and challenges in maintaining reliable electrode placement
950 Holmqvist and Andersson (2017). As a result, EOG is less suitable for field applications and has been
951 largely replaced by non-invasive techniques.

952

953 4.1.2 Scleral Contact Lens/Search Coil Systems

954 Scleral contact lens/search coil systems use a wire coil embedded in a contact lens worn on the sclera,
955 which moves within a controlled magnetic field to induce an electric current proportional to eye position.

956 Evolving from early mechanical methods that fixed markers directly on the cornea Delabarre (1898),
957 modern scleral coils provide exceptional accuracy and high temporal resolution, historically serving
958 as a reference standard for calibrating other eye-tracking systems Young and Sheena (1975). However,
959 the method's invasive nature causes significant discomfort and poses risks such as corneal irritation or
960 infection, restricting session durations to typically under 30 minutes Holmqvist and Andersson (2017).
961 Operation within a Faraday cage is necessary to shield against electromagnetic interference, confining use
962 to specialized laboratory settings and prohibiting mobility Young and Sheena (1975). The complex setup,
963 involving magnetic fields and precise calibration, is costly and inaccessible for most applications. Due to
964 these limitations, scleral coil systems are increasingly obsolete, replaced by non-invasive methods like
965 video-oculography for most research and practical purposes Holmqvist and Andersson (2017). Their use
966 persists only in niche calibration tasks.

967

968 4.1.3 Infrared Oculography (IROG)

969 Infrared Oculography (IROG) tracks eye movements by measuring the intensity of reflected infrared
970 light, often using dual Purkinje imaging (DPI). DPI compares reflections from the cornea's anterior surface
971 — first Purkinje image — and the lens's posterior surface — fourth Purkinje image — which shift relative to
972 each other as the eye rotates, providing measurements robust to eye translation Cornsweet and Crane (1973).
973 IROG offers high spatial and temporal resolution, making it suitable for precise laboratory studies Crane
974 and Steele (1985). However, its limitations are notable. Precise head stabilization, typically via chinrests or
975 head mounts, is required to maintain alignment with infrared cameras, restricting applications to controlled
976 environments Cornsweet and Crane (1973). The method is limited to a visual angle of approximately
977 15 degrees from the center, as the fourth Purkinje image becomes occluded by the iris at larger angles,
978 reducing accuracy Crane and Steele (1985). Sensitivity to ambient infrared light or reflective surfaces, such
979 as glasses, can degrade performance, necessitating controlled lighting conditions Holmqvist and Andersson
980 (2017). The complex setup and calibration requirements further increase cost and user effort, making IROG
981 less practical for mobile or real-world applications compared to video-based systems.

982

983 4.1.4 Video-based Eye Tracking (VOG)

984 Video-based Eye Tracking, or Video-Oculography (VOG), uses one or more cameras, typically with
985 near-infrared light, to capture eye appearance and track features like the pupil and corneal reflection — first
986 Purkinje image. By computing the vector between the pupil center and corneal reflection, VOG maps eye
987 positions to points in the visual field Hansen and Ji (2009). Its non-invasive nature and flexibility make it the
988 most widely used eye-tracking method, supporting variants such as limbus or iris-sclera boundary tracking
989 Cognolato et al. (2018). A significant limitation is its reliance on a calibration procedure, where participants
990 fixate on predefined targets to establish a mapping between eye features and gaze points, which is time-
991 consuming and requires cooperation Hansen and Ji (2009). VOG is sensitive to environmental factors,
992 including ambient light, occlusions (e.g., eyelids, glasses), and reflections, which can reduce accuracy
993 in uncontrolled settings Holmqvist and Andersson (2017). Significant head movements disrupt tracking,
994 necessitating stabilization or additional compensation techniques Cognolato et al. (2018). Accuracy also
995 decreases at large visual angles — e.g. beyond 30 degrees — due to pupil distortion or occlusion Hansen
996 and Ji (2009). Despite these challenges, VOG remains the most versatile and practical eye-tracking method
997 for both research and commercial applications.

998 EOG, scleral contact lens/research coil, and IROG are specialized methods used in controlled
999 environments for high-precision research, particularly in neurophysiology, vision, and ophthalmology. In
1000 contrast, VOG is easier to implement and has become the dominant eye-tracking technique, widely used in
1001 commercial systems. While eye-gaze tracking was once complex and expensive, recent advancements have
1002 lowered costs and improved VOG efficiency. Unlike other systems requiring specialized training, VOG is
1003 accessible to a broader range of researchers. However, with many commercial options available, selecting
1004 the right equipment can be challenging. To assist in this, we review the technical specifications of VOG
1005 systems and discuss their applicability to different experimental paradigms in the subsequent sections.

1006 4.2 Technical Specifications

1007 A typical VOG eye tracker comprises a camera, a lighting system, and software for detecting and tracking
1008 eye movements. A key metric for evaluating eye-tracker spatial quality is *gaze accuracy*, defined as the
1009 average angular distance between the true and recorded gaze positions, with smaller distances indicating
1010 better accuracy (Feit et al. (2017)). *Spatial resolution*, related to accuracy, refers to the smallest detectable
1011 eye movement, while *gaze precision* measures the consistency of gaze position over time, often quantified
1012 as the root mean square sample-to-sample (RMS-s2s) deviation. Accuracy and precision are typically
1013 assessed separately in horizontal and vertical directions, though manufacturers often provide a single
1014 aggregated value for each.

1015 System *latency* refers to the delay between actual eye movement and the corresponding time reported by
1016 the eye tracker, while variability in latency is described as temporal precision (Holmqvist et al. (2012)).
1017 This latency can be critical in certain experimental setups, particularly in gaze-contingent tasks where
1018 visual stimuli dynamically update based on gaze position. End-to-end latency encompasses multiple factors,
1019 including camera exposure time, image readout and transfer, processing delays, data transmission, and
1020 display refresh rate.

1021 *Data loss*, on the other hand, indicates the proportion of samples during which no gaze coordinate was
1022 reported compared to the reported sampling rate of the eye tracker. These losses could result from blinks
1023 or from the recording device's inability to effectively track eye movements, particularly for eccentric eye
1024 movements. Also, it is sometimes desirable to differentiate blinks from other sources of data loss. For
1025 instance, this differentiation may be necessary when blinks serve as a behavioral measure (Leal and Vrij
1026 (2008)) or as inputs for gaze-based interactions, such as selection inputs.

1027 Lastly, the *sampling frequency* of an eye tracking system denotes how often the eye tracker records the
1028 position of the eyes per second. A higher sampling frequency enhances the accuracy of estimating the
1029 actual trajectory of eye movements. However, this increased frequency comes with certain drawbacks, such
1030 as the need for more expensive cameras, higher illumination requirements, possibly increased levels of
1031 noise, and ultimately, a larger amount of data to be stored.

1032 Standardized criteria for reporting eye-tracking data quality are lacking, with many studies relying on
1033 manufacturer specifications. However, discrepancies often exist between reported accuracy and actual
1034 performance, even in controlled conditions (Nyström et al. (2013a); Blignaut et al. (2014)). This highlights
1035 the need for standardized quality assessments and independent validation, similar to practices in other
1036 technology fields. Benchmarking eye-tracking systems against a gold standard, such as the Scleral Contact
1037 Lens or Search Coil System, is essential for ensuring reliability. For detailed guidance on data quality
1038 assessment, see Holmqvist et al. (2012).

1039 4.3 Eye-Trackers and Experimental Paradigms

1040 This section focuses on video-based eye trackers, as other methods in Section 4.1 serve specialized needs.
1041 Video-based systems fall into four types: fixed, remote, wearable, and integrated. The following sections
1042 outline each, with their strengths and limitations. Table 1 summarizes the main types of video-based
1043 eye trackers, highlighting their typical applications and limitations. Table 2 provides an overview of
1044 commercially available devices with key technical specifications.

1045

1046 4.3.1 Tower-Mounted Eye Trackers

1047 Tower-mounted eye trackers, such as the *EyeLink 1000 Plus* and *Tobii Pro Spectrum*, are high-precision
1048 systems designed for controlled environments. These devices use high-resolution cameras and infrared
1049 illumination to capture detailed eye movements, often requiring head stabilization via a chinrest or bite
1050 bar to minimize external interference. They achieve superior spatial accuracy and sampling rates up to
1051 2000 Hz, enabling the study of fine fixational eye movements, saccades, and rapid phases of nystagmus,
1052 critical for neurophysiological and vision research Nyström et al. (2021). These systems capture raw
1053 monocular eye position data, including pupil center coordinates and corneal reflection positions for each
1054 eye, at high temporal resolution. Algorithms process this into cyclopean eye position, averaging binocular
1055 data to estimate gaze direction, or compute gaze coordinates mapped to a stimulus plane via calibration
1056 Holmqvist and Andersson (2017). Access to raw monocular data, crucial for detailed oculomotor analyses
1057 like microsaccades, often requires premium software licenses — e.g. EyeLink Data Viewer, Tobii Pro Lab
1058 — while processed gaze data is standard Nyström et al. (2016).

1059 Traditionally, tower-mounted eye trackers, such as the EyeLink 1000 Plus, have employed classic
1060 computer vision algorithms for pupil detection, corneal reflection tracking, and gaze estimation, avoiding
1061 reliance on artificial intelligence (AI) (Holmqvist et al. (2011)). These deterministic approaches, utilizing
1062 techniques like thresholding and geometric modeling, are tailored for highly controlled laboratory settings
1063 where precision, speed, and reliability are paramount, particularly at sampling rates up to 2000 Hz
1064 Holmqvist et al. (2011). Head stabilization via chinrests and consistent lighting ensure robust performance
1065 without AI Gibaldi et al. (2017). Recent advancements in eye-tracking technology, however, highlight
1066 growing exploration of AI and machine learning, particularly in less controlled environments (Klaib
1067 et al. (2021); Tonsen et al. (2016)). Although not yet a standard feature in high-precision tower-mounted
1068 systems like the *EyeLink 1000 Plus*, AI algorithms demonstrate potential for improving pupil detection
1069 under challenging conditions, such as blinks, minor head movements, or reflections from glasses, and for
1070 enabling adaptive calibration and predictive gaze estimation to mitigate brief tracking losses (Klaib et al.
1071 (2021); Fuhl et al. (2017)). Deep learning models are integrated cautiously in high-precision systems due to
1072 potential latency, which can undermine the millisecond-level accuracy required for experimental research
1073 (Andersson et al. (2017)).

1074 A few key considerations are worth noting. First, while these eye trackers can achieve high sampling rates
1075 and spatial accuracy under head-constrained conditions, studies have identified certain limitations in pupil-
1076 based systems when recording the dynamics of saccadic eye movements Nyström et al. (2016). Indeed,
1077 during saccadic movements, the rapid accelerations exerted by the eye muscles induce significant forces
1078 on the eyeball, causing changes in pupil size and center position. These changes can distort the velocity
1079 profiles of saccades recorded by pupil-based trackers, and thus variations in saccadic measurements across
1080 participants and experimental conditions should be interpreted with caution. For experimental paradigms

1081 that require precise measurement of oculomotor dynamics, alternative tracking technologies discussed in
1082 Section 4.1 may be more suitable, although these require highly controlled environments.

1083 Second, some tower-mounted systems can be adapted for head-free eye tracking, which is advantageous
1084 in studies where head stabilization is impractical but high accuracy is still required — *e.g.* in developmental
1085 research involving infants Hessel and Hooge (2019). This head-free adaptation may lead to a slight
1086 reduction in sampling frequency and accuracy, thereby blurring the line between tower-mounted and
1087 remote eye trackers, despite technical and price differences between the two categories as discussed in
1088 subsequent sections.

1089

1090 4.3.2 Remote Eye-Trackers

1091 Remote eye trackers, such as the *Tobii Pro Spark*, *GazePoint GP3*, and *EyeLogic LogicOne*, are compact
1092 systems positioned below a stimulus display, typically a computer screen, using infrared light and cameras
1093 for gaze tracking. With sampling rates of 60 to 250 Hz, they prioritize ease of use and participant comfort,
1094 eliminating the need for head stabilization, thereby allowing participants to engage in a natural and
1095 unobstructed viewing experience. This less intrusive setup is advantageous for usability testing, a range of
1096 human behavior and visual psychology studies, as well as screen-based market research Niehorster et al.
1097 (2018). These systems collect raw monocular eye position data, such as pupil center and corneal reflection
1098 coordinates, but typically output processed gaze coordinates mapped to a screen-based calibration plane
1099 using polynomial regression or neural network models Morimoto and Mimica (2005). Raw monocular data,
1100 useful for studying binocular coordination, is often accessible only through premium subscriptions — *e.g.*
1101 *Tobii Pro SDK*, *GazePoint SDK* — as processed gaze data is the default Niehorster et al. (2018).

1102 These systems typically allow for some degree of head movement accommodation, but excessive motion
1103 can result in data gaps, inaccuracies, and artifacts. Specifically, remote eye-tracking systems feature
1104 a constrained functional area, known as a *head box* and often restrict gaze tracking to a designated
1105 *calibration plane*, usually the computer screen. If a participant moves outside the head box or looks beyond
1106 the calibration plane, tracking may pause temporarily. High-quality systems can rapidly reacquire eye
1107 movements with minimal data loss when the participant's gaze returns to the calibration plane. However,
1108 substantial shifts in distance from the screen can necessitate recalibration, and changes in vergence — eye
1109 convergence — may introduce additional error in tracking data.

1110 Artificial intelligence (AI) is transforming the capabilities of remote eye trackers, enhancing their
1111 robustness, accuracy, and usability across diverse environments. Traditionally, remote eye trackers, which
1112 rely on infrared illumination and corneal reflection without physical contact, required controlled lighting,
1113 stable head positioning, and careful calibration (Holmqvist and Andersson (2017)). Early systems mainly
1114 used rule-based image processing methods for pupil and glint detection, but these approaches struggled
1115 with real-world challenges like head movements, glasses reflections, partial occlusions, and changing
1116 ambient lighting (Santini et al. (2018)). To address these issues, AI-driven methods, particularly deep
1117 learning models, are now widely adopted for tasks such as real-time pupil detection, gaze estimation, and
1118 dynamic head pose compensation Santini et al. (2018). Convolutional neural networks (CNNs) enable
1119 robust eye feature extraction even under suboptimal imaging conditions, while machine learning models
1120 trained on large datasets predict gaze direction more accurately across a wide range of head positions,
1121 facial geometries, and lighting environments Zhang et al. (2017); Fuhl et al. (2017); Ansari et al. (2023).
1122 Deep learning also supports user-adaptive gaze estimation, fine-tuning calibration based on individual

1123 anatomical or behavioral differences Byrne et al. (2025), thus facilitating "*low-calibration*" operation (Liu
1124 et al. (2018)).

1125 When selecting an eye-tracker, researchers often weigh specifications such as spatial accuracy, precision,
1126 and head box dimensions. Manufacturers typically present these metrics as representative for any participant
1127 within the head box, though they may overlook the limitations of non-ideal head positioning. However,
1128 empirical studies Niehorster et al. (2018) have shown that these specifications are most reliable only when
1129 participants closely adhere to instructions and maintain optimal positioning. When participants deviate
1130 from these optimal conditions Hessels et al. (2015b), or when recording from challenging groups — like
1131 infants Hessels et al. (2015a) — both accuracy and precision can degrade significantly, even if the eyes
1132 remain within the head box. This can lead to considerable data loss and reduced data quality, with important
1133 implications for subsequent data analysis and interpretation.

1134

1135 4.3.3 Wearable Eye-Trackers

1136 Wearable eye tracking systems, often referred to as head-mounted or mounted eye tracking systems,
1137 typically consist of lightweight and ergonomically designed eyewear or headbands, such as *Pupil Labs*
1138 *Neon* and *Tobii Pro Glasses 2/3*. These systems generally incorporate one or more cameras positioned
1139 within the visual field of one or both eyes, alongside an additional camera that captures the surrounding
1140 scene or field of view. In head-mounted configurations, gaze tracking is performed relative to the entire
1141 field of view, making these systems particularly well-suited for real-world experimental settings. Wearable
1142 eye trackers are employed across a diverse range of research applications, including decision-making
1143 studies in marketing Gidlöf et al. (2017), analysis of viewing behaviors among various professional groups
1144 McIntyre et al. (2019), investigations into shared manipulation in human–robot interaction Aronson et al.
1145 (2018), and examinations of social interactions among adults Macdonald and Tatler (2018). They capture
1146 raw monocular eye position data and output gaze coordinates MacInnes et al. (2018b). Pupil Labs provides
1147 raw data openly via Pupil Capture, but Tobii restricts unprocessed data and advanced mapping tools — see
1148 below — to premium subscriptions — e.g. Tobii Pro Lab Glasses Edition) Macdonald and Tatler (2018).

1149 The miniaturization and portability of wearable eye-tracking systems, while advantageous for real-world
1150 applications, come with trade-offs in terms of performance. For instance, while high-end fixed laboratory
1151 eye trackers can record eye positions at frequencies up to 2000 Hz, modern wearable eye-tracking glasses
1152 typically have lower recording capacities, with most devices operating within the 50 – 100 Hz range,
1153 and the upper limit rarely exceeding 250 Hz. This reduced sampling rate limits the utility of wearable
1154 eye trackers in studies requiring high temporal precision, such as investigations into fine fixational eye
1155 movements, or the recordings of saccades and fast phase of the VOR and OKN. For example, exploring the
1156 non-linearity of saccade trajectories or examining microsaccades is generally considered unfeasible with
1157 eye-tracking systems that sample below 250 Hz, as these phenomena require higher-frequency data capture
1158 for accurate analysis Martinez-Conde et al. (2009). Additionally, maintaining an unobstructed view of the
1159 eyes is essential for accurate tracking, making it difficult to capture peripheral eye movements. This can
1160 lead to a decrease in tracking accuracy, particularly in dynamic or less controlled environments.

1161 Artificial intelligence (AI) has become integral to modern wearable eye trackers, significantly enhancing
1162 their flexibility, accuracy, and usability in real-world environments. Unlike fixed, laboratory-based systems,
1163 wearable devices must contend with constant head movements, changing lighting conditions, partial
1164 occlusions from eyelids or glasses, and variations in individual anatomy (Holmqvist and Andersson (2017);
1165 Tonsen et al. (2016). To address these challenges, AI-driven algorithms, particularly deep learning models,

1166 are employed for real-time pupil detection, gaze estimation, and robust calibration without extensive
1167 manual setup (Klaib et al. (2021); Yiu et al. (2019)). For instance, the DeepVOG framework utilizes
1168 fully convolutional neural networks for pupil segmentation and gaze estimation, demonstrating robust
1169 performance across multiple datasets (Yiu et al. (2019)). Similarly, YOLO-based models have been applied
1170 for accurate pupil center detection in visible-light conditions (Ou et al. (2021)).

1171 Neural network-based approaches adeptly handle issues such as reflections from glasses, variable
1172 illumination, and motion artifacts, ensuring reliable gaze tracking during dynamic activities like walking,
1173 driving, or sports analysis (Chaudhary et al. (2019); Tonsen et al. (2017)). Trained on diverse datasets,
1174 these models adapt to the complex visual conditions typically encountered outside controlled environments
1175 (Garbin et al. (2019); Tonsen et al. (2016)). In settings where lighting is consistent and computational
1176 resources are limited, simpler techniques like edge detection can complement AI-based tracking for greater
1177 efficiency (Holmqvist and Andersson (2017)). Wearable eye trackers require compact AI models optimized
1178 for lightweight cameras and minimal infrared illumination, with fast, adaptive calibration to maintain
1179 tracking accuracy on the move (Fuhl et al. (2017); Tonsen et al. (2017)). Recent advancements, such as
1180 lightweight convolutional neural networks, have improved real-time pupil detection for mobile eye tracking,
1181 although challenges related to model compression and energy efficiency remain critical for deploying deep
1182 learning on embedded systems (Marvasti-Zadeh et al. (2021)).

1183 Furthermore, wearable eye-tracking devices generate gaze data based on a coordinate system defined
1184 by both the wearable tracker and the recorded scene video, rather than being anchored to fixed objects
1185 in the observer's visual field. When the participant's head and body movements are unconstrained, a
1186 disassociation between eye movements and gaze shifts can occur. This creates a challenge, especially as
1187 many recent studies aim to investigate gaze dynamics in naturalistic environments, where it is crucial
1188 to translate gaze data into a consistent, fixed frame of reference. To overcome this challenge, manual
1189 mapping of gaze coordinates to a fixed reference frame can be time-consuming and typically feasible only
1190 for short recordings. Several automated solutions have been developed to address this issue. For example,
1191 certain systems use markers to delineate a consistent tracking area, such as a section of the visual field or a
1192 screen, to maintain reference during data collection. In addition, techniques exist to map eye-tracking data
1193 onto a more static representation of the scene. *Tobii*, for instance, offers the *Real World Mapping* (RWM)
1194 solution, while *Pupil Labs* has developed the *Reference Image Mapping* (RIM) module, both of which
1195 enable the conversion of dynamic gaze data into a fixed spatial framework. It should also be mentioned that
1196 open-source pipelines for gaze mapping can be found in the literature MacInnes et al. (2018b,a).

1197

1198 4.3.4 Integrated Eye-Trackers

1199 This category includes eye-tracking devices embedded within a variety of technological systems. Notable
1200 examples include aiming systems in eye surgery technologies, other medical devices, and eye-tracking
1201 systems integrated into vehicle dashboards. Recent advances in virtual and augmented reality (VR/AR)
1202 technologies have significantly enhanced the quality and accessibility of integrated eye-tracking systems,
1203 facilitating their widespread adoption in research environments. VR provides a fully immersive experience,
1204 while AR augments the user's real-world environment by overlaying digital elements onto live visual
1205 input—more detailed information on this can be found in the review by Clay et al. (2019). These systems
1206 collect monocular eye position data (pupil coordinates, corneal reflections) but prioritize processed 3D
1207 gaze coordinates or vergence-based depth in virtual environments, using calibration to map gaze to stimuli
1208 Duchowski et al. (2000). Raw monocular data, valuable for custom research — e.g. vergence studies —

1209 often requires premium licenses — *e.g.* Tobii’s XR SDK — while processed gaze data is standard for
1210 applications like foveated rendering Lang et al. (2018).

1211 Eye tracking in VR/AR is a relatively recent innovation, first emerging in the literature around the turn
1212 of the century Duchowski et al. (2000), and offers substantial potential for advancing research on human
1213 perception and behavior. In contrast to traditional eye-tracking methods, VR/AR enables the creation
1214 of controlled experimental settings while granting participants the freedom to move within a relatively
1215 naturalistic environment Clay et al. (2019); Drewes et al. (2021). Participants can explore their surroundings
1216 by moving their heads, and the precise spatial relationship between stimuli and the participant’s gaze can
1217 be tracked concurrently with head movements.

1218 Similarly to wearable and remote eye trackers, artificial intelligence (AI) is playing a critical role in
1219 advancing AR/VR eye tracking systems, making gaze estimation faster, more accurate, and more adaptive to
1220 immersive environments. Deep learning algorithms enable personalized calibration by modeling individual
1221 anatomical variations, such as corneal curvature and interpupillary distance, reducing setup time and
1222 improving user comfort (Liu et al. (2018)). AI also supports predictive gaze models, allowing systems to
1223 anticipate eye movements for foveated rendering, where high-resolution graphics are focused only where
1224 the user is looking, enhancing performance and realism (Arabadzhiyska et al. (2017); Patney et al. (2016)).

1225 Eye tracking in virtual and augmented reality enables diverse applications across multiple domains,
1226 including education and training Lang et al. (2018), clinical diagnostics Miao et al. (2020), and marketing
1227 and consumer research Meißner et al. (2019), among others. Gaze-based pointing and target selection
1228 introduce intuitive multimodal interaction methods Jacob and Stellmach (2016); Majaranta and Bulling
1229 (2014); Plopski et al. (2022), while awareness of a user’s gaze direction enables novel approaches for
1230 navigation and subtle manipulation of virtual environments Langbehn et al. (2018); Marwecki et al. (2019).
1231 The broad applications of VR-based eye tracking span numerous fields. For a comprehensive overview see
1232 the recent work by Adhanom et al. (2023).

1233 In terms of hardware, key manufacturers in the field include *Tobii* and *Pupil Labs*. *Tobii* integrates its
1234 eye-tracking technology directly into VR headsets such as the *HTC Vive Pro Eye*, while *Pupil Labs* provides
1235 modular add-ons that can be attached to commercial headsets without built-in eye tracking, such as the *Pico*
1236 4. Due to the relatively recent development of eye tracking in VR, assessing the quality of specific hardware
1237 can be challenging at times. Similar to *traditional* eye-tracking systems, there is a growing demand for
1238 standardization of data quality reporting in VR. Notably, B. Adhanom et al. (2020) introduced an open
1239 source package to measure gaze precision and accuracy within the Unity rendering engine.

5 DISCUSSION

1240 Much of our understanding of the role of various oculomotor control circuits in complex tasks is derived
1241 from extrapolating results obtained in simple laboratory experiments. The fundamental characteristics
1242 of eye movements under these controlled conditions are well-documented in the eye-tracking literature,
1243 and such environments allow for reproducibility and comparison across studies. Laboratory settings offer
1244 several advantages, particularly in terms of stimulus design. Visual stimuli can be carefully constructed
1245 based on known physiological parameters, including those of theoretical relevance to the experiment. The
1246 tasks are typically designed to be simple, with the key experimental parameters clearly defined, allowing
1247 the stimulus to contain most of the relevant information needed for the task. As a result, behaviors can be
1248 easily quantified in parametric terms, such as reaction times to stimulus presentation, and the task can be

1249 explicitly instructed and its difficulty level precisely controlled. This creates a situation akin to a toy model,
1250 where nearly all variables are controlled, enabling a detailed understanding of the processes involved.

1251 However, this approach has notable limitations. The controlled, simplified nature of laboratory
1252 experiments creates nonphysiological scenarios that may not accurately reflect real-world conditions.
1253 Although laboratory research can provide valuable information on the neurophysiological mechanisms
1254 underlying basic oculomotor control, it may have limited applicability to the characterization of more
1255 complex behavioral processes that occur outside of these controlled settings. As a result, while such studies
1256 are invaluable for understanding the fundamental building blocks of eye movement control, they may not
1257 fully characterize more complex behavioral processes expressed in more naturalistic, real-world contexts.

1258 In this respect, research carried out under less controlled conditions is interesting from two points of view.
1259 Firstly, as discussed in Section 3, a comprehensive understanding of the visual system requires an analysis
1260 that integrates not only the visual processes themselves but also their interaction with other body segments
1261 and functions, such as head and upper limb movements. Secondly, studying visual function in more natural
1262 contexts allows for a more ecologically valid analysis of integrative visual behavior, something that is
1263 typically not achievable with brain imaging techniques like fMRI or basic neurophysiological methods.
1264 Therefore, it may appear paradoxical that the study of visual behavior, particularly when integrated with
1265 physical or behavioral tasks, has been so limited in scenarios where the participant's head movement is not
1266 restricted.

1267 While naturalistic research is essential for understanding which visual strategies, enabled by the flexibility
1268 of the human oculomotor system, are employed in real-world tasks, and what role eye movements play
1269 in these strategies, extrapolating findings from laboratory experiments to natural settings is not always as
1270 straightforward as it might seem. One of the key challenges in naturalistic environments is designing and
1271 parameterizing stimuli in ways that reveal essential behavioral components. Furthermore, characterizing
1272 natural eye movements remains complex as they are often the result of the interaction between multiple
1273 neural pathways. For example, vestibular inputs combine with visual information to accomplish a motor
1274 task, making it difficult, if not impossible, to isolate the contribution of each system to a given movement.
1275 This suggests that the modular approach to oculomotor control, which posits that each eye movement is
1276 governed by a distinct neural circuit, is insufficient to adequately describe natural eye movements (Steinman
1277 et al. (1990)).

1278 Interestingly, this issue reflects the broader *real-world or the lab* dilemma in cognitive science and
1279 psychology, as outlined by Hammond (Hammond and Stewart (2001)). Specifically, the artificial nature
1280 of experimental environments may differ from real-world contexts in ways that make the results less
1281 relevant to the phenomena that researchers aim to explain. The field has experienced what has been referred
1282 to as an *ecological validity crisis* (Aanstoos (1991)), many authors have noted that "*what is missing is
1283 an independent, objective, and operational definition of the concept of ecological validity*" (Lewkowicz
1284 (2001)) which could jointly cover the nature of the stimuli, the nature of the task and the nature of the
1285 research context. These concerns are central to recent discussions on the limitations of ecological validity
1286 in eye-tracking research (Holleman et al. (2020)). Although these questions remain unresolved, they
1287 encourage researchers to clearly specify and describe the environmental contexts they study, which helps
1288 uncover contextual and general principles of behavioral and physiological mechanisms.

1289 To address the limitations described above, two main approaches have emerged in the literature. The first
1290 approach involves studying gaze behavior under laboratory conditions. This approach aims to isolate the
1291 contributions of different systems involved in eye movement control, indirectly returning to a modular

1292 perspective of the oculomotor system. Typically, participants are asked to direct their gaze to a specific
1293 location when a stimulus appears, and a set of metrics is used to characterize the coordination and
1294 interdependence of the subsystems involved in gaze control. However, this approach is not without
1295 limitations, as it relies on reductionist paradigms that may not accurately reflect real-world behavior. The
1296 second approach focuses on recording natural eye movement behavior, acknowledging that determining the
1297 precise neural sources of each movement is unlikely. This approach shifts the focus to the analysis of eye
1298 movements from a task-oriented perspective, a relatively new area in eye tracking research (Lappi (2016)).
1299 Ultimately, there exists a continuum between control and realism, and it is up to each researcher to balance
1300 these two perspectives in their experimental design. The challenge lies in finding an appropriate balance
1301 between simplifying the system for robust experimental outcomes and capturing the rich complexity of
1302 real-world behavior while navigating the potential limitations of both approaches.

CONFLICT OF INTEREST STATEMENT

1303 The authors declare that the research was conducted in the absence of any commercial or financial
1304 relationships that could be construed as a potential conflict of interest.

AUTHOR CONTRIBUTIONS

1305 QL: Formal Analysis, Methodology, Writing – original draft, Writing – review & editing. AR: Formal
1306 Analysis, Writing – original draft, Writing – review & editing. MPR: Validation, Writing – review &
1307 editing. AA: Validation, Writing – review & editing. NV: Supervision, Methodology, Validation, Writing –
1308 review & editing. IB: Supervision, Methodology, Validation, Writing – review & editing. LO: Supervision,
1309 Methodology, Validation, Writing – review & editing. PPV: Supervision, Methodology, Validation, Writing
1310 – review & editing.

ACKNOWLEDGMENTS

1311 Part of this work has been founded by the Industrial Data Analytics And Machine Learning chairs of ENS
1312 Paris-Saclay.

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Table 1. Summary of main types of video-based eye-tracking devices, together with typical usages and main limitations.

Type of Device	Example of Use	Main Limitations
Fixed/Head Stabilized	<ul style="list-style-type: none"> Screen-based visual tasks High-precision research in neuroscience and physiology exploring oculometric dynamics 	<ul style="list-style-type: none"> Commonly requires head stabilization Limited to laboratory conditions Unsuitable for certain populations
Remote	<ul style="list-style-type: none"> Screen-based visual tasks Research in neuroscience, cognitive science, psychology and marketing Participants with neurological impairments, infants 	<ul style="list-style-type: none"> Viewer must stay within the device headbox Excessive head and body movements can cause inaccuracy and data loss Generally not suitable for analyzing fine oculomotor dynamics
Wearable	<ul style="list-style-type: none"> Behavioral experiments outside the laboratory Research in neuroscience, human factors, ergonomics and marketing Driving experiments and high-fidelity simulators 	<ul style="list-style-type: none"> Data recorded relatively to the viewer field of view, requiring further analysis Interpreting the results is more complicated due to increased viewer freedom Generally not suitable for analyzing fine oculomotor dynamics
Integrated	<ul style="list-style-type: none"> Augmented/virtual reality research in neuroscience, cognitive science and psychology Medical analysis tools 	<ul style="list-style-type: none"> Generally highly-specialized to a specific use-case Participant has to tolerate augmented/virtual reality

Table 2. This comparison focuses on the technical specifications of commercial video-based eye-trackers. When available, the specifications are those provided by the manufacturers; otherwise, the data presented are based on observations reported in the research community. Notably, we include the *SMI ETG 2*, a video-based eye tracker frequently referenced in the literature. Although this device has been widely used in various studies, it has been discontinued following Apple's acquisition of SMI in 2017.

Device	Type	Accuracy (deg)	Sampling rate (Hz)	Head-box (cm)	Latency (ms)	Price point (\$)
Arrington ViewPoint	Tower-mounted	0.3 – 1 (accuracy) 0.25 (precision)	90 – 400	—	< 20	< 15000
Tobii Pro Spectrum	Tower-mounted	0.3 – 0.4 (accuracy) 0.06 (precision)	60 – 1200	34 × 26 at 65 cm (free-head)	< 10	> 15000
EyeLink 1000 Plus	Tower-mounted	0.3 – 0.5 (accuracy) 0.01 (fixed-head precision) 0.05 (free-head precision)	250 – 2000 (fixed-head) 250 – 1000 (free-head)	40 × 40 at 70 cm (free-head)	< 10	> 15000
Gazepoint GP3	Remote	0.5 – 1 (accuracy) 0.1 (precision)	60 – 150	35 × 22	< 50	< 5000
Tobii Pro Spark	Remote	0.5 (accuracy) 0.3 (precision)	33 – 60	35 × 35 at 65 cm	< 50	< 5000
EyeLogic LogicOne	Remote	0.5 (accuracy) 0.1 (precision)	60 – 250	30 × 20 at 60 cm	< 20	< 15000
SmartEye Aurora	Remote	0.3 (accuracy) 0.1 (precision)	60 – 250	50 × 40 at 65 cm	< 20	< 15000
Tobii ProGlasses 2	Wearable	1.4 (accuracy) MacInnes et al. (2018b) 0.3 (precision) MacInnes et al. (2018b)	50 – 100	—	< 50	< 15000
SMI ETG 2	Wearable	0.5 – 1 (accuracy) MacInnes et al. (2018b) 0.2 (precision) MacInnes et al. (2018b)	60 – 120	—	< 50	< 15000
PupilLabs Core	Wearable	0.6 (accuracy) 0.2 (precision)	200	—	< 50	< 5000
HTC Vive Pro Eye	Integrated	0.5 – 1.1 (accuracy) 0.4 (precision) Schuetz and Fiehler (2022) Schuetz and Fiehler (2022)	120	—	< 50	~ 1000
Pupil Labs Neon Pico 4	Integrated	1 (accuracy) 0.08 (precision)	200	—	< 20	< 15000
Varjo XR-4	Integrated	1 (accuracy) 0.2 (precision)	200	—	< 30	< 10000