

Running head: EYE MOVEMENTS AND DECISION MAKING

Eye movements as a window into decision making

Miriam Spering^{1,2}

¹Dept. of Ophthalmology & Visual Sciences, University of British Columbia, Vancouver,
Canada

²Djavad Mowafaghian Center for Brain Health, University of British Columbia, Vancouver,
Canada

Word count: 8,367

Figure count: 4

Author's address:

miriam.spering@ubc.ca

ABSTRACT

For over 100 years, eye movements have been studied and used as indicators of human sensory and cognitive functions. This review evaluates how eye movements contribute to our understanding of the processes that underlie decision making. Eye movement metrics signify the decision stimulus and task context in which information is accumulated and weighed. They indicate the efficiency with which we evaluate decision-task instructions, the timing and duration of decision formation, the expected reward associated with a decision, the accuracy of the decision outcome, and our ability to predict and feel confident about a decision. Because of their continuous nature, eye movements provide an exciting opportunity to probe decision processes non-invasively in real time.

KEYWORDS:

decision making, choice, eye movement, saccade, value, confidence

1. INTRODUCTION

Seeing and perceiving the visual world is an active process that involves orienting eyes, head and body toward an object of interest. It is also a highly dynamic process during which the eyes continuously scan the environment to sample visual information. Eye movements are used by many research disciplines—ranging from developmental and cognitive psychology to computer science and art history—to measure visual perception, object recognition, memory function, and other cognitive processes. This review focuses on the link between eye movements and decision making.

We make decisions frequently throughout the day. Perceptual decisions are usually simple and binary—such as whether to drive through a changing traffic light or whether to stop. They require selecting, discriminating, and weighing the accumulated sensory evidence. Value-based decisions might be more complex and involve options with multiple attributes—for example, which lunch option to choose, gym to join, or stock option to invest in. They require identifying and deliberating expected costs and benefits. Perceptual and value-based decisions have been the focus of neuroscience for over three decades. Single-neuron and population recording studies in nonhuman primates have unraveled some of the brain circuits underlying the transformation of a sensory signal into a perceptual choice (Gold & Shadlen, 2007; Najafi & Churchland, 2018; Schall, 2001; 2013), and the timing, accuracy, and confidence with which this choice is made (Shadlen & Kiani, 2013). Nonhuman primate neurophysiology, human imaging and neuropsychological studies have elucidated how value is represented in neuronal activity across different brain areas (Platt & Glimcher, 1999; Padoa-Schioppa & Conen, 2017; Kennerley & Walton, 2011; Vaidya & Fellows, 2020). In many of these studies, primates indicate their choice by moving their eyes into a preferred direction or location while neuronal activity is being

recorded. For example, a classic paradigm involves asking monkeys to discriminate the motion direction of a stimulus (e.g., left versus right) by making a saccade in the perceived direction (to the left or right). In this task, saccade choice accuracy is related to neuronal activity in motion-sensitive brain areas (Newsome, Britten, & Movshon, 1989). More critically, choice accuracy is also predicted by activity in decision-related brain areas, making this a key task to elucidate aspects of perceptual decision making (Levi & Huk, 2020; Shadlen & Kiani, 2013). Such tasks have contributed to detailed neuronal and computational models of decision making that rely on the idea that neuronal activity itself acts as a decision signal and predicts upcoming choices (Glimcher, 2001; Gold & Shadlen, 2007; Najafi & Churchland, 2018; Schall, 2001; 2013; Shadlen & Kiani, 2013).

More recently, neurophysiological studies have been complemented by behavioral eye movement studies that focus not only on where we look, but also on the metrics of the movement itself. In these studies, eye movements are used as indicators of target selection, choice or deliberation processes and performance monitoring (confidence), as well as indexes of stimulus and task features such as uncertainty or value. Whereas traditional reaction-time measurements (e.g., of button presses or verbal responses) provide basic insights into the mental processes that mediate decision processes, eye movements can provide a much finer temporal resolution than reaction time. They allow us to investigate not only the relation between neuronal activity and behavior, but also how this relationship unfolds.

In cognitive psychology and neuroscience, the terms “choice” and “decision” are often used interchangeably. Both processes are commonly studied by evaluating simple actions or movements, such as button presses, saccadic eye movements, or pointing movements. Strictly speaking, a choice directly implies a response (or an action), whereas the decision is the process

leading up to it. Definitional distinction of these terms can help categorize and evaluate the available evidence, and identify gaps in our understanding of decision making (Schall, 2001; 2013). In this review, I will attempt to refer to choices when I speak about the action itself, and to decisions when I speak about the deliberation process. I will discuss studies that employ parameters of physical actions—for example, a movement’s latency, amplitude, velocity, vigor—as indicators of a decision’s characteristics (**Fig. 1**). This review is organized as follows.

I will first introduce eye movement types along with a selective overview of underlying brain pathways. I will then review experimental eye movement studies in human and non-human primates engaging in a variety of laboratory decision tasks. In five sections, I will discuss studies that utilize eye movements (1) as models of sensory evidence sampling and accumulation to maximize information gain, (2) as predictors of sensorimotor decision timing and temporal expectation, (3) as measures of response execution and inhibition, (4) as indicators of reward and value, and (5) as markers of decision certainty and confidence. I will propose new directions for future research focusing on clinical populations, new technologies, and real-world tasks. Together with recent discoveries, these new directions can lead to insights into the function and dysfunction of decision processes across populations and applications, and into the pathophysiology of diseases that impact decision making.

2. PRIMATE EYE MOVEMENTS ARE TUNED TO A DYNAMIC SENSORY WORLD

Because the resolution of peripheral vision is limited, eye movements are needed to align the eyes’ foveae with visual objects or areas of interest, allowing us to examine them in detail.

Different types of visually-guided eye movements cooperate to achieve gaze-alignment with a target (Leigh & Zee, 2015). Saccades are high-velocity and short-duration movements that shift

the eyes to a new spatial area of interest. During fixation, the eyes focus on a small area and only make miniature movements (Rolf, 2009). Smooth pursuit eye movements are continuous eye rotations often made in conjunction with saccades to track a moving object and hold it steady near the fovea. Even though these different gaze-aligning eye movements are usually prompted by different stimuli in the laboratory, they interact to achieve high-accuracy vision (Goettker & Gegenfurtner, 2021; Orban de Xivry & Lefèvre, 2007). We make about three to five eye movements per second, meaning that it is the most common movement primates engage in (Bargary et al., 2017). Yet, the extraocular muscles do not fatigue (Fuchs & Binder, 1983), allowing us to move our eyes continuously. It is this continuity at high accuracy and precision that makes eye movements such an appealing model of sensorimotor behavior and allows us to infer cognitive processes.

In the context of decision making, eye movement metrics such as the latency, amplitude, peak velocity or frequency of a saccade and the position error or velocity gain of smooth pursuit (**Fig. 1**) have been linked to the timing or accuracy of the choice. Some studies have defined specific eye movement parameters that signify decision processes. For example, saccade vigor (**Fig. 1**) reflects the economic utility of a decision outcome, i.e., the interaction of the subjective reward associated with a decision outcome, and the effort that has to be exerted to obtain this reward (Shadmehr et al., 2019). Pupil dilation and blink rate are two relatively novel markers of decision-task features, and have the potential to shed light on longer-scale or sequential decision processes. Under constant luminance, pupil diameter tends to be modulated by arousal and responds sensitively to a large range of decision-related processes, including value, effort, confidence, uncertainty, and surprise (Ebitz & Moore, 2019); spontaneous eye blinks have been correlated with decision outcome and stimulus predictability (Jongkees & Colzato, 2016).

Figure 1 here

The detailed knowledge of the brain mechanisms that control eye movements (reviewed in detail elsewhere, e.g., Krauzlis, 2005; Lisberger, 2015; Munoz & Coe, 2011) allows us to link oculomotor neuronal activity to decision-related neuronal activity. In brief, a visual signal is sensed by the retina, and relayed via the thalamus to primary visual cortex. Neurons in these brain areas encode stimulus features which will ultimately allow the observer to localize, categorize, and select a stimulus as the basis for the following choice. In parallel, the retina projects directly to the midbrain's superior colliculus (SC). Visual cortex and SC have rich connections with a network of fronto-parietal oculomotor areas such as the frontal eye field (FEF) and lateral intraparietal cortex (area LIP), where sensory signals are integrated and transformed into a motor command to move the eyes. The motor command is adjusted and optimized in the cerebellum and passed on to motoneurons in brainstem nuclei that innervate the extraocular muscles.

Of interest for the current review is the question how the sensory signals that drive eye movements might be modulated by top-down decision signals. One prime candidate for the integration of sensory and decision signals is FEF, which contributes to the generation of saccades and pursuit. Independent of its role in generating eye movements, it is also involved in visual-cognitive functions such as visual search and target selection (Schall, 2013; 2015). Similarly, SC carries signals that correlate with choice accuracy in decision tasks, and with related variables such as target uncertainty (Basso & May, 2019); microstimulations in area SC can directly modulate decision outcome (Herman, Katz, & Krauzlis, 2018). There is general consensus that FEF and SC are implicated in sensorimotor transformations through which visually-driven activity changes affect eye movement metrics (Kimmel & Moore, 2007;

Stanford, Freedman, & Sparks, 1996). Neuronal firing rates in these areas encode decision thresholds (Gold & Shadlen, 2000; Stanford et al., 2010). However, the exact mechanisms of how decision processes might influence eye movement metrics are not yet fully understood.

Pupil constriction and dilation are primarily driven by brainstem projections to the Edinger-Westphal nucleus in the midbrain, which signals the pupillary sphincter muscle to contract. This circuit receives descending cortical inputs (via the locus coeruleus or the SC, for example) that might be responsible for cognitive modulation of pupil size (Joshi & Gold, 2020). Both locus coeruleus and SC have been linked directly to pupillary changes via cortical inputs, for example, from FEF (Ebitz & Moore, 2017; Lehmann & Corneil, 2016), but the detailed pathways for this cortical modulation are unclear.

Spontaneous eye blinks are driven by activity in three motor systems (facial, oculomotor and retractor bulbi systems; Delgado-García, Gruart, & Trigo, 2006), but the exact circuitry underlying cognitive modulations of blinks is not known. Clinical studies indicate abnormalities in spontaneous blinks in disorders associated with dopamine dysfunction, such that reduced or increased dopamine activity are associated with low or high eye blink rates, respectively. Blinks appear to reflect dopamine receptor type 2 (D2) function (Groman et al., 2014), linked to decision thresholds in go/no-go circuits in the basal ganglia (Bahuguna, Aertsen, & Kumar, 2015). Correspondingly, blink rate correlates with performance in tasks associated with dopamine function, such as reward-driven learning or decision making (Jongkees & Colzato, 2016). In the following section I will discuss how a systematic investigation of eye movement metrics in decision tasks can shed light on some of the unanswered questions in decision research.

3. EYE MOVEMENTS AS INDICATORS OF DECISION PROCESSES

3.1. Eye movements as models of sensory evidence sampling and accumulation

In its simplest form, choosing an item over another involves perceptually detecting or locating a target and then selecting it from amongst distractors. The underlying choice processes are usually automatic and happen outside of our conscious awareness. This basic form of decision making follows a stage model of human information processing (Sternberg, 1969) that includes decoding a stimulus, retrieving information from memory, and deciding based on the available information before producing an appropriate response. At a more fine-grained level, a decision process involves accumulating noisy sensory samples until an evidence threshold is reached, at which point the decision is considered final (Ratcliff & McKoon, 2008). The information accrual process is driven by goals such as maximizing choice accuracy, timing, or reward (Gold & Shadlen, 2007). Eye movements directly contribute to this optimization process by achieving high-acuity vision of objects or locations of interest. They also reflect the steps of sensory information accrual (Gottlieb & Oudeyer, 2018)—ranging from which target is selected first, how evidence is weighed and integrated with prior knowledge and expectations, to when the information accrual process is stopped, inhibited, or reassessed.

Simple perceptual decisions have been studied using paradigms such as visual discrimination, target selection, or visual search. Visual search paradigms present multiple response alternatives and involve scanning or foraging the search array or image before settling on a response (Eckstein, 2011). Visual search could be considered a sequence of choices (where to move next) leading to a final decision (target present or absent). Eye movement patterns are related to how successful observers are in finding the target, and when they stop the search. Which target is prioritized reflects how we process visual saliency, task and target information,

statistical regularities, and value (Eckstein, 2011). Moreover, how we interact with real-world scenes through eye movements can give important insights into how we interpret the content of the image and why errors occur in target present/absent decisions (e.g., whether the image contains a malignant growth or not; Krupinski, 2010; Wu & Wolfe, 2019).

Typically, eye movement analyses during visual search have focused only on where we look, and less on the spatiotemporal characteristics of saccades and fixations (Godwin et al., 2021). Considering each saccade during search as a read-out of a perceptual decision, it can be interesting to investigate situations in which the initial saccade is “captured” by a distractor, not the target (Theeuwes, 2004). Features of saccades in such oculomotor-capture paradigms reveal target saliency and target probability information, in line with predictions of priority or salience models (Fecteau & Munoz, 2006; Itti & Koch, 2000). Initial saccade landing position and saccade latency reflect the similarity between target and distractor, the frequency with which a target appears, and the probability of a distractor appearing in a certain location within the search display. For example, saccades were less likely to land on distractors when they appeared in a location with high distractor (and low target) probability, and fixation duration at those locations was shorter. These findings indicate that saccade properties sensitively signal the probability with which a target or distractor appear at a certain location, and the related process of disengaging the eyes from a location that has been identified as irrelevant (Sauter et al., 2021). Moreover, saccades can be attracted to non-salient stimuli (or distractors) that signal the availability of reward, especially at short saccade latency; saccade accuracy scales with the magnitude of the reward (McCoy & Theeuwes, 2016). It appears that the oculomotor system competitively integrates external salience and internal value information when deciding where to look (Meeter, van der Stigchel, & Theeuwes, 2010).

According to classic saliency models, already fixated objects should be inhibited in order to drive efficient search until the target has been found. Neurophysiological studies have identified parts of the oculomotor decision network (e.g., areas FEF and LIP) as critical structures that keep track of refixations and determine where to look next (Mirpour et al., 2019; Mirpour & Bisley, 2021). Despite behavioral and neurophysiological evidence for inhibition-of-return (Klein & MacInnes, 1999; Mirpour & Bisley, 2021), eye movements during search and free viewing often follow a pattern of making a saccade to a novel object (exploration) and revisiting a previously fixated object (exploitation). Refixations usually occur shortly after the first fixation, within one (intervening) saccade. Compared to saccades to novel locations, they are of longer duration (approx. +50 ms) and occur most frequently in areas of high salience and where objects similar to the target are located, i.e., in areas where it is easy to miss the target (Zhang et al., 2021). It follows that refixations might serve an important purpose in reducing sensory uncertainty during visual search or foraging tasks. Eye movement metrics such as fixation patterns and potentially pupil size could further elucidate the factors that determine the trade-off between exploration vs. exploitation—both at the level of the environment (e.g., scene complexity and predictability) and the individual (e.g., confidence, prior knowledge, or memory capacity), emphasizing the importance of cognitive signals in guiding where we look.

How cognitive factors interact with salience is also reflected in findings that show a causal relation between fixation duration and choice outcome, i.e., fixation duration on a response alternative is closely related to which object is ultimately chosen. Typically, the longer a response alternative is viewed (e.g., in a non-urgent choice task, such as a choice between different food items) the higher the likelihood that it will be selected, irrespective of its value (Armel, Beaumel, & Rangel, 2008; Pärnamets et al., 2015; Shimojo, Simion, Shimojo, &

Scheier, 2003; Thomas et al., 2019). This process is presumably amplified by visual spatial attention to the fixated location or object (Cavanagh et al., 2014; Krajbich, Armel, & Rangel, 2010) and interacts with salience (Towal, Mormann, & Koch, 2013). In a reanalysis of four choice datasets from previous studies, in which observers had to select and rate or bid on an object out of a choice set, Thomas and colleagues (2019) calculated the positive or negative gaze advantage for each trial, computed as the fixation time on the selected object relative to the total time spent fixating. They found that 98% of a large sample of observers had positive scores, indicating an overall positive relationship between gaze allocation and choice. Individual choice behavior could be predicted by a gaze-weighted linear accumulator model, which assumes accumulation of sensory evidence at a rate that is discounted for objects that are fixated for a shorter period of time. The authors propose that this model can also account for individual behavior in multi-alternative, multi-attribute choices (Thomas, Molter, & Krajbich, 2021), such as when selecting an item from a vending machine. Similar claims have been made for decisions involving moral questions (e.g., “murder is sometimes justifiable” vs. “murder is never justifiable”). When observers’ fixation duration was restricted in a gaze-contingent display, in which a (randomly predefined target) choice alternative was shown for longer than the other alternative, they were systematically biased toward this target. These findings show that gaze-dependent decision models, according to which observers choose what they fixate, apply even to high-level moral decisions (Pärnamets et al., 2015).

An interesting discussion point is that many of the studies reviewed above assume implicitly that information accumulated throughout a trial or search process is weighed uniformly in contributing to a choice. However, it is known that this is not the case: observers instead commonly rely more heavily on sensory information acquired early (Levi & Huk, 2020;

Nienborg & Cumming, 2009; Yates et al., 2017). Using pupil size measurements, Kawaguchi and colleagues (2018) were able to show that this early weighing of information is modulated by confidence. When the animal was confident about their decision (dilated pupil), they were more biased toward early information than when they were overall less confident (pupil constriction; Kawaguchi et al., 2018).

In summary, these findings shed light on aspects of the sensory evidence accumulation process, such as how visual and task features (such as salience and probability) are processed to guide initial target selection or the goal of a first saccade, how and why sensory information is revisited by refixations, and why acquired evidence is not necessarily weighed uniformly across the course of a trial or task. Eye movements can also affect choice processes and outcomes in constructive ways and need to be factored into models of sensory evidence accumulation (Li & Ma, 2021).

3.2. Eye movements as indicators of decision timing and temporal expectation

Because of the relatively shorter latency of eye movements as compared to button presses, eye movements can reveal just how fast a perceptual choice can be made. Standard center-out saccades are usually made at latencies of 200-250 ms (Bekkering et al., 1994), and express saccades can be initiated even faster, after around 100 ms, with the fastest saccades starting at around 75 ms (Fischer, 1986). The fastest smooth tracking response, ocular following, has similar minimum latencies to the fastest express saccades (70-75 ms; Gellman, Carl, & Miles, 1990). By contrast, button press responses take around 300-350 ms to simple objects (Bekkering et al., 1994), and even longer (450 ms on average) to more complex scenes (Fabre-Thorpe et al., 2001). In a simple perceptual choice task, Kirchner and Thorpe (2006) showed two images of

natural scenes and asked human observers to make a saccade to the image that contained an animal. Strikingly, observers were able to reliably saccade to the correct image after only 120 ms, implying that the image can be processed and categorized within less than 100 ms (considering a 20 ms delay for saccade preparation). These results show how fast the visual system can accumulate information to inform a choice.

These findings are congruent with results obtained in tasks specifically designed to investigate the temporal evolution of decision making. When a stimulus is presented in a choice paradigm, neuronal activity begins to differ based on whether the stimulus that falls into the recorded neuron's receptive field is a cued target or distractor about 150 milliseconds (ms) after cue presentation (Stanford & Salinas, 2021). Just before a saccade is made, neuronal activity in areas such as FEF and LIP is unambiguously aligned with the upcoming choice (Glimcher, 2011; Huk & Shadlen, 2005; Schall & Hanes, 1993; Stanford & Salinas, 2021), establishing the link between neuronal activity and saccadic choices. But given that the time interval to evaluate response alternatives, to reach a decision, and to prepare a saccade is long (typically >500 ms), it is not possible to pinpoint the exact time when the decision is made. To investigate the temporal dynamics of this process, Seideman, Stanford and Salinas (2018) utilized an urgent saccadic choice task, in which monkeys were trained to make a rapid color discrimination between a target and a distractor. Importantly, the color cues revealing target and distractor identities were only presented after the monkey received the command to move, ensuring that the motor plan is already initiated when choice alternatives are evaluated (**Fig. 2A**; Stanford et al., 2010). Perceptual processes are therefore determined solely by the raw processing time (rPT)—the amount of time during which the visual cue can be evaluated—and can be assessed independently of the motor processes related to making the choice. Tachometric curves

(percentage of correct choices per raw processing time bin) reveal that accuracy increased with increasing processing time. Moreover, it took approx. 150 ms for the cue to be read out (timepoint at which the rise in performance is halfway between chance and asymptotic; **Fig. 2B**). The rapid transition from guesses to correct responses within approx. 50 ms indicates a short overall perceptual processing time and sensory information accumulation to reach a decision in this task, implying that the decision duration was around 50 ms.

Figure 2 here

Recall that longer processing times are associated with a higher proportion of correct choices. Saccade peak velocity also varied as a function of processing time. Peak velocity was significantly higher (and saccade amplitude longer, endpoints less variable) in trials with correct as compared to those with incorrect choices. Interestingly, velocity profiles started to diverge at around the time at which perceptual processing transitioned from guesses to correct estimates (~125 ms; **Fig. 2C**). Together, these findings indicate that eye movement metrics are strongly driven by how perceptual information is accumulated and weighed. Differences in saccade metrics co-occur with the formation of a decision. The overall timing that can be inferred here implies that perceptual decisions might be completed sooner than previously believed, between 50-100 ms after choice alternatives or relevant visual cue information is available. It could be argued therefore that some of the neuronal responses in areas FEF, LIP and SC, interpreted as related to differentiating between decision alternatives, might instead be related to post-decisional evaluations, attentional shifts, or performance monitoring (Stanford & Salinas, 2021; see also Huk, Katz, & Yates, 2017; Katz et al., 2016).

Urgent choice tasks are also prevalent in real-world situations. Hitting a baseball is arguably one of the most difficult tasks to achieve in sports. Traveling at speeds of around 100 mph, a

fastball arrives at the plate in less than 400 ms. Given a bat travel time of approx. 180 ms (Shaffer et al., 1993), this leaves a mere ~200 ms for the hitter to process visual trajectory information to decide whether or not to swing and where to intercept, essentially rendering this task an urgent choice task. Eye movements play a critical role during this process, and are used to continuously track the ball until shortly before interception (Toole & Fogt, 2021). In a laboratory simulation of the decision process required for baseball hitting, Fooker and Spering (2019; 2020) asked observers to view a 2D display with a ball moving toward a dedicated strike zone (**Fig. 3A**). Shortly after launch, the ball disappeared from view and observers had to extrapolate its trajectory in order to decide whether the trial was a hit or a miss. If they estimated a hit, observers had to rapidly intercept the ball within the strike zone (go trials), if they estimated a miss, observers had to withhold the interceptive hand movement (no-go trials). An analysis of observers' eye movements—a combination of smooth pursuit and saccades—revealed a close link between eye movement accuracy and go/no-go decision outcome, akin to findings of a link between neuronal activity in Supplemental Eye Fields (SEF) and decision outcome in a similar task (Kim, Badler, & Heinen, 2005). The position error of the smooth pursuit part of the response as well as the time at which observers made a saccade into the strike zone predicted decision outcome (go vs. no-go) in this task (Fooker & Spering, 2019). Moreover, the rate of targeting saccades during pursuit (the last saccade made before interception) started to differ between go and no-go decisions prior to hand movement onset, with higher saccade rates in go versus no-go trials (**Fig. 3B**). Akin to findings in the urgent saccadic choice task (Stanford et al., 2010), smooth pursuit properties similarly provide a signature of the evolving decision process that precedes an interceptive choice response. Of note, findings by Fooker and Spering (2019; 2020) also point to a role of pursuit in enhancing go/no-

go decisions, not unlike what has been reported for fixation duration and choice preference above (Thomas et al., 2019). Pursuit velocity (between the time of the initial and the final targeting saccade) was correlated with decision timing (i.e., a well-timed interception) on an individual observer basis. These findings indicate that eye movements not only differentiate between different decision outcomes, but are also related to better-timed decisions.

Figure 3 here

When choice alternatives are presented sequentially and not simultaneously (i.e., rapid serial visual choice task), eye movements provide information about temporal expectations of events. When searching for an item in a display, observers are believed to activate a search template, a working-memory representation of target features. Recent studies have revealed that these search templates are not continuously active, but are transiently and rapidly activated and deactivated before and after the onset of each search episode, tuned to the observer's temporal expectation of search. These findings were obtained by evaluating observers' microsaccades in response to the presentation of a rapid serial visual presentation of colored disks, presented during a delay preceding a search display (in which a target color had to be found; Olmos-Solis et al., 2017). Microsaccades were suppressed close to the time when the search display was anticipated. Their direction was biased toward task-irrelevant distractors that matched the target color, and these biases increased in strength as the appearance of the next search display grew closer. Microsaccade suppression and biases are indicators of observers' search template activation in expectation of the upcoming search display (Olmos-Solis et al., 2017), and therefore of the upcoming information-weighting process for target selection. Generally, response-related suppression of saccades or microsaccades (oculomotor freezing) appears to be linked to active response preparation and efficiency across modalities and tasks, and provides a marker of

temporal expectation (e.g., Abeles et al., 2020; Badde et al., 2020). This measure could therefore serve as a tool to track the time course of decision formation in classic choice tasks as well.

Other real-time indicators of decision processes that focus on the timing of when the decision is being made, are blinks and pupil responses. Studies in the visual domain have already related the timing of blinks to information processing. Blinks occur at breaks in the information flow or immediately after a manual response has been given (Wascher et al., 2015). Blinks can be suppressed prior to predictable temporal events (Abeles et al., 2020; Hoppe et al., 2018), making blinks a potential marker of temporal uncertainty. Blinks might even enhance visual processing in a detection task (Ang & Maus, 2020), indicating that blinks are not only a useful real-time measure of visual processing and temporal uncertainty, but might be functionally linked to performance.

To summarize, in binary choice tasks, eye movement metrics directly reflect the transition from perceptual evidence evaluation to when a decision threshold is reached, within 50-100 ms after complete visual information is available. Results obtained in urgent choice tasks reveal that decisions might only take tens of milliseconds, much faster than previously believed. Similarly, eye movement signatures characterize different outcomes in real-world urgent choice tasks (such as a simulated baseball paradigm). Oculomotor freezing can indicate the dynamics of cognitive expectations during decision formation, and blinks provide a novel tool to delineate the decision time course further.

3.3. Eye movements as indicators of response inhibition

A binary choice might involve a process of inhibiting a planned or ongoing action. Eye movement and blink characteristics reflect how fast or how well the choice to inhibit a response

is made. McSorley and McCloy (2009) showed that saccades curve away from a non-selected object, and land progressively further away from it, as the signal strength of a motion direction cue increases. For example, saccades following a direction cue with a strong motion signal were deviated away more strongly, and landed further away from the non-target direction than saccades following a weak motion signal direction cue. These findings reveal a signature of inhibition, scaling with signal strength, in saccade curvature and endpoints. They also show that oculomotor output can be continuously affected by a decision signal, even after the choice (e.g., saccade left or right) has been made. Decision formation affects eye movements even when the decision task does not involve an eye movement (Joo, Katz, & Huk, 2018), emphasizing the tight link between decision-related activity and decision-unrelated oculomotor processes. Overall, these results point to a continuous interaction between decision signals and eye movement responses during action execution and inhibition.

Countermanding, stop-signal, go/no-go and anti-saccade tasks are examples of paradigms that have specifically been developed to investigate action inhibition processes. In countermanding or stop-signal tasks, observers are asked to execute a speeded response, such as a button press or a saccade, to a go signal—for example, the disappearance of a fixation spot. In a small subset of trials, they have to abort that response when a stop signal—for example, the reappearance of a fixation spot—is shown (Logan, 1994). This task allows researchers to study the initiation and cancellation of planned movements, and how movement consequences are monitored—processes that are mediated by neuronal activity in area FEF and in the Supplementary Eye Field (SEF), respectively (Schall, Hanes, & Taylor, 2000). Responses are believed to be the outcome of a competitive process between generating (go) and cancelling (stop) a movement. The stop signal reaction time (or movement latency) quantifies the time

needed to cancel a movement and is approx. 100 ms in monkeys (Hanes & Schall, 1995) and 130 ms in humans for saccades (Hanes & Carpenter, 1999). Saccade cancellation is increasingly harder as the delay between target onset and stop signal increases. During saccade cancellation, microsaccades are also suppressed (Godlove & Schall, 2016). Therefore, saccade latency and rate of microsaccade suppression provide two possible measures of movement (or choice) cancellation in the saccade domain. Even though pursuit and saccades differ in terms of movement characteristics such as speed and latency, the mechanisms underlying the release of and transition back to fixation (as in the stop signal task) appear to be similar in both systems. Both movements are made at a shorter latency when the fixation spot is extinguished before the onset of the target (gap paradigm), and both movement latencies scale similarly with gap duration (Krauzlis & Miles, 1996). Kornyló, Dill, Saenz and Krauzlis (2003) directly compared stop signal performance in saccades and in pursuit. Estimated pursuit stop signal reaction times were overall shorter than for saccades (50-60 ms in humans and 60-70 ms in monkeys). The authors argue that the inhibitory mechanisms for both systems are similar, based on these latencies. The saccade system includes a point of no return (starting at the offset of omnipause neuron activity, which usually helps the eye to maintain fixation and to suppress saccades) placed up to 20 ms before the start of the saccade, but the pursuit system might not include such a ballistic interval. Therefore, the stop signal reaction times might in fact be comparable across eye movement types when taking this interval into account. Congruent with pursuit countermanding, Jarrett and Barnes (2003) found that anticipatory pursuit (made before the onset of an expected target) could also be stopped at will when an auditory cue is given. This is particularly interesting, given that anticipatory pursuit cannot be initiated at will. Finally, ongoing pursuit can be stopped in a gradual transition to fixation. This gradual stopping is likely

achieved through a combination of activating the fixation (omnipause neuron) system, through online feedback (efference copy) and through predictive mechanisms (Missal & Heinen, 2017).

In addition to countermanding activity in voluntary or visually-driven movements, spontaneous eye blink rate, a marker of dopamine function, predicts how efficiently human observers are able to inhibit unwanted action tendencies in this task. In a standard version of the stop-signal task, Colzato and colleagues (2009) related the go-signal reaction time (indicator of response execution) and the stop-signal reaction time (indicator of response inhibition efficiency) to the rate of eye blinks. Whereas blinks were unrelated to response execution, they were positively correlated with response inhibition efficiency: increased blink rate was associated with lower inhibition efficiency. Blinks might therefore serve as an additional indicator of inhibitory control. However, the assessment of eye movements in countermanding tasks merely links saccade latency, microsaccade inhibition, and blink frequency to task outcome, and not to the choice inhibition process itself. Moreover, most studies rely on correlations and do not manipulate eye movement behavior (which would be admittedly difficult—but possible—for blinks) to investigate the constructive contribution of blinks to decision efficiency.

In the anti-saccade task, observers have to suppress a saccade toward a cued distractor (pro-saccade) and instead voluntarily direct it toward an uncued target. This task has been used to evaluate the timing of saccade direction errors (in addition to saccadic latencies) as a measure of response inhibition (Munoz & Everling, 2004). Direction errors can occur early in the trial as an express-latency (90-140 ms) reflexive response to the cued target, indicating that suppression might start (and fail) pre-emptively, before the peripheral visual target can even trigger a saccade command. Later direction errors (latency >140 ms) indicate that there is a voluntary suppression mechanism as well that can override an erroneous (automated) pro-saccade. The detailed timing

of these different processes was revealed by saccade behavior in compelled antisaccade task, in which observers had to start programming a saccade before knowing the direction of the correct response (Salinas et al., 2019). Analysing observers' success rate as a function of raw processing time (analogously to **Fig. 2B**) reveals that the initial draw to the cued target yielded an almost 0% success rate (at 100 ms after cue onset), which was recovered when endogenous control took over (within an additional 40 ms). These different temporal processes and error types reveal different forms of suppression that might be mediated by separate neuronal pathways (Coe & Munoz, 2017). Pre-stimulus suppression could be controlled by direct cortical inputs from key frontal lobe areas (e.g., dorsolateral prefrontal cortex or area FEF) to intermediate layers of the SC. Suppression during a later stage might be distributed across different pathways providing SC input, including through the caudate nucleus in the basal ganglia, where signals for automatic, exogenously triggered pro-saccades and voluntary, endogenously controlled anti-saccades are known to interact (Watanabe & Munoz, 2009). The involvement of the SC is also supported by the finding that pupil dilation scales with saccade latency and errors, indicating a close relation between pupil size and saccade preparation. Pupil dilation is larger for short-latency vs. regular anti-saccades, and for correct anti-saccades and erroneous pro-saccades as compared to correct pro-saccades (Wang, Brien, & Munoz, 2015). The involvement of dopaminergic pathways, e.g., through the basal ganglia, is supported by consistent observations of increased antisaccade errors in patients with Parkinson's disease (Waldthaler et al., 2021), a potential biomarker of impulse-control disorders in these patients (Barbosa et al., 2019).

In sum, the ability to inhibit a response is a critical feature of choice processes in situations that require adaptation to changing contexts or goals. Saccade and pursuit latency and blink frequency during the stop-signal task reflect the cost and resource efficiency of response

inhibition—saccades and pursuit are initiated later and are less correct when the inhibition process is challenging (e.g., due to long delays or low saliency). Saccade direction errors and pupil dilation in the antisaccade task reveal the characteristics and time course of inhibition mechanisms—an early automatic mechanism and a later voluntary one, mediated by different brain pathways—during binary saccadic choice tasks. The stop-signal and antisaccade task bear some resemblance to the urgent saccadic choice task. In both types of tasks, vital stimulus or cue information have to be detected or interpreted when a motor plan is already ongoing, and an original movement plan (developed within 100 ms of cue onset) has to be either halted or inhibited (within an additional 40 ms) by voluntary mechanisms. These tasks therefore allow us to determine at which point in time automatic and voluntary mechanisms are engaged to control eye-movement indicated choice behavior.

3.4. Eye movements as indicators of reward and value in decision tasks

In real-world economic decisions, such as whether to buy a house or continue renting, observers have to choose from amongst multiple options with different subjective values. In order to understand how values are converted into choices we must first understand how the brain encodes value. Just as eye movements can be used to read out decisions, eye movements also directly reflect the value or expected reward associated with a choice. Saccade and pursuit metrics, blink rate and pupil size are all determined by activity in dopaminergic systems in regions that are also important for reward processing, such as the direct pathway connecting the basal ganglia (caudate nucleus and substantia nigra) to the SC (Hikosaka et al., 2014). This link between reward modulation and eye movement control implies that these metrics can sensitively signal how we process reward information.

It is well-documented that expected reward leads to shorter saccade latency and higher peak velocity. Saccade velocity scales with the probability or expected rate of receiving a reward (Thura et al., 2014). Congruently, the value associated with a saccadic choice also modulates peak velocity as a function of amplitude, a metric known as saccade vigor (Shadmehr et al., 2019). When observers deliberate between two choice alternatives with different values—a smaller monetary reward paid out immediately, or a larger reward, paid out later—the eyes initially move with the same vigor to both options. But as the process continues, vigor increases for the response alternative that is ultimately chosen. Immediately after the choice (button press) is made, vigor drops, with a steeper rate of decline in trials in which the decision was made fast. This temporal evolution of vigor—its rise as the observer identifies a preferred option and its drop after the choice has been made—provides a marker of decision timing (Reppert et al., 2015). Moreover, observers tended to make their last saccade before the button press to the alternative they chose later. The target of this last saccade reliably predicted the explicit choice in a given trial (for equivalent findings for targeting catch-up saccades during pursuit, see Fooker & Spring, 2019; **Fig. 3B**). Vigor also increases as a function of value difference between options and differentially scales with two aspects of economic utility—reward and effort: it increases with expected reward and decreases with anticipated effort (Shadmehr et al., 2019). It appears that human observers are able to keep accurate track of reward and effort over time. When observers were asked to look at images that differed in reward (manipulated via image content) and effort (eccentricity between images), reward and effort history across previous trials affected saccade velocity and fixation or harvest duration (as a measure of how much reward is being collected) in following trials. A history of rewarding images led to increased vigor and decreased harvest duration; less time spent at a given image means more images can be viewed

and more reward can be accumulated (Yoon et al., 2018). These findings show that saccade vigor reflects decision optimality (according to the marginal value theorem; Yoon et al., 2018), i.e., maximizing the rate of gain associated with reward and effort of a current action, given the rate of gain in recent history. Recent history of reward also modulates performance in antisaccade tasks. Saccades are more error-prone if antisaccade trials are preceded by trials in which the target was associated with a high (vs. no or low) reward (Preciado & Theeuwes, 2018). This reward-history driven selection bias or capture was mainly found for short-latency saccades, indicating that reward predominantly modulates automatic control mechanisms, possibly by interacting with stimulus salience and overriding voluntary control mechanisms.

The value associated with a choice is also predicted by the frequency of blinks. For example, blink rate correlates with the outcome of value-based choices after reinforcement learning (Slagter, Georgopoulou, & Frank, 2015) and predicts observers' strategies in assessing low-value vs. high-value alternatives. Van Slooten and colleagues (2018) asked observers to view pairs of colored squares that were each associated with a different reward probability. Observers had to learn to select the most rewarding option and received feedback about whether they earned a reward. In a subsequent transfer phase, observers viewed the same options in novel pair combinations and had to again choose the most rewarding option, but without receiving feedback. Lower blink rate predicted higher choice accuracy during the learning phase, but only when the difference in expected value between options was large. The same data set also revealed that pupil size fluctuations tracked choice behavior and value beliefs (Van Slooten et al., 2018). Prior to making a value-based choice, pupil dilation reflected the value of the to-be-selected option. After receiving feedback, pupil dilation reflected uncertainty about the value of the most recent choice options, and pupil constriction reflected reward prediction errors. In

addition to signifying the arousal associated with an expected reward, pupil dilation is also associated with riskier choices (Cherkasova et al., 2018). In summary, saccade metrics such as vigor, and parameters such as blink rate and pupil size, determined by activity in dopaminergic systems, signal reward processing during decision making. This link has important implications for our understanding of value-based decision making in diseases associated with dopamine dysfunction.

Insert sidebar here

3.5. Eye movements as markers of decision certainty and confidence

When sensory information is insufficient, unreliable, or inconclusive, decisions have to be made under uncertainty. Most decisions we make are accompanied by a feeling of confidence that the decision is accurate—internally estimated probability of a correct choice (often equal to the estimated probability of receiving a reward), given the evidence (Pouget, Drugowitsch, & Kepecs, 2016). Confidence can be overtly measured by soliciting a confidence rating at the end of a given trial, or covertly and analytically derived. For example, in a drift-diffusion model describing performance in a two-alternative sensory discrimination task, in which evidence is accumulated over time until it reaches a decision threshold or boundary, decision confidence could be defined as the distance between the decision signal and the decision threshold (Kepecs et al., 2008; Nienborg et al., 2018). Seideman and colleagues (2018) defined decision confidence statistically as the probability of a correct choice, given the available sensory evidence—which in the case of their task is equivalent to information processing time (more processing time means more evidence). They considered saccade peak velocity to reflect the degree of certainty with which a decision is made because peak velocity was associated with choice accuracy and

scaled as a function of processing time, meaning it increased with increasing evidence. The finding that saccade metrics not only reflect choice accuracy but also the statistical confidence in the choice implies that decision making and confidence might rely on the same underlying mechanisms.

Pupil diameter reveals nuanced and dynamic information about the decision time course and is linked to how beliefs about one's own decision change over time (Colizoli et al., 2018; Urai, Braun, & Donner, 2017). Throughout a decision process, the pupil is continuously dilated (de Gee, Knapen, & Donner, 2014). Several studies have investigated the relationship between pupil size and internal belief states about the decision, before and after feedback about the decision outcome has been received. For example, Colizoli and colleagues (2018) monitored pupil size while observers performed a motion direction discrimination task at different levels of task difficulty, resulting in different levels of uncertainty. Importantly, the authors introduced long and variable delays before and after response feedback to investigate the effect of reward anticipation and reward prediction error on pupil dilation. During both delay intervals, observers showed sustained pupil dilation. Larger increases in pupil size during the pre-feedback interval were associated with larger decision uncertainty (Urai et al., 2017). Larger pupil size changes during the post-feedback interval were observed in trials in which feedback indicated that the given response was incorrect, suggesting that pupil size scales with prediction error and the perceived violation of the internal belief state. Input signals to the pupil therefore continuously signal uncertainty about the upcoming decision (pre-feedback interval) and the comparison with feedback (post-feedback interval). Pupil dilation correlates with confidence in humans (Lempert, Chen, & Fleming, 2015) and monkeys (Kawaguchi et al., 2018). It also indexes the occurrence of surprising events (Preuschoff, 't Hart, & Einhäuser, 2011; Satterthwaite et al., 2007). A detailed

analysis of the time of peak of pupil dilation during a perceptual decision task can reveal the time course of information accumulation for perceptual and confidence judgments (Balsdon, Wyart, & Mamassian, 2020). This novel approach might allow researchers to link pupil dilation to information-seeking behavior as a function of confidence (see also Kawaguchi et al., 2018), thus revealing the time course of the interplay between current decision confidence and future evidence accumulation (for an example using manual tracking, see Locke, Mamassian, & Landy, 2020).

In sum, tracking pupil size during decision making not only scales with uncertainty and confidence, but might also reveal the dynamics of evidence accumulation and how information seeking is adjusted based on individual differences in metacognitive confidence or perceived uncertainty. This is especially important when considering demanding real-world tasks that commonly require a sequence of decisions, and in which confidence in the first decision might affect information accumulation in following decisions (Van den Berg et al., 2018), or in which evidence accumulation must be adapted to a changing environment (Murphy et al., 2021). The known link between pupil size and confidence might allow outcome predictions in multi-step complex decision sequences.

SUMMARY POINTS

1. Eye movement metrics add a continuous dimension to the discrete outcomes of decision tasks; they provide direct, real-time insight into the dynamics of deliberation processes, at a fine spatial and temporal scale (**Fig. 4**).

2. Saccade metrics in urgent choice tasks reveal the timing and duration of perceptual decisions, taking as little as 50 ms and made within 50-100 ms of when complete visual information about choice alternatives and task is available.
3. The dynamics of smooth pursuit and the frequency of saccades track the time course of decision formation, and the temporal expectation of future events.
4. Saccade endpoints, fixation duration and saccade exploration-exploitation patterns reflect scene and task complexity and signify working-memory efficiency in search-selection and decision tasks.
5. Choice preference is linked to fixation duration, and decision timing accuracy is linked to eye movement accuracy, indicating that eye movements not only reflect upcoming choices but might also contribute to them.
6. Saccade and pursuit latency and blink frequency reflect the efficiency with which a response can be inhibited, and saccade direction errors and pupil dilation reveal two separate inhibition mechanisms.
7. Saccade vigor scales with the expected reward and anticipated effort of a decision and tracks reward history, indicating that it reflects an optimal integration of reward and effort.
8. Saccade metrics and pupil dilation reflect decision confidence and internal belief states, linking eye movements not only to the process of making the decision, but also to its predicted outcome.

Figure 4 here

FUTURE ISSUES

1. **Clinical models:** Eye movement measures have mostly been applied to studying decision making in healthy, young adults. Given the impact of neurological and psychiatric disease on decision making, eye movements could be applied to pathological decision making with the ultimate aim of developing neurobiologically plausible models of dysfunction as well as bedside decision tests.
2. **Enhancement:** The functional link between eye movements and decision outcome is underexplored. Relations have been reported for pursuit, blinks, and fixation duration, but few studies have systematically manipulated eye movements' effects on the timing and accuracy of decisions.
3. **Technology:** Researchers should take advantage of the rapid advance of eye-tracking technology to investigate eye movements during real-world decision tasks, such as gambling. Eye movements could also be used to indicate social and interpersonal factors in multiplayer economic decision tasks.
4. **Dynamics:** The main focus in the eye movement and decision literature has been on saccades to stationary targets. Smooth pursuit has the added benefit of being sensitive to dynamic visual stimulation, allowing researcher to create decision tasks that reflect the natural, dynamic properties of our visual environment.

ACKNOWLEDGEMENTS

This work was supported by a Humboldt Foundation Fellowship for Experienced Researchers and a University of British Columbia Killam Research Fellowship. The author would like to

thank members of the Spering lab, Jolande Fooker, and Aenne Briemann for comments on manuscript drafts.

LITERATURE CITED

- Abeles, D., Amit, R., Tal-Perry, N., Carrasco, M., Yuval-Greenberg, S. (2020). Oculomotor inhibition precedes temporally expected auditory targets. *Nature Communications*, *11*(1):3524.
- Ang, J.W.A. & Maus, G.W. (2020). Boosted visual performance after eye blinks. *Journal of Vision*, *20*(10):2.
- Armel, K.C., Beaumel, A., & Rangel, A. (2008). Biasing simple choices by manipulating relative visual attention. *Judgment and Decision Making*, *3*, 396-403.
- Badde, S., Myers, C.F., Yuval-Greenberg, S., Carrasco, M. (2020). Oculomotor freezing reflects tactile temporal expectation and aids tactile perception. *Nature Communication*, *11*(1), 3341.
- Bahuguna, J., Aertsen, A., & Kumar, A. (2015). Existence and control of Go/No-Go decision transition threshold in the striatum. *PLoS Computational Biology*, *11*(4), e1004233.
- Balsdon, T., Wyart, V., & Mamassian, P. (2020). Confidence controls perceptual evidence accumulation. *Nature Communications*, *11*, 1753.
- Barbosa, P., Kaski, D., Castro, P., Lees, A.J., Warner, T.T., & Djamshidian, A. (2019). Saccadic direction errors are associated with impulsive compulsive behaviours in Parkinson's disease patients. *Journal of Parkinson's Disease*, *9*, 625-630.
- Bargary, G., Bosten, J.M., Goodbourn, P.T., Lawrance-Owen, A.J. Hogg, R.E., & Mollon, J.D. (2017). Individual differences in human eye movements: an oculomotor signature? *Vision Research*, *141*, 157-169.
- Basso, A.M. & May, J.P. (2019). Circuits for action and cognition: a view from the superior colliculus. *Annual Review of Vision Science*, *3*, 197-226.
- Bekkering, H., Adam, J.J., Kingma, H., Huson, A., Whiting, H.T.A. (1994). Reaction time latencies of eye and hand movements in single- and dual-task conditions. *Experimental Brain Research*, *97*, 471-476.
- Cavanagh, J.F., Wiecki, T.V., Kochar, A., & Frank, M.J. (2014). Eye tracking and pupillometry are indicators of dissociable latent decision processes. *Journal of Experimental Psychology: General*, *143*, 1476-1488.
- Cherkasova, M.V., Clark, L., Barton, J.J.S., Schulzer, M., Shafiee, M., Kingstone, A., Stoessl, A.J., & Winstanley, C.A. (2018). Win-concurrent sensory cues can promote riskier choice. *Journal of Neuroscience*, *38*, 10362-10370.
- Cherkasova, M.V., Corrow, J.S., Taylor, A., Yeung, S.C., Stubbs, J.L., McKeown, M.J., Appel-Cresswell, S., Stoessl, A.J., & Barton, J.J.S. (2019). Dopamine replacement remediates risk aversion in Parkinson's disease in a value-independent manner. *Parkinsonism and Related Disorders*, *66*, 189-194.
- Coe, B.C., & Munoz, D.P. (2017). Mechanisms of saccade suppression revealed in the anti-saccade task. *Philosophical Transactions of the Royal Society of London B*, *372*(1718), 20160192.

- Colizoli, O., De Gee, J.W., Urai, A.E., & Donner, T.H. (2018). Task-evoked pupil responses reflect internal belief states. *Scientific Reports*, 8, 1-13.
- Colzato, L.S., van den Wildenberg, W.P.M., van Wouwe, N.C., Pannebakker, M.M., & Hommel, B. (2009). Dopamine and inhibitory action control: evidence from spontaneous eye blink rates. *Experimental Brain Research*, 196, 467-474.
- de Gee, J.W., Knapen, T., & Donner, T.H. (2014). Decision-related pupil dilation reflects upcoming choice and individual bias. *Proceedings of the National Academy of Sciences USA*, 111, 618-625.
- Delgado-García, J.M., Gruart, A., & Trigo, J.A. (2003). Physiology of the eyelid motor system. *Annual Reviews of the New York Academy of Sciences*, 1004, 1-9.
- Ding, L., & Gold, J.I. (2010). Caudate encodes multiple computations for perceptual decisions. *Journal of Neuroscience*, 30, 15747-15759.
- Ding, L., & Gold, J.I. (2012). Neural correlates of perceptual decision making before, during, and after decision commitment in monkey frontal eye field. *Cerebral Cortex*, 22, 1052-1067.
- Ebitz, R.B., & Moore, T. (2019). Both a gauge and a filter: cognitive modulations of pupil size. *Frontiers Neurology*, 9, 1190.
- Eckstein, M.P. (2011). Visual search: a retrospective. *Journal of Vision*, 11(5):14.
- Eckstein, M.P., Lago, M.A., & Abbey, C.K. (2018). Evaluation of search strategies for microcalcifications and masses in 3D images. *Proceedings of the International Society of Optical Engineering*, 10577: 105770C.
- Fabre-Thorpe, M., Delorme, A., Marlot, C., & Thorpe, S.J. (2001). A limit to the speed of processing in ultra-rapid visual categorization of novel natural scenes. *Journal of Cognitive Neuroscience*, 13, 1-10.
- Fecteau, J.H., & Munoz, D.P. (2006). Saliency, relevance, and firing: a priority map for target selection. *Trends in Cognitive Science*, 10, 382-390.
- Fischer, B. (1986). Express saccades in man and monkey. *Progress in Brain Research*, 64, 155-160.
- Fooker, J., & Spering, M. (2019). Decoding go/no-go decisions from eye movements. *Journal of Vision*, 19(2): 5.
- Fooker, J., & Spering, M. (2020). Eye movements as a readout of sensorimotor decision processes. *Journal of Neurophysiology*, 123, 1439-1447.
- Fuchs, A.F., & Binder, M.D. (1983). Fatigue resistance of human extraocular muscles. *Journal of Neurophysiology*, 49, 28-34.
- Gellman, R.S., Carl, J.R., & Miles, F.A. (1990). Short-latency ocular following responses in man. *Visual Neuroscience*, 5, 107-200.
- Glimcher, P.W. (2001). Making choices: the neurophysiology of visual-saccadic decision making. *Trends in Neuroscience*, 24, 654-659.
- Godlove, D.C., & Schall, J.D. (2016). Microsaccade production during saccade cancellation in a stop-signal task. *Vision Research*, 118, 5-16.

- Godwin, H.J., Hout, M.C., Alexdóttir, K.J., Walenchok, S.C., & Barnhart, A.S. (2021). Avoiding potential pitfalls in visual search and eye-movement experiments: a tutorial review. *Attention, Perception, & Psychophysics*, epub ahead of print.
- Goettker, A., & Gegenfurtner, K.R. (2021). A change in perspective: The interaction of saccadic and pursuit eye movements in oculomotor control and perception. *Vision Research*, *188*, 283-296.
- Gold, J.I., & Shadlen, M.N. (2000). Representation of a perceptual decision in developing oculomotor commands. *Nature*, *406*, 390-394.
- Gold, J.I., & Shadlen, M.N. (2007). The neural basis of decision making. *Annual Review of Neuroscience*, *30*, 535-574.
- Gold, J.I., & Shadlen, M.N. (2010). Representation of a perceptual decision in developing oculomotor commands. *Nature*, *404*, 390-394.
- Gottlieb, J., & Oudeyer, P.-Y. (2018). Toward a neuroscience of active sampling and curiosity. *Nature Reviews Neuroscience*, *19*, 758-770.
- Groman, S.M., James, A.S., Seu, E., Tran, S., Clark, T.A., Harpster, S.N., Crawford, M., Burtner, J.L., Feiler, K., Roth, R.H., Elsworth, J.D., London, E.D., & Jentsch, J.D. (2014). In the blink of an eye: relating positive-feedback sensitivity to striatal dopamine D2-like receptors through blink rate. *Journal of Neuroscience*, *34*, 14443-14454.
- Gray, R., & Cañal-Bruland, R. (2018). Integrating visual trajectory and probabilistic information in baseball batting. *Psychology of Sport & Exercise*, *36*, 123-131.
- Hanes, D.P., & Carpenter, R.H.S. (1999). Countermanding saccades in humans. *Vision Research*, *39*, 2777-2791.
- Hanes, D.P., & Schall, J.D. (1995). Countermanding saccades in macaque. *Visual Neuroscience*, *12*, 929-937.
- Herman, J.P., Katz, L.N., & Krauzlis, R.J. (2018). Midbrain activity can explain perceptual decisions during an attention task. *Nature Neuroscience*, *21*, 1651-1655.
- Hoppe, D., Helfmann, S., & Rothkopf, C.A. (2018). Humans quickly learn to blink strategically in response to environmental task demands. *Proceedings of the National Academy of Sciences*, *115*, 2246-2251.
- Huk, A.C., Katz, L.N., & Yates, J.L. (2017). The role of the lateral intraparietal area in (the study of) decision making. *Annual Review of Neuroscience*, *40*, 349-372.
- Huk, A.C., & Shadlen, M.N. (2005). Neural activity in macaque parietal cortex reflects temporal integration of visual motion signals during perceptual decision making. *Journal of Neuroscience*, *25*, 10420-10436.
- Itti, L., & Koch, C. (2000). A saliency-based search mechanism for overt and covert shifts of visual attention. *Vision Research*, *40*, 1489-1506.
- Jarrett, C.B., & Barnes, G.R. (2003). The volitional inhibition of anticipatory ocular pursuit using a stop signal. *Cognitive Brain Research*, *17*, 759-769.
- Jongkees, B.J., & Colzato, L.S. (2016). Spontaneous eye blink rate as predictor of dopamine-related cognitive function - a review. *Neuroscience & Biobehavioral Reviews*, *71*, 58-82.

- Joo, S.J., Katz, L.N., & Huk, A.C. (2018). Decision-related perturbations of decision-irrelevant eye movements. *Proceedings of the National Academy of Sciences*, *113*, 1925-1930.
- Joshi, S., & Gold, J.I. (2020). Pupil size as a window on neural substrates of cognition. *Trends in Cognitive Science*, *24*, 466-480.
- Katz, L.N., Yates, J.L., Pillow, J.W., & Huk, A.C. (2016). Dissociated functional significance of decision-related activity in the primate dorsal stream. *Nature*, *535*, 285- 288.
- Kawaguchi, K., Clery, S., Pourriahi, P., Seillier, L., Haefner, R.M., & Nienborg, H. (2018). Differentiating between models of perceptual decision making using pupil size inferred confidence. *Journal of Neuroscience*, *38*, 8874-8888.
- Kepecs, A., Uchida, N., Zariwala, H.A., & Mainen, Z.F. (2008). Neural correlates, computation and behavioural impact of decision confidence. *Nature*, *455*, 227-231.
- Kennerley, S.W., & Walton, M.E. (2011). Decision making and reward in frontal cortex: complementary evidence from neurophysiological and neuropsychological studies. *Behavioral Neuroscience*, *125*, 297-317.
- Kim, Y.-G., Badler, J.B., & Heinen, S.J. (2005). Trajectory interpretation by supplementary eye field neurons during ocular baseball. *Journal of Neurophysiology*, *94*, 1385-1391.
- Kimmel, D.L., & Moore, T. (2007). Temporal patterning of saccadic eye movements signals. *Journal of Neuroscience*, *27*, 7619-7630.
- Kirchner, H., & Thorpe, S.J. (1996). Ultra-rapid object detection with saccadic eye movements: visual processing speed revisited. *Vision Research*, *46*, 1762-1776.
- Klein, R.M., & MacInnes, W.J. (1999). Inhibition of return is a foraging facilitator in visual search. *Psychological Sciences*, *10*, 346-352.
- Kornylo, K., Dill, N., Saenz, M., & Krauzlis, R.J. (2003). Cancelling of pursuit and saccadic eye movements in humans and monkeys. *Journal of Neurophysiology*, *89*, 2984-2999.
- Krajbich, I., Armel, C., & Rangel, A. (2010). Visual fixations and the computation and comparison of value in simple choice. *Nature Neuroscience*, *13*, 1292-1298.
- Krauzlis, R.J. (2005). The control of voluntary eye movements: new perspectives. *Neuroscientist*, *11*, 124-137.
- Krauzlis, R.J., & Miles, F.A. (1996). Release of fixation for pursuit and saccades in humans: evidence for shared inputs acting on different neural substrates. *Journal of Neurophysiology*, *76*, 2822-2833.
- Krupinski, E.A. (2010). Current perspectives in medical image perception. *Attention, Perception, & Psychophysics*, *72*, 1205-1217.
- Lehmann, S.J., & Corneil, B.D. (2016). Transient pupil dilation after subsaccadic microstimulation of primate frontal eye fields. *Journal of Neuroscience*, *36*, 3765-3776.
- Lempert, K.M., Chen, Y.L., & Fleming, S.M. (2015). Relating pupil dilation and metacognitive confidence during auditory decision-making. *PLoS One*, *10*(5), e0126588.
- Leigh, R.J., & Zee, D.S. (2015). *The neurology of eye movements*. Oxford, UK: Oxford University Press.

- Levi, A.J., & Huk, A.C. (2020). Interpreting temporal dynamics during sensory decision-making. *Current Opinions in Physiology*, *16*, 27-32.
- Li, Z.-W. & Ma, W.J. (2021). An uncertainty-based model of the effects of fixation on choice. *PLoS Computational Biology*, *17*(8), e1009190.
- Lisberger, S.G. (2015). Visual guidance of smooth pursuit eye movements. *Annual Review of Vision Science*, *1*, 447-468.
- Locke, S.M., Mamassian, P., & Landy, M.S. (2020). Performance monitoring for sensorimotor confidence: a visuomotor tracking study. *Cognition*, *205*, 104396.
- Logan, G.D. (1994). On the ability to inhibit thought and action: a users' guide to the stop signal paradigm. In D. Dagenbach, & T.H. Carr (Eds.), *Inhibitory processes in attention, memory and language* (pp. 189-239). San Diego, CA: Academic Press.
- McCoy, B. & Theeuwes, J. (2016). Effects of reward on oculomotor control. *Journal of Neurophysiology*, *116*, 2453-2466.
- McSorley, E., & McCloy, R. (2009). Saccadic eye movements as an index of perceptual decision-making. *Experimental Brain Research*, *198*, 513-520.
- Meeter, M., Van der Stigchel, S., & Theeuwes, J. (2010). A competitive integration model of exogenous and endogenous eye movements. *Biological Cybernetics*, *102*, 271-291.
- Mirpour, K., & Bisley, J.W. (2021). The roles of the lateral intraparietal area and frontal eye field in guiding eye movements in free viewing search behavior. *Journal of Neurophysiology*, *125*, 2144-2157.
- Mirpour, K., Bolandnazar, Z., & Bisley, J.W. (2019). Neurons in FEF keep track of items that have been previously fixated in free viewing visual search. *Journal of Neuroscience*, *39*, 2114-2124.
- Missal, M., & Heinen, S.J. (2017). Stopping smooth pursuit. *Philosophical Transactions of the Royal Society B*, *372*, 20160200.
- Munoz, D.P., & Coe, B.C. (2011). Saccade, search and orient – the neural control of saccadic eye movements. *European Journal of Neuroscience*, *33*, 1945-1947.
- Munoz, D.P., & Everling, S. (2004). Look away: the anti-saccade task and the voluntary control of eye movement. *Nature Reviews Neuroscience*, *5*, 218-228.
- Murphy, P.E., Wilming, N., Hernandez-Bocanegra, D.C., Prat-Ortega, G., & Donner, T.H. (2021). Adaptive circuit dynamics across human cortex during evidence accumulation in changing environments. *Nature Neuroscience*, *24*, 987-997.
- Najafi, F., & Churchland, A.K. (2018). Perceptual decision-making: a field in the midst of a transformation. *Neuron*, *100*, 453-462.
- Newsome, W.T., Britten, K.H., & Movshon, J.A. (1989). Neuronal correlates of a perceptual decision. *Nature*, *341*, 52-54.
- Nienborg, H., & Cumming, B.G. (2009). Decision related activity in sensory neurons reflects more than a neuron's causal effect. *Nature*, *459*, 89-92.
- Nowell-Smith, P.H. (1958). Choosing, deciding, and doing. *Analysis*, *18*, 63-69.

- Olmos-Solis, K., van Loon, A.M., Los, S.A., & Olivers, C.N.L. (2017). Oculomotor measures reveal the temporal dynamics of preparing for search. *Progress in Brain Research*, 236, 1-12.
- Orban de Xivry, J.J., & Lefèvre, P. (2007). Saccades and pursuit: two outcomes of a single sensorimotor process. *Journal of Physiology*, 584, 11-23.
- Padoa-Schioppa, C. & Conen, K.E. (2017). Orbitofrontal cortex: a neural circuit for economic decisions. *Neuron*, 96, 736-754.
- Pärnamets, P., Johansson, P., Hall, L., Balkenius, C., Spivey, M.J., & Richardson, D.C. (2015). Biasing moral decisions by exploiting the dynamics of eye gaze. *Proceedings of the National Academy of Sciences, USA*, 112, 4170-4175.
- Platt, M.L., & Glimcher, P.W. (1999). Neural correlates of decision variables in parietal cortex. *Nature*, 400, 233-238.
- Pouget, A., Drugowitsch, J., & Kepecs, A. (2016). Confidence and certainty: distinct probabilistic quantities for different goals. *Nature Neuroscience*, 19, 366-374.
- Preciado, D., & Theeuwes, J. (2018). To look or not to look? Reward, selection history, and oculomotor guidance. *Journal of Neurophysiology*, 120, 1740-1752.
- Preuschoff, K., 't Hart, B.M., & Einhäuser, W. (2011). Pupil dilation signals surprise: evidence for noradrenaline's role in decision making. *Frontiers in Neuroscience* 5, 1-12.
- Ratcliff, R., & McKoon, G. (2008). The diffusion decision model: theory and data for two-choice decision tasks. *Neural Computing*, 20, 873-922.
- Reppert, T.R., Lempert, K.M., Glimcher, P.W., & Shadmehr, R. (2015). Modulation of saccade vigor during value-based decision making. *Journal of Neuroscience*, 35, 15369-15378.
- Rolfs, M. (2009). Microsaccades: small steps on a long way. *Vision Research*, 49, 2415-2441.
- Salinas, E., Steinberg, B.R., Sussman, L.A., Fry, S.M., Hauser, C.K., Anderson, D.D., Stanford, T.R., (2019). Voluntary and involuntary contributions to perceptually guided saccadic choices resolved with millisecond precision. *Elife*, 8, e46359.
- Satterthwaite, T.D., Green, L., Myerson, J., Parker, J., Ramaratnam, M., & Buckner, R.L. (2007). Dissociable but inter-related systems of cognitive control and reward during decision making: evidence from pupillometry and event-related fMRI. *NeuroImage*, 37, 1017-1031.
- Sauter, M., Hanning, N.M., Liesefeld, H.R., & Müller, H.J. (2021). Post-capture processes contribute to statistical learning of distractor locations in visual search. *Cortex*, 135, 108-126.
- Schall, J.D. (2001). Neural basis of deciding, choosing and acting. *Nature Reviews Neuroscience*, 2, 33-42.
- Schall, J.D. (2005). Decision making. *Current Biology*, 15, R9-R11.
- Schall, J.D. (2013). Macrocircuits: decision networks. *Current Opinion in Neurobiology*, 23, 269-274.
- Schall, J.D. (2015). Visuomotor functions in the frontal lobe. *Annual Review of Vision Science*, 1, 469-498.
- Schall, J.D., & Hanes, D.P. (1993). Neural basis of saccade target selection in frontal eye field during visual search. *Nature*, 366, 467-469.

- Schall, J.D., Hanes, D.P., & Taylor, T.L. (2000). Neural control of behavior: countermanding eye movements. *Psychological Research*, *63*, 299-307.
- Seideman, J.A., Stanford, T.R., & Salinas, E. (2018). Saccade metrics reflect decision-making dynamics during urgent choices. *Nature Communications*, *9*(1), 2907.
- Shaffer, B., Jobe, F.W., Pink, M., & Perry, J. (1993). Baseball batting: an electromyographic study. *Clinical Orthopaedics and Related Research*, *292*, 285-293.
- Shadlen, M.N., & Kiani, R. (2013). Decision making as a window on cognition. *Neuron*, *80*, 791-806.
- Shadmehr, R., Reppert, T.R., Summerside, E.M., Yoon, T., & Ahmed, A.A. (2019). Movement vigor as a reflection of subjective economic utility. *Trends in Neuroscience*, *42*, 323-336.
- Sharp, M.E., Viswanathan, J., Lanyon, L.J., & Barton, J.J.S. (2012). Sensitivity and bias in decision-making under risk: evaluating the perception of reward, its probability and value. *PLoS ONE*, *7*(4), e33460.
- Shimojo, S., Simion, C., Shimojo, E., & Scheier, C. (2003). Gaze bias both reflects and influences preference. *Nature Neuroscience*, *6*, 1317-1322.
- Simioni, A.C., Dagher, A., Fellows, L.K. (2012). Dissecting the effects of disease and treatment on impulsivity in Parkinson's disease. *Journal of the International Neuropsychological Society*, *18*, 942-951.
- Slagter, H.A., Georgopoulou, K., & Frank, M.J. (2015). Spontaneous eye blink rate predicts learning from negative, but not positive, outcomes. *Neuropsychologia*, *71*, 126-132.
- Stanford, T.R., Freedman, E.G., & Sparks, D.L. (1996). Site and parameters of microstimulation: evidence for independent effects on the properties of saccades evoked from the primate superior colliculus. *Journal of Neurophysiology*, *76*, 3360-3381.
- Stanford, T.R., Shankar, S., Massoglia, D.P., Costello, M.G., & Salinas, E. (2010). Perceptual decision making in less than 30 milliseconds. *Nature Neuroscience*, *13*, 379-385.
- Sternberg, S. (1969). The discovery of processing stages: Extensions of Donders' method. In W.G. Koster (Ed.), *Attention and performance II* (pp. 276-315). Amsterdam: North-Holland.
- Theeuwes, J. (2004). Top-down search strategies cannot override attentional capture. *Psychonomic Bulletin & Review*, *11*, 65-70
- Thomas, A.W., Molter, F., & Krajbich, I. (2021). Uncovering the computational mechanisms underlying many-alternative choice. *Elife*, *10*, e57012.
- Thomas, A.W., Molter, F., Krajbich, I., Heekeren, H.R., & Mohr, P.N.C. (2019). Gaze bias differences capture individual choice behaviour. *Nature Human Behavior*, *3*, 625-635.
- Thura, D., Cos, I., Trung, J., & Cisek, P. (2014) Context-dependent urgency influences speed-accuracy trade-offs in decision-making and movement execution. *Journal of Neuroscience*, *34*, 16442-16454.
- Toole, A.J., & Fogt, N. (2021). Review: head and eye movements and gaze tracking in baseball batting. *Optometry & Vision Science*, *98*, 750-758.

- Towal, R.B., Mormann, M., & Koch, C. (2013). Simultaneous modeling of visual saliency and value computation improves predictions of economic choice. *Proceedings of the National Academy of Science*, *110*, 3858-3867.
- Urai, A.E., Braun, A., & Donner, T.H. (2017). Pupil-linked arousal is driven by decision uncertainty and alters serial choice bias. *Nature Communications*, *8*, 14637.
- Vaidya, A.R., & Fellows, L.K. (2020). Under construction: ventral and lateral frontal lobe contributions to value-based decision-making and learning. *F1000 Research (F1000 Faculty Review)*, *9*, 158.
- Van den Berg, R., Zylberberg, A., Kiani, R., Shadlen, M.N., & Wolpert, D.M. (2018). Confidence is the bridge between multi-stage decisions. *Current Biology*, *26*, 3157-3168.
- Van Slooten, J.C., Jahfari, S., & Theeuwes, J. (2019). Spontaneous eye blink rate predicts individual differences in exploration and exploitation during reinforcement learning. *Scientific Reports*, *9*, 17436.
- Van Slooten, J.C., Jahfari, S., Knapen, T., & Theeuwes, J. (2018). How pupil responses track value-based decision-making during and after reinforcement learning. *PLoS Computational Biology*, *14*(11), e1006632.
- Von Mises, L. (1998). *Human action. A treatise on economics*. Ludwig von Mises Institute, Auburn, AL.
- Waldthaler, J., Stock, L., Student, J., Sommerkorn, J., Dowiasch, S., & Timmermann, L. (2021). Antisaccades in Parkinson's disease: a meta-analysis. *Neuropsychological Reviews* online ahead of print, doi: 10.1007/s11065-021-09489-1.
- Wang, C.A., Brien, D.C., & Munoz, D.P. (2015). Pupil size reveals preparatory processes in the generation of pro-saccades and anti-saccades. *European Journal of Neuroscience*, *41*, 1102-1110.
- Wascher, E., Heppner, H., Möckel, T., Kobald, S.O., Getzmann, S. (2015). Eye-blinks in choice response tasks uncover hidden aspects of information processing. *Journal of Experimental and Clinical Sciences*, *14*, 1207-1218.
- Watanabe, M., & Munoz, D.P. (2009). Neural correlates of conflict resolution between automatic and volitional actions by basal ganglia. *European Journal of Neuroscience*, *30*, 2165-2176.
- Wu, C.-C., & Wolfe, J.M. (2019). Eye movements in medical image perception: a selective review of past, present and future. *Vision*, *3*(32).
- Yates, J.L., Park, I.M., Katz, L.N., Pillow, J.W., & Huk, A.C. (2017). Functional dissection of signal and noise in MT and LIP during decision making. *Nature Neuroscience*, *20*, 1285-1292.
- Yoon, T., Geary, R.B., Ahmed, A.A., & Shadmehr, R. (2018). Control of movement vigor and decision making during foraging. *Proceedings of the National Academy of Sciences*, *115*, 10476-10485.
- Zhang, M., Xiao, W., Rose, O., Bendtz, K., Livingstone, M., Ponce, C., & Kreiman, G. (2021). Look twice: a computational model of return fixations across tasks and species. *arXiv*, 2101.01611.

FIGURES

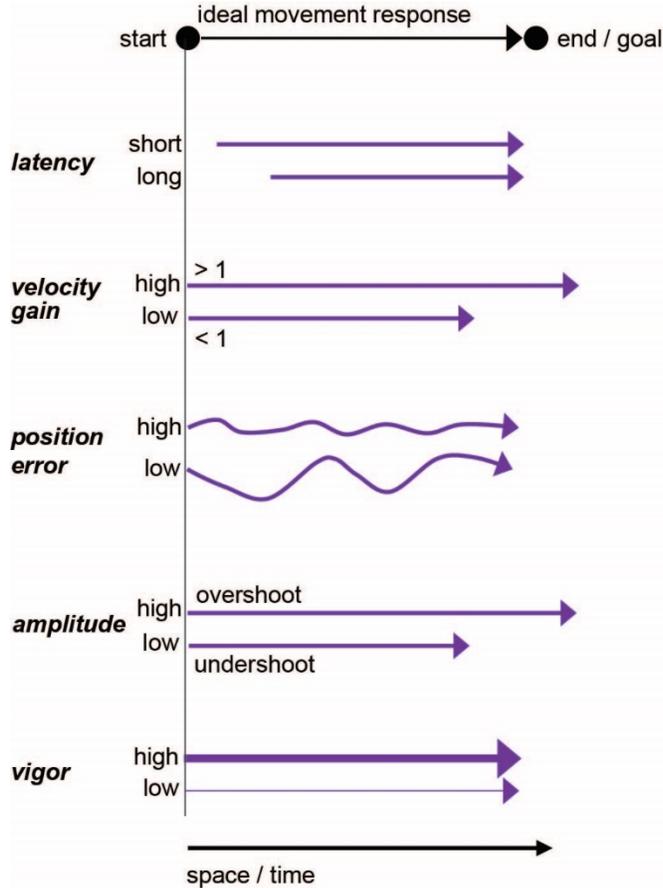


Figure 1. Selected eye movement metrics as a function of space or time, shown relative to an idealized movement between a start time / position and an end time / position. The **latency** of a movement describes the time interval between stimulus onset at start and movement onset. The **velocity gain** of a pursuit movement describes the magnitude of the movement, and how well the velocity of the eye matches the velocity of the target (sometimes also described as velocity error). The **position error** is the spatial accuracy and equivalent to gain; it describes how well eye position matches target position. This measure can be described for pursuit or saccades (and microsaccades); for saccades it is more commonly described as the **amplitude**, which can either fall short of the target and undershoot (hypometric saccade) or overshoot (hypermetric saccade). Movement **vigor** is the time it takes for the movement relative to its amplitude; it describes the strength, effort or energy expenditure of a movement.

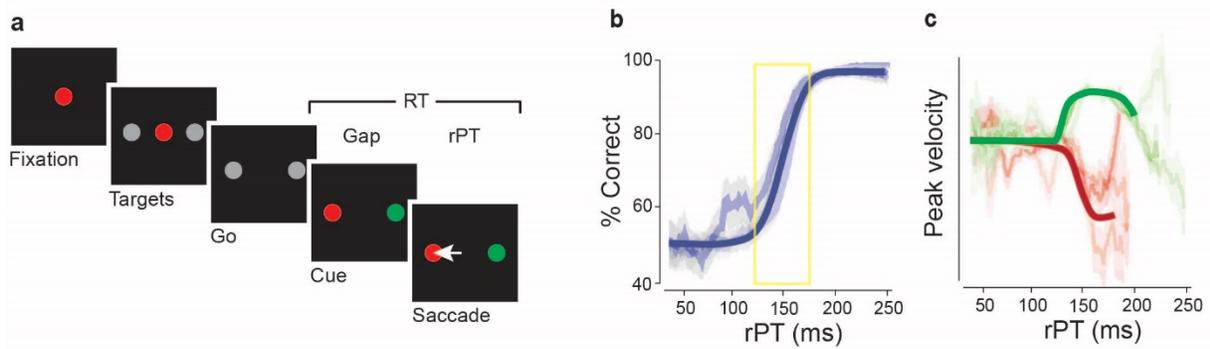


Figure 2. The urgent saccadic choice task (Stanford et al., 2010). **(a)** Time sequence of events in a rapid color discrimination task, in which the target’s color matches the fixation spot. The presentation of potential target locations is followed by the offset of fixation (go signal), compelling a response. Color cues are withheld for a variable amount of time (gap), determining task difficulty. Choices are indicated by a saccade. **(b)** Cartoon tachometric curve (bold blue) plotted as a function of raw processing time, with three original data sets (faint blue) adapted from Seidman and colleagues (2018). The yellow box marks the rise time of the tachometric curve, as responses transition from choices (50% correct) to correct estimates (saturation of the tachometric curve), reflecting the time course of the perceptual decision. **(c)** Cartoon eye velocity as a function of raw processing time in trials with correct (bold green) and incorrect (bold red) choices. Each point on the velocity curve represents average peak velocity for many saccades as a function of rPT. Faint colored data profiles are original data from three monkeys (adapted from Seidman et al., 2018). Original data have been scaled to correct for magnitude differences in individual eye velocity, and aligned to the velocity peak for clarity.

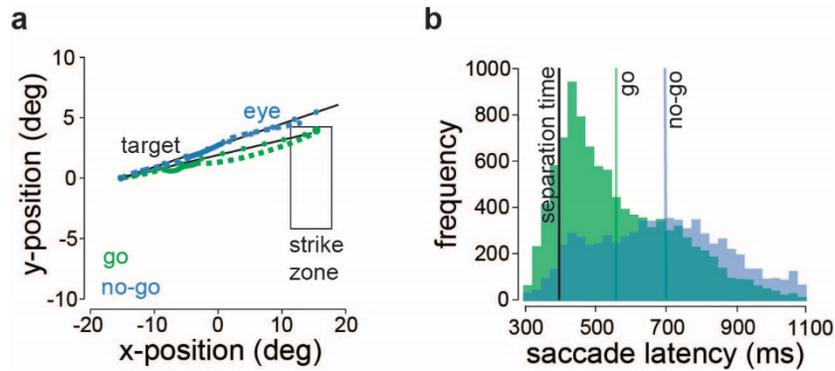


Figure 3. The rapid go/no-go interception task (Fookien & Spering, 2019). **(a)** Observers tracked a ball moving toward a strike zone with their eyes. The ball was initially visible and then disappeared from view so that its trajectory had to be extrapolated in order to estimate a hit (manual intercept) or miss (withhold interception). Feedback indicated the ball’s true position and interception location. Eye and hand movements were recorded. Green single trace from a representative correct “go” trial, blue trace from a correct “no-go” trial. Intervals between dots on target trajectories (straight lines) indicate 100-ms intervals; here, ball was visible for 200 ms. Solid traces are pursuit, dotted traces denote saccades. **(b)** Frequency of targeting saccades (last saccade made before interception) as a function of time bin relative to target onset ($n=45$; adapted from Fookien & Spering, 2019). Vertical black line denotes the separation time as the mean time point at which frequency distributions for go and no-go trials started to differ significantly.

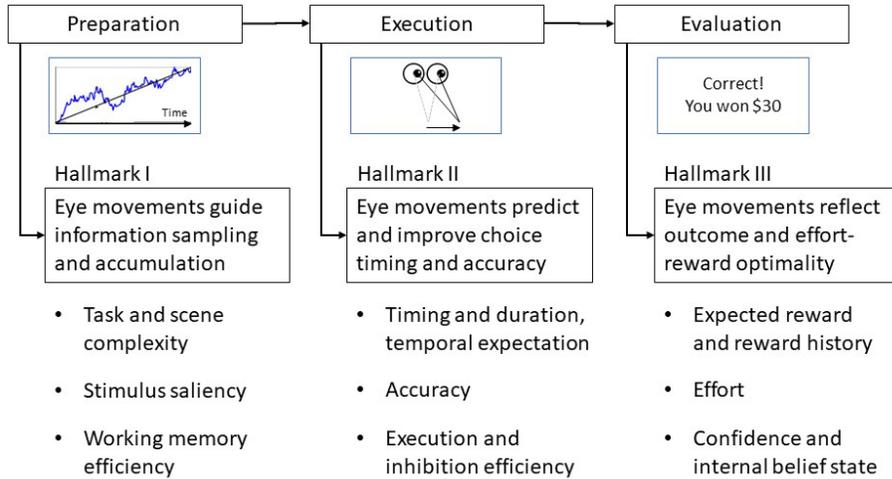


Figure 4. Decision-making framework and hallmark features reflected by eye movement metrics. In the preparation phase, eye movement responses during information sampling and accumulation reflect properties of the task, stimulus, and scene, and how efficiently information is stored and retrieved from working memory. During and just before response execution, eye movement responses predictively scale with the timing and accuracy of the upcoming choice; they also reflect processes of response inhibition. After a decision has been made, eye movements scale with the value of a decision and the subjective feeling of confidence; they also reflect the optimal integration of effort and reward.

SIDEBAR: Decision processes in Parkinson's disease

Dopamine function—critically associated with decision competence and impaired in conditions such as Parkinson's disease (PD)—is also involved in impulsivity, a psychological construct affecting how we evaluate risk and time (Simioni, Dagher, & Fellows, 2012). Eye movement studies reveal deficits in both aspects of impulsivity in PD. When trading off two choices with different reward magnitudes and probabilities in a simulated lottery task developed by Sharp and colleagues (2012), unmedicated PD patients are risk-averse for gains—an effect that was normalized by medication (Cherkasova et al., 2019). The same patients were also more driven by expected value or reward regardless of medication state. Eye movement measures (e.g., fixation duration) can quantify the relative use of reward and probability information (Cherkasova et al., 2018). Assessing eye movements in a time-critical go/no-go interception task (**Fig. 3A**), Fooker and colleagues (2021) found relatively preserved decision competence in PD patients, but only as long as they did not rush their decision (indicated by targeting saccade timing, **Fig. 3B**). Together these findings support the notion that abnormal impulsivity in PD is related to abnormal risk-taking behavior as well as a tendency to make more errors when a decision is rushed. Eye movement indicators of decision can therefore inform neurobiological models of PD.

TERMS AND DEFINITIONS (roughly in order of occurrence in the text)

Choice: selection of an option, often through a motor action, when faced with two or more alternatives

Decision: cognitive process of comparing and deliberating alternatives before a choice can be made.

Perceptual decision: based on weighing sensory evidence

Value-based decision: based on weighing reward expectations

Saccade: quick (high-velocity and short-duration) eye movement toward an object or location of interest

Microsaccade: small-amplitude saccade made during fixation

Fixation: period between saccades when the eyes are relatively focused on an object or location

Smooth pursuit: continuous tracking response to moving objects of interest during which smooth periods are interspersed with catch-up saccades

Latency: time period between the onset of a target, cue or go signal and the start of a movement

Vigor: saccade peak eye velocity (sometimes also: saccade latency plus movement time) normalized by saccade amplitude

Spontaneous eye blink rate: frequency of eye blinks per time unit

Superior colliculus (SC): layered midbrain structure receiving direct retinal input and contributing to orienting movements and preceding cognitive processes, attention and decision making

Frontal eye field (FEF): visual and oculomotor area in prefrontal cortex contributing to visual processing, target selection, and generation of eye movements

Lateral intraparietal cortex (LIP): visual and motor area in parietal cortex involved in eye movement control and selection processes, attention and decision making

Oculomotor capture: likelihood with which the first saccade toward a search display is made to a distractor, and not the target

Salience: subjective perceptual property of an object or stimulus (relative to its context) that attracts an observer's attention and orienting response

Receptive field: area of sensory space (here: visual) that can elicit neuronal responses when stimulated

Antisaccade: instructed saccade away from a cued or salient target, usually to a target 180° opposed

Confidence: metacognitive ability to internally estimate the probability of a correct choice, given the evidence

Parkinson's disease (PD): neurodegenerative disease primarily affecting the motor system, with cardinal symptoms tremor, bradykinesia, and postural instability, and sensory and cognitive abilities