

From Vision to Decision: The Role of Visual Attention in Elite Sports Performance

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Abstract: Elite sports performance fundamentally relies on a complex set of brain functions engaged once visual signals are relayed from the eye. In this review, we overview a series of these neural mechanisms—focusing specifically on the critical role of attention in sculpting the visual processing that takes place leading up to a decision. These brain functions are introduced within the theoretical concept of the ‘Perception–Action Cycle.’ Vision does not stop at the eye but requires a coordinated set of brain mechanisms called on to convert visual input into rapid decisions about action.

Key Words: Sports neuroscience—Attention—Top-down control.

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The Perception–Action Cycle

At the apex of on-field athletic performance, and flexible human behavior more generally, is a coordinated set of cortical and subcortical brain networks that bridge the gap between perception and action. Although the brain has long been recognized as the “executive controller” of behavior, it is only in the past half century that a multidisciplinary research effort has begun to crack open the mysteries of this ‘black box’ to uncover its inner workings. The explosion of empirical data emerging from functional neuroimaging (e.g., functional magnetic resonance imaging) and other new research technologies has laid the empirical groundwork detailing how the brain solves the range of problems it confronts during the ‘perception–action cycle.’

The perception–action cycle^{1,2} is a theoretical construct encompassing the multilevel chain of neural operations that are required to effectively guide action based on one’s multimodal sensory experiences. In the visual domain, this cycle is embodied in the form of *visuomotor integration*³—a more specific term referring to the computations within multiple levels of the visual system that provide real-time sensory updates to action-planning and action-execution regions in the parietal and frontal lobes. Whether the goal of action is to successfully operate a moving car on a highway or successfully execute a screen pass in the face of a pass rush, a hierarchical set of distributed cortical systems is rapidly called on

to render a coherent representation of the realtime visual environment needed to guide decisions about action.

Elite athletes face intense visuomotor demands requiring millisecond-level decision making to convert vision into action. In fact, elite athletics falls into a small class of human behaviors in which the perception–action cycle is required to function under intense temporal demands but with an incredibly high level of decision-making accuracy and action execution. The goal of this review is to highlight some of the neural machinery that allows athletes to successfully manage these intense demands by rapidly incorporating expert knowledge and past experiences into low-level visual processing. By flipping the perception–action cycle on its head, the brain is able to use representations of ‘action goals’ to directly modify incoming visual input in favor of those stimuli that are most relevant for behavior.

At the top of this neural architecture are neural assemblies in the prefrontal cortex (PFC) and posterior parietal cortex (PPC) that orchestrate this control by means of extensive reciprocal connections with multiple levels of the visual system. Rather than being a passive processor of incoming visual signals, the brain is a dynamic and predictive organ that buys critical milliseconds by increasing the efficiency and fidelity of visual processing in a proactive, as opposed to reflexive, manner.⁴ This boost in efficiency contributes to a wide range of on-field situations, and throughout the course of this review, we highlight what happens to visual signals after they enter the brain and, more specifically, how visual attention plays a direct role in sports by impacting the amplitude and speed of visual signals in the brain.

FUNDAMENTAL THEMES: THE BRAIN AND HAND–EYE COORDINATION

If the conceptual framework of the perception–action cycle strikes a familiar chord within the field of sports vision, it is because popular terms describing skills within this class of brain operations use common conjunctions of a perceptual input mechanism (e.g., eye) with an action output effector (e.g., hand). As the names suggest, hand–eye and foot–eye skills within sports fundamentally rely on a range of visuomotor integration functions forming the link between visual input and biomechanical output. Although the brain has long been recognized as part of the equation driving elite athletic performance, empirical evidence delineating the specific neural substrates of on-field performance remains limited and the evidence out there has a disproportionate focus on motor control and action-related components (for a recent review, see Yarrow et al.⁵). One primary reason for this challenge is methodologic. Within the confines of a laboratory setting and with the use of neuroscientific technologies (e.g., fMRI, electroencephalography),

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it is exceedingly difficult to simulate the real-world demands athletes face on the field. Despite this, the neuroscience of sports is informed by an extensive multidisciplinary research tradition into the neural basis of visuomotor skills. The goal of this review, then, is to focus on the role of visual attention in the perception–action cycle by drawing on the large neuroscience literature investigating visual attention in general while supplying sports-specific evidence when appropriate to bridge the gap between the laboratory and athletic skill.

Two On-Field Scenarios and Major Themes

To anchor these discussions, we will highlight two common on-field sports scenarios that we use as examples throughout to demonstrate different principles of visual attention and visuomotor integration at play during gametime situations:

Scenario A

A baseball hitter deciding to swing or not to swing at a pitch in the ~150 to 225 millisecond time window after the release of the pitch (see Fig. 1).

Scenario B

A football quarterback (QB) dropping back and making multiple decisions (e.g., if, where, and when to pass the football) in the presence of a defensive pass rush.

These two scenarios represent both the common and divergent challenges placed on each athlete’s visuomotor abilities across a range of sports. In both of these examples, athletes are forced to rapidly identify and recognize task-relevant information in their environment to make a range of decisions about action execution (e.g., if, when, and how to act). Before discussing the role of visual attention in these scenarios, however, here are a few key overarching principles about the neural properties underlying these abilities:

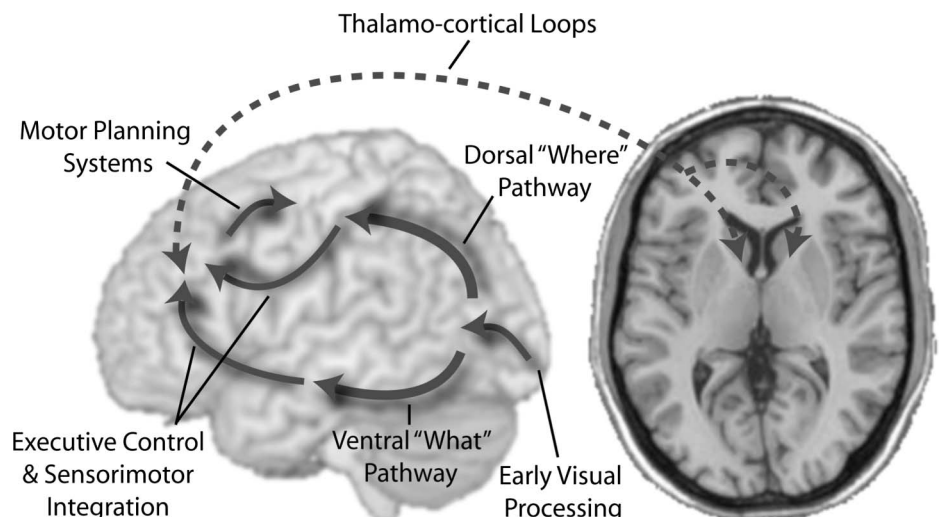
Hand–eye coordination is not a unitary concept or skill but rather a chain of critical visuomotor functions engaged in a coordinated manner during performance: Often in sports vision and sports training, hand–eye coordination is often treated as

a unitary concept to refer to the function of the brain intervening between the eye and movement. The different challenges faced by the hitter and QB in their respective on-field situations, however, suggest that particular on-field skills evoke different flavors or subcomponents of hand–eye coordination. Although a hitter must direct focus to the release point and rapidly synthesize information about speed, rotation, and direction to identify a pitch, a QB must rapidly conduct a visual search across receiver options in space to evaluate the best target for his throw. Both these require a rapid synthesis of visual information in time and space but suggest that rather than one distinct function, hand–eye coordination is a collection of operations in the brain that are differentially called on depending on the particular demands of the on-field context.

The brain regions forming the link between vision and action are hierarchical in nature with increasingly complex response properties: The networks that intervene to guide hand–eye coordination are organized in a synaptic hierarchy that proceeds through multiple cortical levels with increasing representational capacities.⁶ At the base of this hierarchy are ‘low-level’ unimodal sensory cortices that are specialized to extract particular components of the visual scene. These neural assemblies are engaged automatically in a feedforward manner and signals emanating from these unimodal (i.e., one sensory modality) visual regions converge into higher areas of unimodal association cortices integrating basic attributes features into representations of objects. At the peak of the hierarchy are heteromodal (i.e., multisensory modality) control regions in the PFC and PPC that form the direct link between vision and action.

Specific hand–eye coordination functions do not map to specific brain areas but rather each function requires a coordinated interaction of reciprocally connected neural networks: Although the functional architecture of the neocortex is organized based on a specialization of functions to particular subdivisions, the execution of even simple behaviors requires the distributed interactions of these areas across networks. This is true for all brain functions falling within the perception–action cycle. One intrinsic feature of these networks is that their dynamics are reciprocal. As a result, network interactions within the hierarchical

FIG. 1. The neural substrates of the perception–action cycle involve a hierarchic set of brain areas concerned with different components of visual processing, attention, and control/selection of appropriate responses. This figure shows a general landscape of these functions including a schematic of the ventral and dorsal “what” and “where” attention systems.



structure of the visual system are bidirectional so that there are mutual influences: both feedforward (bottom-up) and feedback (top-down) interactions.

THE FUNCTIONAL ARCHITECTURE OF THE VISUAL SYSTEM: THE CONVERGENCE OF BOTTOM-UP AND TOP-DOWN SIGNALS

Bottom-Up Processing: From Elements to Units

To successfully execute visually guided movement, it is critical to have a representational architecture that renders a sufficient internal model of the external visual world (for an overview of these brain systems, see Fig. 2). The neural chain by which the visual word is broken down into meaningful units begins when the first volley of evoked visual signals reach the athlete's primary visual cortex (layer 4 of area V1) after relay through the lateral geniculate nucleus (LGN) of the thalamus. V1 neurons begin to spike 30 to 40 millisecond after transduction of the neural impulses from the retina⁷ and begin to extract rapid information about the orientation of elemental units making up the visual scene. Importantly, at this foundational level of the visual system, each neuron's response is restricted to focal receptive fields and positioned retinotopically across the striate cortex to preserve exquisite spatial information. Alternating ocular dominance columns are found in V1 and refer to cells with the same eye preference being grouped together. Information from each eye, then, converges at the primary visual cortex (V1) to form one unitary representation.

The onset of physiological signals suggests that these signals then move in a parallel manner to higher and higher levels of the visual hierarchy. From V1, there is a rapid flow of feedforward signals to a set of visual regions (e.g., V2, prestriate cortex) that are selective for basic features in the environment. Distributed neural assemblies have been shown—through recordings of single neurons—to have specific response properties to different fundamental stimulus attributes. For example, color (area V4,⁸) and motion (area MT,⁹) are preferentially processed with distinct neural scattered across subregions of the extrastriate cortex. For any given neuron, there is the property of neural tuning which refers to the fact that each neuron may respond most strongly to only a subset of stimuli that are within its receptive field. At the early visual areas (V1), these neuron preferences are simple (e.g., neurons respond to any vertical stimulus) and become more complex as you move further up the visual hierarchy. At higher levels in the visual chain, certain neurons may be tuned to fire only to specific stimuli (discussed below).

After basic feature extraction, visual signals diverge into two general visual streams sending signals to higher levels of the visual hierarchy: one ventral "what" pathway involved in object identification,^{10,11} and one dorsal "where" pathway involved in spatial processing.¹² The dorsal pathway courses by means of rapid magnocellular pathways that relay signals to targets involved in spatial attention (more below). The visual information contained in these rapid signals is rudimentary and low-spatial frequency¹³ but provides the raw materials necessary for higher-order areas to gain the 'gist' of the spatial configuration of the visual field. At the peak

NEURAL PROCESSES ENGAGED DURING AN AT BAT

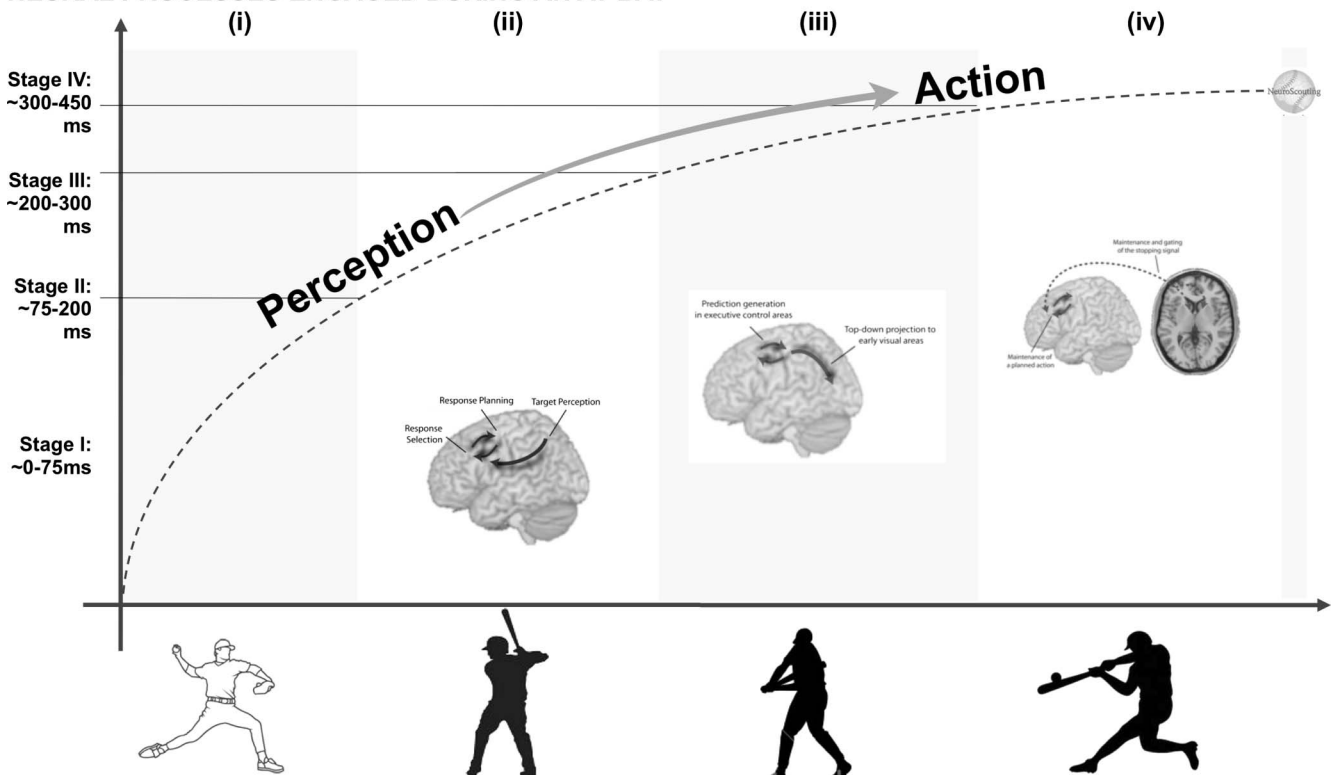


FIG. 2. During the course of an on-field event—in this case, hitting a baseball pitch—a series of brain systems become rapidly engaged over time to successfully mediate performance.

of this dorsal stream are regions in the frontal cortex, comprising area 6, also known as the frontal eye fields (FEF). This region controls the shift of eye movements with spatial attention consistent with the role of the dorsal stream in identifying important signals across space. The ventral stream relays through parvocellular pathways to areas in inferior temporal cortex (ITC; comprising extrastriate visual cortex) that are specialized for particular categories of objects. For example, single neuron recordings across the ITC have found individual cells (e.g., Scialoja et al.¹⁴) and populations of cells (e.g., Kanwisher et al.¹⁵) that exhibit selective responses to faces, scenes, and other larger-scale objects. This pathway terminates into regions of the PFC that integrate object and space-based information to guide appropriate decisions about action.¹⁶

Regions in the frontal and parietal cortex, then, represent a massive convergence zone for spatial and object information in vision. Consistent with this convergence, zones of frontal areas show varying degrees of domain specificity to certain classes of objects (e.g., Romanski¹⁷), and recent evidence suggests that both frontal and parietal circuits also have topographic maps of retinotopic space.^{18,19} These areas with some preference to domain and spatial information in the PFC are part of an increasing hierarchy of prefrontal areas leading to integration of space and object information into flexible action.²⁰

Passive Versus Active Perception: An Ongoing Paradigm Shift

Early models of vision proposed that signal flow and information processing within this hierarchic set of visual regions moved in a serial manner with the sequential extraction and recombination of features at increasing levels of the visual hierarchy. The end result was a faithful representation of the external world that was context invariant and whose general purpose was to provide the accurate internal models to cognitive centers in the brain. More recently, several lines of empirical evidence have challenged these classical models of vision and propose a more dynamic model of vision with a larger role for top-down feedback at even the earliest stages of visual analysis. The first piece of evidence emerges from the temporal properties of physiologic signals throughout the visual system.⁷ Several lines of neurophysiologic evidence indicate that visually driven neurons as high as the FEF receive bottom-up sensory signals much more rapidly than would be predicted from a strict serial flow of information processing through the visual system (within ~70 millisecond after stimulus onset). These rapid temporal parameters in the dorsal stream suggest that control regions in the PFC are within a temporal window to exert modulatory feedback onto the slower ventral stream signals extracting object information.¹³ These attentional signals could be a driving force by which previous experience and long-term memories could rapidly bias processing in favor of specific targets in the visual environment. Along these lines, other evidence shows that disruption to heteromodal control regions by stroke²¹ or transient disruption with transcranial magnetic stimulation²² has a causal impact on the magnitude of bottom-up signaling in addition to the spatial characteristics of the evoked visual response. New lines of physiological evidence²³ are uncovering more evidence for direct feedback signals to multiple levels of the visual system proceeding in a top-down manner from higher visual areas down to

responses at the level of V1 and potentially even the LGN of the thalamus.²⁴

Collectively, these empirical findings have been incorporated into theoretical models of vision (e.g., Engel et al.⁴) that incorporate an expanded role for top-down modulation. These models detail the active role of PFC and PPC regions in the constructive nature of visual processing. In the next section, we highlight how this convergence of top-down feedback with early sensory signals is involved in a range of gametime athletic situations to amplify those features and objects in the environment that are most important for on-field action.

ON-FIELD ATHLETIC PERFORMANCE: A DYNAMIC INTERPLAY BETWEEN STIMULUS-DRIVEN AND GOAL-DIRECTED VISUAL ATTENTION

At any given moment on the field, an athlete is bombarded with a barrage of visual information about rapidly changing situations on the field. The visual system, however, has inherent capacity limitations (e.g., Tsotsos²⁵). Visual inputs reflecting the location of the ball in space, positions of teammates, threats posed by defenders along with extraneous information (e.g., the crowd) all compete for these limited resources of the visual system. Amid this continuous influx of visual signals, however, only a small subset of inputs are particularly relevant for the athlete's ongoing action selection. A fundamental challenge for goal-directed behavior generally, and on-field sports performance in particular, is the brain's need to manage the capacity limitations of vision by favoring the neural representation of those inputs that are most relevant for current action.

For these task-relevant visual signals to guide decision making at higher levels in the perception-action cycle, they must achieve stable representations through a process known as 'perceptual binding.' Several leading models of vision (e.g., Treisman feature integration theory²⁶) propose a two-step architecture of visual processing. The first is an initial parallel 'preattentive' stage where basic features are extracted, followed by a second stage where ~1 object is selected for binding. Although this model has been tested and refined,²⁷ they all agree that at some level in the visual chain, a set of mechanisms pool independent feature representations into coherent 'bound' objects in the visual world.^{28,29} Binding has been a major focus of research in perceptual neuroscience, earning the name 'the binding problem' (e.g., Riesenhuber and Poggio³⁰) because of a lack of clear consensus on the specific mechanisms by which features are integrated into distinct objects that can guide action. As outlined in the previous section, the crux of the problem stems from the fact that early preattentive vision breaks down complex objects into distinct and spatially segregated neural modules representing distinct features in extrastriate cortex. Several models make predictions about how these features are pooled together into coherent objects later in the visual stream. The Temporal Binding model,³¹ just to provide an example, purports that binding is mediated by distributed synchronization of neural activity across the specific feature modules that comprise the bound object. Although researchers continue to test these and other theoretical models, for our purposes, it has become clear that visual attention plays a primary role in selecting the to-be-bound objects.

The fact that only a limited number of visual representations are selected for binding and further processing is referred to as the 'bottleneck' of attention. By limiting neural resources to those incoming inputs that are most critical for current action, the brain ensures that the athlete has the most sensitive representation of the most important features in his or her environment to guide decision making. Before reviewing the prefrontal and parietal control networks underlying visual attention, it is important to understand the mechanism by which attention works in early visual processing. One of the leading models of attentional selection—the 'biased competition model'—has laid the theoretical groundwork for how incoming sensory signals are biased in the service of behavior.³² This model is based on three fundamental principles that are informative for our discussion^{33,34}: (1) Because of limited resources, the earliest stages of visual processing are competitive as task-relevant and irrelevant visual inputs go head to head, and biases in favor of one object will be at the expense of the rest of the visual scene. (2) This neural competition can be resolved in two different manners³³: First is by means of particularly salient stimuli that violate ongoing predictions. These stimuli are markedly distinctive relative to the rest of the visual scene or are threatening stimuli in the environment (stimulus driven). Second is by goal-directed biasing through top-down resources (goal driven) that control biasing mechanisms. (3) The results of selective competition are integrative, meaning that biasing at one level of the visual hierarchy (i.e., at extrastriate cortex) leads to increasing likelihood that the object will receive competitive advantage at higher levels of the visual system (e.g., PFC).

PREDICTIVE MODELS OF THE VISUAL ENVIRONMENT: NEURAL MACHINERY TO GUIDE VISUAL ATTENTION

Elite athletics represents a special class of behaviors in which the perception-action cycle is forced to execute under incredible time constraints. Many decisions ranging from returning a tennis serve to committing to a baseball swing must be executed within 100 to 200 millisecond after first visual signals initiating the on-field event. If the brain's functional architecture is left to respond to these demands in a purely reflexive manner, the physiological lags of bottom-up signaling alone would extend beyond the time windows available to athletes during many on-field situations. To increase the efficiency of the perception-action cycle and to manage extreme situations such as on-field athletics, the brain evolved a set of mechanisms that speed up perception by leveraging two different knowledge sources to guide predictions: (1) knowledge from past experience and (2) knowledge about current goals and means to those goals. The impact of bringing in this extra information is that humans are better and faster at recognizing objects in the visual world when they know something in advance about the features or potential location of the relevant target. This is because of a collection of neural mechanisms that allow the brain to rapidly form 'predictive models' of future sensory experience. Even more importantly, these predictive models provide expectations that are actively used to prepare sensory systems for likely events in the near future and, in doing so, actually facilitate the bottom-up signaling in lower visual areas once those events occur or do not occur.⁴ The brain has two primary mechanisms for forming these rapid predictions about

upcoming sensory input: (1) top-down mechanisms originating in the PFC, (2) bottom-up mechanisms in which visual signals automatically trigger perceptual and motor representations that have been associated with them through past experience and skill development. Although both of these are absolutely critical to on-field athletic performance, the second is beyond the immediate scope of this review, so we will focus on the first mechanism, which has a direct role in the top-down deployment of goal-directed attention.

The PFC—by virtue of its position at the apex of the perception-action cycle and its extensive connectivity throughout the visual system³⁵—generates a range of predictive models by activating representations of the stimulus-response mappings that are relevant within the current 'rules of the game.' Stimulus-response mappings are the specifics defining the input-output relationships that make up the ongoing perception-action cycle the individual is engaged in. Within the context of an athletic sport, such as baseball, these top-down driven models define the fundamental components of ongoing behavior that are relevant for success within the game. For example, linked with any large-scale goals (e.g., hitting a homerun) is a set of relevant perceptual targets (e.g., the pitcher, a ball, the fence in left center) and relevant action output (e.g., a swing, running the bases). Within the context of the game, these linkages are temporally dependent and consequently must proceed in a time-invariant manner (e.g., running the bases cannot precede hitting the ball). This time invariance allows the brain to constantly make predictions about the future based on the recent past. Even specific subgoals within these larger level goals have specific task sets governing them. The subgoal of hitting the ball, for example, has its own set of perceptual targets (e.g., the pitcher's hand grip, the ball, and the ball's direction and spin as it reaches the hitter) and action output (e.g., initiating a swing). At both the goal and subgoal levels, neural circuits maintain representations about the structure of the task, its important stimulus-response mappings, and the temporal contingencies of the situation. By dynamically activating these representations, predictive models provide a mechanism to bias lower-level sensory systems in a top-down manner³⁶ in favor of likely upcoming events.

Given the moment-by-moment nature of ongoing behavior, predictive models must be continuously updated as the context of the perception-action cycle evolves. This rapid updating happens through a rapid convergence of top-down and bottom-up mechanisms that activate representations that are relevant based on the latest sensory events. By rapidly monitoring the sensory world, the PFC rapidly switches and updates task sets correspondingly. One implication of this is that systems involved in detecting targets must be capable of rapid switches in the types of stimuli that are targets on a moment-by-moment basis.³⁷ Before hitting the ball, for example, the hitter must temporarily activate all the stimulus-response mappings relevant for the first subgoal of the game: successfully meeting the target with the behavioral output of the swing. At this point, the representation of the action 'run the bases' is not currently relevant and therefore should not be active. This changes abruptly once the brain receives cues that the first subgoal is executed (e.g., the hit dropping safely in the left field), and the hitter must now transition to the next phase of behavior. This switching of task set (i.e., 'task switching') is a hallmark feature of human behavior that allows the predictive models of ongoing actions to be continuously updated.³⁸ One of the most valuable

behavioral implications of these rapidly updated models is that the brain is able to draw on all this knowledge to rapidly direct several modes of attention. We will now highlight three specific modes of attention that use these predictive models to alter early visual processing.

PREDICTIVE ORIENTING AND VISUAL SEARCH: USING EXPERIENCE TO DRIVE VOLUNTARY ATTENTION

How does the brain become aware that early visual information competing for neural resources is relevant and should be biased in a top-down manner? This set of mechanisms begins with a process neuroscientists term “target detection”—that is, the ability to rapidly identify stimuli in the environment that are relevant for ongoing action. ‘Visual targets’ refers to a heterogeneous set of visual objects that are activated by current representations of the stimulus–response mappings relevant to ongoing behavior. The class of visual targets within the realm of on-field athletics is a large group that varies both within sports (across different gametime situations) and across sports (given sport-specific rules of the game). Targets could be objects (e.g., a moving ball), people (e.g., teammates), a particular spatial location (e.g., the release point of a pitch), or particular spatial relationships between objects in the environment (e.g., a pattern indicating separation between a receiver and defenders). As mentioned in the previous section, given that predictive models are rapidly updated based on changing events, targets themselves can rapidly be relegated to non-target status as action goals change.

Knowing Where in Space: Spatial Attention Facilitates Target Detection and Visual Processing

At certain points during gametime situations, knowledge of the current task set provides reliable cues about the likely spatial location of upcoming targets. In these cases, spatial attention works analogously to a spotlight illuminating a particular sector of a stage: By focusing the ‘spotlight of attention’ on a particular spatial location, these attentional signals bias the incoming responses of retinotopic visual areas representing any feature within the spotlight.

Any facilitation of visual processing by spatial attention would have an impact on gametime situations such as hitting in baseball. As the pitcher begins his windup, the batter is cued to the location in space where the pitch will be released. Given the importance of early pitch attributes (e.g., speed, direction, rotation) to making an effective decision about whether to swing, allocating spatial attention to the release point in the milliseconds leading up to the pitch affords the opportunity to enhance the response properties of visual neurons processing multiple attributes of the ball after release (e.g., motion, direction, pattern of seams).

The mechanism by which spatial attention facilitates the processing of incoming visual signals has been a focal area of recent research. After input signals from predictive centers in the PFC, the dorsal frontoparietal attention network is engaged to direct spatial attention to the target location.^{39,40} Even before the onset of visual targets within that spatial location, this frontoparietal network sends top-down signals to increase the baseline activity of visual neurons with receptive fields in the attended location.⁴¹ These prestimulus baseline shifts have been shown in both fMRI⁴² and single unit neurophysiology where baseline neural spiking

increased by as much as 30% to 40% before appearance of the target.⁴³ In addition to impacting the amplitude of prestimulus activity in these areas, spatial attention modulates anticipatory oscillatory patterns (in the alpha band) reflecting larger-scale synchrony in expectation of the target.⁴⁴ These prestimulus amplitude and oscillatory shifts serve as preparatory biases to provide a competitive advantage to features within that location relative to others outside the spotlight of attention.

Several lines of evidence suggest that these prestimulus shifts have a direct and powerful effect on the efficacy of bottom-up processing and target detection, specifically. Spatial attention has been shown to modulate stimulus-evoked responses at both the single neuron⁴⁵ and population level.⁴⁶ Recent evidence⁴² comparing the relationship between prestimulus activity and the magnitude of evoked signal enhancement suggests that preparatory signals and the degree of sensory enhancement are directly related. The size of the prestimulus top-down effect and the magnitude of evoked activity are linked even on a trial-by-trial basis.⁴⁷

Evidence also demonstrates that these spatial attention effects have a pronounced effect on target detection. By transiently disrupting the frontoparietal network with transcranial magnetic stimulation in the time leading up to target presentation, Capotosto et al.⁴⁴ showed disruption of anticipatory alpha patterns in visual areas—consistent with a direct role of frontoparietal feedback on prestimulus patterns in the visual system. Most importantly, this frontoparietal disruption had behavioral impact leading to decreased identification of relevant targets. Further evidence suggests that these attentional effects improve the bottom-up processing of multiple attributes of visual stimuli. Sapir et al.,⁴⁸ for example, showed that prestimulus activity in the dorsal parietal network predicted accuracy in a motion discrimination judgment.

The role of spatial attention in bolstering target detection and motion discrimination has a direct impact for on-field performance. In a study exploring expert cricket players, for example, researchers found that the primary difference between elite players and novices was *where* in space the experts were attending at critical time periods during the pitch.⁴⁹ Early in the pitch, expert batsmen focus on a particular cue during the pitcher’s delivery—specifically, the motion of the bowling arm.⁵⁰ This then allows them sufficient cue information to rapidly shift spatial attention to the predicted bounce spot of the ball—a critical point in the travel of the pitch. By focusing the spotlight of attention on particular locations during these critical timepoints, the batter is able to leverage spatial attention to ramp up visual processing in motion-selective areas to better detect any deviations from their ongoing prediction of the balls temporal and directional trajectory.

Knowing the Features of Targets: Top-Down Contributions to Visual Search

Although situations such as hitting are conducive to expectations about the spatial location of targets, in many other situations, athletes must search for particular targets without specific expectation of their spatial location. These situations call on a range of brain functions underlying “visual search.” What complicates visual search is that it is conducted in the presence of a range of distractors with more or less similarity to the target stimuli of interest. The classic example used to illustrate the challenges of visual search is looking for a particular friend (i.e., the target)

within a crowd (i.e., the distractors). The demands of the visual search task, and the resulting time required to successfully identify your friend, depends on the level of distinctiveness of the target relative to the rest of the background distraction. If your friend happens to wear neon green among a crowd of people with more mainstream clothing selections (e.g., all wearing red), he or she would almost effortlessly grab your attention because of large feature distance between the signal (i.e., your friend in neon) and the noise (i.e., the background crowd with more conservative fashion sense). When this signal-to-noise difference⁵¹ decreases (as it does during most sporting crowds where fans collectively don the team's colors), the taxes on visual search and the need for top-down resources to guide successful identification are both increased.

A great deal of research has focused on the degree to which visual search proceeds in a parallel or serial manner. That is, when searching for your friend in a crowd, do you serially go through each crowd member and subjectively compare their match with an internal representation of your friend? Or do you instead scan the crowd in parallel guided by critical features that make up the internal representation of your friend until he or she pops into your awareness? Given the increased speed of parallel search, the mechanisms supporting this feature-based search operation become particularly relevant within the realm of on-field athletics which is defined by the rapid nature in which successful search must be executed. In the case of finding your friend in the crowd, as time goes on, it becomes a source of frustration, but there is an open temporal window to ensure completion of the search. This is not the case on the athletic field where often times search must be completed rapidly or else the player gets tackled, forced into a turnover.

Given these time demands, several lines of evidence suggest that even in complex search—presumed to be the domain of serial search strategies—there are top-down mechanisms that aid search in parallel. Specifically, when a stimulus with specific features is the target of visual search, neurons in visual areas that process those features show elevated neural activity during the course of the search.⁵² This evidence is consistent with theories suggesting that the PFC converts representations of relevant targets into attentional templates⁵³ that are activated and maintained in working memory during the course of the search. These temporary activations serve as prospective codes to bias visual areas representing features of that template. Much like spatial attention, then, temporary activation of relevant targets in the PFC leads to prestimulus biasing of relevant representations at multiple levels of the visual system. Also like spatial attention, these prestimulus codes have been shown to lead to increased evoked-sensory responses to targets sharing those features.⁵⁴ This phenomenon of 'match enhancement'⁵⁵⁻⁵⁷ leads to increases in the magnitude,^{55,58} synchrony,⁵⁹ and speed⁶⁰ of neural activity when bottom-up sensory maps have a high correspondence with top-down expectation maps. Further work shows that the numerous attributes of a target can help guide visual attention during search.²⁷ The end result is a set of mechanisms that bias the visual system in favor of detecting certain attributes that help pull attention in favor of stimuli matching features of the target.

The recent review by Bichot and Desimone⁵² highlights these feature detectors but suggests a hybrid model involving serial search in conditions of increased complexity. It is clear that on-field

game situations also sometimes call on a hybrid of serial and parallel visual search and that these can be determined based on the temporal constraints of the particular situation. One example of these different constraints can be illustrated through the example of a QB dropping back for a pass aiming to decide which receiver to target in a passing play. Although parallel search offers the most efficiency, many plays have priority reads and—providing the offensive line is doing its job—the QB has time to survey the available options. He does this by initiating a rapid visual search to the spatial location his playbook knowledge and practice experience highlights as the top priority read. In this example, the visual target is a peculiar one: a pattern of separation between a target receiver multiple defenders within the visual scene. The QB rapidly evaluates the presence of this target situation before deciding to pull the trigger or switch his search to the secondary, tertiary, options. Unfortunately for the QB, many plays do not permit this serial search through receivers. In the presence of a pass rush, QBs are forced to rely on more rapid parallel search strategies to rapidly identify target receivers before time runs out. These targets may still rely on a quick search of receiver–defender separation or a more basic feature-based search for where the appropriate colored jersey(s) are in space. This example suggests that athletes too must use a hybrid search strategy to accomplish on-field goals in the face of stiff time constraints.

STIMULUS-DRIVEN ATTENTION: THE 'CIRCUIT BREAKER' OF ATTENTION

Despite the critical role played by the dorsal frontoparietal network in voluntary attentional control, numerous lines of evidence suggest that there is a distinct attentional network⁶¹ performing competitive functions⁶² that are also relevant to on-field athletic performance. Although target detection and visual search rely on top-down resources, certain gametime situations require control of attention to be wrestled away from the voluntary attention network so that it can be grabbed by nontargets that suddenly become salient within the environment. In these situations, high priority information demands that attention be controlled by an external event rather than ongoing voluntary attention. As an example, consider the QB just mentioned who is faced with the quick temporal constraints of a defensive pass rush. Often times in these situations, the QB may be rifling through his normal visual search patterns—evaluating targets out in the field—when suddenly a rapidly moving defender emerges out of nowhere in his periphery indicating an impending sack and the rapid need to adjust his behavior.

Importantly, even this stimulus-driven form of visual attention is impacted by predictive models formed by the PFC. By setting up likely expectations, these models pave the groundwork for detecting low probability, salient events that violate the predictive model. On detection of these violations, exogenous orienting of attention is performed by a functionally distinct neural machinery that is localized largely on the right hemisphere and is called the ventral frontoparietal network³⁹ and calls on several critical areas (including the right temporoparietal junction).⁶³ During normal on-field behaviors where voluntary attention is advantageous, this ventral network is suppressed so that it is not drawn by irrelevant information.⁶² During times of highly salient, unexpected stimuli,

however, this network becomes rapidly engaged to serve as a ‘circuit-breaker’ for voluntary attention to override ongoing cognition and voluntary attention when visual resources are necessary to deal with unpredictable stimuli of importance.

CONCLUSIONS

This review highlights several mechanisms by which visual attention impacts critical situations in sports vision. The interplay of stimulus and goal-driven attention in elite athletics is only the tip of the iceberg in the brain’s multifaceted role in guiding on-field decision making and action. Although a range of other neural mechanisms become engaged throughout the evolution of the perception–action cycle culminating in movement execution, visual attention represents a major class of neural functions that are engaged rapidly to facilitate visual function at the earliest stages of cortical (and potentially even subcortical) function.

Although most research investigating visuomotor function (including visual attention) has focused on ‘normal control’ populations, it is important to emphasize that the brain of an elite athlete—because of years and years of focused training in the intense demands of the perception–action cycle—has adapted during the course of skill acquisition to become optimized relative to normal controls in many of the brain systems covered in this review. Across a range of expertise in skill domains ranging from perceptual skills (e.g., elite videogamers⁶⁴) to motor skills (e.g., expert musicians⁶⁵), neuroscientists have reported a range of structural and functional adaptations at the normal level that support elite performance. Although the study of elite performance within neuroscience is still an emerging field and data within top performers are limited, numerous lines of evidence suggest that elite athletics are supported by a range of training-induced neural changes. Development of certain perceptual skills, for example, has been shown to lead to a range of alterations to primary visual cortex (e.g., Schoups et al.⁶⁶) likely because of training-dependent changes in top-down control functions. By better understanding these neural alterations that support elite athletics, future neuroscience research stands in a position to identify the particular brain systems that separate elite athletes from the rest of the pack.

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