Review

Visual processing, learning and feedback in the primate eye movement system

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We present an overview of recent paradigms used for studying visual information and reward processing in the human and monkey oculomotor pathways. Current evidence indicates that eye movements made during visual search tasks rely on neural computations similar to those employed when eye movements are planned and executed to obtain explicit rewards. These data suggest that human eye movements originate from the processing of (predominantly visual) sensory information, feedback about previous errors, and expectations about factors, such as reward. We conclude that these properties make the saccadic system an ideal model for studying both the behavioral and neural mechanisms for human voluntary and involuntary choice behavior.

Introduction

Humans are a largely visually driven species, responding strongly to visual information of many different kinds. Here, we review recent experimental and computational work concerned with uncovering, in both the monkey and human oculomotor system, the neural computations underlying visual processing, target selection and eye movement initiation. We summarize the behavioral evidence obtained during saccadic choice tasks in both species and provide an overview of existing computational models designed to explain the behavior observed in these experiments. We present a model framework which describes how the primate brain might program saccadic eye movements based on a representation of the *relative expected subjective value* of individual eye movements, and then updates this representation based on dopaminergic feedback loops. We hypothesize that human eye movements result from the processing of predominantly (although certainly not exclusively) visual information, from feedback about saccadic accuracy, and expectations caused by remembered information, and only rarely reflect simple stimulus-response associations. These properties make the saccadic system an ideal model system for studying the processes underlying human choice behavior.

Eye movements and neural pathways of visual input

Eye movements serve the purpose of shifting a stimulus into the region of highest visual acuity, the fovea. From the retina, visual information reaches the striate cortex via the *lateral geniculate nucleus* (LGN) along retinotopically organized connections. A second, parallel pathway links the LGN directly with the oculomotor system via connections in the superior colliculus [1]. This pathway is, among other things, probably involved in the generation of short-latency *express saccades* [2].

Visual information arriving at the cortex is first processed in the occipital lobe. From there, visual information is processed via two main pathways, the dorsal and the ventral stream [3]. Both streams begin in the primary visual cortex (V1) and then separate into two parallel pathways, with one stream (the ventral) ending in the cortex of the inferior temporal lobe, and the other processing information forward into the parietal lobe (dorsal stream). Even though both streams are highly interconnected, information processed in the two streams is widely believed to serve different functions: the dorsal pathway is hypothesized to be the major pathway for the computation of spatial information for eye and hand movement control [4]. From caudal to rostral, the dorsal stream projects from primary visual areas to the posterior parietal cortex. The dorsal stream is interconnected with the ventral stream, which is assumed to largely process information for perception and object recognition. Information processed via the dorsal pathway connects to the parietal lobe, where visual information is integrated with sensory information from other modalities into a spatial representation of the world [5]. From caudal to rostral, the ventral stream consists of visual areas V1 (primary visual cortex), V2, V4, and the areas of the inferior temporal lobe: posterior inferotemporal, central inferotemporal and anterior inferotemporal (AIT) in the monkey. Each of these visual areas is hypothesized to contain a full representation of visual space in retinotopic coordinates. Moving along the ventral stream from V1 to AIT, it is generally assumed that receptive fields increase in size, latency and complexity [6].

Activity in the human brain, monitored during spatial saccadic tasks with functional magnetic resonance imaging (fMRI), reveals similar findings. These data indicate that the dorsal stream from V1 to the posterior parietal cortex (PPC) in the human is composed of a set of separate retinotopic topographic maps [7–14]. The spatial relations represented in the PPC probably play a critical role in the representation of upcoming movements [8,15,16] (see Ref. [17] for related work in monkeys); however, the PPC has

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also been found to show activity during spatial attention tasks – independent of preparatory motor activity [12,14,18] (see Refs. [19–21] for related work in monkeys).

Target selection and eye movement generation

In the presence of multiple visual targets, the brain must generate a representation of the entire stimulus configuration and select a single target for each saccadic eye movement. In many experiments that have examined this process, the subject is rewarded for foveating circular targets, presented at various locations on the display. These saccadic tasks, which offer rewards for eye movements, have become a key paradigm for studying the neural processes underlying voluntary and involuntary choice behavior. Single cell activity measured in monkey area LIP (lateral intraparietal area), in the parietal cortex during these types of tasks has been hypothesized to correspond to an attentionally filtered spatial map of the stimulus array and/or a spatial map of the repertoire of available movements [21–24]. LIP presaccadic activity has also been observed to be influenced by the presence of additional stimuli within the search array (outside the classically defined response field), a finding which suggests that LIP neuronal activity might reflect visual processing, saccade preparation [25] and/or some form of cortical normalization [26].

These conclusions are strengthened by results obtained during the memory-guided saccade paradigm. In the memory-guided saccade paradigm, stimulus presentation in the periphery is followed by a delay period of a few seconds until eye movement initiation. Gnadt and Andersen [17] found elevated activity in area LIP in response to visual target onset in this paradigm, as well as specific eye movement-related activity during the memory delay period. Activity recorded during this delay period requires neither the presence of a visual stimulus nor the immediate execution of an eye movement, and therefore has been suggested to distinguish sensory-driven information from (spatial) intentional motor planning information [27], although this conclusion has been controversial [23]. Indeed, the enhanced response in LIP to target onset is similar during both spatial saccadic tasks and spatial detection tasks (which requires no movement) and appears to be distinct from spatially organized motor preparatory activity recorded in the frontal eye fields (FEFs) and superior colliculus (SC) (see Ref. [23] for references). Activity in area LIP has also been found to modulate depending on the reward magnitude associated with eye movement completion [28–31] and the presence of explicit rewards has been demonstrated to change the search behavior of primates in sequential eye movement search tasks [32].

These results led Glimcher et al. [33] to propose a frontoparietal decision model for saccadic eye movements (Figure 1 shows an extended version of the model framework). According to this model, area LIP contains a map of the relative expected utility (or more precisely the "relative expected subjective value") for each possible eye movement in the oculomotor repertoire [26]. The output of this map is

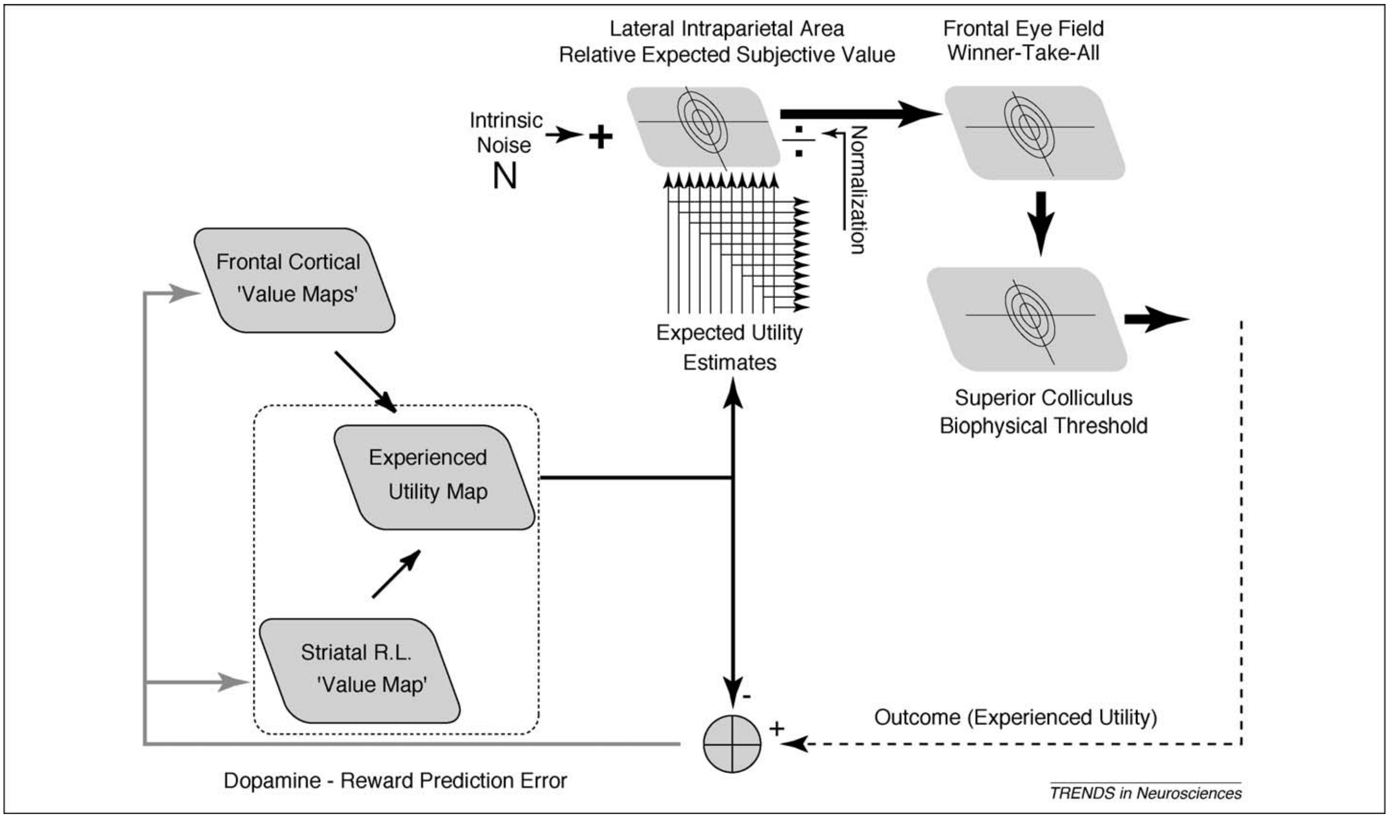

Figure 1. Schematic representation of the visual-saccadic decision-making process in primates. According to this model, area LIP contains a map of the relative expected subjective value for each possible eye movement. The output of this map is passed to the FEFs and the SC (with which it is reciprocally interconnected) where a ''winner-take-all'' rule determines direction and amplitude of the next eye movement. The relative expected subjective value estimates encoded in this map are assumed to derive from frontal and basal ganglia circuits updated by error-related feedback arising at least partially via dopaminergic cortical and striatal pathways [33].

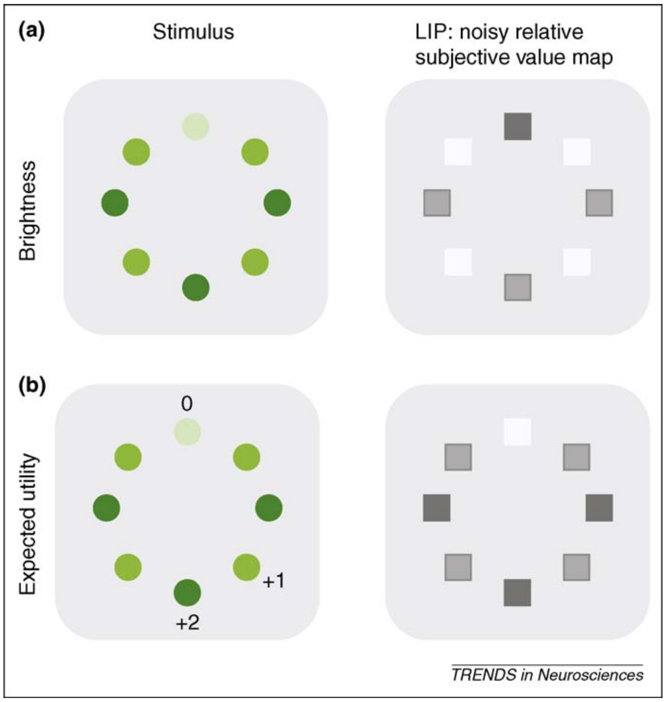

Figure 2. Schematic representation of hypothetical LIP activity of relative subjective value in visual search tasks without and with reward coding. (a) Visual search task. The subject is instructed to detect the brightest stimulus (the light green target); the brightness search yields a peak in the subjective value map in LIP which corresponds to the brightest stimulus (presented at 0°). (b) Visual search task with reward coding. The subject is instructed to maximize monetary gain, i.e. to try and fixate any of the dark green targets. According to the model proposed in Figure 1, the activity in area LIP, shown on the right, is predictive of the changes in decision strategy which reflect the change in subjective value that the subject places on each of the visual targets. For the visual search task illustrated in (a), the brightness search yields a peak in the subjective value map which corresponds to the brightest stimulus (presented at 0°). For the search task illustrated in (b), the peak(s) in the subjective value map distribution correspond to the stimulus option coding the highest reward magnitude (presented at 90°, 180°, 270°).

passed to the FEFs and the SC (with which it is reciprocally interconnected) where a "winner-take-all" rule determines the direction and amplitude of the next eye movement, effectively selecting the movement having the highest value to the subject [34,35]. The relative expected utility estimates encoded in this map are in turn assumed to derive from frontal and basal ganglia circuits updated by error-related feedback arising at least partially via dopaminergic cortical and striatal pathways.

Following the observations in saccadic choice tasks, one could conclude that reward should shift the implicit decisions subjects make in visual search tasks. A subject instructed to detect the brightest stimulus in a visual search task, for example (illustrated indicated by the light green target in Figure 2A) might be expected to fixate at a different location on the search display than a subject aiming to maximize monetary gain (i.e. trying to fixate any of the dark green targets, Figure 2B). According to the model proposed by Glimcher *et al.* [33], the activity in area LIP should be predictive of this change in decision strategy which reflects a change in the subjective values that the subject places on each of the visual targets. For the task illustrated in Figure 2, the brightness search yields a peak in the subjective value map in LIP which corresponds to the brightest stimulus (presented at 0°). The distribution of activity in the expected subjective value map changes in the presence of monetary or fluid reward, shifting the most likely eye movement response to the stimulus option coding for the highest reward magnitude, which now serves as the point of highest relative expected subjective value to the subject.

In accordance with the predictions of this model framework, LIP neurons have been found to be responsive to categorical boundaries [36] when subjects are reinforced in a manner contingent on these categorical boundaries. In this study by Freedman and Assad [36], monkeys were first trained to categorize motion stimuli into one of two possible categories ("upward right", "downward left"). The monkeys were trained in a delayed match to category task in which the monkey first viewed a sample stimulus, followed by a delay and a test stimulus. The monkey received a reward if he correctly classified test and sample by lever press. After training with a set of 12 directional motion stimuli, LIP activity correlated robustly with the category of the classified motion stimulus. After retraining the monkeys to group the same stimuli into two new sets, LIP selectivity shifted to encode the motion directions according to the newly learned categories. These results are consistent with the assumption that area LIP contains a reward expectation signal which modulates the gain of visual neurons in LIP in a manner that reflects the learned contingencies of rewards presented under these conditions [37].

Neural time integration of sensory evidence of LIP neurons has been studied using a very similar paradigm, which can be interpreted as yielding largely concurrent results [38–42]. In this work by Shadlen, Newsome and colleagues, monkeys perform a two alternative motion direction-discrimination task. The monkey views the direction of a noisy dynamic random dot stimulus and indicates his decision (the perceived direction of motion) by making an eye movement in the perceived motion direction. The recorded LIP spike rates in these experiments reflect the temporal integration of the sensory signal; spike rates ramp up faster with increased stimulus strength (formally, motion coherence) and are predictive of observed decisions and reaction times [43–45].

Saccadic latencies have been demonstrated to be modulated by the presence of reward and are significantly shorter when followed by a big reward than when followed by a small reward [46–48]. Along with modulations of latency by expected reward, modulations of expected reward have been found to change or even reverse the original direction selectivity of some projection neurons in the caudate nucleus [49]. This reward-dependent latency bias can be reduced by injections of dopamine D1 receptor antagonist and can be facilitated by injections of D2 antagonist [47,50].

Lau and Glimcher [51] recorded from phasically active neurons in the caudate nucleus while monkeys performed a probabilistically rewarded delayed saccade task and tested explicitly whether neurons in the caudate nucleus encode saccade direction, whether a reward had been received, or both. Encoding of the eye movement and the outcome was found to be performed by separate populations of post-movement phasically active neurons. One subset of neurons was tuned for the direction of the immediately preceding saccade. Another subset of neurons responded differentially on rewarded versus unrewarded trials and was relatively untuned for saccade direction. Using a related approach, these authors [52] demonstrated the existence of neurons which encode the values associated with individual saccades presaccadically. (A result closely paralleling earlier work by Samejima et al. [53].) Taken together, these results suggest that the reward modulation of saccadic eye movements, at least partly, originates from the caudate nucleus, that dopaminergic input to caudate nucleus projection neurons is responsible for the reward modulation and that the dopaminergic effect is mediated, at least in part, by D1 and D2 receptors in a differential manner.

A second substructure of the basal ganglia, the subthalamic nucleus, appears to contribute to the control signal for saccade switching apparently employed for the suppression of habitual unwanted saccades and the facilitation of controlled alternative saccades [54]. The majority of "switch neurons" found in the subthalamic nucleus appear to inhibit an automatic undesirable saccade, whereas some appear to facilitate a more "cognitively desired" saccade, and yet other neurons appeared to perform both roles. Similarly in humans, neurons in the subthalamic nucleus do show directional selective activity during saccades directing gaze to visual targets [55].

In humans, several brain areas have been linked to eye movement generation. Area(s) *intraparietal sulcus (*IPS*)* (1 and 2) has been found to topographically code both visual stimulus information and the direction of intended saccadic eye movements [8–10]. The IPS and the frontal and supplementary eye fields (FEFs and SEFs) are three highly interconnected frontoparietal eye fields with neuronal activity that is related to the generation of saccades [56–58].

Saccadic response times observed in laboratory tasks suggest that the processing of sensory information and eye movement initiation occur largely in parallel. Saccadic latency, for example, is strongly influenced by the presence or absence of a visual fixation stimulus. The removal of a fixation stimulus 200 ms before target presentation in so-called gap trials results in shorter latencies [59]. Gap trials constitute stimulus conditions in which the fixation stimulus has already disappeared, but the target has not yet been displayed. Brain activity recorded with high temporal resolution techniques (such as EEG) during the gap period is therefore probably motor preparatory activity, and (it has been argued) can be conceptually distinguished from sensory processes (sensory information about the target position is not yet available) and from motor processes (the eye movement has not been initiated). Activity labeled as motor preparatory during the gap period has, however, been hypothesized in the FEF and SEF [60], confirming closely related electrophysiological evidence from single cell recordings in the FEF of monkeys [61].

In the monkey brain, a reduction of saccadic latencies in gap trials has been attributed to the disinhibition of cells in the anterior SC which are active during fixation [62,63]. Following a trigger signal from the SC, omnipause neurons in the brainstem are known to pause in their firing, a pause which is hypothesized to disinhibit "burst" neurons in the SC via a negative feedback circuit. This disinhibition evokes a burst of activity in these cells, the duration of which corresponds to the amplitude of the elicited saccade under at least some conditions [64].

Recordings during spatial saccadic tasks indicate that the SC functions as an interface at which visual input is converted into a saccadic output; it contains a retinotopic map of motor goals, coding the distance from fixation to the target position [65]. Some SC neurons, however, show elevated activity for targets compared with simultaneously presented distractors, with a delay that is locked to stimulus onset, suggesting that these neurons play a role in target selection [66]. It should be noted that this activity in SC buildup neurons predicts changes in saccade latency along with changes in target probability [67,68]. Other SC neurons discriminate the target with timing that is well correlated with latency, suggesting that these neurons are more directly involved with triggering saccades [69,70].

The SC and its contribution to the generation of saccades in humans has not been studied much, but as in the monkey brain, the SC in humans has been found to be involved in the control of reflexive saccades [71–74].

In summary, whereas the exact processing routes of visual and reward-related information need to be determined by future research, existing evidence suggests that the parietal cortex might serve as part of a decision module for the selection of movement relevant visual information linked to eye movement generation.

We next review behavioral experimental evidence for seemingly effortless and highly efficient processing of information in visual search tasks and discuss recent computational work that models the behavior observed in these tasks.

Visual search and saccadic decisions

Visual search tasks are the most commonly used paradigm for the study of neural processing underlying visual target selection. Subjects in these tasks are typically instructed to press a response button as soon as they detect the target among a set of visually similar distractors [75]. Successful detection of the target does not require foveating the target, but search accuracy increases with fixation [76]. Reaction times and the percentage of correctly detected responses vary depending on the stimulus set size, the visual similarity between target and distractors, and on the discriminability of target and distractors from background noise [75,77–79]. The circuits for driving saccades seem to be specifically tuned to vision in natural environments. Given equal visibility, saccadic latencies are much shorter when target stimuli are presented on noisy backgrounds rather than uniform backgrounds [78].

Recent work by Najemnik and Geisler [80] combines computational and behavioral methods to study human search strategies. Najemnik and Geisler have proposed a Bayesian model of optimal visual search which models human search behavior in visual search tasks. The optimal search strategy of this Bayesian ideal searcher is defined as the strategy which maximizes the information gained across successive eye movements. The ideal searcher starts his search with initial assumptions about the distribution

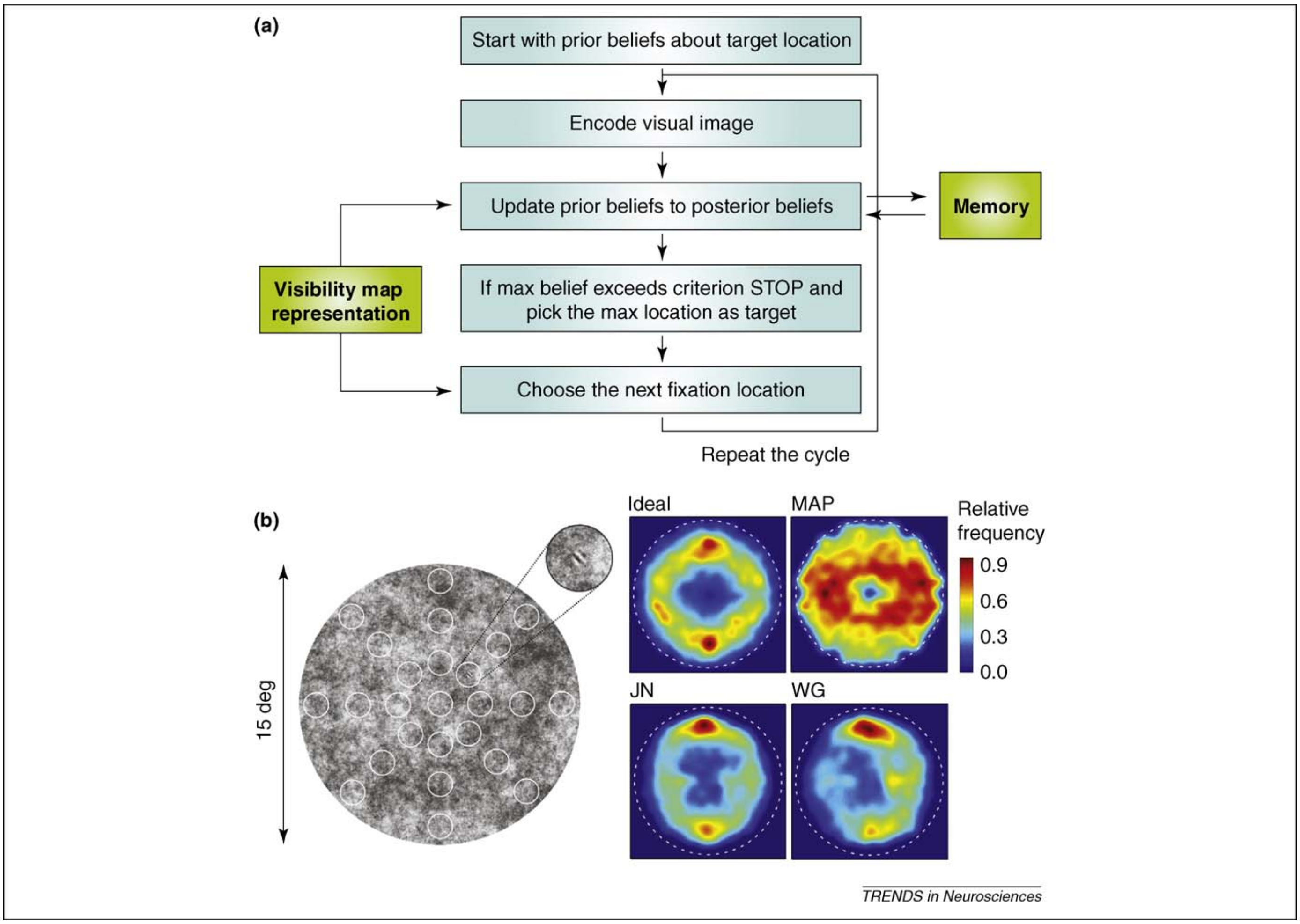

Figure 3. (a) Ideal searcher model. (b) Average spatial distribution of fixation locations across the search area for ideal, map and human searchers (Figures 1 and 3 in Najemnik and Geisler [80]). Note that the search strategy of the Bayesian ideal searcher (a) is different from the search strategy of a feature based maximum *a posteriori* (b) searcher that plans the next eye movement towards the position in the display which contains the target with highest probability. The Bayesian ideal searcher (a) will not look for the most probable target location but will search the display to maximize information about the available visual information – until the target is detected. The MAP searcher (b) plans his next eye movement to the most probable target location, independent of information collected during previous fixations. For displays containing uniformly distributed targets, MAP search strategies result in an almost uniform distribution of fixations across the entire display, whereas the fixations of the Bayesian ideal searcher cluster in a ring around the position of initial fixation.

of possible target locations and then updates this representation based on visibility information collected across successive eye movements (Figure 3).

An experimental test of the model showed that human searchers employ highly efficient search strategies which are very similar to the search strategies of the Bayesian ideal searcher (Figure 3). This implies that human searchers efficiently process visual information across the entire visual display, select fixation locations to maximize the information processed by the visual system, and that their search strategies include inhibition of return, i.e. the ability to remember and process information across successive fixations [80–82]. Inhibition of return [83] prevents the repeated fixation of previously fixated targets and has been demonstrated to reflect remembered information processed during the past three fixations [84]. Recent data obtained during a visual search task of targets embedded in natural images indicate that inhibition of return seems to be a strategic attentional component that mostly operates during visual search tasks, although less so under free viewing conditions [85]. These results suggest that inhibition of return does vary strongly with task constraints and is in effect when task performance benefits from a bias toward new objects, such as in visual search. Studies using the Posner cueing paradigm [86] in general also indicate that inhibition of return operates along with delays in the shifts of attention back to recently attended locations and motor processing – and correspondingly the parietal cortex has been suggested to play a crucial role in the neural computations underlying inhibition of return [87,88].

Geisler and colleagues found that human search strategies differed from the predictions for the Bayesian ideal searcher in two ways: first, the model in general underestimated saccade amplitudes and the increase in the number of fixations for eye movements towards targets presented at larger eccentricities and second, the model failed to account for the spatial inhomogeneities in the distribution of fixations across the search display [80,81]. Some of the differences between the predictions by the Bayesian ideal searcher model and the observed fixation pattern are probably due to the asymmetric enhancement of apparent contrast with shifts in spatial attention [89]. Consistent with the predictions for a Bayesian ideal searcher, expectations about scene context in natural scenes bias observers' fixation strategies towards more fixations into regions with expected context [90].

Interestingly, eye movement strategies change when explicit rewards are associated with the final eye position in tasks of the same type [91]. In this study by Milstein and Dorris [91], subjects searched for a visual target among a set of visual distractors. Subjects controlled their choice strategy to maximize reward by choosing among the possible targets. The number of fixation errors to the distractor decreased when larger relative rewards were assigned to the visual target and saccadic reaction times were correlated significantly with the relative sizes of the rewards offered for target and distractor. In a similar study, Stritzke *et al.* [92] examined human saccadic decisions in an eye movement task in which monetary rewards and losses were awarded depending on parameters of the motor component of the action, saccadic endpoint and variability. The decision strategies observed in this experiment were very similar to the strategies of an optimal decision maker maximizing expected value [93].

In both these latter studies, the presence of reward altered the observed search strategies. Typically, visual search tasks differ from saccadic choice tasks mostly with regard to the type of feedback provided for the selected response. Whereas subjects typically do not receive any feedback for their performance in visual search tasks, correct performance in saccadic choice tasks is rewarded with juice in studies with monkey subjects or with a small monetary bonus in (many) experiments with human subjects. The change in search strategy observed in the presence of reward in the studies by Milstein and Dorris [91] and Stritzke *et al.* [92] indicates that visual search tasks probably recruit at least some neural processes that are distinct from those employed in saccadic choice tasks that yield explicit rewards.

Learning in visual discrimination tasks

We finally review evidence for changes in visual discrimination performance induced by (non-monetary) feedback about correct performance. The results obtained in the context of these experiments indicate that even the fully developed adult visual system exhibits significant and long-lasting improvements in performance after repeated training with near threshold visual detection tasks. Perceptual learning has been observed in a variety of perceptual tasks, such as enhancement in visual hyperacuity [94], size perception [95], contrast discrimination [96], orientation discrimination [97–99] and discrimination of motion perception [100]. Perceptual learning is, however, slow. It occurs gradually over hundreds of trials and mostly does not transfer between tasks [97,101]. However, transfer of perceptual learning across several perceptual tasks has been observed following extensive unspecific training with action video games [102]. In a typical perceptual learning experiment, subjects are instructed to repeatedly execute the same visual discrimination task and receive positive feedback about correct responses. Following extensive practice they gradually learn to deploy attention to stimulus relevant features [103]. Consistent with this hypothesis, Droll *et al.* [104] reported changes in the learning rate for stimulus orientation changes with increased practice. The observed improvement in performance coincided with an increase in the average number of fixations on the detected stimulus during the detection task, suggesting that subjects acquired more focused search strategies with increased practice.

Observed changes in attentional search strategies during perceptual learning are paralleled by neural changes in early visual areas (calcarine sulcus) during texture discrimination tasks [105]. Similarly, perceptual learning during contrast discrimination correlated significantly with a decrease of fMRI activity in visual cortex and several cortical regions associated with the attentional network (IPS) and eye movement generation (FEF, SEF) [96] and transfers about retinal locations [106].

In monkeys, perceptual learning has been found to accompany changes in the tuning characteristics of individual neurons. Extended training of orientation identification increased the tuning amplitude and narrowed the orientation tuning of neurons in the primary visual cortex [107]. Single cell measurements during perceptual learning of orientation discrimination at a later stage of processing in the ventral pathway showed similar changes in the response properties of V4 neurons [108]. In both studies, the slope of the orientation tuning curve that was measured at the trained orientation increased only for the subgroup of trained neurons, providing clear evidence for electrophysiological correlates of perceptual learning on a single neuron level.

Conclusion

We summarize evidence which suggests that human eye movements serve as an indicator of a human or monkey subject's knowledge about the distribution of possibly interesting and previously fixated target locations, as well as expectations about possibly interesting target locations. Eye movements serve the purpose of gathering and updating information across successive eye movements. Furthermore, we discuss recent experimental and behavioral evidence obtained during saccadic choice tasks in humans and non-human primates and the computational models which aim to explain the neural computations underlying this behavior. We present a computational framework which can account for the updating of eye movement goals based on the outcome of previous eye movements. This model framework can account for the observation that feedback provided repeatedly about the success of a visual decision induces persistent changes in sensory and motor processing. Similarly, feedback provided for correct performance during visual discrimination tasks causes gradual, long-lasting changes in early visual processing. These changes in visual processing are mostly shifts in attentional strategies and largely independent of the eye movement system.

Our model framework makes distinct predictions about the neural computations underlying voluntary and involuntary eye movement generation. According to our model, area LIP constitutes one part of a multi-area decision module where computations occur that assign the *relative* expected subjective value to any potential target for the next eye movement. Activity in area LIP also reflects updating and learning across sequences of eye movements as performed elsewhere in the brain. Future research is needed to test these assumptions and to determine the neural implementation of these computations (see Ref. [109] for an overview and introduction into non-spatial network models of LIP function).

Here, we highlight recent experimental evidence which demonstrates that the tracking of eye movements in visual search tasks allows one to track the neural processes underlying voluntary search behavior and involuntary reflexive behavior. We conclude that the tracking of eye movements constitutes a useful tool to assess how humans gather, integrate and process information in the context of simple laboratory experiments, as well as under natural viewing conditions.

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