

CHAPTER 23

Saccadic decision-making

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Abstract

The generation of a saccade may be considered the outcome of some decision-making process. Functional models of saccadic decision-making are based on the accumulation of sensory evidence in favour of various alternative movement programmes in a race to a decision threshold. The outcome of this race is affected by a number of decision-related variables such as the quality of sensory evidence, the prior probability of alternative movements, and the reward associated with the different movements. I review a selection of behavioural and neurophysiological studies on the influence of these variables on saccadic decisions, and relate these variables to the distinct mechanisms posited by models of decision-making.

Decision-making may be regarded as that internal process which produces behaviour, as manifest in the motor output of an organism (Glimcher, 2003b, 2003a). Behaviour may be in response to sensory stimulation, triggered by non-sensory factors or, most typically, some combination of the two. Motor responses to sensory stimulation may be anything from what are often thought of as primitive reflexes—indeed, these were the starting point of the physiological study of decision-making—to more complex patterns of motor output that are less deterministically linked to the sensory input.

Clearly saccadic eye movement generation is a long way removed from what may be regarded as 'volitional' decision-making that we typically associate with human behaviour. Nevertheless, it is appropriate to view these movements as the consequences of some decision-making process that is more complicated than those underlying the most direct sensory-motor responses. That is, saccades may be internally generated on the basis of non-sensory factors (e.g. I can choose to look to the right and up even in absence of any sensory stimulation), may be withheld altogether even when presented with a highly salient stimulus, and may be triggered in response to sensory stimulation. The mapping between sensory stimulation and saccadic eye movement response may be direct (such as in a typical visually guided saccade task) or more arbitrary and symbolic. Regardless of the complexity of the sensory-motor mapping, a decision is made: 1) to move the eyes, 2) where to move the eyes to, and 3) when to move the eyes. The limited resolution of human vision dictates that such decisions are made at regular, relatively short intervals (around 3 or 4 times every second).

In this sense, any chapter in this volume on saccadic eye movements may be regarded as being about saccadic decision-making. As a result, there will inevitably be some overlap between the topics addressed in this chapter and issues reviewed elsewhere in the volume. I will restrict the focus of this review to a discussion of: 1) the functional mechanisms that serve saccadic decision-making; 2) the representation within the saccadic system of decision-related variables such as sensory evidence,

prior probability and reward; and 3) whether and how these variables impinge on the mechanisms identified in models of saccadic decision-making.

Models of saccadic decision-making

Over the past two decades both behavioural and neurophysiological research on the saccadic system has started to address how saccade targets are selected in situations in which the system is confronted with a number of possible objects to look at (reviewed in Fecteau and Munoz, 2006; Schall and Thompson, 1999). Selectivity is studied by examining the accuracy and latency of target selection, as well as more dynamic variables such as saccade trajectories. The logic is straightforward: a more difficult selection process will be evidenced by less accurate saccades, triggered with longer latencies, and executed with more biased trajectories (either towards or away from the competing object location; see Chapter 5, this volume, as well as McSorley et al., 2006). Single-cell recordings from primate superior colliculus (SC) (McPeck et al., 2003; McPeck and Keller, 2002b, 2002a) and frontal eye fields (FEF) (Bichot et al., 2001; Schall et al., 1995; Thompson et al., 2005) in such paradigms have reinforced a view of target selection as a competitive process that is gradually resolved over time. Neurons with visual and/or motor responses in these structures will typically respond to any item that falls within their receptive or movement field. Over time, responses to non-selected items are suppressed in favour of neurons coding the selected, target location. This competitive process has been formalized at the functional level in the form of decision-field models.

Decision-field models

Decision-field models assume that the relevant parameters of movements towards the various response alternatives are coded in a continuous and dynamic activation field (Arai and Keller, 2005; Arai et al., 1999; Erlhagen and Schoner, 2002; Kopecz, 1995; Kopecz and Schoner, 1995; Ludwig et al., 2007; Trappenberg et al., 2001; Wilimzig et al., 2006). For instance, a generic saccadic 'motor map' may be conceptualized as a one or two-dimensional topographic representation of visual space (e.g. the amplitudes and directions of all different possible eye movements; see Fig. 23.1). Maps in which neighbouring units code nearby movement vectors are found throughout the saccadic eye movement system (e.g. in SC and FEF). An input into the system, which may be a localized visual stimulus or an internally generated movement plan, results in a broadly distributed pattern of activity. The peak of activity is centred on the movement vector associated with the input, but neighbouring vectors are also activated in the population code (e.g. Ottes et al., 1986; Goossens and Van Opstal, 2006; C.K. Lee et al., 1988; McIlwain, 1986). Fig. 23.1 illustrates a simple, two-item input which gives rise to two separate, broadly distributed activation patterns on the motor map.

The activity on the map evolves over time. For instance, the activity associated with one pattern may rise faster than that associated with the other, perhaps because of experimental instructions which may render one type of pattern more relevant than the other (e.g. 'look for squares'). Such computations are captured by the $f(input)$ term in Fig. 23.1, where f may represent anything from a simple linear transducer to more complicated and non-linear transformations of the sensory input. Units representing distant portions of space may mutually inhibit each other and nearby units may activate each other, in accordance with neurophysiological evidence from SC (Munoz and Istvan, 1998). In addition, units may 'leak' a certain proportion of the activity they are accumulating, which may be countered by some degree of recurrent self-excitation (Usher and McClelland, 2001; Wang, 2002; Wong and Wang, 2006). Regardless of the precise dynamics, the competition may be thought of as a parallel race to a response threshold. The saccade is executed soon after the threshold is reached, its target corresponding to the vector that won the race.

For such models to produce realistic variability in choice, latency and landing position, one or more sources of noise need to be assumed. For example, the input into the decision field may vary upon repeated presentation of the same stimulus configuration, as a result of internal noise in the transformation of the input. Additional noise is often added to the gradual evolution of activity on

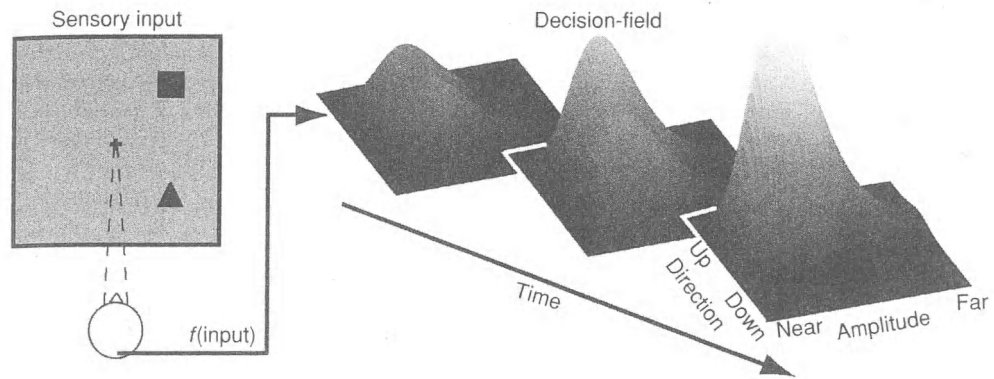


Fig. 23.1 Decision-field model of saccadic decision-making. An observer is presented with a test display and told to saccade to the square. The two potential saccade targets are represented by broadly distributed populations in a two-dimensional decision-field (r, θ). Due to the prioritization of squares over triangles (an operation assumed to occur in $f(input)$), the units representing the location of the square receive a stronger input. Over time the activity associated with the non-target is completely suppressed. The activity distributions in the decision field are based on a mapping of a 0.5-mm Gaussian activity profile in collicular coordinates to polar coordinates, according to the model of Ottes et al. (1986). Note that only the right visual field is represented.

the motor map over time. Together, this set of assumptions can account for an impressive array of data from a range of simple saccade target selection paradigms (Trappenberg et al., 2001). Decision-field models can provide an excellent functional description of the competitive interactions that take place throughout the saccadic eye movement system.

Evidence integration models

More abstract evidence integration models are based on a similar principle of the gradual evolution of noisy activity towards a response threshold (Luce, 1986; Ratcliff and Smith, 2004; Smith and Ratcliff 2004). Such models have been widely used in cognitive psychology to account for relatively simple decisions such as whether a string of letters is a word or non-word, whether a test item featured on a study list presented earlier, etc. Models in this class include a variety of sequential sampling models that are characterized by temporally dynamic noise (often referred to as 'wiener noise' in the continuous time domain) that is added to each sample. Examples of sequential sampling models are random walk models (Laming, 1969; Link and Heath, 1975), the widely used diffusion model (Ratcliff, 1978; Ratcliff and Rouder, 1998; Ratcliff and Smith, 2004), and accumulator models (Usher and McClelland, 2001; Vickers, 1970). Other evidence integration models do not assume that the temporal samples themselves are noisy (Brown and Heathcote, 2005, 2008; Carpenter and Williams, 1995). These models are often also referred to as accumulator models, but they are technically not in the same class as the sequential sampling models. The feature that unites both noisy and ballistic accumulator models is their absolute stopping rule: the decision process finishes as soon as an accumulator reaches a criterion amount of evidence. In the random walk and diffusion models, the criterion is a relative one: it corresponds to a certain amount of *net* evidence in favour of one particular alternative, relative to the other alternative(s).

In the saccadic domain one particularly simple model is the LATER (linear accumulation to threshold with ergodic rate; Carpenter and Williams, 1995) model developed by Roger Carpenter and colleagues (see also Sumner, Chapter 22, this volume). LATER assumes that activity associated with a particular saccade programme (i.e. movement vector) rises gradually towards a threshold. Importantly, the accumulation rate is assumed to vary randomly from one saccade to the next, according to a Gaussian distribution. This single noise source is sufficient to account for the latency

variability observed in simple visually guided saccade tasks. Application to competitive situations in which there are multiple items to choose from requires an extension of this basic idea to multiple accumulators racing against each other. As in the dynamic field models, this competition may involve lateral inhibition, self-excitation, and leakage, which would make the accumulation paths non-linear (Brown and Heathcote, 2005; Leach and Carpenter, 2001; Ludwig et al., 2005a; Usher and McClelland, 2001). Fig. 23.2A illustrates this competitive process, with lateral inhibition, for the same two-alternative decision that was illustrated in Fig. 23.1. As in that example, the activity associated with one particular saccade programme (e.g. the one for the square) rises more rapidly than the activity associated with the competitor and ends up winning the race.

One way to view this accumulator model is as a reduced version of a full decision-field, consisting of just a small number of units that represent the discrete choices available to the decision-maker. Each of these units may be thought of as representing the mean activity of the different neural populations encoding the response alternatives (Wong and Wang, 2006). In many experimental paradigms the different potential saccade targets are well separated, so that the movements can be clearly and discretely classified as being directed towards one pattern or another. To model choice and latency variability in such paradigms then, this simplified representation is sufficient.

Finally, it should be noted that models involving competitive accumulation towards an absolute threshold are difficult to distinguish empirically from the noisy accumulation of net evidence towards a relative criterion, as assumed by the bounded diffusion model (Bogacz et al., 2006; Ratcliff and Smith, 2004). In the diffusion model, as applied to two-choice tasks, there is only a single 'accumulator' which moves through a decision space (analogous to the Brownian motion of a particle) towards one of two boundaries which represent the available response alternatives. The consequence is that motion towards one particular alternative necessarily implies a shift away from the competing alternative. The same inhibitory dynamics may be achieved through lateral inhibition between multiple accumulators that race to a single, common threshold.

Representation of decision-related variables

Evidence integration models suggest what functional mechanisms may underlie selection from multiple competing peripheral targets. I will now turn to the question of whether the saccadic eye

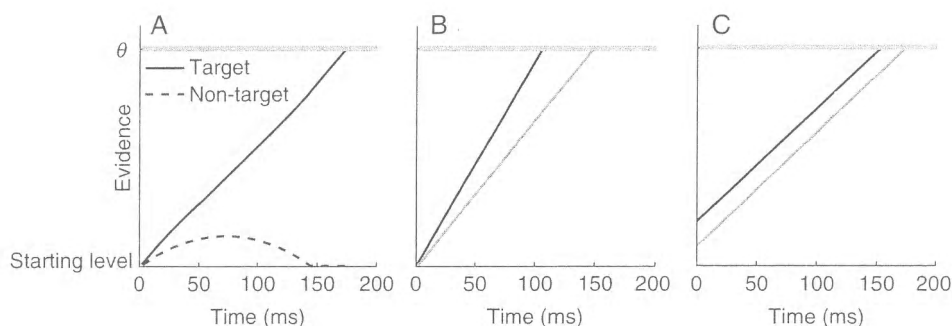


Fig. 23.2 Accumulator model of saccadic decision-making. A) Competition between two potential saccade targets is resolved over time through lateral inhibition, just as in Fig. 23.1. A saccade is initiated when one accumulator reaches threshold. The saccade target is determined by the winning accumulator. B) As reviewed in the 'Representation of decision-related variables' varying the quality of sensory evidence is best represented by changing the rate of accumulation. Weaker evidence is indicated by the lighter shaded, slower accumulators. C) The effect of varying the prior probability of a particular movement vector is best represented by changing the starting level of accumulation. Less probable responses are represented by lower initial levels of activation, as indicated by the lighter shaded accumulators.

movement system is capable of representing information that a sensible decision-maker would take into account. Neurophysiological, and to some extent behavioural, work has focused on three decision-related variables: strength of sensory evidence, prior probability, and reward (or, more precisely, relative expected utility). I will discuss each of these three variables in turn and attempt to link them to the functional mechanisms described in the previous section.

Sensory evidence

Evidence refers to the extent to which the sensory data provide support for one hypothesis relative to one or more competing hypotheses. In the context of saccadic decisions, the hypotheses correspond to the different possible saccade targets. The question is then whether the sensory evidence calls for a saccade to one potential target in favour of the others, and whether the strength of that evidence affects the decisions made in a predictable and adaptive manner.

Possibly the most straightforward manipulation of sensory evidence is simply to vary the visibility of a peripheral target (Ludwig et al., 2004; White et al., 2006). Unsurprisingly, in visually guided saccades to a single target the latency of the saccade decreases as the luminance contrast of the peripheral target increases. This is consistent with the idea that improving the sensory evidence enhances the rate of accumulation, which results in a shorter decision latency (see Fig. 23.2B). However, the visually guided saccade paradigm does not involve a decision between multiple competing response alternatives.

To examine saccadic decision-making in such competitive conditions, Ludwig et al. (2005a) (see also Caspi et al., 2004) presented human observers with two peripheral luminance patterns. The luminance contrast of both patterns was re-sampled every 25 ms, independently from partly overlapping probability distributions, so that one of the patterns had a slightly higher average contrast. Observers were asked to saccade to this higher contrast pattern. As a result of the temporal noise in the stimulus sequence, the sensory evidence provided in this paradigm is uncertain. Under these conditions, temporal integration of the evidence is a good strategy to decide which pattern to look at.

The sensory uncertainty introduced by the external noise enabled Ludwig et al. (2005a) to identify over what time window the sensory evidence was taken into account. Imagine a trial on which, through random sampling, the designated 'non-target' pattern (i.e. the one with the lower average contrast) happened to be a little brighter than the actual target for some brief period of time, shortly after the onset of the two patterns. If the observer chose to fixate the non-target pattern on that trial, this would indicate that the sensory evidence provided in this period of time was taken into account in the decision process. Over the course of many trials, this type of regression of the decisions against the noise in the stimulus reveals the temporal window of evidence integration.

Surprisingly, given average saccade latencies on the order of ~300 ms, this window was restricted to approximately the first 100 ms of stimulus presentation. Subsequently, Ludwig (2009) has demonstrated that the results from this study can be accounted for using the evidence integration framework. In this instance, the evidence is represented by temporally blurred versions of the sequence of luminance contrast values. The net evidence is computed as the difference between these temporally filtered internal responses. This difference is integrated over time to one of two boundaries, corresponding to the two decision alternatives. As a result, temporary variations in the strength and direction of sensory evidence result in corresponding temporary, blurred variations in the rate of accumulation. This model could account for the overall accuracy of the saccadic decisions, the latency distributions of correct and error decisions, as well as results from a different experiment in which the temporal availability of *useful* sensory evidence was manipulated systematically (Ludwig et al., 2005b, experiment 2).

Newsome, Shadlen, and colleagues have examined the neural mechanisms underlying the integration of sensory evidence during perceptual decisions about visual motion (Britten et al., 1992; Ditterich et al., 2003; Gold and Shadlen, 2003, 2000; Kim and Shadlen, 1999; Newsome et al., 1989; Palmer et al., 2005; Roitman and Shadlen, 2002). Figure 23.3 illustrates the classic paradigm.

The observer (mostly non-human primates) fixates a point on the screen and is presented with a central random dot kinematogram (RDK). This is a pattern consisting of a number of randomly moving dots. A subset of the dots, however, moves in the same direction. For instance, 10% of the dots may move coherently to the left, in which case the observer has to make a saccade to the marker object located left of the central RDK pattern. By varying the proportion of coherently moving dots (the motion coherence), the strength of the sensory evidence is manipulated. The evidence in favour of either option is weak when the coherence is close to 0%, but less and less ambiguous for higher coherence values.

Note that although the task calls for a saccadic decision, the mapping between the available saccade targets and the sensory evidence used to make the saccadic decision is symbolic and rather arbitrary. The main focus of these studies is on *perceptual* decision-making, but saccadic responses are used because the basic neurophysiological mechanisms underlying saccade generation are relatively well understood. In terms of the definition of decision-making provided at the start of this chapter, the saccadic system is treated as a model system to study the neural signature(s) of 'that internal process which produces behaviour'. It is important to bear in mind that in more naturalistic conditions, the sensory evidence in favour of a peripheral saccade target is typically bound to that peripheral location. In that regard, it could be argued that the decision-making task of Ludwig et al. (2005b) has greater ecological validity.

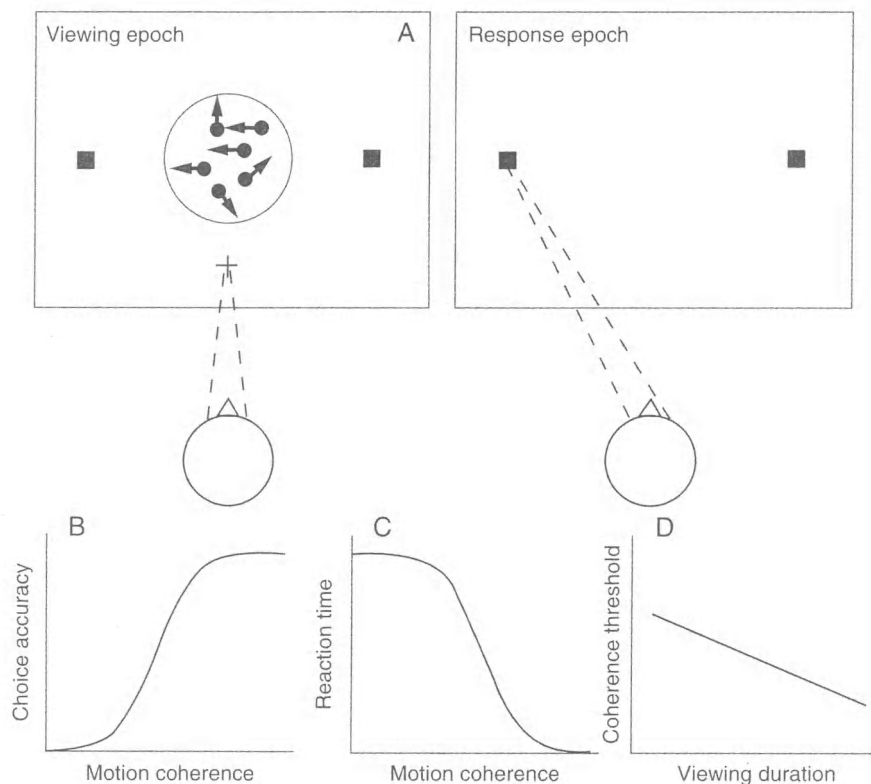


Fig. 23.3 Visual-saccadic decisions about perceptual motion. A) The observer views a RDK pattern in which only a subset of the dots move coherently in one direction. After a delay (determined by the experimenter or by the observer) the motion direction is signalled with a saccade to one of the two peripheral markers. B–D) Fictitious data showing how choice accuracy (B) and reaction time (C) vary as a function of motion coherence, and how motion coherence thresholds (D) for direction discrimination improve with viewing time.

In the RDK task observers do clearly adjust their behaviour in accordance with various manipulations of the sensory evidence. Their choice accuracy improves monotonically as a function of motion coherence (see Fig. 23.3B for a hypothetical example). For a typical viewing duration, performance ranges smoothly from close to chance for weak coherence to nearly perfect for high coherence (typically >25%; Gold and Shadlen, 2003). More interestingly, accuracy improves with increasing viewing duration in that motion coherence thresholds decrease as a function of viewing time (see Fig. 23.3C). This finding suggests strongly that the observers are taking advantage of the increase in viewing time by collecting more sensory evidence. Finally, in a reaction time version of the task (in which the viewing epoch is terminated by the observer's saccadic response) the decision time decreases with increasing coherence (Roitman and Shadlen, 2002; see Fig. 23.3B). This result indicates that when the evidence is weak, observers elect to wait longer and collect more data in order to make a more informed decision. Behaviourally then, it is clear that the saccadic system is capable of taking sensory evidence into account.

In terms of the underlying physiological mechanism, it is well established that directionally selective neurons in primate brain area MT respond to such motion patterns (Britten et al., 1992). A pool of MT neurons with the same direction preference (say leftward) then provides an ongoing, momentary estimate of the sensory evidence in favour of responding to the marker object that corresponds to this direction. Of course, a pool with the opposing directional selectivity will encode the evidence in favour of the alternative choice option. It is important to note that this evidence is momentary: due to the stochastic nature of the RDK pattern the evidence in favour of one or the other alternative will fluctuate over time.

Two pieces of evidence suggest very strongly that brain structures that are involved in saccade generation perform a gradual accumulation of the fleeting sensory evidence. First, micro-stimulation of the frontal eye fields results in evoked saccades with endpoints that are biased in the direction of the ensuing target-directed saccade (Gold and Shadlen, 2000). This bias indicates that the evoked saccade is some weighted combination of the vector coded by the stimulated site and the decision-related vector (i.e. to the marker that corresponds to the perceptual decision). Critically, the magnitude of this bias increases with viewing duration and motion coherence in a similar manner as behavioural choice accuracy, suggesting that the decision to make a saccade to the peripheral marker evolved gradually over time. Second, single cell recordings from LIP show that the activity of neurons coding the decision-related movement gradually increases over time (Gold and Shadlen, 2003; Huk and Shadlen, 2005; Roitman and Shadlen, 2002). The rate of increase is systematically related to the motion coherence so that strong evidence results in a faster increase than weak evidence. In the reaction time version of the task it appears that, when aligned to movement onset, neural activity reaches a critical level that is independent of motion coherence (see also Horwitz and Newsome, 2001; Kim and Shadlen, 1999, for similar signals in SC and in dorsolateral pre-frontal cortex).

These data can be modelled by assuming that LIP neurons integrate sensory evidence over time up to a criterion threshold, where evidence is the *difference* in the sensory response of pools of MT neurons coding the alternative directions used in the experiment (Ditterich, 2006b, 2006a; Mazurek et al., 2003). This variable is closely related to the optimal decision variable, namely the (log) likelihood ratio (Gold and Shadlen, 2001; Green and Swets, 1966). Human data from this paradigm are also successfully modelled under the assumption that the strength of sensory evidence affects the (mean) rate of evidence accumulation up to a decision threshold (Reddi et al., 2003).

Prior probability

The prior probability of an event or state is the probability of that event occurring, regardless of the momentary evidence. Consider the domain of medical diagnosis. A set of symptoms (evidence) may typically be attributed to various different possible underlying causes (hypotheses). Unless the evidence overwhelmingly points to one particular condition over any other, a sensible diagnosis takes into account how likely the various conditions are to occur in the first place. This idea is formalized in Bayes rule, which combines the current evidence (likelihood) with the prior probability of

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some event. In the present context, the question is whether the prior probability of a particular movement vector being required plays a role in saccadic decision making.

In this domain, a straightforward manipulation has been to vary target location (un)certainly. For instance, in a simple visually guided saccade task variation in the probability of the target appearing in one location results in a strong modulation of the saccade latency (Carpenter, 2004; Carpenter and Williams, 1995). Unsurprisingly, saccade latency increases with greater target uncertainty. Using LATER, the change in the reaction time distributions was best accounted for as a change in the separation between the starting point of accumulation and the threshold (Carpenter and Williams, 1995): increased target uncertainty results in an increase in this separation. Note that such a change may be brought about either by decreasing the starting point or increasing the threshold. However, in the context of a probabilistic interpretation of this kind of model, it is most natural to assume that variations in prior probability affect the starting point (see Fig. 23.2C). Saccade vectors that are unlikely to be called for will start off from a lower level, compared to movement programmes that are relatively more likely to be executed. It is distinctly possible that this modulation represents a purely local effect (Waltheve and Gilchrist, 2006), in that every time one particular saccade (say leftward) is executed the starting point for that (left) programme is increased for the next trial. Over the course of a whole experiment then, this would result in a relatively decreased (mean) starting point for less likely saccade vectors.

Another way to vary target uncertainty is to manipulate the number of choice alternatives. Hick's law states that (manual) reaction time increases logarithmically with the number of choice alternatives (Hick, 1952). Hick's law has been observed with saccadic responses, provided that the task involves a transformation between the stimulus and saccadic response (e.g. antisaccades in Kveraga et al., 2002; mapping a colour cue to a location in K.-M. Lee et al., 2005). The latency distributions from K.-M. Lee et al. (2005) (where the number of alternatives varied from 1–8) were fit with the LATER model. These fits were—again—more consistent a change in the starting point of accumulation with varying numbers of alternatives.

Basso and Wurtz (1998, 1997) performed a series of similar experiments while recording from SC. Monkeys were presented with an array of objects arranged around a central fixation point. The size of the array ranged from 1–8. After a delay one of the items dimmed; this item was the saccade target. When the central fixation point extinguished the monkey was required to make the target-directed saccade. The critical interval in this paradigm is that between array onset and target specification. Build-up neurons in the intermediate layer of the SC showed a reduction in their activity as target uncertainty increased. Once the target was specified these neurons increased their activity more when target uncertainty was high, presumably to cover the extra ground needed to reach the common saccade trigger threshold. Indeed, the immediate, presaccadic burst of both build-up and burst neurons was not affected by target uncertainty. A similar modulation of activity may be seen in LIP neurons when a central cue signals which of two targets to saccade to and the prior probability of one or the response is varied (Platt and Glimcher, 1999).

Both modelling of behavioural results and neurophysiological evidence then suggest that effects of prior probability are mediated by varying the separation between the starting point of evidence integration and the decision criterion (see K.-M. Lee and Keller (2008) for tentative evidence for an effect of prior probability on the threshold of FEF visual-movement neurons). However, a recent study by Liston and Stone (2008) suggests that prior probability may also affect the sensory response that, presumably, forms the input into the oculomotor system. In this study, observers performed a two-AFC saccadic contrast discrimination task. A bias in the location of the higher contrast target influenced the saccadic decisions in a predictable fashion: choice was biased towards the more probable location and saccade latency was shorter. After completing the saccade a test disc appeared and observers were asked to indicate whether the previously fixated saccade target or the subsequent test stimulus was brighter. The perceptual decision task essentially probed the perceived contrast of the saccade target. If the bias induced by the prior probability variation affects the sensory response to the target, this should be manifest in the perceptual judgement. Indeed, Liston and Stone (2008) reported that increased estimates of contrast gain and internal noise for the more likely target location. These results are consistent with a multiplicative weighting mechanism that amplifies the noisy

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internal sensory response, before being transmitted to the oculomotor system. In the context of accumulating sensory evidence, this scheme is more consistent with an effect of prior probability on the rate of accumulation.

Finally, even in the absence of any real variation in the prior probability of certain locations becoming behaviourally relevant, humans (Anderson et al., 2008; Carpenter, 2001) and monkeys (Fecteau and Munoz, 2003) frequently develop idiosyncratic motor biases in that a particular response is favoured (e.g. a preference for successive movements in the same direction; Anderson et al., 2008). Such biases may be interpreted as internally generated, misguided estimates of prior probability and seem to be best accounted for in terms of an offset in the starting point of accumulation (Gold et al., 2008). Again, it is possible this offset is the result of a purely local mechanism that generates trial-by-trial adjustments of the starting point.

Reward

As with movements that are a priori more likely to be commanded, responses that are associated with larger expected rewards may also be expected to be weighted more heavily in the saccadic decision-making process. Indeed, the effect of reward magnitude on LIP activity is very similar to that of prior probability in the cued saccade paradigm of Platt and Glimcher (1999). Early activity (i.e. before specification of the movement target and the associated pre-motor ramp to threshold) is higher for neurons representing higher value choices, even when the prior probability of both responses is equal (see also Dorris and Glimcher, 2004).

These neurons also appear to be involved in tracking local variations in reward in a free-choice paradigm (Sugrue et al., 2004). In this paradigm the monkey is presented with two choice alternatives of different colours and is free to choose to look at either target. In blocks of 100–200 trials the response alternatives were associated with different rewards, which changed unpredictably. Behaviourally, the challenge is to match choice to the relative rewards. The monkey's performance was modelled by computing the expected relative reward from the different options, through leaky integration of the recent reward history (see also Corrado et al., 2005). This quantity, termed 'local fractional income', guides decision-making on the current trial. Importantly, LIP activity during the delay between the onset of the targets and a subsequent 'go' signal was correlated on a trial-by-trial basis with local fractional income: activity was higher for the option that was more generously rewarded in a relatively short window of recent choices. Interestingly, unlike in the cued saccade paradigm (Platt and Glimcher, 1999) this modulation evolved gradually over time during the delay period. That is, the LIP response to the onset of the two targets was independent of local fractional reward (perhaps because the reward was related to the colour of the peripheral target, rather than the location), but this dependency manifested itself gradually and lasted up to the onset of the saccade.

Reward-related modulations of neural activity can be found in a variety of brain areas (Sugrue et al., 2005), but in the context of saccadic decision-making the basal ganglia are a structure of particular interest. The basal ganglia are important for motor control in general. The caudate nucleus (CN) in the dorsal striatum and the substantia nigra pars reticulara (SNr) are involved in saccade generation. Briefly, the SNr tonically inhibits the SC motor map. For a saccade to occur the SC needs to be disinhibited, which is mediated by the inhibitory projection from CN to SNr (Hikosaka and Wurtz, 1989; Hikosaka et al., 2006). Activation of the CN, in turn, is achieved through cortical inputs from a variety of areas, including the FEF and LIP. The modulation of SC build-up neurons with prior probability reviewed above (Basso and Wurtz, 1998, 1997) appears to be preceded by a pause in SNr activity, the extent of which is also related to the level of target uncertainty (Basso and Wurtz, 2002).

In a similar vein, CN neurons are responsive to reward magnitude in that larger rewards trigger greater levels of CN activity (Lauwereyns et al., 2002). In a visually guided saccade task with unequal rewards associated with different target locations, the CN neurons coding 'richer' target locations showed elevated levels of activity before the target is presented (i.e. in the delay between fixation point onset and target presentation). Given the inhibitory connection between CN and SNr, it appears that the increase in CN activity would manifest itself as increased oculomotor readiness at

the collicular level, similar to that seen in manipulations of prior probability. Indeed, the latency of saccades to the high-reward target location is typically reduced. It has been hypothesized that the reward-modulation of CN neurons is shaped through dopaminergic inputs into the CN that modulate the synaptic efficacy of the cortical inputs (Hikosaka et al., 2006). These dopamine neurons appear to encode a quantity related to the difference between predicted and obtained rewards (Hollerman and Schultz, 1998): a larger obtained reward than expected results in an increased response and a smaller than expected reward results in response suppression. As a result, these neurons may be regarded as computing a prediction error term that enables learning of the reward structure of an environment (Nakahara et al., 2004; Schultz, 1998).

These physiological data seem to point towards reward affecting the oculomotor readiness, which corresponds to the functional mechanism of the starting point of evidence accumulation. However, human behavioural evidence on this issue is scarce. The study reviewed in the previous section by Liston and Stone (2008) also included a manipulation of reward frequency to induce a saccadic motor bias. Like the variation in prior probability in that study, the bias in reward frequency associated with different locations affected the internal perceptual response, which a priori is more consistent with an effect on the rate of accumulation.

Conclusions

It should be noted that many of the reviewed studies on decision-related variables in the oculomotor system are not so much concerned with the saccadic system itself, but use the system in order to learn about more general principles of decision-making that may apply to more complex decision-problems and more complex patterns of motor behaviour. Nevertheless, what these studies show is that variables such as evidence, prior probability and (expected) reward are represented in neural mechanisms that play a role in saccade planning and generation. Moreover, the behavioural effects of these variables can be mapped onto functional mechanisms posited by decision-field and evidence integration models of saccadic decision-making. These models are based on the idea of accumulating sensory evidence up to a response threshold. Neurophysiological and behavioural work indicates that the (momentary) strength of sensory evidence acts upon the rate at which activity rises to the response threshold. Variations in prior probability and reward appear to act predominantly upon the starting level of accumulation, giving more likely and rewarding saccade targets a head-start in the race to threshold.

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