OPINION

Seeing at a glance, smelling in a whiff: rapid forms of perceptual decision making

Naoshige Uchida, Adam Kepecs and Zachary F. Mainen

Abstract | Intuitively, decisions should always improve with more time for the accumulation of evidence, yet psychophysical data show a limit of 200–300 ms for many perceptual tasks. Here, we consider mechanisms that favour such rapid information processing in vision and olfaction. We suggest that the brain limits some types of perceptual processing to short, discrete chunks (for example, eye fixations and sniffs) in order to facilitate the construction of global sensory images.

For many years, psychologists have used human psychophysical data to build abstract models of information processing in various cognitive and perceptual tasks. These models focus mainly on two key variables from the data: the speed and the accuracy of decisions. More recently, the application of psychophysical techniques to animals has made it possible to test these models directly, using techniques for recording from individual neurons. Studies in monkeys performing a visual motion discrimination task have provided remarkable confirmation of several key assumptions of a widely used model known as an integrator or accumulator model[1]. Because integration in these data extends over timescales of seconds or more, whereas the intrinsic timescales of most neuronal and synaptic mechanisms are relatively short (<200 ms), these studies raise what seems to be an important conundrum: how can relatively fast neural processes be assembled to produce such slow integration processes? As a result, a great deal of recent experimental and theoretical attention has focused on understanding the mechanisms underlying integration and the accumulation of evidence[2–7].

Despite the importance of long timescale integration in certain perceptual tasks, here we review psychophysical data that demonstrate that a much wider range of perceptual decisions are not only performed relatively rapidly, but, perhaps surprisingly, cannot be improved by deliberation beyond a much shorter timescale (~200–300 ms). The immediate implication of these data is that special circuits for neural integration are not required to explain most types of perceptual decision made by animals or humans. Therefore, we argue that integrators should not be considered as a universal mechanism of decision making, but rather as specialized higher cognitive mechanisms engaged under a circumscribed set of conditions. So, to understand the basic process of decisions, attention needs to be focused elsewhere.

The goal of this perspective is to provide insights into which types of task admit integration, which do not, and, most importantly, why. We take the following strategy. First, we provide some background on how temporal integration is modelled and inferred from data. Next, we take a closer look at psychophysical data from different types of perceptual discrimination in two contrasting sensory modalities: vision, for which a wealth of psychophysical and neural data are available, and olfaction, for which studies in rodents have begun to explore similar issues. We then discuss the mechanisms that might determine the relevant timescale of temporal integration in different types of task, highlighting the importance of sensory adaptation, temporal correlations in noise sources and mechanisms of integration. Finally, we consider the advantages of rapid perceptual decision making. Specifically, we suggest that the discrete nature of sensory sampling — saccades in vision and sniffs in olfaction — may reflect evolutionary adaptations for rapid information processing that limits the processing of low-level information to short chunks to facilitate the assembly of global perceptual images.

Temporal integration: models

For some time psychophysicists have studied the mechanisms of decision making by making quantitative measurements of behaviour in simple tests in which a participant repeatedly chooses between two responses. The crucial measurement in these studies is the distribution of response times[8]. Response times fluctuate from trial to trial, and their distribution varies systematically depending on experimental conditions (for example, easy or difficult problems) or instructions (for example, asking the subject to choose accurately or rapidly). To account for both the variability and the dependency of response times on different factors, psychophysicists constructed various mathematical models, the most widely used of which are known as integrator or accumulator models[8,9]. In one of the simplest of this class of models, the diffusion or random walk model, a decision device accumulates evidence (signals derived from sensory systems) for or against alternative options (typically two choices). A decision is reached when the accumulated evidence (the decision variable) crosses a specified threshold (FIG. 1).

A key assumption of integrator models is that uncertainty in choices and the variability in response times are due to the presence of noise. Noise may be present in the stimulus itself or may be introduced by the nervous system. Regardless of the source of noise, a decision-making device should average out noise in order to achieve more accurate decisions, and integrator models readily capture this function. Despite their simplicity, integrator models can explain a wide range of response time data from human psychological experiments[8,10–13] (BOX 1).

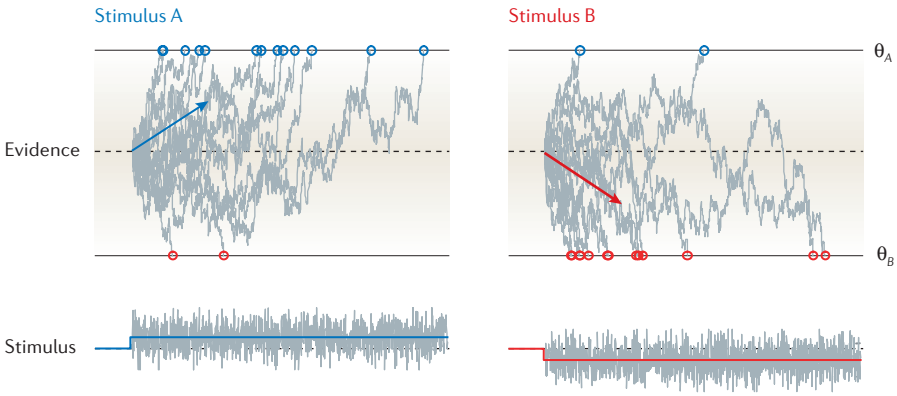


Figure 1 | **Integrator model.** Integrator models have been used successfully to explain various types of response time data. One class of integrator model, the drift diffusion model, is depicted. The decision device receives stochastic input (stimulus, bottom) representing evidence for two competing alternative choices (A and B). The integrator accumulates evidence until it reaches one of the two thresholds (θ_A, θ_B), at which point a decision is emitted. The graphs show the time course of accumulated evidence for several trials for two different stimuli with different mean signal strengths or drift rates (slope of the arrows). The input noise introduces stochasticity in the accumulation of evidence (grey traces represent different trials with different instantiations of noise). This creates trial-by-trial variability in response times and choices (blue circles, choice A; red circles, choice B).

Psychophysics: timescales of integration

Although the basic assumptions of integrator models dictate the qualitative relationship between speed and accuracy, they do not specify the timescale over which information accrues. Integration might occur over only a few milliseconds or across several seconds, depending on the parameters of the model. As we discuss in the following section, psychophysical experiments shed light on the timescales of integration for different perceptual tasks.

Vision: evidence for integration. One of the best-studied perceptual decision tasks is based on the motion of random dots. In this task, participants view a field of flickering dots, some of which move randomly and some of which move coherently in one of two possible directions. The participant must report the net direction of motion. As the fraction of coherently moving dots is decreased, motion signals get weaker and the task becomes more difficult. The impact of temporal integration in this task has been investigated in humans and monkeys in two ways. First, by varying the viewing time and measuring the discrimination threshold for each duration it was shown that sensitivity increases with viewing times up to ~2 s[14,15]. Then, in a reaction time version of this task, it was found that as motion coherence was decreased, reaction times increased from 300 to >800 ms[16,17].

These behavioural results provide a sterling example of an apparently elementary perceptual discrimination (albeit a rather unnatural one) that can benefit from prolonged integration over many hundreds of milliseconds. Moreover, not only can the data be fit quantitatively with a simple diffusion model[17] (BOX 1), but neurophysiological recordings and manipulations have provided a remarkable picture of a neural integrator that might actually explain these behavioural observations[16,18–20]. In a series of elegant studies, Shadlen, Newsome and colleagues showed that neuronal activity in the parietal cortex (the lateral intraparietal area, LIP) ramps up at a rate correlated with the strength of the motion signal until the activity reaches a level that is constant across motion strengths, as if a decision threshold was reached[16,19,21–23]. This pattern of firing matches quite closely to what is expected of the decision variables posited by integrator models[1,22]. Further evidence supporting the integrator model comes from microstimulation experiments used to read out the state of the decision variable[24,25]. Although behavioural data might be fit by different types of model (for an example, see REF. 26; for a detailed discussion, see REF. 17), these and related physiological experiments provide relatively direct evidence supporting the idea that a process of accumulation of evidence, as posited by integration models, underlies the decision process during the random dot motion task.

Olfaction: reaction time studies. For a comparative view of a strikingly different sensory modality, we consider odour perception. Despite the conventional idea that olfaction is a slow sense, Karpov[27] reported some time ago that rabbits can discriminate odours in a single sniff of ~250 ms. Several subsequent studies have shown that elementary olfactory discrimination or detection tasks can be executed rapidly[28–30]. However, if performance on such tasks saturates rapidly simply because the problem is too easy, there would be no room for improvement by the accumulation of more evidence. Therefore, it is important to challenge participants with perceptually difficult discriminations.

Two recent studies addressed the issue of olfactory integration in rodents[31,32]. Uchida and Mainen measured response times in rats using a two-alternative choice reaction time task[31]. In this task, rats were trained to respond to different odours at a left or right spatial choice port. Discrimination difficulty was varied, first by using odour pairs with different levels of similarity and then by requiring the rat to respond to the dominant component in binary odour mixtures. With interleaved mixture stimuli, performance accuracy ranged from ~95% for pure odours to ~60% for the hardest mixture stimuli. Regardless of the stimulus, rats performed rapidly: median odour sampling times were ~300 ms, increasing by only ~35 ms from the easiest to the most difficult problems. Using a similar task, Abraham and colleagues also found rapid olfactory decisions (~300 ms) and a larger increase in sampling times with stimulus difficulty (~80 ms)[32]. Nevertheless, the small effect of difficulty on response time in these studies indicates that integration was limited to a much shorter time window than for random dot motion. Because performance on the hardest stimuli in the rat olfactory experiments was not as good as it could be (that is, not saturated), it would appear that these decisions might benefit from longer integration times, but they did not. Therefore, a central question raised by these studies concerns what accounts for this apparent failure to integrate.

Motivation and the speed–accuracy tradeoff. It is well known from human reaction time studies that it is possible to change the apparent integration time by instructing participants to perform more accurately or more rapidly, a phenomenon known as 'speed–accuracy tradeoff' (BOX 1). Speed–accuracy tradeoff could account for different timescales of integration using the same universal integrator mechanism. In principle, this could explain the longer integration period in the random dot task compared with the much shorter periods of integration

Box 1 | **Three speed–accuracy relationships**

Speed and accuracy in perceptual decisions show characteristic relationships. There are at least three psychophysical experimental contexts in which the relationship between speed and accuracy has been studied, each of which can be explained well by simple integrator models.

Sampling time manipulation

Psychophysics. When the experimenter limits the duration of the stimulus and/or sets a deadline for response time, performance accuracy decreases with shorter sampling times[93].

Model. When accumulation of evidence is halted and/or a response is forced before reaching threshold, integration is abridged (that is, less averaging or improvement in signal-to-noise ratio occurs), resulting in poorer performance. Panel **a** shows a comparison between longer and shorter stimulus sampling. Left, a sample path and path distributions (grey arrow) are shown. Right, a schematic of the relationship between sampling time and accuracy.

Speed–accuracy tradeoff

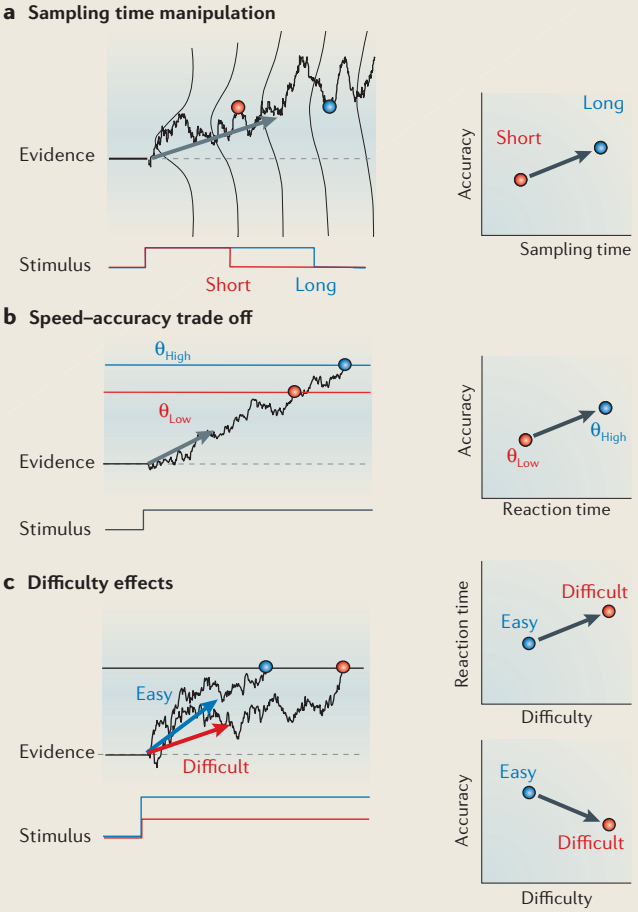
Psychophysics. When humans are instructed to perform rapidly, accuracy drops. When instructed to emphasize accuracy, performance slows. Traditionally, this is the technical definition of 'speed–accuracy tradeoff'[8,94].

Model. In the integrator model, when the decision threshold (θ) is high, more accumulation is required before making a decision, producing more averaging and therefore slower but more accurate decisions[8]. Panel **b** shows a comparison between a high and low decision threshold.

Difficulty effects

Psychophysics. When a participant is free to choose when to respond (a reaction time task), average reaction times increase with difficulty[8].

Model. Evidence for difficult problems accrues more slowly; therefore, it takes more time on average to cross the decision threshold. Panel **c** shows a comparison between an easy and a difficult stimulus.



observed in the olfactory discrimination task. The primates might have been working at a higher accuracy while sacrificing speed, whereas the rodents could have performed quickly by sacrificing accuracy. Of course, the much smaller difference between rats and mice in similar olfactory tasks could also be explained in the same manner[33]. With respect to the integrator model, all that is required is a change in the decision threshold (BOX 1).

The ideal way to test this idea would be to ask the rodents to slow down and be as accurate as possible, which is obviously not possible with animals. Instead, the animals' performance must be manipulated by changing task parameters such as reinforcers (rewards and punishments) that motivate behaviour. Zariwala *et al.* varied a number of task parameters in order to motivate rats to slow down and improve performance[34]. Longer and fixed delays to reward, sessions with higher reward rates, and punishments with time outs (inter-trial intervals) or air puffs all resulted in the rats slowing down (independent of difficulty) without improving their performance[34]. Although the rats were sensitive to the incentives to respond more carefully, they did not readily translate these incentives into the increase in performance and reaction times expected for increasing the threshold in an integrator model (BOX 1). Although the ability of rats to integrate beyond tens of milliseconds during other types of olfactory discrimination cannot be strictly ruled out, the results of these experiments suggest that a short apparent integration timescale is neither a result of saturation of performance nor a question of motivation. Rather, they point to the conclusion that integration mechanisms are not universal, and may depend instead on specific properties of the task and the neural structures that underlie performance.

Limits on integration. Although the two examples described above represent contrasting sensory modalities as well as contrasting integration timescales, it does not seem to be the case that vision is always slow and deliberative. We know that natural images can be classified reliably using very brief (20–40 ms) viewing times[35,36], even when the effect of afterimages was blocked using backward maskers[37]. Nevertheless, it may be noted — as we did when considering easy odour tasks — that such stimuli are too easy and performance may saturate after brief exposures owing to a ceiling effect. However, the impact of viewing time has also been considered in studies that probe psychophysical thresholds (for example, by reducing the contrast of a stimulus) and thereby avoid ceiling effects. These studies show that for many tasks the timescale of performance improvement in human vision is limited, as it appears to be in olfactory discrimination tasks in rats, to 100–300 ms. Such tasks include line detection[38], vernier acuity[38], contrast sensitivity[39,40], motion velocity discrimination[41,42] and stereoscopic depth discrimination[43,44] (but, for a contradictory report, see REF. 45). It is instructive to note that even motion discrimination in a random dots task fails to benefit from long integration when the difficulty is varied by changing the contrast of each dot while keeping motion coherence constant. In this

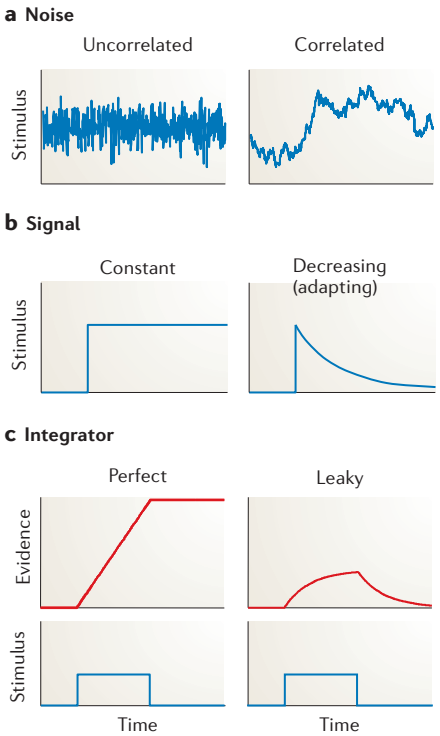


Figure 2 | **Mechanisms that may limit the timescale or effectiveness of temporal integration. a** | Temporal correlation in noise. Integration improves the signal-to-noise ratio by averaging out noise over time. This process is more effective when noise is temporally uncorrelated (left). When noise has temporal correlations (right), the efficiency of integration decreases. Temporal correlations may be present in the stimulus or introduced by the nervous system. **b** | Decrease in information rate. Integrator models typically assume that the information rate (left) over time is constant during stimulus presentation. However, sensory adaptation may result in a decrease in rate over time (right). **c** | Leaky neural integrator. Many integrator models assume perfect accumulation (left, red), but neural integrators may be leaky (right, red). Sensory signals are shown in blue. Leak affects the timescale and the efficiency of temporal integration.

version of the task, the contrast threshold reached an asymptote at viewing time of just 200–300 ms[14].

So, experiments in vision demonstrate that the timescale over which integration can improve performance is strongly dependent on the nature of the task. There are some perceptual tasks within a modality that do not admit improvement by integration beyond a few tenths of a second, even when participants are motivated to do so, whereas others may benefit from integration over seconds.

Within olfaction, the task of odour discrimination — judging whether an odour belongs to one learned category or another — is an elementary perceptual judgement that can apparently be solved with a very short period of integration. It is quite possible that other olfactory tasks admit longer processing or integration times. For example, tasks working at near-threshold odour concentrations might, in principle, tap into different underlying neural substrates from those at higher concentrations[46]. There is also evidence that tasks that require the extraction of more information, such as identifying individual components from a multi-component mixture, might require longer processing times than binary discriminations[47]. This illustrates a fundamental point that not only the nature of the stimulus, but also the complexity of the behavioural response required, is crucial to response times[48].

Mechanisms limiting temporal integration

That integration timescales are evidently not universal begs the question: what limits the ability of an organism to improve decisions through accumulation of evidence? Nervous systems face physical and biological constraints that might limit the benefits gained through integration. Although abstract models accumulate evidence arriving at a constant signal-to-noise ratio with uncorrelated noise using long timescale integration mechanisms, violations of these assumptions are likely to limit the useful timescales for integration (FIG. 2).

Adaptation: decreasing information rates. Integrator models typically assume that the signal arriving at the decision device is of constant amplitude (FIG. 2b, left). However, most sensory neurons tend to respond with a brief transient after stimulus onset, followed by a lower sustained firing rate for prolonged stimulation. Reduction in firing rates suggests, but does not strictly imply, a decrease in information rate. Quantitative studies have shown that these transient responses carry the bulk of the stimulus information, whereas later responses carry less information[43,49–54]. These decreases in information rate have been attributed not only to spike-frequency adaptation, but also to changes in tuning specificity, response gain and response variability[43,49–54]. Of course, information rates that decrease over time will not eliminate the ability to improve signal-to-noise ratios, but may greatly reduce the effectiveness of temporal integration. Interestingly, for neurons in the middle temporal (MT) area, which provides a critical motion signal to the LIP, direction information from random dot motion does not saturate over prolonged periods (~2 s), in accord with psychophysics[15], but information in MT spike trains about coherent motion or disparity stimuli saturates much more quickly, within ~200 ms[43,50,54].

This issue is likely to be important in olfaction as well as vision. Olfactory sensitivity decreases profoundly during long exposures to odours[55–57], and olfactory receptor neurons typically show decreases in activity rates[58–60] (FIG. 2b, right). Recordings from neurons in the olfactory bulb of fish have led to the proposal that information rates might actually increase over hundreds of milliseconds[61]. However, these observations depend on the method used to read out information. Recent studies using classifiers suggest that near-perfect discriminability is reached in <400 ms in fish and insects[62–64].

Temporal correlations. Temporal integration benefits decision making by averaging out noise over time, thereby increasing the signal-to-noise ratio. Averaging is an efficient way of reducing noise as long as the noise is not correlated across the relevant dimension — correlations along this dimension will reduce the ability to suppress noise. For instance, correlated noise in the activity across a neuronal population can dramatically limit the usefulness of pooling spikes across more neurons in order to increase the signal-to-noise ratio[65]. Similarly, correlations of noise across time can reduce the ability of integrators to suppress noise. Therefore, the effectiveness of temporal integration depends on the nature of the limiting noise, which could be due to either neural mechanisms or the stimulus itself. In this regard, random dot kinematograms are a special case, as they are specifically designed to have extremely high levels of temporally uncorrelated (white) stimulus noise, a situation most favourable to a temporal integration strategy (FIG. 2a, left). In some situations it may be difficult to identify and characterize the nature of the limiting stimulus noise (for example, with odour stimuli; see FIG. 2a, right). Nevertheless, a useful approach is to characterize information rates or temporal correlations in the spike trains of neurons believed to underlie a particular task[43,50].

Leaky, noisy integrators. The nature of the accumulation mechanism itself is also a crucial factor in determining the timescale and effectiveness of integration. Whereas the simplest accumulator models (BOX 1) assume perfect 'leakless' accumulation (that is, an infinite time constant; FIG. 2c, left), it is

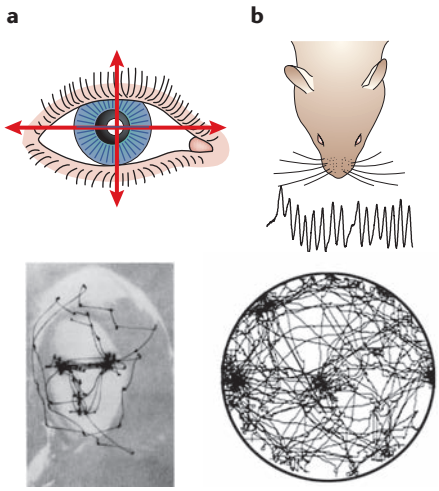


Figure 3 | **Discrete sampling of sensory information in vision and olfaction.** Psychophysical data indicate that a single eye fixation or sniff cycle can provide a high acuity snapshot of local sensory information in 200–300 ms. A larger scene is constructed by combining information abstracted from multiple individual snapshots (but not simply integrating across snapshots). We suggest an analogy between saccades and fixations in primate vision and locomotion and sniffs in rodent olfaction. **a** | Saccadic eye movements during visual scanning in humans. Humans scan visual scenes using a series of short eye fixations separated by saccades (top). Eye movements recorded while a human participant scanned this image (bottom). **b** | Sniffing during exploratory locomotor behaviour in rats. Rodents 'scan' their environment by navigating through it, sampling olfactory sensory information using a series of discrete sniffs (top). Trace shows a 3-s segment of nasal respiration recorded during exploration (centre)[25]. Bottom panel shows a movement path recorded as a rat explored an environment. Panel **a** (bottom) reproduced, with permission, from REF. 91 © (1967) Plenum. Panel **b** (bottom) reproduced, with permission, from REF. 92 © (2005) Blackwell Publishing.

unlikely that such an abstraction can be realized in the brain. How the brain accumulates information and what the intrinsic time constant of neural integrators might be are still open questions. Single neurons are generally leaky devices with short time constants — 10–50 ms — but through a process of feedback, longer time constants could be achieved. A number of computational studies have focused on creating perfect integrators from neural networks[2–7]. These studies show that leakiness is a natural feature of most[5] but not all[7] simple networks. Studies of decision making using biophysically detailed networks show that the timescale of integration depends on the biophysical parameters of their cellular and synaptic components[66,67]. It is likely that different brain regions, endowed with different biophysical properties, have their own intrinsic integration limits.

Indeed, psychologists have made efforts to reduce strong assumptions in the simplest models by introducing a 'leak' in the integrator or transient response characteristics of a sensory encoder. These studies found that such modifications can lead to a better fit to some empirical reaction time data[11,68–73]. From a neurobiological point of view, although such leak may be a manifestation of an imperfect integrator, when the timescale of apparent integration reaches 150–300 ms, much closer to the intrinsic timescales of various neuronal mechanisms, integrator models lose their unique explanatory power. At these timescales, various sensory, motor and computational processes could readily contribute to the relationship between speed and accuracy.

Discrete sampling: sniffing and saccades

Adaptation and temporal correlations in inputs and the leakiness of neural integrators are three specific phenomena that illustrate various ways in which acquisition of elementary perceptual information often departs from abstract decision models. Rather than viewing these as 'bugs' in an otherwise perfect integrator, we finally consider them as adaptive strategies that arise from the discrete nature of the active sampling methods involved in both sensory systems: saccades in vision and sniffing in olfaction. We suggest that rapid and short integration time is a sensible strategy for rapid processing of low-level sensory information in order to form more complex sensory images, both in vision and olfaction.

Visual information within and across saccades. The active movement of sensors has a fundamental role in the acquisition of sensory information, a fact that has long been appreciated in the visual system. Humans scan scenes in a series of saccades that bring different spatial locations sequentially into the high acuity region of the fovea (FIG. 3a). Therefore, rather than processing full visual scenes in detail at one time, we get brief snapshots of high acuity information from small regions of the visual field that must be assembled over time into a larger-scale image of the visual field[74,75]. The impression of a large and detailed visual scene has been called the 'grand illusion' of vision[76].

We suggest that the limited timescale of performance improvement in many types of low-level visual signal can be understood as an adaptation that goes hand in hand with the short duration of individual fixations. The timescale of fixations (200–400 ms)[77] is well-matched to the visual integration times measured in the various perceptual tasks described above, and may reflect the timescale of integration intrinsic to lower-level visual cortical areas[78]. Moreover, the saccade itself has an impact on processing. Psychophysical experiments show that the ability to compare images is greatly reduced when two images are separated by an eye movement[74,79], which indicates that detailed information about an image is erased or reset by the saccade.

Although higher-order properties of visual scenes must still be assembled across saccades, and therefore integrated over time, the process must also be highly selective. If information from different spatial positions were combined indiscriminately, the features of a scene would be degraded rather than improved over time. So, as an example from the familiar case of random dot kinematograms, motion signals can be integrated across saccades, but only if the stimuli maintain a constant retinotopic or spatiotopic position[80].

Finally, to understand why some low-level or elementary perceptual tasks do not admit integration, it is important to consider that the processing of information over larger temporal (and spatial) scales is carried out by higher cortical areas that work with relatively abstract representations. Therefore, tasks probing low-level perceptual acuity (such as vernier acuity) tap into primary visual processing areas (such as the primary visual cortex, V1) that might have a limited intrinsic capacity for integration and limited access to areas with greater capacity.

Sniffing as a unit of odour information acquisition. Rodents lack high-acuity foveal vision and probably use different mechanisms from primates for constructing large-scale impressions of the world. These species are thought to rely more on non-visual information, especially tactile and olfactory information. In addition, rather than absorb a scene at a distance by sequential scanning, rodents assemble a map of an environment by physically navigating through its spaces[81]. We suggest that despite the profound differences in these modes of sensory acquisition, similar issues will arise from the need to integrate detailed but rapid snapshots into a complex whole.

In olfaction, as in vision, the process of active sampling is discrete and the duration of the individual sniff seems to form the main limit on the timescale of olfactory

information processing[46,82]. Familiar, dissimilar odours can be identified by humans in a single sniff[46], and odour detection threshold and perceived intensity are unaffected by increasing the number of sniffs[82,83]. However, owing to the relatively slow breathing rates of humans, even one or two human sniffs can translate to relatively slow performance. One study found 420 ms to be the minimum duration of a human sniff[46]. This could explain the relatively slow performance observed in olfactory reaction time studies in humans[84].

For rodents and other animals that are more reliant on smell, sniffing is comparatively fast. When performing olfactory discrimination, rats sample odours at ~8 Hz, but still perform even very difficult discriminations in just 1–2 sniffs[31], or just 125–250 ms (FIG. 3b). In these experiments, the integration timescales seem to be closely matched to the timescale of the sniffing cycle. Presumably, the neural mechanisms processing olfactory information are likewise adapted to the timescale of sampling.

The results of these studies demonstrate directly that precise olfactory information can be conveyed in a single sniff cycle, just as precise visual information can be conveyed in a single glance. Although so far there is no direct evidence that the sniff cycle resets or erases olfactory information, this idea is consistent with the available data, and is analogous to the impact of saccades on visual integration. We suggest, in analogy to vision, that indiscriminate temporal integration of olfactory information would limit the ability of an organism to form an accurate representation of the world. Rapid and independent olfactory samples would allow animals to associate specific odours precisely with specific spatial locations in the environment, especially for the less volatile components of the olfactory world that are only sensed at closer proximity. For more volatile odours conveyed over longer distances, short and independent samples would provide advantages for estimating absolute concentrations and their gradients, which would facilitate localization or tracking.

Therefore, considering binary odour discrimination as a low-level perceptual task, the detailed sensory information contributing to this task (that is, activation patterns of individual receptors) may be restricted to low levels of olfactory processing that might lack intrinsic mechanisms for integration (for example, the olfactory bulb). Higher-order olfactory cortical areas (for example, the posterior piriform cortex) that may be capable of integration would operate on more abstract representations of olfactory scenes that lack the low-level details of individual odours required for the fine perceptual discriminations.

Conclusions

Although the framework of integrator models provides an important theoretical basis for understanding certain types of perceptual decision that admit long integration times, the relevance of these models to understanding the more common case of rapid decision making is less clear. Whereas accumulation of evidence over periods of a second or longer seems likely to tap into a relatively unique set of cognitive mechanisms, for various reasons discussed here such accumulation is not possible for many (perhaps most) types of perceptual decision. We have discussed how limits on perceptual integration might originate from features of the sensory encoding process — adaptation and temporal correlations — and might also reflect lack of access of certain types of information to integrator circuits (or perhaps the absence of such circuits in some species). At the timescale of rapid decision making (~200–300 ms), a multitude of mechanisms involved in sensory processing, motor initiation and the processes in between can start to contribute to the relationship between speed and accuracy of decisions. For example, in olfaction, delays in odour-specific signal transduction on a timescale of 100 ms have been observed[85], and may contribute to reaction times[32]. Because of the multiplicity of such effects, it is unlikely that studying the reaction times and speed–accuracy tradeoffs at the 50–100 ms range will provide enough constraints to implicate unique mechanisms. Direct comparison of behavioural performance and neuronal data in decisions with different apparent integration times will be important to resolve these issues.

As to the question of why the brain does not choose to integrate, we conclude with the observation that, in nature, animals face numerous, sometimes contradictory selective pressures. Accumulation of evidence is important for selecting actions appropriately, but the costs of deliberation may often override the benefits. In a foraging situation, the decreasing rate of income may counteract gains from improved accuracy. In the presence of predators, slow decisions could be even more costly. Furthermore, because animals are usually either scanning or moving through the environment with their sensors, non-stationarity will confound temporal integration. So, in an ecological context, integration seldom involves summing long stretches of constant signals, but rather the selective assembly of complex images that are accrued over time but must also be stitched together across space. As evidenced by various psychophysical experiments, the neural mechanisms for elementary or low-level sensory discriminations seem to be optimized for rapid execution, whereas higher-order integration mechanisms must operate selectively rather than globally. These constraints might, ultimately, be reflected in the discrete, often cyclic, nature of sensory processes ranging from saccadic eye movements to sniffs[86]. Far from viewing this as a limitation, short discrete information processing cycles may provide important benefits for neural coding[85,87–90]. Discrete sensory snapshots might also facilitate the coordination and integration of information across different sensory modalities and with the motor system, and may give rise to neural encoding strategies that take advantage of these temporal frames[90]. The evaluation of neuronal activity during natural active sampling (that is, saccades and sniffing in freely behaving animals) will be important to understanding perceptual decision making in these contexts.

Naoshige Uchida, Adam Kepecs and Zachary F. Mainen are at Cold Spring Harbor Laboratory, 1 Bungtown Road, Cold Spring Harbor, New York 11724, USA.

Naoshige Uchida is now at the Center for Brain Science and Department of Molecular and Cellular Biology, Harvard University, 16 Divinity Avenue, Cambridge, Massachusetts 02138, USA.

Correspondence to Z.F.M.
e-mail: zach@cshl.org

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