Strategies optimize the detection of motion transients

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Strategies are implicitly formed when a task is consistent and can be used to improve performance. To investigate how strategies can alter perceptual performance, I trained animals in a reaction time (RT) detection task in which the probability of a fixed duration motion pulse appearing varied over time in a consistent manner. Consistent with previous studies suggesting the implicit representation of task timing, I found that RTs were inversely related to the probability of the pulse appearing and decreased with training. I then inferred the sensory integration underlying responses using behavioral reverse correlation analysis. This analysis revealed that training and anticipation optimized detection by improving the correlation between sensory integration and the spatiotemporal extent of the motion pulse. Moreover, I found that these improvements in sensory integration could largely explain observed changes in the distribution of RT with training and anticipation. These results suggest that training can increase detection performance by optimizing sensory integration according to implicitly formed representations of the likelihood and nature of the stimulus.

Keywords: temporal summation, reaction time, decision variable, reverse correlation, temporal strategy, adaptive filtering

Introduction

Attention increases behavioral performance and decreases reaction times (RTs) in perceptual tasks (Bowman, Brown, Kertzman, Schwarz, & Robinson, 1993; Bravo & Nakayama, 1992; Pashler, Johnston, & Rurtuff, 2001; Posner, Snyder, & Davidson, 1980). In sequential sampling decision models, these effects have been explained by increases in sensory evidence, giving rise to a decision (Carpenter, 2004; Carpenter & Williams, 1995). Because these models have typically relied on trials in which the stimuli have stationary statistics, it remains unknown whether they are sufficient to explain the timing of decisions based on nonstationary stimulation. Of particular interest are cases in which the statistics of stimulus presentation are known to the observer (Chun & Jiang, 1999; Olson & Chun, 2001). In such a case, improvements in performance and RT might arise from optimizing the integration of sensory information. For example, if a stimulus is always particularly strong at a particular point in time, performance would be improved if decisions preferentially weighted information then. Indeed, behavioral and physiological evidence suggests that attention can be implicitly directed to specific epochs of time as a consequence of training (Coull, Frith, Buchel, & Nobre, 2000; Janssen & Shadlen, 2005; Naccache, Blandin, & Dehaene, 2002; Nobre, 2001; Olson & Chun, 2001). Similarly, if a stimulus has a characteristic spatial and temporal extent, performance would be improved if the integration of sensory information was matched to the stimulus. Thus, an optimal observer would alter the integration of sensory information to reflect both the likelihood and the spatiotemporal extent of the stimulus to be detected.

To study whether such changes in stimulus integration can occur, I trained monkeys to detect a brief pulse of motion of consistent velocity and duration embedded in motion noise. The probability of the motion pulse was systematically varied over time in a consistent manner throughout training. To study the behavioral effect of task timing representations, I correlated mean RTs with pulse probability. I then examined the stimulus integration associated with the detection of these pulses using reverse correlation analysis of the motion noise (Borghuis et al., 2003; Caspi, Beutter, & Eckstein, 2004). Finally, a simple probability summation model was introduced to relate RT distributions to the sensory integration inferred by reverse correlation. The results from these analyses suggest that implicitly formed representations of the nature and likelihood of behaviorally relevant stimuli can be used to improve behavioral performance.

Methods

Two monkeys (Macaca mulatta) performed a peripheral RT motion detection task. Animals were rewarded by juice or water when they saccaded to the location of a coherent motion pulse embedded in a sequence of motion noise. Animals were treated in accordance with use and care guidelines established by the NIH. Behavior control, stimulus presentation, and data acquisition were computer controlled using customized software (http://www.ghoselab.cmrr.umn.edu/software.html). Eye position was monitored monocularly by scleral search coil (Robinson, 1963) and digitized with a temporal resolution of 5 ms.

Visual stimuli

Stimuli were presented on a CRT display on a gray background (15.6 cd/m², CIE color space x = 0.33, y = 0.33). Each RGB gun of the display was gamma corrected (8 bits),
and the display resolution was $1280 \times 1024$ pixels at a frame refresh rate of 120 Hz. Vertical retrace pulses were digitized with a resolution of 1 or 0.1 ms to ensure an accurate synchronization of behavioral events and stimulation. The stimuli were two arrays of achromatic Gabors symmetrically located with respect to the vertical meridian in the left and right hemifields. Each array was composed of 31 Gabors that were identical in spatial frequency (1 cycle/deg), contrast (100%), orientation, and Gaussian envelope ($\sigma = 0.35–0.5$ deg) but varied in spatial phase. Upon each frame update, each Gabor shifted a quarter cycle ($\pm 90$ deg) in spatial phase (0, 90, 180, and 270 deg), corresponding with a temporal frequency of 30 Hz and a velocity of 30 deg/s. The Gabors were arranged according to hexagonal spacing (1.4–2 deg) to form a symmetric array (Figure 1). The direction of the quadrature phase shifts of each Gabor was randomly chosen according to a binary m-sequence to provide a noisy motion background. The sequence was used to ensure that movements between any two Gabors were uncorrelated, and the average motion was zero over all spatial scales within the array. The phase directions were updated on each frame by selecting 31 adjacent entries in the sequence, and the starting point was advanced by 32 entries every frame. To minimize potential periodicities from the wrapping of this 1-D m-sequence (Sutter, 1991) into a 3-D space–time sequence (Reid, Victor, & Shapley, 1997), I performed Fourier analysis on the 3-D sequences associated with all possible seeds, and the seed associated with the maximally flat space–time spectrum was chosen. Array center location (eccentricities from 5 to 15 deg) and Gabor orientation were varied between experimental sessions. Stimuli were retinally stabilized by translating the arrays according to the most recent eye position.

Pulses of motion were created by moving all Gabors within an array in the same direction (+1 in Figure 1). To ensure that this did not create a contrast artifact in which alternate frames were always opposite in polarity, I alternated frames of uniform motion with motion noise frames (complete movie: Movie 1). After training, subjects were tested with motion pulses with a total duration of 8 frames (67 ms), containing 4 frames of uniform motion interleaved with 4 frames of random motion.

**Task design**

Trials commenced with the subjects fixating on a small dot (0.1 deg) within a 1.5 to 2 deg window. After 500 ms of fixation, the two arrays appeared. Animals performed a motion detection task in which they were required to break fixation and make an eye movement to one of the Gabor arrays immediately after a motion pulse was presented at that array. Only eye movements to the correct array, initiated from 150 to 600 ms after the start of the motion pulse, were rewarded. Trials immediately ceased without reward for inappropriate eye movements. For the standard 67-ms motion pulse, performance was between 45% and 60% correct, with most errors arising from false alarms in which subjects made saccades to an array without any motion pulse being presented.

The occurrence of motion pulses was randomized according to an exponential distribution to minimize expectations during the course of the trial (decay constant for Monkey P, 2 s; for Monkey B, 2.5 s). Thus, the hazard function, representing the instantaneous probability of a pulse occurring given that one has not yet occurred, was flat throughout the trial. Four to five percent of trials were catch trials, in which motion noise without any pulse was presented for a time consistent with the exponential distribution ($\approx 6$ s), and the monkeys were required to maintain fixation throughout the trial to receive a reward. For all other trials, a single motion pulse was presented.
The probability of a motion pulse appearing at a particular location (left or right) was consistently modulated by a square wave (TF = 0.5 Hz) of amplitude 0.98. Thus, if a motion pulse occurred during the first second of a trial, there was a .98 probability that it would be on the right array, whereas in the following second, if a pulse occurred, there was a .98 probability of occurrence on the left array. The temporal variation in the probability of a motion pulse occurring at a particular hemifield was therefore described by the product of a square wave and an exponential. Because no explicit sensory cues were given for any changes in task-relevant probability (Ghose & Maunsell, 2002), any internal representations of spatiotemporal probability must be formed implicitly during training.

Monkeys performed 2,000 to 4,000 trials per day, typically containing two to four experimental sessions. Gabor orientation and array location were fixed within each session but varied between sessions. Thus, within each session, the two potential locations of the motion pulses, as well as their direction and velocity, were predictable. As described previously, all sessions shared a common hazard function (Figure 2) and pulse duration. Each session consisted of advancing through the m-sequence of length 217 by using sequential entries to update the phase of each Gabor on every frame. The sequence was advanced by 32 for each frame, so that each session contained a total of 212 random motion frames. Each session typically took about 30 to 45 min to complete. Progress through the m-sequence within a trial was halted as soon as an erroneous eye movement was made or a motion pulse was presented, and resumed at the beginning of the following trial.

**Results**

**Effect of anticipation and training on RT**

To assess the effects of training, I grouped consecutive experimental sessions spanning several weeks together. I defined the first group as Early and the second as Late, with the Late group of sessions beginning about 2 months after the Early group. Each group contained between 99 and 109 experimental sessions. To assess anticipatory effects, I analyzed RTs as a function of time within trial for each group and animal. Because the hazard function for right array pulses is a square wave (Figure 2, bottom right), a perfect representation of these statistics would lead to a square wave modulation of RT over the course of the trial with RTs remaining at a constant low value during epochs of high probability and at a constant high value during epochs of low probability. Changes in RT should follow changes in probability by a period corresponding to the RT. As shown in Figure 3, the behavioral data of two subjects are only partially consistent with a perfect representation of task statistics. As expected, sharp increases in RT are observed after the decreases of probability at 1, 3, and 5 s for both subjects and training epochs. Moreover, the 1-s epochs preceding these transitions have relatively constant RTs, as expected with a flat hazard function over these epochs. However, RT is not constant during the epochs of low probability and falls during the course of the following second. While training produces a decrease in the RT of both
animals for anticipated pulses, the effect of training on unanticipated pulses varied between the animals: In Monkey P, there was no improvement in RT with training, whereas in Monkey B, both anticipated and unanticipated pulse RTs decreased.

In both animals and training groups, the largest RTs are observed after decreases in pulse probability (green, Figure 3). Conversely, the fastest RTs are observed during the initial second of the trial (purple, Figure 3). I therefore defined these epochs as “anticipated” and “unanticipated” for subsequent analyses. To examine the temporal integration underlying correct saccades initiated during these epochs, I computed cumulative RT distributions. I tested whether these distributions were consistent with previous observations. In most RT studies, the distribution of reciprocal RT is normal (Carpenter, 1988; Ratcliff, 1993). This can be readily visualized by plotting cumulative RT on a probit-inverse scale, in which cumulative frequency is plotted on a z scale versus 1/RT (Carpenter & Williams, 1995; Ratcliff, 2001). To test the consistency of the RT data in this study with such observations, I applied linear regression to the data plotted on the probit-inverse scale. Normality was tested by fitting a straight line over the .05–.95 range of cumulative RT and comparing this prediction to observed RTs using KS statistics (Figure 4). For both animals and training groups, the anticipated RT distributions were significantly different than normal ($p < .001$). Unanticipated RT distributions were different ($p < .05$) from normal for all but one case (Monkey P, late).

One specific model of RT variability, which was inspired by the normal distribution of reciprocal RT, postulates that a response is initiated when a linearly rising decision variable crosses a threshold level (Carpenter & Williams, 1995). RT variability is explained by variability in the linear rate wherein the decision variable rises. The model also makes specific predictions regarding the effect of prior probability on RT distributions: prior probability influences the starting point of the decision variable but not its rise rate or threshold. On the probit-inverse scale, this appears as a “swivel” because the infinite-RT intercept, reflecting the threshold, does not vary (Carpenter & Williams, 1995; Reddi & Carpenter, 2000). A common infinite-RT intercept implies that the slope of the anticipated RT distribution is smaller than that of the unanticipated distribution; if this is not the case, the two distributions will never intersect. As shown in Figure 4, changes in prior probability do not result in distributions with a common infinite-RT intercept in either training group or animal. This suggests that models in which probability solely affects distance to threshold are unlikely to be able to fully explain the observed RT distributions.
Reverse correlation analysis of motion integration

If changes in threshold are unable to fully account for the effects of anticipation, then it is possible that anticipation is altering the progress of the decision variable reflecting sensory information. When stimulus strength is increased, the reduction in RTs can be modeled by an increase in decision variable rise rate (Kim & Shadlen, 1999; Roitman & Shadlen, 2002). In a detection task, optimal performance is obtained when sensory information is integrated according to the spatiotemporal extent of the stimulus. If anticipation could optimize the integration of sensory information, then it would increase the speed wherein the decision variable approaches threshold in a manner analogous to changes seen with increases in stimulus strength. To investigate this possibility, I measured the integration of motion information using reverse correlation analysis. I computed the average stimulus sequence that preceded false alarm saccades during anticipated and unanticipated epochs (Figure 3). The motivation for this technique is that, with a challenging stimulus, detection false alarms are more likely to occur when there are variations in the noise that are consistent with sensory integration used by the observer. Thus, by averaging the stimulation that immediately precedes false alarms, one can, with the assumption of linear summation, infer the sensory integration used by a subject to arrive at a perceptual decision. Being interested in the integration of motion information, I averaged the intraframe phase shifts at each position over the 500 ms preceding each false alarm saccade.

Because of the high contrast sensitivity of motion perception, motion strength was assumed to be uniform throughout individual Gabor elements. To examine spatial biasing along the direction of motion, I rotated the array of each experimental session according to Gabor orientation presented in that session. Figure 5 shows the space–time linear kernel associated with incorrect saccades made during the anticipated epoch in the late training phase of Monkey P. In the temporal dimension, data were convolved with a Gaussian ($\sigma = 2$ frames or 16.67 ms). Three time slices are shown, corresponding to the spatial sensitivity profiles at the peak temporal interval (217 ms) and before (150 ms) and after the peak (250 ms; complete movie: Movie 2). At the peak time, sensitivity is concentrated at the edges of the stimulus array with a weak bias near the direction of motion (+45 deg). Because the radial variation is roughly consistent across all angles, the 2-D spatial data were collapsed into a single angular measure relative to array center, where 0 deg corresponds with the direction of positive motion. The resulting profile is largely space–time separable: the sensitivity profile is not clearly oriented in space–time. This means that the complete sensitivity profile can be well described by the 1-D spatial and 1-D temporal profiles containing the peak. The temporal profile (orange) indicates that temporal integration is well contained within the 100-ms window between 150 and 250 ms and has a peak width (FWHM = 92 ms) that closely corresponds with the temporal extent of the pulse (67.7 ms). Moreover, the spatial integration is broad: As shown in the 217-ms slice, positive correlation is observed at points on opposite ends of the Gabor array, which was up to 14 deg of visual angle in diameter. When collapsed according to spatial angle, positive values were observed for all angles (purple). Thus, the integration of motion signals revealed by this analysis is well matched to the statistics of the motion pulse the subjects were looking for: temporally limited and spatially extensive.

To quantify the correspondence between the reverse correlation profiles and the motion pulse, I computed correlation coefficients between the two space–time profiles separately for all eight data sets (Table 1). This metric defines a perfect match between the motion pulse and reverse correlation profile with a value of 1.0. Temporal
profiles were convolved with a Gaussian (1 frame, 8.83 ms) and peak aligned, and space was binned in 10 deg angular steps. The analysis specifically examines the match between the spatiotemporal profiles of the pulse and the inferred sensory integration. Although a temporal shift without any change in profile might be sufficient to explain RT differences, because of peak alignment, the correlation metric is unaffected by such shifts. Similarly, changes in sensitivity, as reflected by changes in the amplitude of the reverse correlation kernel, would also not change the metric. All correlation coefficients were significantly different from zero \((p \leq 0.001)\) and from each other (corrected for multiple comparisons). In all data sets, correlation was higher during epochs in which the pulse was likely (anticipated vs. unanticipated). Additionally, for both animals, training increased the correlation seen during anticipated epochs. The effect of training and anticipation cannot, therefore, be simply described as a scaling with respect to sensitivity or a change in postintegration latency. Rather, both training and anticipation refined sensory integration to better match the spatiotemporal extent of the motion pulse.

Sensory integration RT model

Because the reverse correlation profiles are based on false alarms, it is possible that they reflect only the stimulus integration associated with errors. If mistakes solely arose because of improper stimulus integration, these profiles would not necessarily reflect the processes underlying correct detection. For example, imagine that an animal occa-

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Table 1. Space–time correlation coefficients between sensory integration and the motion pulse.

Figure 6. A model relating the temporal reverse correlation profile based on false alarm trials to correct trial RT distribution. Data from the saccades during the anticipated epoch of the early training trials of Monkey P are shown. Observed RT distributions (top) were deconvolved with the motion pulse stimulus to infer a temporal kernel (middle). The kernel is then compared with the reverse correlation temporal kernel after thresholding (bottom, black). Thresholds are determined by minimizing mean square error between the RT-derived kernel and the normalized suprathreshold kernel derived by reverse correlation.
temporal profile. A variety of thresholds were tested, and a best fit to the inferred correct-detection kernel was found by minimizing mean square error.

For all data sets except one (unanticipated early from B), kernel peaks are within 50 ms of each other (Figure 7). For anticipated data sets, other temporal aspects, including kernel onset and offset, are within 20 ms of each other. For the unanticipated data sets, the correspondence between the reverse correlation and RT-derived kernels is considerably poorer. This is likely because the unanticipated kernels are derived from far fewer trials (usually by a factor of 10) than the anticipated kernels. It is also likely that the assumption of perfect temporal integration, used to derive kernels from the RT data, is less justified for unanticipated epochs. Imperfect integration is further suggested by the observation that the largest discrepancies in all cases are seen along the trailing edges of the temporal kernels.

Discussion

Temporal strategies in motion detection

Because consistent statistics concerning both the probability and nature of motion pulse were used throughout training, animals in this study could form expectations and use them to improve performance. Although behavioral effects of temporally varying probability are well established (Luce, 1986), the results of this study are unlikely to be explained by modulation in overall vigilance because the hazard function describing the overall likelihood of a pulse occurring was flat. Instead, the results suggest that likelihood in both space and time was encoded by the animals during training. The exact dynamics of the observed changes in RT as a function of time within trial suggest that certain probability changes were particularly salient. Specifically, the most rapid changes in RT to events at a particular location occurred in conjunction with sharp decreases in the probability of an event at that location. These decreases in probability (from .98 to .02) occurred at 1, 3, and 5 s within the trial (Figure 3). In both animals, consistent increases in mean RT followed these probability decrements.

One notable aspect of the modulation of mean RT is that the decreases in mean RT associated with sharp increases in local probability at 2 and 4 s are considerably smaller than the increases associated with decreased probability. There are two possible explanations for this asymmetry. The first is that there is a nonlinearity in the relationship between the internal representation of probability and mean RT. For detection tasks with stationary statistics, it has been shown that mean RT varies logarithmically with probability (Carpenter & Williams, 1995). This could arise from a ceiling effect, in which there are fundamental physiological limits to RT brevity. Because only two levels of probability were present in this study, the exact relationship between probability and mean RT remains to be established. The second possibility is that mean RTs actually reflect an asymmetry in the animals’ representation of the task. Indeed, there is evidence for such asymmetry: Both animals displayed an overall spatial bias toward the right array in their false alarms. This spatial bias might have arisen because of the phase of the spatiotemporal statistics of the task. Because the instantaneous probability is highest during the first second when the right location is probable, there is an overall spatial bias when pulses are considered, irrespective of their timing within the trial. In short, the task statistics of this study were balanced with regard to time but not with regard to space. Although these biases in choice and RT suggest that spatial probabilities can potentially dominate task representations, further studies involving a variety of space–time probabilities will be required to fully elucidate probability representations.

Adaptive sensory integration

I used behavioral reverse correlation analysis to reveal the spatial and temporal integration of motion information underlying the detection of a predictable motion pulse. The analyses revealed that subjects integrated information in accordance with the spatiotemporal extent of the pulse. The results cannot be explained by intrinsic periodicities in the motion noise for several reasons. Fourier analysis was used to verify the absence of periodicities in the motion noise. Similarly, the reverse correlation kernels in this study are not periodic and have zero amplitude at time intervals larger than 100 ms. Therefore, these results suggest that the spatiotemporal statistics of the task do not generate periodicities in the motion noise.
than the longest RT (Figure 7). Finally, the observation that they are significant changes in the reverse correlation kernels (Table 1) as a function of training and pulse probability in the same animal with the same random sequences demonstrates that there is no intrinsic tendency of the analysis to produce a particular integration profile.

Moreover, the spatial and temporal pooling of motion signals is not strongly constrained. Previous studies have shown that motion integration is highly dependent on stimulation parameters and task designs (Vergheese, McKee, & Grzywacz, 2000): Spurious correlations can strongly effect measurements of spatial summation (Todd & Norman, 1995), and reports on the extent of temporal pooling range from several hundreds of milliseconds (Barlow & Tripathy, 1997; Snowden & Braddock, 1991) to 1 to 2 s (van Doorn & Koenderink, 1984). The data from this study suggest that extraretinal factors can also alter the integration of motion information underlying detection and, specifically, that anticipation can optimize this integration. This contrasts with previous behavioral reverse correlation analyses in two respects. First, the results of this study show a change in the integration profile and not simply a change in sensitivity, such as was seen in a reverse correlation study of spatial attention (Eckstein, Shimozaki, & Abbey, 2002). Second, sensory integration is not necessarily well matched to the stimulus that is to be detected: In a bar detection task, for example, reverse correlation revealed that subjects integrated contrast information 100 ms prior to the presentation of a target (Neri & Heeger, 2002).

The consistency of this study’s reverse correlation data with the observed RT distributions suggests that, at least for the narrowband stimulation in this study, the method accurately characterizes the stimulus integration underlying detection of transient motion. However, it is unclear whether the reverse correlation method, and its assumptions of linear summation, would accurately reveal the integration underlying behaviors based on more broadband stimulation, such as random dot fields. In the case of broadband stimulation, decisions may be based on the recruitment of motion detectors with different preferred spatial displacements (Mikami, Newsome, & Wurtz, 1986) or temporal sampling rates. This introduces the additional complication of explaining how motion signals over multiple spatial scales are combined prior to a decision (Barlow & Tripathy, 1997). Several lines of evidence suggest that the activation of multiple scales of motion detectors by broadband stimulation has a profound influence on sensory integration. First, the dependence of random dot detection performance on duration suggests the presence of a second stage of temporal integration for such stimuli with a time constant on the order of 3 s (Burr & Santoro, 2001). Thus, behavioral reverse correlation would be unlikely to yield a well-defined temporal integration profile such as I have observed here. Further evidence for a difference in the temporal integration of motion information is seen in studies of the relationship between RT and stimulus strength, which differs between narrowband (Burr & Corsale, 2001) and broadband (Dzhafarov, Sekuler, & Allik, 1993) stimuli. Second, the dependence of performance on size suggests a spatial constant of integration on the order of tens of degrees (Burr, Morrone, & Vaina, 1998), much larger than is seen for narrowband motion stimuli (Watson & Turano, 1995) such as those used in this study. Finally, temporal probability summation, which was used in this study to correlate RT distributions with reverse correlation data, is unlikely to be applicable for the highly variable responses to broadband motion stimuli (Fredericksen, Verstraten, & van de Grind, 1994c).

Although the results of this study suggest that sensory integration can be altered, the exact implementation of this adaptive filtering remains to be determined. Although the observed integration might be the product of a multistage network of sensory filters, several aspects of the stimulus suggest that early motion detectors may be responsible. First, the peak spatial frequency and bandwidth of the individual Gabor elements are close to the optimal motion stimulus for detection (Watson & Turano, 1995). Second, several studies of contrast sensitivity as a function of stimulus duration have described a critical duration of motion integration, between 100 and 200 ms (Fredericksen, Verstraten, & van de Grind, 1994a; Watson, Barlow, & Robson, 1983; Watson & Turano, 1995), below which Bloch’s law is observed (Watson, 1986). This closely matches the temporal width of anticipatory integration seen in Figure 7.

One attractive candidate for the locus of such adaptive changes is the middle temporal area (MT), which has been strongly implicated by electrophysiological (Britten, Shadlen, Newsome, & Movshon, 1992; Maunsell & Van Essen, 1983), lesion (Newsome, Wurtz, Dursteler, & Mikami, 1985) and microstimulation (Salzman, Murasugi, Britten, & Newsome, 1992) studies to play a critical role in motion perception. The vast majority of MT neurons are direction selective, and the detection of high TF signals (>1 cycle/s) is mediated by direction-selective mechanisms (Watson, Thompson, Murphy, & Nachmias, 1980). MT neurons carry temporal precise information about motion transients, especially when random sequences of motion, such as those used in this study, are presented (Bair & Koch, 1996; Buracas, Zador, DeWeese, & Albright, 1998). MT responses are enhanced by spatial attention (Cook & Maunsell, 2002; Seidemann & Newsome, 1999; Treue & Maunsell, 1996), and the temporal integration seen in single-neuron responses can be altered by anesthetized state (Puck, Berezovskii, & Born, 2001) and the statistics of stimulation (Bair & Movshon, 2004). Finally, models based on MT response physiology have been constructed to explain the dynamics and statistics of motion-based decisions (Mazurek, Roitman, Ditterich, & Shadlen, 2003).

**Temporal evolution of a decision**

The integration of stimulus information over time can be fundamentally important to perceptually based decision
making (Mazurek et al., 2003). If there are behaviorally irrelevant rapid fluctuations in sensory signals, for example, integration over time provides a means of minimizing the behavioral consequences of such noise (Ratcliff, 2001). These noise sources may be neutral in origin, such as synaptic unreliability (Manwani & Koch, 2001), or extrinsic, due to eye movements or luminance variations (Buracas et al., 1998). As mentioned previously, in the case of broadband motion stimuli, there is evidence of extensive temporal integration, on the order of seconds (Burr & Santoro, 2001), with certain tasks. However, many cases of visually guided behavior necessarily involve dynamic stimuli in which such prolonged integration of information would significantly degrade performance. For example, the rapidness with which smooth pursuit can be updated when an object changes direction suggests that the underlying motion signals are integrated over a very limited period, on the order of 100 ms (Krauzlis & Lisberger, 1994).

In this study, animals have been trained to detect a pulse of motion, on the order of tens of milliseconds. Extensive temporal integration is clearly nonoptimal for the detection of such a pulse because, as integration is expanded beyond the pulse duration, increasing amounts of noise are incorporated. The results of this study demonstrate that subjects are able to employ a more effective means of noise reduction for such situations by optimizing the spatiotemporal window over which stimulus information is accumulated. Moreover, because subjects changed their integration without any explicit cueing, this study suggests that such optimization can automatically occur for tasks with predictable stimuli.

This potential for stimulus integration to vary with task has important implications on the modeling of perceptual decision making. Sequential sampling models of decision timing typically postulate that a signal derived from sensory information, which represents the likelihood of the stimulus, increases over time either in a strictly linear fashion (Carpenter & Williams, 1995) or around some average slope (Ratcliff, 1978). These models specify that such a signal will tend to increase over time, even after transient sensory signals (Ratcliff & Rouder, 2000). The data from this study suggest, on the other hand, that if the transient nature of stimulus is known to the subject, this decision variable does not necessarily increase over time: As seen in Figure 7, only motion information over limited temporal windows was correlated to behavior. Because I did not explore a variety of stimulus durations, it is not clear exactly how malleable the sensory signals used for detection are.

The correspondence between the temporal integration seen with reverse correlation and the integration responsible for correct decisions relies on several assumptions. Because a single temporal correlation function was constructed by a weighted average of the full spatiotemporal reverse correlation profile, the analysis assumes linear spatial summation. Such linear summation has been observed for broadband stimuli, such as random dot patterns (Fredericksen et al., 1994b), and narrowband stimuli (van Doorn & Koenderink, 1984), such as those used in this study. The probability summation over time (Watson, 1979), used to derive the integration associated with correct decisions, makes three assumptions: (1) that stimulus responses are consistent, (2) that the probability at one time interval is independent from the probabilities at other intervals, and (3) that detection occurs if a threshold is reached in any time interval. Because the deviations between correct trial motion kernel and the reverse correlation kernel (Figure 7) tend to increase with time, it suggests that there was an imperfect temporal integration of sensory information (Gorea & Tyler, 1986), especially when the appearance of the pulse is unanticipated. However, the close match between the overall shape and peak position of the two kernels suggests that, especially for anticipated stimuli, the assumptions of temporal probability summation are largely reasonable for modeling the detection of sensory transients.

Conclusions

Using a fixed duration motion pulse and consistent statistics concerning occurrence of that pulse, I have shown that animals automatically form internal representations of both task and stimulus statistics. Anticipation of task statistics is evidenced by systematic increases in mean response time, which are coincident with sudden decreases in the probability of pulse occurrence. Anticipation of stimulus statistics is evidenced by quantifying the perceptual integration after training, using the reverse correlation method. As a consequence of training, the sensory integration underlying detection decisions is refined to better match the spatial and temporal extent of the motion pulse. These results show that extraretinal modulations can enhance perceptual performance not only by increasing sensitivity but also by optimizing the integration of sensory information.

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