Stimulus probability directs spatial attention: an enhancement of sensitivity in humans and monkeys

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Abstract

We examined whether improvements in sensory processing, defined as changes in sensitivity, could be elicited in a simple luminance discrimination task without eliciting concomitant changes in decision processing. To this end we developed a task, for use in both humans and monkeys, in which prior knowledge about where a discriminative stimulus was likely to appear (1) offered no decisional advantage in solving our task and (2) could be parametrically varied to yield a psychometric function. We found that if we parametrically varied the quality of prior knowledge, by increasing the probability, and thus the certainty, that a discriminative stimulus would appear at a particular location under these conditions, luminance discrimination improved for both human and monkey subjects. This improvement was correlated with an enhancement in sensory processing, but not with any systematic changes in decisional processing, as assessed by signal detection theory. These results suggest that (1) sensory processing and decision processing can be separated by task design and (2) systematic changes in prior knowledge about where a stimulus may appear can lead to systematic changes in sensitivity; providing a psychometric function for the influence of prior knowledge on perceptual sensitivity. Importantly, these results were obtained from both human and monkey subjects. Similar task designs could be used in physiological studies attempting to generate linking hypotheses between psychometric and neurometric functions, ultimately allowing changes in perceptual sensitivity to be linked to changes in an underlying neural substrate. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The accuracy or speed with which human or animal subjects evaluate a stimulus can be influenced by prior knowledge about the nature of the stimulus before it appears. For example, cues which indicate the probable location of a stimulus can improve the accuracy or reduce the reaction time with which subjects report stimulus detection (c.f. in humans: Posner, Nissen, & Ogden, 1978; Posner, Snyder, & Davidson, 1980; in non-human primates: Witte, Villareal, & Marrocco, 1996). According to classic signal detection theory, the improvements in accuracy or speed elicited by prior knowledge can be produced by two separable and independent processes, either by local improvements in the quality of the sensory signals themselves, or by

changes in the decision criteria by which these sensory signals are evaluated (Green & Swets, 1966). This distinction between perceptual improvements due to changes in sensitivity versus changes in decisional criteria has been a subject of psychophysical inquiry since the 1960s (c.f. Kinchla, 1969a, 1992; Palmer, Ames, & Lindsey, 1993; Shaw, 1980, 1984; Sperling, 1984; Sperling & Dosher, 1986; Lu & Dosher, 1998; Yeshurun & Carrasco, 1999; Carrasco, Penpect-Talgar, & Eckstein, 2000). Only recently has it also become the subject of physiological studies which seek to test empirically the closely related hypothesis that sensory processes, decision-making processes, and even purely movement-related processes, may be neurobiologically separable (cf. Andersen, 1995; Bracewell, Mazzoni, Barash, & Andersen, 1996; Colby, Duhamel, & Goldberg, 1993, 1996; Gnadt & Andersen, 1988; Goldberg, Colby, & Duhamel, 1990; Gottlieb, Kusunoki, & Goldberg, 1998; Leon & Shadlen, 1998; Mazzoni, Bracewell, Barash, &

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Andersen, 1996a,b; Platt & Glimcher, 1997, 1999; Shadlen & Newsome, 1996; Snyder, Batista, & Andersen, 1997, 1998).

One approach to testing this hypothesis, which seeks to link discrete mental processes with neural events, would involve a three step process (cf. Parker & Newsome, 1999): First it would be necessary to demonstrate, at a behavioral level, that sensory, decision-making, and movement-related processes are separable. Second, it would be necessary to develop continuous and quantitative measures of how one or more environmental variables influence sensory, decision-making, and/or movement-related processes; measurements that would take the form of psychometric functions. Finally, one could begin to test the hypothesis that these psychometric functions are related to discrete physiological events by measuring the effects of these same environmental variables on neuronal activity levels and then correlating these neurometric functions with the psychometric functions described above.

The first element in this approach, the notion that human perceptual performance can be viewed as the product of at least two separable and mathematically independent processes, emerged explicitly with the application of signal detection theory to perceptual psychology. In this framework, overall performance on a perceptual task is viewed as the product of processes which influence the quality of sensory signals directly, and processes which influence the decision criteria by which sensory signals are evaluated. The initial psychological studies of how human subjects use information about where a stimulus is likely to appear to improve their performance on simple perceptual tasks suggested an effect of prior knowledge about the stimulus on decision processing but not on sensory processing. For example, in Marilyn Shaw's set size experiments (1984), subjects were asked to identify a stimulus at one of either two or four locations. By changing the number of possible locations at which a stimulus could appear, Shaw manipulated prior knowledge, in this case the subject's certainty that a stimulus would appear at a particular location. Not surprisingly, human subjects performed better in this task when target location was more certain and worse when target location was less certain. A signal detection theoretic analysis of these data revealed that the improvement in performance on this simple luminance increment detection task could be totally accounted for by changes in decision processing. Other studies, however, have begun to identify a number of simple perceptual tasks in which improvements in performance produced by prior knowledge about the upcoming stimulus might well be attributable to changes in sensory processing, not solely changes in decision processing (cf. Bashinski & Bacharach, 1980; Downing, 1988; Hawkins et al., 1990; Luck et al., 1994; Luck, Hillyard, Mouloua, & Hawkins, 1996; Muller &

Humphreys, 1991; Lu & Dosher, 1998; Carrasco et al., 2000).

If prior knowledge can, at least under some conditions, influence both sensory processing and decision processing, then physiological researchers intent upon testing the separability of sensory, decisional and motor processes may need to design behavioral tasks which uniquely influence each of these processes in their subjects. One strategy for developing a task that uniquely influences sensitivity would be to assure that prior knowledge about the location at which the stimulus is likely to occur provides subjects with no information about the correct decision, or response, required on a given trial. In this way prior knowledge could, in principle, be used by the subject to enhance sensory processing without offering any decisional advantage.

If the changes in sensory processing can be separated from changes in decision processing, then the effects of prior knowledge on sensitivity can be studied systematically and quantitatively with psychometric functions. Sperling and Dosher (1986) proposed just such an approach for studying sensitivity, suggesting a methodology for manipulating prior knowledge by manipulating the utility structure of the sensory environment. In their formulation, utility refers to the gain an observer can expect to realize from devoting additional perceptual resources to a particular spatial location. The observer's expected gain is presumed to reflect prior knowledge about stimulus properties. The utility of devoting perceptual resources to a particular location might be high, for example, when the subject is certain that a stimulus will appear at that location or when the gain associated with a correct judgement at that location will be higher than the gain associated with a correct judgement at another location. In retrospect, one of Shaw's earlier papers (Shaw & Shaw, 1977) supports this notion, demonstrating that the distribution of perceptual performance can be tightly correlated with the utility structure of the visual environment.

In the experiments presented here, we wanted to isolate the effects of prior knowledge on perceptual performance to effects only on sensitivity and we attempted to develop a psychometric function for the effects of prior knowledge on sensitivity. To this end, we designed a task in which the parameter used by subjects to guide the allocation of perceptual resources (1) provided no information about the nature of the correct response and (2) was a variable which could be systematically adjusted, allowing us to provide subjects with many discrete levels of prior knowledge along a psychometric continuum. Finally, and perhaps most importantly, we designed a task (3) that could be performed by both human and monkey subjects so that similar task designs could be used in physiological studies attempting to generate linking hypotheses between psychometric and neurometric functions of perceptual sensitivity as defined by signal detection theory.

2. Experiment 1: effects of uncertainty on sensitivity in humans

We assessed performance on a discrimination task, in which the luminance of a stimulus had to be judged either bright or dim, when the location of the discriminative stimulus was uncertain. Uncertainty was systematically controlled by varying the probability with which the discriminative stimulus would appear at each of two possible locations, a manipulation of the spatial probability structure of the visual environment (Sperling & Dosher, 1986). We hoped to determine whether prior knowledge of the spatial probability structure could guide subjects in their allocation of perceptual resources, leading either to an improvement in performance at the location likely to contain the discriminative stimulus and/or a decrement in performance at the location unlikely to contain the discriminative stimulus. Importantly, regardless of where the discriminative stimulus was presented, the luminance of the discriminative stimulus was equally likely to be bright or dim. The spatial probability structure was therefore independent of the sensory properties of the discriminative stimulus, and thus of the correct decision required on any trial. For this reason, any improvement in perceptual performance that was correlated with an increase in the probability of discriminative stimulus occurrence should be attributable to a change in sensitivity, not to changes in decision processing.

2.1. Experimental design and general methods

Four adult human subjects participated in these experiments, which were reviewed and approved by the New York University Committee on Activities Involving Human Subjects. Written informed consent was obtained from all subjects. Subjects LB, BM and CS received $10/h for their participation. Subjects had normal or corrected-to-normal vision. To maintain stable head position during the experiment, a chin and forehead rest was used and subjects were instructed to maintain stable eye position at a central fixation point during the task. Eye position was not monitored.

2.1.1. Task and stimulus design

Experiment 1 was a reaction time luminance discrimination task. On each trial, a circular luminance stimulus was presented for a very brief duration in the periphery, at one of two possible locations. The stimulus was presented at one of two intensities which had been selected to yield approximately 80% correct performance when subjects knew, in advance, where the discriminative stimulus would be presented. On experimental trials, subjects had to judge whether the discriminative stimulus that supported threshold performance, was bright or dim, irrespective of its location.

Luminance stimuli were generated using light emitting diodes (LEDs) which subtended 0.25° of visual angle and were presented on a tangent screen placed 57 in. from the subject's eyes. The LEDs serving as discriminative stimuli were calibrated to have equal luminance to within 2%, and appeared green to normal human subjects.

The brightness of the discriminative stimulus was controlled by varying the pulse-width modulation of the LED during a 52–54 ms interval. According to Bloch's law (cf. Schiffman, 1990), for stimulus durations less than 100 ms, the perceived brightness of a stimulus depends only on the total energy, which is the product of its duration and intensity. Thus, varying the proportion of time an LED was illuminated during the 52–54 ms interval allowed us to vary the perceived brightness of the discriminative stimulus. In terms of absolute luminance, our standard bright LED was 80 cd/m^2 and our dim LEDs were 60, 48, 40, 30, and 21 cd/m^2.

All discriminative stimuli were suprathreshold and were presented on a black background (background luminance < 0.1 cd/m^2) in a dimly lit room (< 5 cd/m^2) at 12° eccentricity from the fixation stimulus, at one of two possible locations, one above and one below the horizontal meridian.

Discriminative stimuli were presented in the left hemifield for two subjects (in Cartesian coordinates, 6° to the left and 10° upwards from fixation, and 6° to the left and 10° downwards from fixation) and in the right hemifield for the other subjects.

2.1.2. Stimulus presentation

Subjects were seated in a dimly lit room and given several minutes to adapt to the ambient illumination. A trial (see Fig. 1) began with the illumination of a central red LED that subjects were instructed to fixate. This fixation stimulus was illuminated for 800–1000 ms, then extinguished, and after a 50 ms delay, a peripheral green LED, (the discriminative stimulus), was illuminated, at a bright or dim intensity, for 52–54 ms. Following a further 150 ms delay, two red LEDs, the choice targets, were co-illuminated for 100 ms, one directly above and one directly below the fixation stimulus[1]. The subject had 850 ms, from the time at which the choice targets were extinguished, to indicate by a button press whether the discriminative stimulus had been illuminated bright or dim. All trials were followed by visual feedback: The choice target at the upper location was re-illuminated for 300 ms if the discriminative stimulus had been bright and the choice target at the lower location was re-illuminated for 300

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[1] These LEDs served as saccadic targets in Experiment 2. They appeared in Experiment 1 so that the same visual stimuli would appear in both experiments.
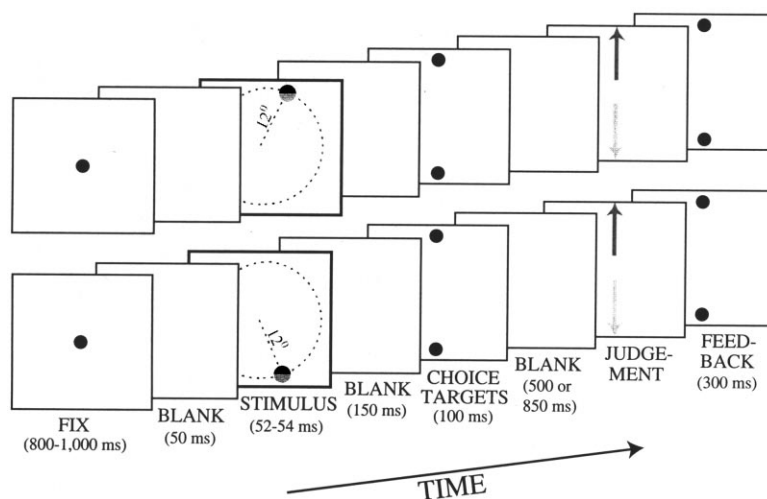
Fig. 1. Trials began with the illumination of a central red LED (fix) for 800–1000 ms. After 50 ms, a 12° eccentric, green LED (stimulus) was illuminated, bright or dim, for 52–54 ms, at one of two possible locations. Following a 150 ms delay, two red LEDs (choice targets) were co-illuminated for 100 ms, one above and one below the *fix* location. The subject judged whether the *stimulus* had been bright or dim by button press (human) or eye movement (monkey). Subjects were required to make their *judgement* within 850 ms (human) or 500 ms (monkey) of choice target offset. Visual and auditory feedback were provided at the end of each trial and monkeys received a juice reward on a randomly selected fraction of correct trials. The inter-trial interval was 600–800 ms, except for aborted trials, in which case the inter-trial interval was 2000–3000 ms.

ms if the discriminative stimulus had been dim. After correct responses, a 300 ms noise burst was delivered. Trials were considered aborted if the subject failed to respond within 850 ms (in which case a warbling tone was presented) or if the subject responded before choice target onset. The inter-trial interval was 600–800 ms for all trials, except for aborted trials, after which the next trial ensued within 2000–3000 ms.

2.1.3. Procedures

In a preliminary investigation, we identified, for each subject, a bright/dim discriminative stimulus pair that would support approximately 80% correct performance when subjects knew in advance the location at which the stimulus would be presented. Following two training sessions, each subject participated in six of these preliminary experimental sessions. Preliminary sessions consisted of one 40 min block of 500 trials during which five discriminative stimulus pairs were presented at a single one of the two possible stimulus locations. Blocks were presented in random order. Each block was subdivided into five sequential 100 trial sub-blocks in which discriminative stimuli were presented, with equal likelihood, at either a standard bright or a single dim intensity. Across sequential sub-blocks, the intensity of the dim stimulus varied randomly. All stimuli were suprathreshold and in this preliminary experiment there was no ambiguity about when or where the discriminative stimulus would appear.

After the discriminative stimulus pair that supported threshold performance had been determined, each subject participated in six (VC) or seven (CS, LB, and BM)

experimental sessions, lasting approximately 75 min each. Each session consisted of a block of approximately 800 trials during which the discriminative stimuli were presented, with a fixed probability, at each of the two possible stimulus locations, a spatial probability structure. The probability that a stimulus would appear at each of the two locations always summed to 100%. A total of six or seven probability structures were tested such that (1) each probability condition was tested twice, once at each location, and (2) on sequential sessions, the high probability conditions were presented at a given location in the following order: 93, 84 and then 69%, with the corresponding low probability conditions, 7, 16 and 31%, respectively, presented at the other location. The high and low probability locations were then switched to collect the complementary data. Several subjects also participated in a session with a spatial probability structure of 50% at each location.

2.1.4. Instructions

Subjects were provided with a detailed description of the stimuli to be presented and the responses required and were instructed to perform the task as accurately and as quickly as possible. To ensure sustained alertness, subjects were encouraged to take breaks every 100 trials. Subjects were informed that during Experiment 1 discriminative stimuli would be presented at each of the two potential locations with an equal likelihood of being bright and dim, regardless of where stimuli appeared. Subjects VC and CS knew in advance the spatial probability structure to be presented in each session. Subjects LB and BM were naive and had to

learn the spatial probability structure during the session. Although eye movements were not monitored, subjects were instructed to maintain stable fixation and the task design helped to preclude the generation of eye movements.

2.1.5. Analysis

To determine threshold, we computed percent correct performance on bright and dim trials at each location, for each sub-block. Average percent correct performance at each location was then plotted as a function of the luminance difference between the bright and dim LED for each luminance pair. These data were fit with a Weibull function, where the upper and lower asymptotes were constrained to be 100 and 50%, respectively. From these functions, the luminance pair supporting approximately 80% correct performance was determined. Sensitivity was then calculated for each luminance pair, using the traditional one-dimensional signal detection theory measure of d'.[2]

For Experiment 1, we computed percent correct performance for correct and error trials, at each of the two locations presented within each block, for all trials in each block. Given that subjects had to learn the spatial probability structure over the course of the 800 trials, we also analyzed the last 200 trials of each block, where subjects should have been most certain of the spatial probability structure. We excluded a session from further analysis if, in either the entire block of 800 trials or in the last 200 trials of each block: (1) the subject had judged 100% of the discriminative stimuli presented to be either bright or dim at one or at both locations or (2) the subject had judged 100% of bright stimuli to be bright or dim or 100% of dim stimuli to be bright or dim at one or at both locations. These patterns of responding were referred to as biased response strategies.

We then computed several measures for each probability condition, averaging across stimulus locations, both for all the trials in each block and for the last 200 trials of each block. (1) *Perceptual performance*: percent correct performance was calculated for each probability condition, plotted as a function of probability, and fit with a Weibull function. The upper and lower asymptotes for the Weibull fits were constrained to be percent correct performance when location was certain (our threshold measurement) and 50%, respectively. (2) *Sensory processing*: sensitivity, d', was calculated for each probability condition, plotted as a function of probability, and fit with a Weibull function. The upper and lower asymptotes for the Weibull fits were constrained to be performance when location was certain and 0, respectively. (3) *Decision processing*: The signal detection theory term response bias, or c,[3] was calculated for each probability condition and then plotted as a function of probability. (4) *Response latency*: for each probability condition, response latency was calculated as the interval from the time at which the choice targets were extinguished (250 ms after the discriminative stimulus was extinguished) to the time at which a button was pressed, and then plotted as a function of probability.

We performed an additional analysis: (5) *calculating the effects of recent stimulus position history*: because repeated presentation of the discriminative stimulus at the same location occurs more frequently at higher probability locations than at lower probability locations, it is possible that a temporally local sensory facilitation, such as position priming or a locally enhanced memory trace could occur. To determine if a temporally local sensory facilitation could have accounted for the improvements we found in sensitivity with increasing probability, we analyzed any changes in sensitivity that we observed as a function of the number of trials in a row in which the discriminative stimulus appeared at the same location. This trial-by-trial sequential analysis provided a measure of the extent to which sensitivity was improved by repeated sequential presentation of the discriminative stimulus at the same spatial location. For the 93, 84 and 69% probability conditions sensitivity was calculated for subsets of the data in which, for a certain number of trials in a row in the past, the discriminative stimulus had been presented at the same location. Sensitivity was then plotted as a function of the number of trials in a row during which the discriminative stimulus had been presented at the same location. We assessed the variance intrinsic to this analytic technique by plotting sensitivity as a function of the number of trials in a row in the future which would be presented at the same location, given that future trials should have had no causal influence on current performance. We averaged data gathered for the same probabilities at each of the two locations tested.

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[2] Sensitivity, $d' = [z(\text{hit rate}) - z(\text{false alarm rate})]$ (from Green & Swets, 1966; Macmillan & Creelman, 1991). In essence, our task is a photon counting task, where the subject judged the stimulus to be either dim or bright. Thus, we applied signal detection theory calculations for a one-dimensional stimulus. We arbitrarily defined the hit rate as the fraction of bright trials where the subject correctly judged a bright stimulus to be bright and the corresponding miss rate as the fraction of bright trials where the subject incorrectly judged a bright stimulus to be dim. The false alarm rate was defined as the fraction of dim trials where the subject incorrectly judged a dim stimulus to be bright.

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[3] Response bias, $c = -0.5[z(\text{hit rate}) + z(\text{false alarm rate})]$ (Green & Swets, 1966; Macmillan & Creelman, 1991). Note that a negative response bias indicated a tendency for the subject to judge the discriminative stimulus to be bright.
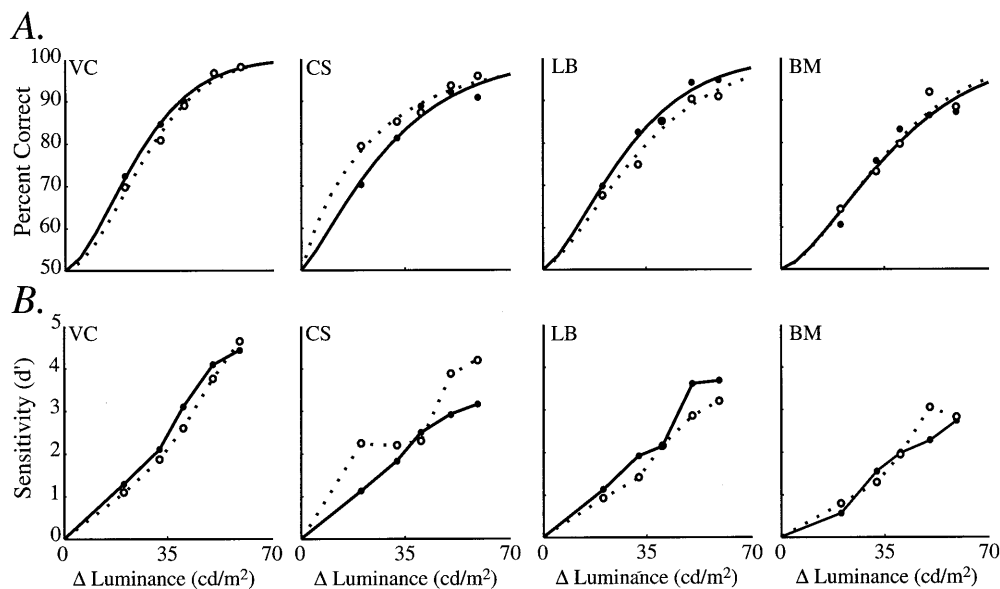
Fig. 2. Average percent correct performance is plotted as a function of the difference in luminance between the bright and dim discriminative stimuli for each of the two locations where the discriminative stimulus was presented, for each human subject. All bright stimuli had an absolute luminance of 80 cd/m². (A) Average percent correct performance as a function of the luminance difference between the bright and dim stimuli. Solid lines are Weibull functions fit to the data when the discriminative stimulus was presented at the upper location within the hemifield (filled dots). Dashed lines are Weibull functions fit to the data when the discriminative stimulus was presented at the lower location within the hemifield (open dots). For the Weibull fits, upper and lower asymptotes were constrained to be 100 and 50%, respectively. Total number of trials: 1672, 1651 (VC), 1650, 1872 (CS), 1474, 1476 (LB) and 1588, 1584 (BM), for the upper and lower location, respectively. Weibull slopes: 1.57, 1.75 (VC), 1.23, 0.9 (CS), 1.43, 1.42 (LB), and 1.51, 1.58 (BM) for the upper and lower location, respectively. Weibull thresholds: 28.39, 31.03 (VC), 32.24, 24.39 (CS), 32.12, 37.52 (LB) and 42.31, 41.11 (BM), for the upper and lower location, respectively. (B) Reanalysis of the data in A. Sensitivity is plotted as a function of the luminance difference. Solid lines reflect data gathered when the discriminative stimulus was presented at the upper location (filled dots). Dashed lines reflect data gathered when the discriminative stimulus was presented at the lower location (open dots).

2.2. Results

2.2.1. Measuring threshold

The luminance pair supporting an average percent correct performance of approximately 80%, threshold performance, across the two locations was determined for each subject when the location of discriminative stimulus occurrence was certain. Fig. 2 plots percent correct performance as a function of the luminance difference between pairs of bright and dim stimuli. Filled circles plot performance at the upper discriminative stimulus location. Open circles plot performance at the lower location. As the luminance difference increased, average percent correct performance improved at both locations and there were no consistent asymmetric trends in performance between the two locations (Fig. 2a). Fig. 2b presents these data reanalyzed in terms of the signal detection measure of sensitivity, d'. During the 4 or 5 week period in which Experiment 1 was conducted on subjects CS, BM, and LB, we found that luminance discrimination functions were stable: Average percent correct at threshold increased from 77 to 79% in subject LB, 81.1 to 83.3% in subject CS and decreased from 81.4 to 72.1% in subject BM. (A second set of luminance discrimination functions were not gathered for subject VC, who completed Experiment 1 in 1 week).

2.2.2. Overall perceptual performance: average percent correct

We then examined discrimination performance on the threshold luminance pair when the location of discriminative stimulus occurrence was made uncertain, by parametrically varying the probability of discriminative stimulus occurrence at each of the two locations studied. Fig. 3 presents data from the human subjects, plotting average percent correct performance on the discrimination task as a function of the probability of discriminative stimulus occurrence. As the probability of discriminative stimulus occurrence increased, average percent correct performance, or accuracy, improved systematically.

Fig. 3a presents this improvement in accuracy with increasing probability, measured across all of the trials presented in each block. Fig. 3b presents an analysis performed on the last 200 trials of each block during which the effect of probability on performance was found to be greatest for both of the naive subjects (LB and BM). To determine whether the increase in performance as a function of probability was statistically significant, using a minimum number of assumptions, we computed linear regressions for these data. Using this technique, the effects of probability on percent correct performance were found to be significant for
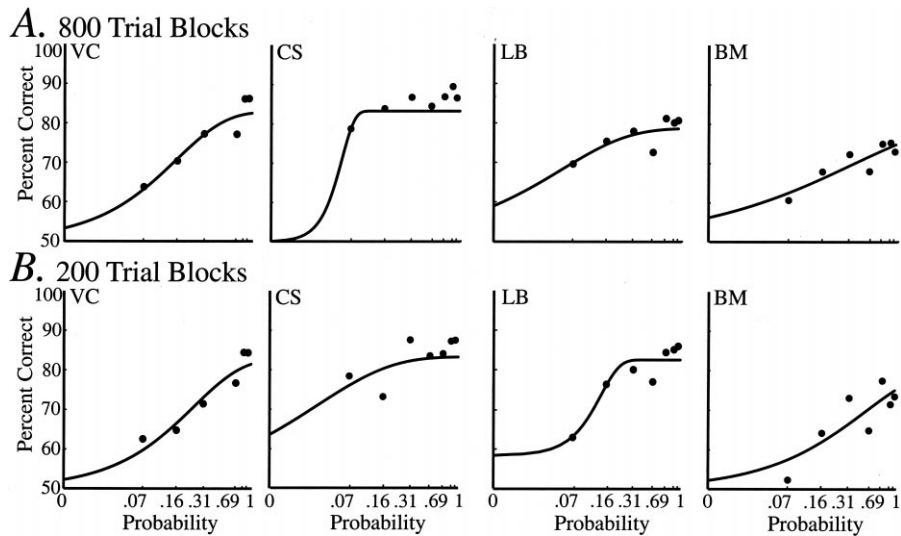
Fig. 3. Average percent correct performance is plotted as a function of the probability of discriminative stimulus occurrence, for each human subject. Solid lines are Weibull functions fit to the data. Upper and lower asymptotes were constrained to be the average percent correct performance when the stimulus location was certain and 50%, respectively. (A) Average percent correct performance for data collected over the entire 800 trials of each block. Total number of trials: 4486 (VC), 5533 (CS), 5309 (LB), and 5394 (BM). Weibull slopes: 0.819 (VC), 3.2 (CS), 0.594 (LB), and 0.335 (BM). Weibull thresholds: 0.157 (VC), 0.056 (CS), 0.052 (LB), and 0.335 (BM). (B) Average percent correct for data collected in the last 200 trials of each block. Total number of trials: 1119 (VC), 1386 (CS), 1323 (LB), and 1401 (BM). Weibull slopes: 0.828 (VC), 0.548 (CS), 2.16 (LB) and 0.681 (BM). Weibull thresholds: 0.247 (VC), 0.033 (CS), 0.141 (LB), and 0.469 (BM).

subject VC (all trials of each block: $F(1,4) = 24.99$, $P < 0.0075$; last 200 trials of each block: $F(1,4) = 124.85$, $P < 0.0037$), CS (all trials of each block: $F(1,5) = 7.5$, $P < 0.041$; last 200 trials of each block: $F(1,5) = 5.86$, $P < 0.06$), LB (all trials of each block: $F(1,5) = 7.91$, $P < 0.037$; last 200 trials of each block: $F(1,5) = 13.20$, $P < 0.015$), and BM (all trials of each block: $F(1,5) = 8.69$, $P < 0.032$; last 200 trials of each block: $F(1,5) = 5.741$, $P < 0.062$). In summary, the accuracy of luminance discrimination improved systematically with increasing probability for all trials of each block and, especially for the naive observers, where accuracy improved most dramatically during the last 200 trials of each block.

2.2.3. Sensory processing: sensitivity

In order to assess the extent to which our improvements in performance were due to a change in sensory processing, we used a signal detection theoretic analysis and plotted sensitivity (d') as a function of probability. Fig. 4 indicates that, like percent correct performance, sensitivity on the luminance discrimination task improved as the probability of discriminative stimulus occurrence increased. An improvement in sensitivity was observed as a function of probability for data from all trials in each block (Fig. 4a) with a more dramatic improvement observed during the last 200 trials of each block for the naive subjects, LB and BM (Fig. 4b). The effects of probability on sensitivity were found to be significant for subject VC (all trials of each block:

$F(1,4) = 10.49$, $P < 0.032$; last 200 trials of each block: $F(1,4) = 68.93$, $P < 0.0012$), CS (all trials of each block: $F(1,5) = 5.55$, $P < 0.065$; last 200 trials of each block: $F(1,5) = 5.408$, $P < 0.068$), LB, (all trials of each block: $F(1,5) = 6.86$, $P < 0.047$; last 200 trials of each block: $F(1,5) = 11.84$, $P < 0.018$) and BM (all trials of each block: $F(1,5) = 6.658$; $P < 0.049$; last 200 trials of each block: $F(1,5) = 6.17$, $P < 0.056$), by linear regression.

2.2.4. Decision processing: response bias

To confirm that decision processing was not being systematically influenced by our manipulation of the spatial probability structure, we also plotted response bias (c), as a function of probability (Fig. 5). Given that the spatial probability structure provided no information about the intensity of the discriminative stimulus, one would expect a response bias close to zero. We observed that response bias was stable and near zero, for most subjects, when measured for all the trials of each block (Fig. 5a) as well as, for the last 200 trials of each block (Fig. 5b). Note that all subjects had a slight tendency to judge stimuli to be bright (negative response bias) and there was a slight decrease in the tendency of subjects to judge stimuli to be bright with increasing probability. For subjects CS and LB, for all 800 trials of blocks, a correlation between probability and bias was observed ($F(1,5) = 7.43$, $P < 0.042$ and $F(1,5) = 15.12$, $P < 0.01$, respectively) by linear regression.
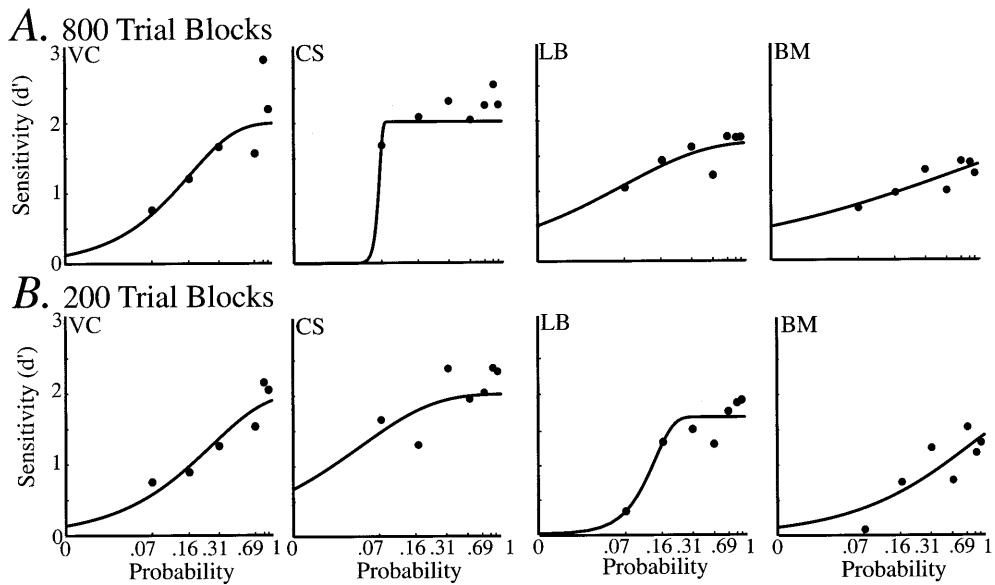
Fig. 4. The signal detection theory measure for sensory processing, sensitivity, is plotted as a function of the probability of discriminative stimulus occurrence, for each human subject. Solid lines are Weibull functions fit to the data. Upper and lower asymptotes were constrained to be the average sensitivity when the stimulus location was certain and 0, respectively. (A) Average sensitivity as a function of discriminative stimulus probability for data collected over the entire 800 trials of each block. Weibull slopes: 0.984 (VC), 13.093 (CS), 0.541 (LB), and 0.311 (BM). Weibull thresholds: 0.163 (VC), 0.067 (CS), 0.067 (LB), and 0.572 (BM). (B) Average sensitivity as a function of discriminative stimulus probability for data collected in the last 200 trials of each block. Weibull slopes: 0.814 (VC), 0.607 (CS), 2.368 (LB) and 0.657 (BM). Weibull thresholds: 0.261 (VC), 0.043 (CS), 0.133 (LB) and 0.69 (BM).
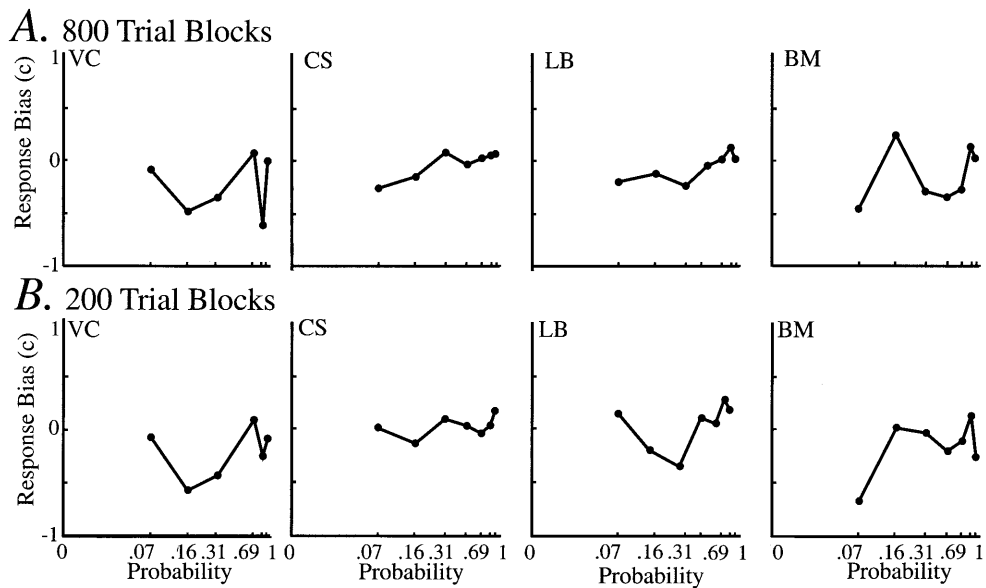

Fig. 5. The signal detection theory measure for decision processing, response bias, is plotted as a function of the probability of discriminative stimulus occurrence, for each human subject. (A) Average response bias as a function of discriminative stimulus probability for data collected over the entire 800 trials of each block. (B) Average response bias as a function of discriminative stimulus probability for data collected in the last 200 trials of each block.

2.2.5. Response latency: a speed–accuracy trade-off

If the improvements we found in percent correct performance and sensitivity with increasing probability were due to an underlying trade-off between accuracy and response latency, then response latency would be expected to increase with increasing probability. Fig. 6

plots mean latency to respond (in ms $\pm$ SEM) as a function of probability. None of the subjects showed an increase in mean response latency with increasing probability in either all trials of each block (Fig. 6a) or the last 200 trials of each block (Fig. 6b). Thus, the systematic improvements in average percent correct perfor-
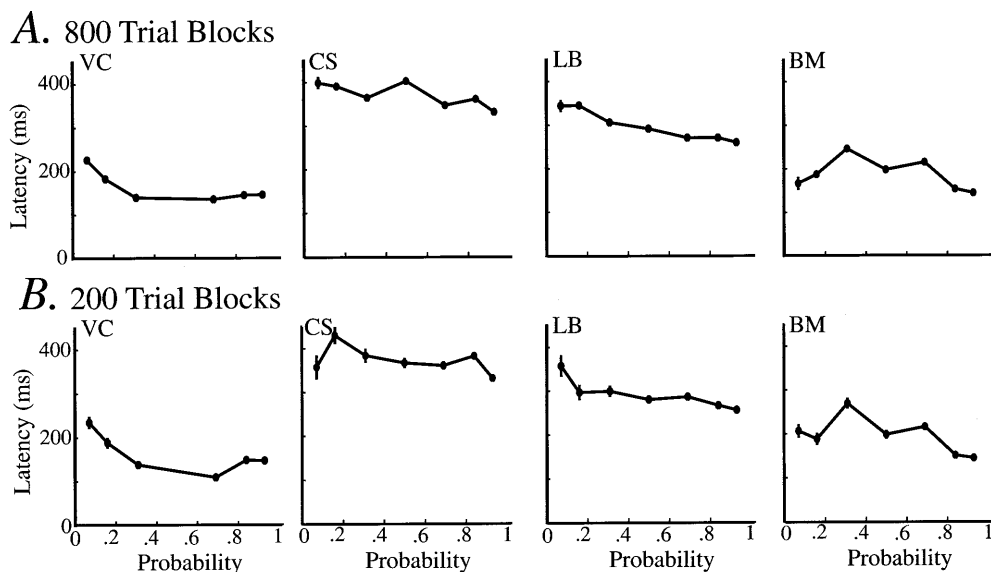
Fig. 6. Average response latency is plotted as a function of the probability of discriminative stimulus occurrence, for each human subject. (A) Average response latency in ms (± SEM) as a function of discriminative stimulus probability, for data collected over the entire block of 800 trials. (B) Average response latency in ms (± SEM) as a function of discriminative stimulus probability, for data collected in the last 200 trials of each block.

mance as a function of probability could not be due to a systematic increase in mean response latency as a function of probability.

2.2.6. Effects of recent stimulus history

Repeated presentation of the discriminative stimulus at the same location, as would occur frequently at high probabilities, could have resulted in a temporally local facilitation, such as position priming or a locally enhanced memory trace. Although this could not account for our finding that naive subjects showed a stronger effect during the last 200 trials of an 800 trial block, we examined the effects of recent stimulus history on sensitivity to determine if a temporally local sensory facilitation could have accounted for some of the improvement we observed in sensitivity. To do this, we plotted average sensitivity, for several probabilities, as a function of the number of trials in a row, or sequential trials, during which the discriminative stimulus appeared at the same location (Fig. 7).

At the probability conditions of 93, 84 and 69%, all subjects showed essentially no change in average sensitivity relative to baseline when, for up to five or eight trials in a row in the *past*, the discriminative stimulus was presented at the same location. For all subjects, the minor fluctuations in average sensitivity observed when up to five or eight trials in a row in the *past* were presented at the same location were similar to the fluctuations due to variance intrinsic to this measure, as assessed by plotting sensitivity when up to five or eight trials in a row in the *future* were going to be presented at the same location (Fig. 7).

The failure to find evidence for sequential effects in the 69% probability condition is particularly important since it suggests that the absence of sequential effects at the higher probabilities is not due to a ceiling effect. Furthermore, our failure to find sequential effects did not arise from measuring sensitivity, since we also found no systematic effects in sequential analyses of percent correct performance, response bias, or response latency (Ciaramitaro & Glimcher, 1999). Finally, given that the sequential analysis was limited by the number of consecutive trials that, by random fluctuations, presented the discriminative stimulus at the same location,
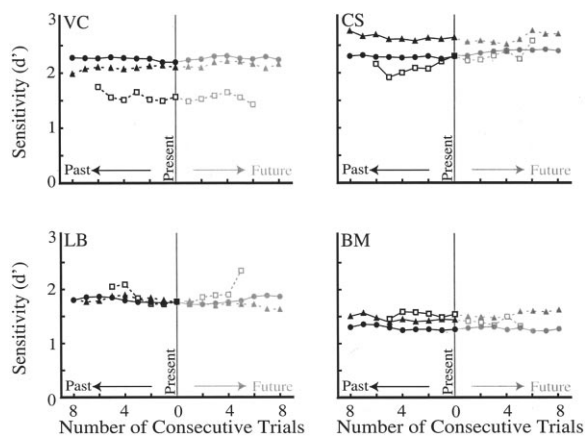

Fig. 7. Average sensitivity is plotted as a function of the number of sequential trials *in the past* (black segment), and *in the future* (gray segment), presented at the same location, for each human subject. Data from the 93% probability condition (filled circle, solid line), the 84% probability condition (filled triangle, dashed line), and the 69% probability condition (open square, dashed line), are shown.

we conducted a memory kernel analysis (Maljkovic & Nakayama, 1994, 1996). Assuming that the effect of repeated presentation was linear, this would allow us to determine the influence of specific preceding trials on sensitivity, irrespective of the location of intervening trials, for any number of trials into the *past*. The memory kernel analysis (data not shown) indicated that there was no systematic improvement in sensitivity when the discriminative stimulus was presented at the same location, up to 12 trials in the *past*.

In summary, we found little evidence for an influence of recent stimulus position history on sensitivity. While this does not exclude the possibility of a middle-term adaptation effect which could arise from the different adaptation histories for stimuli at the two possible locations, the systematic increase in sensitivity we observed as a function of probability was unlikely to be due to a short-term mechanism operating over a time course of 5–12 trials.

3. Experiment 2: effects of uncertainty on sensitivity in monkeys

3.1. Experimental design and general methods

Two juvenile rhesus macaques (*Macaca mulatta*) served as subjects in these experiments. All experimental procedures were approved by the New York University Institutional Animal Care and Use Committee and complied with the PHS Guide for the care and use of animals.

3.1.1. Surgical procedures

To allow for the maintenance of stable head position and to monitor eye position during the experiment, animals were implanted with a head restraint prosthesis and a scleral search coil (for details see Platt & Glimcher, 1997). All surgical procedures were performed using standard aseptic techniques under isoflurane inhalant anaesthesia. Analgesia was provided post-operatively for a minimum of three days. Antibiotics were administered prophylactically during surgery and were continued for a minimum of 3 days.

3.1.2. Behavioral procedures

Subsequent to a post-operative recovery period of 6 weeks, animals were habituated to sitting in a primate chair and to head restraint. Animals were then permitted only limited access to water in their home cages and were trained to perform the task described below for a juice reward. During training and experimental sessions, animals were seated in a primate chair for periods of 1–4 h; otherwise, animals were free to move about in their home cages. The animal's water intake and general health, including weight, were monitored on a daily basis. Eye position was monitored during the task at 500 Hz using the scleral search coil method, which reported the position of the eye with an accuracy of better than 0.25° (Fuchs & Robinson, 1966).

3.1.3. Stimulus design

Monkey subjects were run in the same task, using the same apparatus, as outlined for human subjects. They viewed the same visual stimuli and were provided with the same auditory and visual feedback as the human subjects. However, monkey subjects indicated their judgement (bright or dim) by making an eye movement rather than a button press and when they produced a correct response, they received a fruit juice reward in addition to visual and auditory feedback.

3.1.4. Stimulus presentation

For the monkeys, a trial began with the illumination of a central red LED that subjects were required to fixate within 1000 ms. Subjects had to align their gaze within 2° of the fixation stimulus for a variable fixation interval (800–1000 ms). This fixation stimulus was then extinguished and after a 50 ms delay, the *discriminative stimulus* was illuminated at a bright or dim intensity for 52–54 ms. Following a further 150 ms delay, two red LEDs, the *choice targets*, were co-illuminated (100 ms), one above and one below the fixation stimulus. The subject had 500 ms, from the time of choice targets offset, to align gaze within 4° of one of the choice target locations. The choice target location above the fixation stimulus was the correct response if the discriminative stimulus presented had been bright and the choice target location below the fixation stimulus was the correct response if the discriminative stimulus presented had been dim. All trials were followed by visual feedback: The choice target at the upper location was re-illuminated for 300 ms if the discriminative stimulus had been bright and the choice target at the lower location was re-illuminated for 300 ms if the discriminative stimulus had been dim. Correct responses were indicated by a 300 ms noise burst and a fruit juice reward, which was provided on a VR3 variable ratio reinforcement schedule (on average, one of every three correct trials was rewarded). A trial was considered aborted if the subject failed to respond within 500 ms (in which case a warbling tone was presented) or if the subject responded before choice target onset. The inter-trial interval was 600–800 ms, except for aborted trials, which were followed by a 3000–4000 ms inter-trial interval.

3.1.5. Procedures

To determine threshold performance when the location of the discriminative stimulus was certain, both monkeys participated in six preliminary experimental sessions, lasting roughly 1.2 h each (range: 0.9–1.5 h).

Two of these preliminary experimental sessions were normally collected per day. Sessions, blocks and sub-blocks, were presented as described for human subjects.

For Experiment 2, each monkey subject participated in five (Ahab) or seven (Zed) experimental sessions, lasting roughly 2 h each (range 1.75–2.5 h). Sessions were presented as described in Experiment 1 for human subjects. The 93% and 7% probability conditions were always presented first and, whenever possible, a new spatial probability structure was not presented until data for a given spatial probability structure had been successfully obtained. One subject, Zed, was also presented with a spatial probability structure of 50% at each location.

3.1.6. Instructions

Several months of training were required for monkeys to perform this task reliably, and as quickly and as accurately as possible, without many aborts. During training, if the abort rate was observed to increase over time, the inter-trial intervals were increased.

To determine threshold performance when the location of the discriminative stimulus was certain, animals were trained not to adopt a biased response strategy of judging 100% of the discriminative stimuli to be either bright or dim, a response pattern typically observed at the most difficult discriminations. If a biased strategy emerged, the experiment was terminated and the animal received further training. For example, if all stimuli were judged to be bright, the experimenter increased the proportion of dim stimuli, requiring an increase in the generation of the non-preferred judgement, dim, to obtain a juice reward.

For experiment 2, no cue was provided to indicate the spatial probability structure, rather, the probability structure had to be learned by the subject during the session. Monkey subjects frequently adopted a biased response strategy early in data collection: judging 100% of bright stimuli to he bright (or dim) or 100% of dim stimuli to be bright (or dim) at one or at both locations. If an animal adopted a biased response strategy, the experiment was terminated and the animal received further training. For example, if all stimuli were judged bright at the upper discriminative stimulus location, the spatial probability structure was altered such that all stimuli were dim and were only presented at the upper discriminative stimulus location.

Finally, to stabilize performance on these tasks: (1) On an average of 10% of trials, no discriminative stimulus was presented, but rather, a simple saccade task was presented. In this task, once gaze was aligned within 2° of the central fixation stimulus, one of the choice targets was co-illuminated with the fixation stimulus for 800–1000 ms. The monkey was required to maintain fixation until the fixation stimulus was extinguished and then had 500 ms to align gaze within 4° of the choice target location. Each choice target was presented in this way on

5% of trials. (2) Breaks were given roughly every 100 trials.

3.1.7. Analysis

To determine threshold performance when the location of the discriminative stimulus was certain, data were excluded from analysis if: (1) a complete set of data from all luminance pairs could not be gathered at a given location on a given day, (2) the abort rate for any of the sub-blocks was high (greater than 50% for either the bright or dim stimulus or greater than 30% across both stimuli), (3) a biased response strategy emerged for any of the sub-blocks. For experiment 2, data were excluded from further analysis if, in either the entire block of 800 trials or the last 200 trials of each block, there was evidence of: (1) a high abort rate (> 50%) at either location or (2) a biased response strategy. Data meeting these criteria were analyzed as described previously for Experiment 1.

3.2. Results

3.2.1. Measuring threshold

The luminance pair supporting an average threshold performance of approximately 80% was determined for each subject when the location of discriminative stimulus occurrence was certain. Fig. 8 presents data from the two monkey subjects, plotting percent correct performance at each of the two locations, as a function of luminance difference. As the luminance difference between the bright and dim stimuli increased, percent correct performance improved at each location and subjects did not show a marked asymmetry in performance between locations (Fig. 8a). Fig. 8b presents these data reanalyzed in terms of sensitivity. Despite the 2 or 3 month period during which Experiment 2 was conducted in subjects Ahab and Zed, respectively, we found that luminance discrimination functions gathered during and/or after Experiment 2 remained stable: Average percent correct at threshold varied from 80.2 to 83.8% in subject Zed and from 74.2 to 83.5% in subject Ahab.

3.2.2. Overall perceptual performance: average percent correct

We next examined performance when the location of threshold discriminative stimulus occurrence was uncertain. Fig. 9 presents data from the two monkey subjects, plotting average percent correct performance on the discrimination task as a function of the probability of discriminative stimulus occurrence[4]. As in the human data, we found a systematic improvement in average

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[4] Fig. 9 displays the results from two sets of data at each probability, averaging data obtained for the same probability at each of the two potential discriminative stimulus locations, except for the 93 and 7% probabilities for monkey Ahab, which reflect only one set of data.
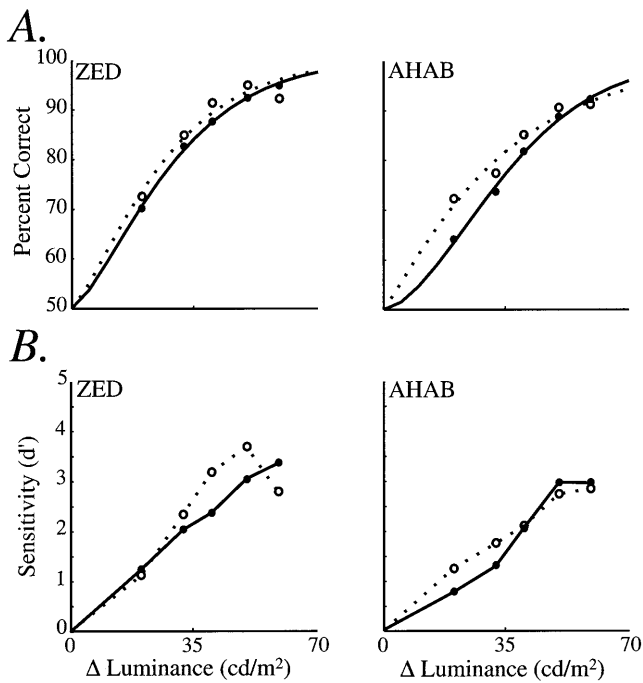
A.

B.

Fig. 8. Average percent correct performance is plotted as a function of the difference in luminance between two discriminative stimuli for each of the two locations where the discriminative stimulus was presented, for each monkey subject. (A) Average percent correct performance as a function of the luminance difference between bright and dim stimuli. Solid lines are Weibull functions fit to the data when the discriminative stimulus was presented at the upper location within the hemifield (filled dots). Dashed lines are Weibull functions fit to the data when the discriminative stimulus was presented at the lower location within the hemifield (open dots). Upper and lower asymptotes were constrained to be 100 and 50%, respectively. Total number of trials: 1177, 1189 (Zed) and 1411, 1394 (Ahab), for the upper and lower location, respectively. Weibull slopes: 1.38, 1.27 (Zed) and 1.67, 1.11 (Ahab), for the upper and lower location, respectively. Weibull thresholds: 31.58, 28.29 (Zed) and 40.08, 34.44 (Ahab), for the upper and lower location, respectively. (B) Reanalysis of the data in A. Sensitivity is plotted as a function of the luminance difference. Solid lines reflect data gathered when the discriminative stimulus was presented at the upper location (filled dots). Dashed lines reflect data gathered when the discriminative stimulus was presented at the lower location (open dots).

percent correct performance as the probability of discriminative stimulus occurrence increased. Note that although monkey subjects required extensive training on this task, the data included for analysis were collected over the course of only 19 days for subject Zed (7 of 19 datasets met criterion), and 11 days for subject Ahab (5 of 11 datasets met criterion). Furthermore, the percentage of aborted trials in these data was low in monkey subjects: an average of 24 and 12% in subjects Zed and Ahab, respectively.

Fig. 9a indicates that the improvement in performance with increasing probability was observed for all trials in each block. However, for both of these 'naïve' subjects, a more dramatic improvement in performance with increasing probability was seen in the last 200

trials of each block (Fig. 9b). The effects of probability on percent correct performance were found to be significant for subject Zed, (all trials of each block: $F(1,5) = 15.92$, $P < 0.01$; last 200 trials of each block: $F(1,5) = 64.22$, $P < 0.0005$), and subject Ahab, (all trials of each block: $F(1,4) = 2.77$, $P < 0.171$; last 200 trials of each block: $F(1,4) = 18.41$, $P < 0.013$) by linear regression. In summary, the accuracy of luminance discrimination improved systematically with increasing probability across all the trials of each block, and especially in the last 200 trials of each block, for both of our monkey subjects.

3.2.3. Sensory processing: sensitivity

We determined the contributions of changes in sensory processing to the improvements in luminance discrimination performance as a function of probability by plotting sensitivity (d') as a function of probability. As indicated in Fig. 10, sensitivity varied systematically as a function of probability: As the probability of discriminative stimulus occurrence increased, sensitivity im-

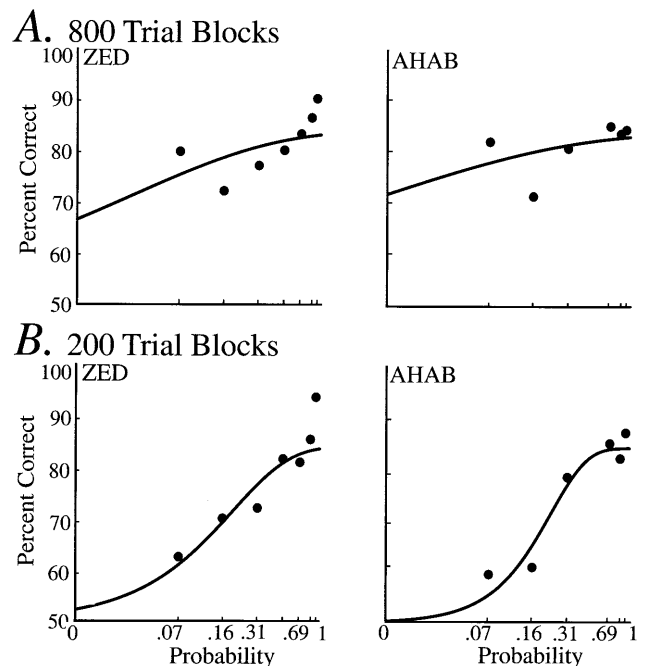**A. 800 Trial Blocks**

B. 200 Trial Blocks

Fig. 9. Average percent correct performance is plotted as a function of the probability of discriminative stimulus occurrence, for each monkey subject. Solid lines are Weibull functions fit to the data. Upper and lower asymptotes were constrained to be the average percent correct performance when the stimulus location was certain and 50%, respectively. (A) Average percent correct performance as a function of discriminative stimulus probability for data collected over the entire 800 trials of each block. Total number of trials: 3881 (Zed) and 3695 (Ahab). Average percent of aborted trials: 24% (Zed) and 12% (Ahab). Weibull slopes: 0.368 (Zed) and 0.253 (Ahab). Weibull thresholds: 0.029 (Zed) and 0.01 (Ahab). (B) Average percent correct for data collected in the last 200 trials of each block. Total number of trials: 957 (Zed) and 753 (Ahab). Weibull slopes: 0.917 (Zed) and 1.467 (Ahab). Weibull thresholds: 0.195 (Zed) and 0.229 (Ahab).
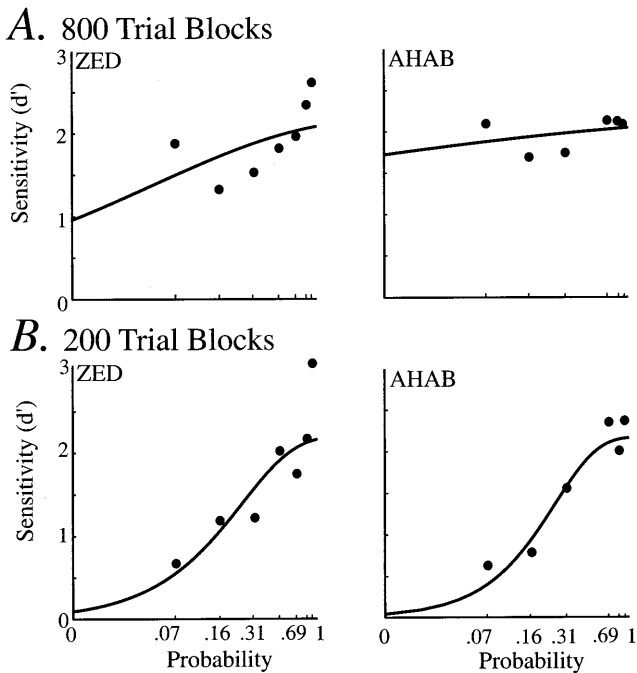
Fig. 10. Average sensitivity is plotted as a function of the probability of discriminative stimulus occurrence, for each monkey subject. Solid lines indicate Weibull functions fit to the data. Upper and lower asymptotes were constrained to be the average sensitivity when the stimulus location was certain and 0, respectively. (A) Average sensitivity as a function of discriminative stimulus probability for data collected over the entire 800 trials of each block. Weibull slopes: 0.354 (Zed) and 0.154 (Ahab). Weibull threshold: 0.048 (Zed) and 0.002 (Ahab). (B) Average sensitivity as a function of discriminative stimulus probability for data collected in the last 200 trials of each block. Weibull slopes: 0.986 (Zed) and 1.285 (Ahab). Weibull thresholds: 0.242 (Zed) and 0.232 (Ahab).

proved. As with percent correct performance, the improvement in sensitivity with increasing probability was seen across all the trials of each block (Fig. 10a). The most dramatic improvement, however, was observed in the last 200 trials of each block (Fig. 10b). The effects on sensitivity as a function of probability were significant for subject Zed, (all trials of each block: $F(1,5) = 11.54$, $P < 0.019$; last 200 trials of each block: $F(1,5) = 28.36$, $P < 0.0031$), and subject Ahab, (all trials of each block: $F(1,4) = 3.94$, $P < 0.118$; last 200 trials of each block: $F(1,4) = 28.43$, $P < 0.006$) by linear regression.

3.2.4. Decision processing: response bias

To confirm that decision processing was not also being influenced by our manipulation of the spatial probability structure, we plotted response bias (c) as a function of probability (Fig. 11). We observed that response bias was fairly stable and near zero for all trials of each block (see Fig. 11a) as well as in the last 200 trials of each block (see Fig. 11b), where the largest effects on sensitivity were observed. As with our human

subjects, monkey subjects exhibited a slight tendency to judge stimuli to be bright.

3.2.5. Response latency: a speed–accuracy trade-off

We assessed whether an underlying change in response latency could explain the improvement we observed in sensitivity with increasing probability. Fig. 12 plots mean latency to respond (in ms ± SEM) as a function of probability. Neither of the two subjects showed an overall increase in mean response latency as a function of probability either across all the trials of each block (Fig. 12a) or in the last 200 trials of each block (Fig. 12b). Thus, the systematic improvements in average percent correct performance with increasing probability were not due to an underlying increase in mean response latency.

Furthermore, we found no evidence for any systematic changes in motor processes. Animals were trained to make accurate eye movements, within ± 4° of the visual stimulus. A very small percentage of trials, 7 and 3% of the total number of trials for subjects Zed and Ahab, respectively, were excluded from analysis due to movements which were inaccurate and exceeded the ± 4° window. The mean amplitude of eye movements was 11.84° (SE 0.026) and 11.19° (SE 0.02) for subjects Zed and Ahab, respectively. For both animals, initial eye position at fixation remained stable over the course
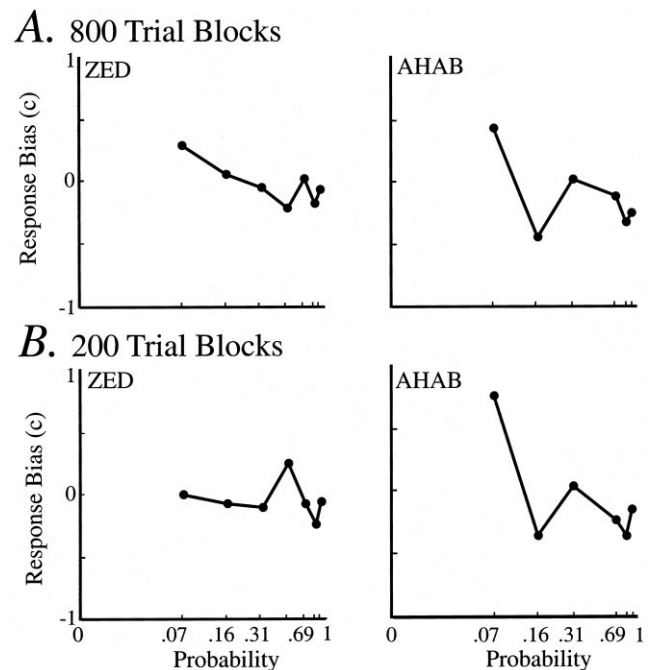

Fig. 11. Average response bias is plotted as a function of the probability of discriminative stimulus occurrence, for each monkey subject. (A) Average response bias as a function of discriminative stimulus probability for data collected over the entire 800 trials of each block. (B) Average response bias as a function of discriminative stimulus probability for data collected in the last 200 trials of each block.
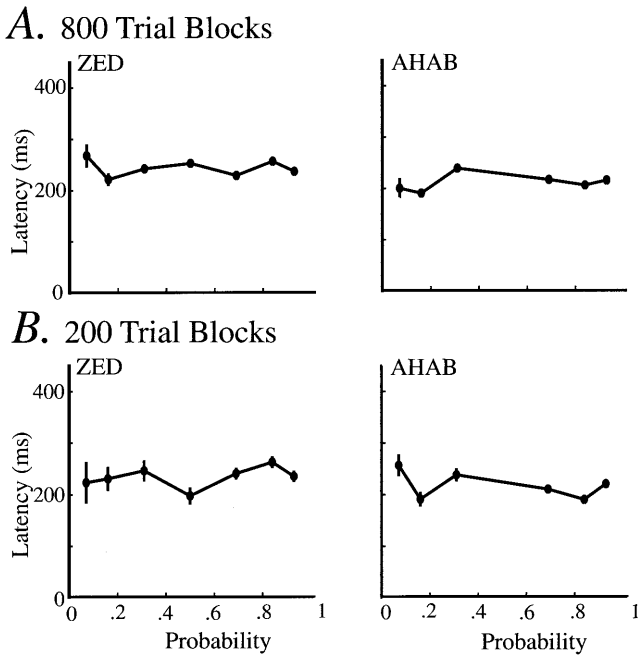
A. 800 Trial Blocks

Fig. 12. Average response latency is plotted as a function of the probability of discriminative stimulus occurrence, for each monkey subject. (A) Average response latency in ms (± SEM) as a function of discriminative stimulus probability, for data collected over the entire block of 800 trials. (B) Average response latency in ms (± SEM) as a function of discriminative stimulus probability, for data collected in the last 200 trials of each block.
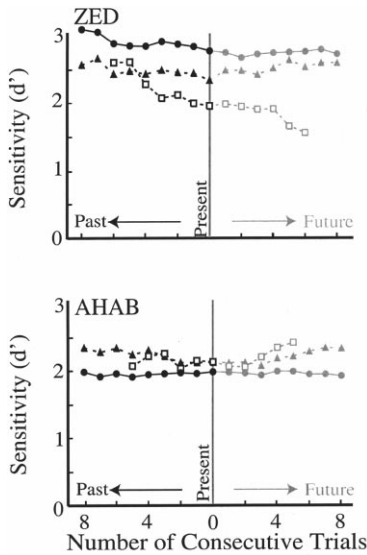

Fig. 13. Average sensitivity is plotted as a function of the number of sequential trials *in the past* (black segment), and *in the future* (gray segment), presented at the same location, for each monkey subject. Data from the 93% probability condition (filled circle, solid line), the 84% probability condition (filled triangle, dashed line), and the 69% probability condition (open square, dashed line), are shown.

of the experiment and the vertical and horizontal component of saccadic eye movements remained stable, to within 1°, despite changes in the spatial probability structure which affected sensitivity (data not shown).

3.2.6. Effects of recent stimulus history

To determine if a temporally local facilitation could have accounted for the improvements we found in sensitivity, we plotted average sensitivity as a function of the number of sequential trials on which the discriminative stimulus appeared at the same location as the location of the high probability discriminative stimulus (Fig. 13). At probability conditions of 93 and 84%, both subjects showed essentially no change in average sensitivity relative to baseline, even when the discriminative stimulus was presented at the same location for up to eight trials in a row in the *past*. Furthermore, for both subjects, the minor fluctuations in average sensitivity observed when up to eight trials in a row in the *past* were presented at the same location were similar to the fluctuations observed when up to eight trials in a row in the *future* were presented at the same location.

At the lower probability condition of 69%, an increase in average sensitivity was observed for one subject, Zed, when five or six trials in a row in the *past* were presented at the same location. This evidence suggests that, for a restricted condition there was an effect of recent stimulus position history. However, the magnitude of this increase in average sensitivity was similar to the magnitude of the decrease observed due to intrinsic variance, as assessed by plotting sensitivity when up to five or six trials in a row in the *future* were presented at the same location.

Importantly, these results did not arise because we were measuring sensitivity. Additional sequential analyses revealed no systematic effects on percent correct performance, response bias, or response latency (Ciaramitaro & Glimcher, 1999). Furthermore, a memory kernel analysis (Maljkovic & Nakayama, 1994, 1996) performed on the data from subject Zed provided no evidence for position priming, up to the 12 trials in the *past*.

In summary, the systematic increase in sensitivity as a function of probability, in our task, was unlikely to be due to a short-term mechanism such as temporally local facilitation, occurring over the course of 5–12 trials.

4. Discussion

The three primary goals of these experiments were to develop a paradigm that (1) separated the effects of prior knowledge on sensitivity from the effects of prior knowledge on the criteria by which decisions are made (2) developed a continuous and quantitative assay for the effects of prior knowledge on sensitivity and (3)

could be used in both humans and monkeys, permitting the examination of a possible animal model for human visual-spatial attention. To this end, we developed a simple luminance discrimination paradigm where the probability that a discriminative stimulus would appear at each of two potential locations, the spatial probability structure of the environment (after Sperling & Dosher, 1986), was varied. The probability that any given perceptual judgement would be required, the decisional probability, was independent of the spatial probability structure and was, in these experiments, held constant. The spatial probability structure should therefore have governed the spatial allocation of resources effecting sensitivity, while the decisional probabilities should have held the criteria by which decisions were made constant.

In fact, we found that the perceptual sensitivities of our human and monkey subjects, as measured by the signal detection term d', varied systematically as a function of the spatial probability structure. The decisional criteria, as measured by the signal detection theory term c, remained fairly constant throughout these experiments in which decisional probabilities were held constant. Our data thus indicate that, even in a task where the available knowledge can not confer an advantage by altering decision processing, prior knowledge (the spatial probability structure) can influence perceptual sensitivity.

While it may be premature to conclude that the effects we observed on sensitivity can be attributed to the psychological process often described as visual-spatial attention, the systematic improvement we found in sensitivity as a function of probability did not appear to be due to a speed–accuracy trade-off. Nor were these effects due to a short-term process (such as position priming or an enhanced memory trace), occurring over the course of 1–12 trials, which could have arisen due to differences in the adaptation histories for stimuli occurring with different probabilities at different spatial locations. Furthermore, the increase in sensitivity with probability was not correlated with systematic shifts in fixational eye position in our animal subjects, whose eye position was continuously monitored. We did, however, observe that the magnitude of this improvement in sensitivity developed over the course of an entire 800 trial block, a time during which the subjects could have accurately learned the spatial probability structure or learned to optimally allocate perceptual resources. Taken together, these data suggest that our manipulation activated a long-term process that influenced sensitivity but not decisional criteria. This unavoidably raises the possibility that our manipulation of the subject's prior knowledge of the spatial probability structure led to a re-allocation of spatial attention in a manner that regulated perceptual sensitivity in this luminance discrimination task. Of course, it is possible

that some process which might not be considered visual spatial attention, with a time course of greater than 12 trials, might account for some of these results. Some classes of perceptual adaptation effects may fall into this category. But perhaps more importantly, these data provide a tool for the manipulation of sensitivity independent of decisional criteria in both humans and monkeys. Physiological studies employing a paradigm of this type could begin to examine whether perceptual sensitivity and decisional processes are neurobiologically separable.

4.1. Sensory processing versus decision-making

The idea that perceptual and decisional criteria can be separated is, of course, nothing new. Many previous studies have demonstrated independent contributions of sensory and decision processing to perceptual performance in probability-cueing paradigms by using signal detection theory (Bashinski & Bacharach, 1980; Downing, 1988; Hawkins et al., 1990; Luck et al., 1994, 1996; Muller & Findlay, 1987; Muller & Humphreys, 1991). However, in some of these studies, task designs may have introduced influences on decision processing which confounded interpretations of effects on sensory processing. Experimental paradigms which place high information and memory demands on subjects, for example, may result in the preferential encoding or retrieval of sensory information at certain spatial locations or may introduce uncertainty in assigning a perceptual judgement to a particular spatial location (c.f. Kinchla, 1992; Luck et al., 1994, 1996; Palmer et al., 1993). In one typical study, Downing (1988) argued that she had demonstrated independent effects of a cue on sensitivity and decision making by using a task in which subjects encoded and retained information for up to four visual stimuli, each presented at one of 12 possible locations, until the trial was over, when subjects were probed about their judgements at each location. Given that the cued location was likely to be probed and that the uncued locations that would be probed could not be predicted, it has been argued that subjects may have encoded information at the cued location more quickly or carefully, and encoded or stored less information from other locations, especially as the limits of short term visual memory were reached. The differential encoding of information could have led subjects to guess more often at uncued locations, resulting in the differences in sensitivity found between the cued and uncued locations in this study. Despite criticisms like these, which can be leveled at many studies, recent work continues to raise the possibility that changes in sensory processing may account for some improvements in performance on perceptual tasks (c.f. Lu & Dosher, 1998; Yeshurun & Carrasco, 1999; Carrasco et al., 2000).

Our experimental study of perceptual performance was specifically designed to separate the contributions of changes in sensitivity from the contributions of changes in decisional criteria. We did this to permit future investigations of the extent to which the nervous system may or may not separate these processes. In our experimental design we adopted two unusual strategies. First, we did not use a pre-trial cue to provide prior knowledge about where a visual stimulus was likely to occur. Rather, we adopted Sperling and Dosher's proposal that changes in the utility of a spatial location could, in principle, be used to induce subjects to produce spatially local shifts in sensory and decisional efficiency: In our experiment, the spatial probability structure of the environment, which was systematically varied, indicated the location in space to which perceptual resources should have been allocated while the decisional probability, which was held constant, indicated the decisional criteria which optimized performance. Thus, sensory processing and decision processing should have been largely independent in our task. Second, we adopted an unusual stimulus design so that even if the subject was unable to perform the required discrimination, there was no ambiguity about when or where the stimulus occurred. We did this by making both bright and dim stimuli suprathreshold for detection. This allowed subjects, in principle, to determine the spatial probability structure of a block of trials, even if they were performing the luminance discrimination at chance. Finally, our task minimized decisional influences by avoiding the introduction of high information or memory loads on observers and by avoiding the use of post-trial probes, distractors, or masks, which might have influenced decision processing.

4.2. A continuous and quantitative analysis of sensitivity

In the human psychophysical literature, techniques have been developed for the quantitative assessment of perceptual resource allocation. The trade-offs between the allocation of perceptual resources and instruction have been formalized in performance–resource functions, the performance operating characteristic (Norman & Bobrow, 1975), and the attention operating characteristic (Kinchla, 1969b; Sperling & Melchner, 1978). Further, the rules that govern and limit the allocation of attentional resources have been the subject of investigation (cf. Sperling & Dosher, 1986; Wickens, 1984). Most recently, linear systems analysis has been applied to quantify some of these effects: Blaser and Sperling (1998) have developed psychophysical tasks which measure attentional effects using an attention modulation transfer function.

In the monkey physiological literature, by contrast, a more quantitative assessment of perceptual performance

as a function of instruction, or prior knowledge, has been rare. The majority of behavioral tasks employed in animals to study attention or attention-related phenomena have examined the influence of prior knowledge on performance as an all-or-none event, where subjects either 'attend' or 'do not attend' (cf. Moran & Desimone, 1985; Motter, 1993; Treue & Maunsell, 1996; Treue & Martinez Trujillo, 1999). To develop a continuous and quantitative method for varying the effect of prior knowledge on the performance of our monkeys, we parametrically controlled the perceptual requirements of the task by systematically manipulating prior knowledge about the sensory environment (the spatial probability structure), as originally suggested by Sperling and Dosher (1986). We were thus able to measure changes in sensitivity more systematically than has been typical in animal studies of attention or attention-related phenomena. The improvements we observed in sensitivity as a function of probability thus serve as a psychometric function for the effects of prior knowledge on sensitivity, where sensitivity is explicitly defined by signal detection theory and is quantified along a continuum.

4.3. Developing an animal model

The experimental design used here allowed us to study the unique influences of prior knowledge on perceptual sensitivity using a similar technique in both humans and monkeys. We obtained similar results on our task for both humans and monkeys, suggesting that similar mechanisms may be involved. Furthermore, the experimental paradigm we employed allowed us to explicitly quantify changes in sensory processing as well as obtain a continuous and quantitative assessment of changes in sensory processing. Once a psychometric function has been established for a well defined psychological process, quantified changes in mental state can then be explicitly correlated with quantified changes in neuronal state. In principle, we are now in a position to begin to examine the closely related hypothesis that changes in sensitivity may be correlated with physiological changes at one or more points in the primate nervous system. Previous studies have accomplished similar linkages by identifying neurometric functions that are tightly correlated with well described psychometric functions (cf. Britten, Shadlen, Newsome, & Movshon, 1992; Celebrini & Newsome, 1994; Newsome, Britten, & Movshon, 1989). Using approaches like the one described here, this should also become possible for studies of perceptual sensitivity.

4.4. Response strategies

The strategy adopted by a subject to solve a perceptual task can greatly influence the results obtained and the strategy selected is, in turn, very sensitive to task parameters such as the penalties imposed for incorrect judge-

ments or for judgements made too quickly or too slowly (cf. Sperling & Dosher, 1986; Shaw, 1982). Given these considerations, we imposed constraints on the strategies that could be used by subjects to solve the problem of how to allocate perceptual resources between the two potential discriminative stimulus locations as a function of discriminative stimulus probability.

In our task, data were not considered for analysis if subjects adopted a biased response strategy, which they occasionally did in judging stimuli presented at low probability locations. Such a solution, of essentially ignoring the low probability location, could have been optimal if subjects incurred a cost to achieve a split allocation of resources between the two locations. While we rarely saw evidence of such a strategy in our human subjects, we did see evidence of this strategy in our monkey subjects. Monkey subjects often developed a biased response strategy at the low probability location, such as identifying all trials at this location as bright. We believe that actively prohibiting our monkeys from adopting such a solution was important since it enabled us to maintain parametric control over the allocation of resources in our task.

Instead, our subjects seem to have been forced to solve our luminance discrimination task by matching the allocation of perceptual resources to the spatial probability structure of the visual environment, a possibility that has been previously considered in humans (cf. Neimark & Estes, 1967; Shaw & Shaw, 1977; Sperling & Dosher, 1986) and animals (cf. Estes, 1976; Hermstein, 1974; Luce, 1959). Of course, our subjects could have achieved this probability matching by adopting either of two strategies: attention sharing, in which perceptual resources are shared across the two locations on a given trial, or attention switching, in which perceptual resources switch between the two locations across trials. The current psychophysical experiment can not disambiguate these two strategies although future physiological investigations employing this approach might very effectively address this issue.

4.5. Limitations of the signal detection theory approach

We used a signal detection theoretic analysis to separate out the contributions of sensory and decision processing in our psychophysical task. However, like most analytic techniques, signal detection theory relies upon a number of critical assumptions (Green & Swets, 1966) and violations of any of these assumptions could challenge some or all of the conclusions drawn here. For this reason, a change in sensitivity, in and of itself, is not adequate proof of an attentional effect. Changes in sensitivity have been observed in tasks which do not require attention (Kinchla, Chen, & Evert, 1995). Furthermore, changes in response bias over time could

occlude, or perhaps even account for, changes in sensitivity under some conditions (Kinchla, 1992). Finally, and perhaps even more importantly, the signal detection theory measure of response bias is not inclusive of all aspects of decision-making (Shaw, 1982).

Nonetheless, given a small set of relatively common assumptions, our data do provide support for our conclusions that (1) sensory processing and decision processing can be separated by task design and (2) that changes in the probability structure of the visual environment can lead to changes in the allocation of sensory processing resources in both humans and monkeys. These data serve as a point of departure for future physiological studies which seek to extend the enormous human literature, which psychophysically examines signal detection in humans, by describing the mechanisms underlying psychophysically measured events in closely related animals.

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