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Deciding about motion: linking perception to action

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Introduction

How do neural systems within the cerebral cortex interact to produce cognitively based behavior? The answer to this question is far from clear, even for simple forms of cognition that can be explored in alert animals in the neurophysiological laboratory. We may anticipate, however, that a satisfactory answer to this question will eventually emerge through the coordinated application of techniques and ideas from several disciplines including neurophysiology, computational modeling, decision theory, and the quantitative measurement of behavior. In this paper I review the efforts of my laboratory to investigate the neural basis of cognition in a particular sensorimotor context: the visual discrimination of motion direction. Our ultimate goal is to understand the neural systems that mediate the complete cycle of discriminative behavior, from coding of the sensory stimulus, through the discriminative mechanisms that form psychophysical decisions, to the motor circuits that program and execute the operant response. I will not describe experimental results in detail; rather, I will provide a general overview of our experimental approach, our primary findings, and the outstanding issues that appear amenable to investigation in the near future. The interested reader may consult published papers for documentation of specific findings.

The discrimination paradigm

All of our experiments involve neurophysiological recording or electrical microstimulation of selected structures in the central nervous system while rhesus monkeys perform a rigorously controlled direction discrimination task. The monkeys are trained to discriminate opposed directions of coherent motion (up vs. down, right vs. left, etc.) in a set of visual stimuli like those schematized in Fig. 1. The stimuli are dynamic random dots plotted sequentially on the face of a CRT screen at a very high rate (6.67 kHz). After 45 ms, a dot is either displaced in a specified direction (coherent motion) or replaced by another dot at a random location on the screen (noise). In one extreme form of the display, illustrated in the lefthand panel of Fig. 1, all dots are positioned randomly so that the display is pure noise. In this form, the display
contains many local motion events due to fortuitous pairings of dots in space and time, but contains no net motion in any single direction. At the other extreme, illustrated in the right-hand panel of Fig. 1, all dots are displaced uniformly so that the display contains noise-free motion in the specified direction. Our software permits us to create any stimulus intermediate between these two extremes by specifying the percentage of dots that carried the “coherent” motion signal. In the center panel of Fig. 1, for example, 50% of the dots are in coherent motion while the remaining 50% provide a masking motion noise. The difficulty of the task is inversely proportional to the percentage of the dots in coherent motion.

This stimulus set has several important virtues. First, it allows us to manipulate the direction and strength of the motion signal while keeping other properties of the stimulus constant. Second, we are able to conduct experiments near psychophysical threshold simply by reducing the strength of the motion signal to an appropriate level. It is near threshold, where the monkey performs imperfectly, that the relationship between neural activity and psychophysical decisions is best revealed. Finally, since the only cue available to solve the task is the direction of global motion, we have the substantial advantage of knowing that directionally selective neurons within the visual cortex are likely to form the primary sensory substrate underlying performance on the task.

**The motion pathway**

In the primate visual cortex, directionally selective neurons are organized in a “motion pathway” which encompasses several distinct visual areas and incorporates both serial and parallel processing strategies (reviews: Maunsell and Newsome 1987; Albright 1993). The pathway begins in layer 4B of striate cortex (V1) which contains an elevated proportion of directionally selective neurons, and ultimately reaches high-level areas of the parietal lobe. Among the key visual areas in the motion pathway are the middle temporal area (MT, or V5) and the medial superior temporal area (MST), whose locations are shown in Fig. 2. Over 90% of neurons in MT and MST are directionally selective, and both areas are organized in a columnar fashion as illustrated schematically in Fig. 3. Neurons within a column tend to have a common preferred direction and receptive field location. Each cortical column therefore encodes a particular direction of motion (arrows) over a restricted region of the visual field. This organization is particularly evident in MT, which contains a topographic representation of all directions of motion within each region of visual space (Albright et al. 1984).

Of greatest importance for present purposes, we know that the direction columns in MT and MST provide sensory signals that underlie performance on the direction discrimination task described above. We demonstrated the role of MT and MST neurons using the paradigm schematized in Fig. 4. At the beginning of each experiment, a single neuron was isolated, its receptive field mapped (shaded circle), and its preferred direction identified (large arrow). During discrimination
trials, the monkey directed its gaze toward a fixation point while a random dot pattern was presented within an aperture covering the neuron’s receptive field (large circle). The coherent motion of the dot pattern was in the neuron’s preferred direction or in the direction 180 degrees opposite (the “null” direction). The monkey viewed the stimulus eccentrically for 2 s while holding his gaze on the fixation point. At the end of the viewing interval, the fixation point and visual stimulus disappeared and two target lights appeared, each corresponding to one of the two possible directions of motion. The monkey then made a saccadic eye movement to the target corresponding to the perceived direction of motion; correct choices resulted in a liquid reward. Eye movements were monitored continuously using the scleral search coil technique; the trial was aborted if the monkey broke fixation inappropriately.

The monkey performed several hundred trials in an experiment, and the stimuli covered a range of motion coherence levels spanning psychophysical threshold. Having recorded both the monkey’s psychophysical decision and the response of the neuron on each trial, we were able to compare psychophysical and neuronal sensitivity to motion signals presented under identical conditions and on the same sets of trials. Our primary finding was that MT and MST neurons are exquisitely sensitive to the weak directional motion signals in the stochastic visual displays; on average, the directional discrimination ability of single cortical neurons was equal to the directional discrimination ability of the monkey measured psychophysically (Newsome et al. 1989; Britten et al. 1992; Celebrini and Newsome 1994; Britten et al. 1996). In separate sets of experiments, we found that chemical lesions of MT can selectively impair performance on the direction discrimination task (Newsome and Paré 1988), and that electrical microstimulation of individual MT or MST columns can shift a monkey’s perceptual judgements toward the direction encoded by the stimulated column (Salzman et al. 1990; Salzman et al. 1992; Murasugi et al. 1993a, b; Salzman and Newsome 1994; Celebrini and Newsome 1995). Clearly, directional signals in MT and MST provide a substantial portion of the sensory evidence used by the monkeys in making perceptual judgements in our direction discrimination task. We have recently developed a quantitative model of the process by which psychophysical performance may emerge from the responses of MT and MST neurons (Zohary et al. 1994; Shadlen et al. 1996).

In one of the most useful consequences of our modelling efforts, we were compelled to realize that psychophysical performance, while constrained by sensory evidence, is influenced just as surely by higher level decision mechanisms that “read-out” or “interpret” the sensory evidence. The reliability of the monkey’s performance depends substantially upon high-level processes such as signal pooling, noise intrusion upon the pooled signals, and the fidelity of the decision mechanism that commits the animal to one or the other choice. This realization naturally led us to consider experiments that might be designed to investigate decision mechanisms with the cerebral cortex.

Decisions

Our general framework for thinking about decision mechanisms can be appreciated by considering Fig. 5, a diagram adapted from Norma Graham’s book, Visual Pattern Analyzers (Graham 1989). The diagram outlines several processing stages that must occur on every discrimination trial performed by a psychophysical subject. The subject views a visual stimulus which varies in luminance as a function of two spatial dimensions and time $L(x, y, t)$. The pattern is filtered and encoded by “low-level analyzers” within the visual system, which in turn provide inputs to higher level mechanisms including

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**Fig. 5** Outline of processing stages required for performance of a single trial of a typical discrimination paradigm. After Graham (1989)
a "decision stage". The result of the decision is revealed by the observer's behavioral responses.

From a neurophysiological perspective, our ultimate goal is to identify and understand the actual neural systems that produce the observer's behavioral responses to a particular stimulus set. What neural systems correspond to the formal processing stages illustrated in Fig. 5? The work reviewed above demonstrates that directional columns in MT and MST can be viewed as "low-level analyzers" in the context of our discrimination task. The neurons in these columns act as microscopic measuring devices, signaling the amount of "motion energy" present within the band of directions to which they respond.

In a similar vein, we have reasonably secure knowledge of the motor centers that govern behavioral output during performance of our psychophysical task. Since the operant responses are saccadic eye movements, the motor circuits governing behavioral output will include oculomotor structures such as the superior colliculus (SC) and the frontal eye fields (FEF) (reviews: Sparks 1986; Goldberg and Seagrraves 1989; Schall 1991, 1995). Both of these structures contain neurons that fire motor bursts immediately prior to saccades into a well-defined region of the visual field, termed the movement field. The movement fields of individual neurons vary systematically across the surface of the SC and FEF so that each structure contains a topographic map of all possible saccade vectors at any point in time, as illustrated in Fig. 6. For example, neurons situated at one pole of the SC fire before short saccades directed toward locations near the current eye position whereas neurons at the opposite pole fire before large saccades to remote locations. Electrical microstimulation of any point within either map elicits a saccade toward the movement field of the stimulated neurons.

The more mysterious portion of the processing pathway outlined in Fig. 5 is the "decision stage". Decision stages, or decision rules, are invoked in virtually all models of detection and discrimination performance, and in numerous other sub-disciplines of cognitive science as well. More often than not, a decision process comprises the critical link between perception and action. The theoretical importance of decision processes contrasts starkly, however, with the dearth of physiological knowledge concerning these important processing stages.

Given our knowledge of the sensory and motor circuits underlying performance on the direction discrimination task, we are now poised to investigate the link between them—the decision process itself. The problem boils down to a very simple question: how do motion signals in MT and MST influence motor structures like the SC and FEF so as to produce correct performance on the task?

A preliminary inquiry

Our first clue for investigating the decision process derives from anatomical analysis of the connections of MT, some of which are illustrated in Fig. 7. MT has three major feedforward projections to other cortical regions: one to neighboring areas within the superior temporal sulcus (MST, FST), a second to areas in the lateral bank and fundus of the intraparietal sulcus (LIP, VIP), and a third to prefrontal cortex (FEF, area 46) (Maunsell and Van Essen 1983; Ungerleider and Desimone 1986). In addition, MT has at least one subcortical projection of importance to us: to the superior colliculus (Fries 1984; Ungerleider et al. 1984). Three of these projections connect MT to structures that have been implicated in the planning and execution of saccadic eye movements: the SC, the prefrontal cortex, and the lateral intraparietal area (LIP). In the context of our discrimination task, therefore, these three structures emerge as high priority targets for investigation of potential neural correlates of the decision process.
We have recently begun physiological analysis of neural activity in two of these structures — LIP and SC — while monkeys perform a modified version of our direction discrimination task. We targeted for study a specific subset of neurons in both structures that carry high-level signals appropriate for planning saccadic eye movements (Mays and Sparks 1980; Gnadt and Andersen 1988; Barash et al. 1991a, 1991b; Glimcher and Sparks 1992; Colby et al. 1993). These signals arise early in the initial stages of saccade planning — up to several seconds before execution of the eye movement — and may therefore be linked to the decision process in a revealing manner. Similar neurons exist in prefrontal cortex, and our investigation must ultimately include this region as well (Funahashi et al. 1989, 1993; Goldberg and Bruce 1990).

As usual, the monkey inspected the random dot pattern and indicated its decision with a saccadic eye movement as in Fig. 8. One of the saccade targets (Target 1) was always placed within the movement field of the neuron under study, while the other (Target 2) was placed in a location remote from the movement field. The important modification of the task was the insertion of a delay period between offset of the random dots and the “go” signal for execution of the saccade (offset of the fixation point). Insertion of the delay period required the monkey to form and remember its decision well in advance of the “go” signal, thus separating in time the decision from the motor response. Our questions were: 1) whether LIP and SC neurons would fire in a manner that would “predict” the monkey’s impending saccade and thus its decision in the discrimination task, 2) whether such “predictive” activity began early or late in the trial, and 3) whether the predictive activity could be explained by purely sensory or motor mechanisms.

Briefly, we have found that neurons in both LIP and SC indeed predict the decision a monkey will make during performance of the discrimination task (Horwitz and Newsome 1996; Shadlen and Newsome 1996). Neurons in both structures elevate their firing rates before saccades to Target 1 relative to their firing rates before saccades to Target 2. The predictive activity typically arises early in the trial, 200–500 ms after onset of the random dot pattern, and is sustained during the delay period until execution of the saccade. The rate of rise, and the final level of predictive activity achieved, is proportional to the strength of the motion signal in the visual display. The variability in neural response with coherence is not explained by subtle aspects of the monkey’s eye movements. These observations suggests that the predictive activity is not simply a motor signal since the same motor act indicates a particular decision (a rightward saccade, for example) irrespective of the degree of motion coherence on a given trial. Neither are these signals purely sensory, however, since robust predictive activity exists: 1) on 0% coherence trials where no net directional signal is present in the visual stimulus, and 2) on error trials in which the direction of motion is opposite to the direction of the saccade (Shadlen and Newsome 1996). In more recent experiments, we have found that microstimulation of LIP and SC can influence the monkey’s choices on the discrimination task, suggesting that both structures participate in the causal flow of neural activity leading to behavior (Seidemann and Newsome 1996; G. Horwitz and W.T. Newsome, unpub. obs.).

While we are still in a relatively early stage of this investigation, the present data suggest that LIP and SC neurons may participate in the integration of weak, slowly arriving sensory signals to generate decisions. If this inference is correct, it becomes vital to inquire more closely about the logic of the circuitry that produces an appropriate association of motion signals with planned saccades.

**A hypothesis**

The logic of the direction discrimination task implies that a precise pattern of circuitry must exist between the direction columns in MT and MST and the movement fields of LIP and SC neurons. In the specific version of the task illustrated in Fig. 8, for example. MT columns preferring rightward motion should excite neurons whose movement fields include Target 1, whereas columns preferring leftward motion should excite neurons whose movement fields include Target 2. In essence, neurons with movement fields in a particular region of visual space should be activated by columns in MT and MST whose preferred directions point toward the movement field, as depicted in Fig. 9. Columns whose preferred directions point away from a particular movement field should have little or no excitatory effect on, and may even inhibit, that LIP or SC neuron. The latter columns would, of course, excite LIP or SC neurons whose movement fields are located elsewhere in space.

Realize that this hypothetical circuitry is little more than a restatement of the logic of the task. If the monkey is to perform correctly, saccade-related neurons anywhere in the brain should be activated only when directional columns in the motion system signal motion
Fig. 9 Proposed functional connectivity underlying the decision process in our direction discrimination paradigm. Information regarding the direction of stimulus motion, originating in directional columns in MT and MST, is routed so as to activate the appropriate region of the map of saccade vectors in oculomotor structures such as the SC and FEF. (Appropriate connectivity can exist between MT, MST and LIP as well, although LIP appears not to contain a topographic map of saccade vectors). The connectivity in this diagram would correspond to the task layout of Fig. 8. Direction columns encoding rightward motion (rightward arrows and connections) must excite a region of the motor map encoding rightward, horizontal saccades. Similarly, leftward columns (leftward arrows and connections) must excite the motor map on the opposite side of the brain that encodes leftward saccades. The diagram is purely heuristic. It should not be construed to indicate the actual number, density or distribution of direction columns in MT. Nor is it a precise depiction of saccadic vector maps in any particular oculomotor structure.

toward their movement fields. The hypothesis does not imply that the proposed circuitry must connect MT and LIP or SC directly; motion signals could be filtered through prefrontal cortex or other structures before activating parietal lobe neurons. The logic of the task requires, however, that such connections exist; however long the pathway.

The simple circuitry summarized in Fig. 9 could, in principle, form the core of the "decision process" that underlies performance on our direction discrimination task. An obvious objection to this hypothesis is a lack of generality in the domain of behavioral responses: the locus of the "decision" lies simply in the pattern of connections between the sensory representation and a specific effector system. Alternatively, one might expect the decision to be held in a more abstract form, which could then activate any desired motor effector system. (Verbal mechanisms undoubtedly perform such an abstracting function for humans, but it is unclear what a simian correlate might be.) This basic objection was put to me pitifully on one occasion by a professional colleague who said: "Bill, a lot of stuff lies between MT and the oculomotor system...it's called 'the brain', and you're ignoring it!".

I plead guilty to this accusation, but I suspect my point of view may be more right than wrong, at least for the current version of our discrimination paradigm. Our monkeys are heavily overtrained on a form of the task in which the direction of motion can indeed be transformed directly into a plan for a saccadic eye movement without the necessity of intervening processing stages. Our monkeys have never been asked to alter their motor responses, either on a long time scale across months of performance or on a short time scale within trials. It seems to me perfectly plausible, if not likely, that direct and simple circuits between direction columns and the oculomotor system have been "trained" into the brains of our monkeys over the course of months (or years) of performance on the task. Certainly appropriate anatomical connections exist at a gross level (i.e., MT and MST to SC); long-term adjustment of synaptic weights according to the logic of Fig. 9 would comprise an efficient solution to the monkey's task. This point of view conforms nicely to recent PET studies indicating that the extent of brain activation decreases considerably as performance on a particular task becomes well rehearsed (e.g. Raichle et al. 1994). Much of the brain comprises a vast learning machine; neural resources can be conserved substantially as task performance becomes routine.

Even if the hypothesis in Fig. 9 ultimately proves incorrect, it is the simplest, most direct scheme available and deserves to be tested. If a test of this simple hypothesis proves impractical, how can we hope to test more sophisticated ideas?

A look at the future: testing the hypothesis

The hypothesis summarized in Fig. 9 incorporates very precise predictions about the functional connectivity between, for example, direction columns in MT and specific locations in the map of eye movement vectors in the intermediate layers of the SC. Our central technical challenge is to devise practical ways of testing this connectivity in neurophysiological experiments. My laboratory is considering several approaches to this problem, some fairly direct, others less so. At the most simpleminded level, it seems possible that the hypothesized directional inputs to SC or LIP neurons might become sufficiently well developed during training so as to comprise visual receptive fields that are measurable by conventional techniques. We would expect such receptive fields to be directionally selective, to be spatially centered in the region of the visual field in which the monkey typically views the dot patterns, and for their preferred directions to point toward the movement fields of the SC or LIP neurons. We have, in fact, observed "visual" responses conforming to this logic in recent experiments, first in LIP and more strikingly in subsequent SC experiments (M.N. Shadlen, G. Horwitz and W.T. Newsome, unpublished observations). The number of experiments is small as yet, and stringent controls need to be performed, but these observations may eventually provide an entree for analyzing circuitry.
The technique of inferring functional connectivity by cross-correlation may offer substantial promise for tracing signal flow in behaving animals (Gerstein et al. 1978; Abeles 1991; Ahissar et al. 1992; Vaadia et al. 1995). For example, we might expect the amount of structure in the cross-correlogram to vary with the degree of functional linkage between a specific MT column and various locations in LIP or SC. The joint peristimulus-time histogram (JPSTH) of Aertsen et al. (1989) may prove to be particularly useful. In principle, this technique can permit measurement in real-time of the formation and dissolution of neural circuits as behavior unfolds during single trials (see below). Another approach that could be tried is to stimulate directional columns in MT or MST with brief electrical pulses while examining selected loci in LIP and SC for evidence of evoked neural activity in the form of orthodromic action potentials or local field potentials. Again, the simple prediction is that sites in the two structures conforming to the logic of Fig. 9 should be linked, while others should not.

If techniques can indeed be developed for monitoring functional connectivity at this level, many fascinating questions can be asked. For example, the functional connectivity between MT and oculomotor structures should not be static, but should be modulated dynamically in time. We know that eye movements are not evoked when MT is electrically stimulated during the intertrial interval, yet the oculomotor system is clearly influenced (via the psychophysical decision process) when MT is stimulated during presentation of our random dot patterns. We infer that the functional connectivity of MT is likely to be dynamically regulated according to the immediate demands of the task. Such rapid changes in connectivity may be detectable with the JPSTH technique, as suggested above.

Another interesting experiment would be to train the monkeys to reverse the association between the direction of stimulus motion and the saccadic eye movement. In Fig. 8, for example, the monkey would saccade to Target 1 in response to leftward motion, and to Target 2 in response to rightward motion. In this case, the functional connectivity between directional columns in MT and the movement map in the SC should be the inverse of that illustrated in Fig. 9. In an ideal case, the monkeys would learn to perform the task according to either algorithm, depending on a cue provided by the experimenter. In this situation, the pattern of connectivity should reverse sign from one block of trials to the next, according to the cue. Any reader with the interest to have come this far can undoubtedly formulate several experiments for himself that would be similarly revealing.

Ultimately, of course, one would be driven to ask questions about the control of connectivity in such situations. What are the circuits that effect such control, and what are the cellular mechanisms by which control is exerted? Speculation about such issues would be gratuitous at this point, but the ability to engage such questions experimentally would clearly signal a substantial step forward for our discipline.

**Conclusion**

In this review, I have considered issues of functional connectivity and its relationship to cognition within the specific context of research carried out in my laboratory over the past decade. Plainly, these issues are not specific to my laboratory, but rather comprise a fundamental challenge for the emerging discipline of cognitive neuroscience as a whole. At the physiological level, most effort in this discipline is devoted to demonstrating neural correlates of cognitive phenomena at particular loci in the brain, whether those correlates be single neuron responses or active voxels in a blood-flow image. The mechanisms by which such signals are created, and by which they influence behavior (succinctly, how the system works!), remain largely obscure. Development of methods for tracing precise patterns of signal flow in behaving animals would ameliorate this problem substantially, and would signal the emergence of a more mature and substantially more powerful discipline.

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