

Cognitive Critique



ON THE EMERGENCE OF COGNITION WITHIN THE SENSORIMOTOR SYSTEMS OF THE CEREBRAL CORTEX

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ABSTRACT

Sensorimotor control is the primary and fundamental function of the cerebral cortex. The cortex performs this function by generating patterns of electrical activity in neuronal networks that encode objects and events in the world and that program effective motor responses. In humans, and most likely higher primates, the engagement of cortical circuits to repeatedly represent stimuli and generate movements leads to the creation of knowledge, the capacity for abstraction, and the emergence of intelligence. One of the most crucial questions confronting cognitive neuroscience is how this occurs. We are far from a full understanding. However, research into neural coding in the posterior parietal cortex of the nonhuman primate is

providing important clues, notably that sensorimotor control and cognition are processes embedded within the same neural architecture. That is, the same neurons and circuits within posterior parietal cortex which participate in processing stimuli and programming movements demonstrate the capacity for abstract representation. In these cells patterns of activity can reflect computational processes that unfold independently of concurrent sensorimotor events, or that encode generalized information akin to a rule, principle or concept that provides the basis for intelligent action in a given circumstance, but that is not directly related to the characteristics of the particular stimuli or movements involved. These neurons appear to participate in forms of information processing that ultimately must enable thinking as we presently understand it, and their existence within the sensorimotor circuits of the cerebral cortex suggests that the capacity for thought may emerge as a byproduct of sensorimotor experience. This is likely to open a new line of enquiry by which it may be possible to discover the biological principles that govern how cortical circuits acquire intelligence by interacting with the world.

INTRODUCTION

Neuroscience has provided very good reason to believe that the human mind is a time-varying pattern of electrical activity in the human brain. Though we can be confident this is true, we do not yet understand how thinking, reason, language, foresight, conscious perception, or any of the other myriad complex processes we associate with human mental life reduce to fleeting electrical signals and chemical events taking place within living brain cells.

There are numerous obstacles between us and an answer. Not the least of these is the problem that we cannot measure mental events, thoughts, ideas, concepts, or anything like them directly. To study the biological basis of mental phenomena, we have to establish experimental conditions in which we can make a relatively strong inference that a given mental event is taking place. Our ability to do this accurately will always be limited. Any observable behavior could potentially result from any of a very large number of very different cognitive processes (though some may be more likely to occur than others in a given behavioral context). Even granting that it is possible, from the outside looking in, to infer exactly what cognitive process is taking place within a given brain at any mo-

ment in time with reasonable confidence and precision, we must still confront the question of how to recognize the biological events in the brain that mediate, or are equivalent to, the cognitive process in question. This is anything but straightforward, because the brain performs many different information processing operations at the same time, only some of which are related to (or responsible for) the cognitive process under study. For example, at the same time that you might be thinking about what you are about to say, you are also seeing the room in front of you, feeling the chair underneath you, and perhaps you are moving your fingers over a keyboard to translate an idea into text. How to separate the biological events responsible for each of these simultaneous but distinct instances of information processing in the brain?

SENSORIMOTOR INDEPENDENCE AND A HIERARCHY OF NEURAL REPRESENTATION IN THE BRAIN

The simple example above makes the point that the brain is doing many things at the same time. Many of these computations are directly involved in basic sensory function and motor control. However, mind must be mediated by a different class of computation, a different class of physiological process taking place alongside of others that encode stimuli and program movements in the brain. Mind, however we ultimately come to understand it, possesses a fundamental property that can be exploited to detect its biological underpinnings – mind has the ability to advance from one thought to the next independently of what is transpiring in the world around it, and in this regard it exhibits *sensorimotor independence*. The implication is that this property must also apply to the biological bases of mind. Specifically, to enable mind, the brain has to have the capacity to progress through a sequence of physiological states that also exhibit sensorimotor independence – that code behaviorally useful information without relating to any specific stimulus or movement. Neural representations meeting these criteria have been described in a number of recent neurophysiological experiments in animals. These experiments have characterized patterns of neural activity that encode abstract, generalized information logically related to the selection of an intelligent response without coding features of specific stimuli or movements. These data make it appear increasingly likely that we will ultimately be able to understand

mental states as biological events; to reduce ideas, concepts, rules and principles to patterns of electrical activity in neurons.

EMERGENCE OF THOUGHT IN SENSORIMOTOR CIRCUITS; A TEST CASE IN THE POSTERIOR PARIETAL CORTEX

The neuronal systems of the brain, and in particular of the cerebral cortex, evolved to enable and support sensorimotor control as their primary function. All areas of the cerebral cortex studied at a cellular level in animals to date have been found to contain neurons that are engaged to represent stimuli or movements. This is true even of the prefrontal cortex, the region of the cerebral cortex most expanded during human evolution and most directly associated with higher cognitive function (Goldman-Rakic 1987). One might expect that prefrontal cortex would be exclusively engaged to represent abstract information by a neural mechanism that exhibits sensorimotor independence. Some prefrontal neurons certainly are engaged to represent abstract information in this manner (Freedman et al. 2001; Wallis et al. 2001; Nieder et al. 2002). However these prefrontal neurons are intermingled with others that code specific stimuli and movements (Funahashi et al. 1989; Funahashi et al. 1993; Chafee and Goldman-Rakic 1998). Sensorimotor information processing is ubiquitous – all cortical areas studied at a cellular level in animals to date have been found to contain neurons that participate in sensorimotor processing. By exclusion there appears to be no “thinking area” of the brain, or region of the cerebral cortex specialized purely and solely for the neural representation of abstract information. If all cortical areas contain neurons that represent stimuli and/or movements, then, how do cortical networks acquire the sensorimotor independence necessary to “think” and how could the capacity for abstraction essential to more complex forms of thought emerge within sensorimotor systems?

The purpose of this paper is to review what new information has been provided on this general question by recent research in posterior parietal cortex, focusing on work in the nonhuman primate. Like the cortex in general, posterior parietal cortex in particular exhibits the dual qualities alluded to above. On the one hand, posterior parietal cortex is a structure that is directly involved in sensorimotor control. A considerable body of research establishes that neural activity in this cortical area represents where objects are

located in space and the direction in which an animal will move. On the other hand, parietal neurons are also directly involved in cognition and code abstract constructs. This functional duality, encompassing sensorimotor and cognitive processing, is reflected in two parallel lines of research into the contributions of parietal neurons and parietal cortex to behavior.

One of these lines of research, beginning in the 1970's and advancing steadily since, has elegantly described how parietal neurons encode the spatial parameters that are crucial to visual sensorimotor control (e.g. the spatial locations of visible stimuli and directions of pending movement). A more recent and parallel line of research has shown that the same neural architecture within posterior parietal cortex that is responsible for supporting spatial sensorimotor control is also capable of generating neural representations that are abstract, code task-relevant information, enable intelligent action, but are irreducible to the parameters of specific stimuli or movements. In this second role, parietal neurons exhibit the property of sensorimotor independence as defined above – they code information that appears to be related to a computational process the brain has undertaken independently of concurrent events at the sensorimotor periphery. The coexistence of these two distinct forms of neural representation within the same cortical area, one concrete and tied to sensorimotor events, one abstract and independent of sensorimotor events, provides an essential clue to the origin of intelligence in cortical systems. Namely, cognition is a set of neural operations embedded within the sensorimotor control circuits of the cerebral cortex, which emerge most probably as the direct result of the repeated engagement of these circuits to represent stimuli and initiate movement.

INFERIOR PARIETAL CORTEX AS SENSORIMOTOR CONTROLLER

Sensory and motor coding in parietal cortex.

The contributions of posterior parietal neurons to behavior were first elucidated by a series of pioneering experiments by Vernon Mountcastle and colleagues (Mountcastle et al. 1975; Yin and Mountcastle 1977; Motter and Mountcastle 1981; Mountcastle et al. 1981), and by Hyvarinen and colleagues (Hyvarinen and Poranen 1974; Hyvarinen and Shelepin 1979; Leinonen et al. 1979; Leinonen et al.

1980). In their seminal experiments, Mountcastle and colleagues recorded the electrical activity of neurons within Brodmann's area 7 in the inferior parietal lobule of the primate cerebral cortex as monkeys directed their gaze and reached their hand toward visual targets. These studies revealed several basic principles about the physiology of parietal neurons that have been repeatedly confirmed by subsequent investigation. First, parietal neurons are visually responsive, possess retinocentric receptive fields that are large and peripheral and that are activated by stationary or moving spots of light (Yin and Mountcastle 1977; Motter and Mountcastle 1981; Mountcastle et al. 1981; Steinmetz et al. 1987). The visual responsiveness of parietal neurons undoubtedly reflects the fact they receive axonal projections from several extrastriate visual areas of the dorsal visual pathway thought to mediate spatial visual processing in the cerebral cortex (Cavada and Goldman-Rakic 1989; Baizer et al. 1991). The visual sensitivity of posterior parietal neurons is confirmed by the fact that these neurons can be activated by visual stimulation in anesthetized monkeys (Blatt et al. 1990).

However, the functions of parietal cortex are not restricted to spatial vision, and parietal cortex is not a visual cortical area in any strict sense. For example, many posterior parietal neurons are phasically activated before the initiation of eye or arm movements. Neurons within the lateral intraparietal area (LIP) for example are selectively activated before the initiation of saccadic eye movements, and the level of activation varies as a function of saccade direction (Andersen et al. 1990a; Andersen et al. 1990b; Blatt et al. 1990; Barash et al. 1991a, b; Bracewell et al. 1996; Mazzoni et al. 1996a, b; Stricanne et al. 1996; Chafee and Goldman-Rakic 1998). LIP neurons project to the superior colliculus (Selemon and Goldman-Rakic 1988; Pare and Wurtz 1997), a brainstem structure directly involved in saccade motor control, and microstimulation within LIP evokes saccadic eye movements (Thier and Andersen 1998). These data provide convergent lines of evidence that LIP neurons participate in oculomotor control. Neurons in the adjacent parietal reach region (PRR) in contrast are activated before reaching arm movements as a function of reach direction (Snyder et al. 1997; Andersen et al. 1998; Batista et al. 1999; Snyder et al. 2000; Batista and Andersen 2001; Andersen and Buneo 2002; Buneo et al. 2002; Cohen et al. 2002; Quian Quiroga et al. 2006). Most LIP and PRR neurons are activated before saccadic eye movements, or reaching arm movements, but not both (Snyder et al. 1997), indicat-

ing that the neurons are effector specific. This is strong evidence that their activity relates to the movement of the effector in question, and not the visual stimulus serving as a movement target (in which case neurons would be activated regardless of which effector was moved).

Coordinate transformation from sensory to motor space.

When considering the use of vision to control arm movements, the following problem must be solved. The visual system initially encodes the two dimensional position of the visual target on the retina. To reach toward the visual target, the brain has to transform neural signals coding the 2D position of the stimulus on the retina into signals coding the 3D position of the stimulus relative to the body. Doing this requires integrating visual and postural information. To compute the body-centered position of a visual target, it is necessary to know where the target is located on the retina, but also where the eyes are directed within their orbits, as well as how the head is oriented relative to the body. All three factors jointly influence the activity of posterior parietal neurons (Andersen and Mountcastle 1983; Andersen et al. 1985; Andersen et al. 1990b; Brotchie et al. 1995; Snyder et al. 1998). Posterior parietal neurons therefore possess properties that suggest they participate directly in the coordinate transformations needed to convert retina-centered spatial representations into body-centered representations. Loss of these neurons following damage to parietal cortex may explain optic ataxia (Battaglia-Mayer and Caminiti 2002), a syndrome in which patients are not able to direct their hand accurately and with precision toward objects that they can clearly see. Given the convergence of neurophysiological and neuropsychological data outlined above, there is little doubt that parietal cortex contributes directly to the visual guidance of movement, and these data identify parietal cortex as central node in distributed cortical systems engaged to mediate sensorimotor control.

“STAGE I” COGNITION: MODIFYING THE AMPLITUDE AND DURATION OF SENSORIMOTOR SIGNALS IN PARIETAL CORTEX

Subsequent research in parietal cortex has made it clear that in spite of, or in addition to, the experimental evidence that parietal cortex operates to enable the visual control of movement, parietal cortex also supports a number of cognitive functions, only some of which bear an obvious relation to sensorimotor control. Given a set of neurons with visual receptive and movement fields, in which firing rate is a function of stimulus position or movement direction, the capacity to modulate either the intensity or duration of neuronal discharge as a function of additional behavioral factors provides the basis for a suite of simple but fundamentally important cognitive functions I collectively refer to as stage I processes. Stage I processes include visual attention, working memory, motor planning, and decision processing, as enumerated below. Each of these essential cognitive abilities appears to be implemented in the brain via a relatively straightforward modification of the basic sensorimotor representations that exist within posterior parietal cortex.

For example, visual attention is thought to be mediated at a neural level by the modulation of activity evoked by a visual stimulus as a function of its behavioral relevance. Working memory is thought to be mediated by the persistence of neural activity evoked by a visual stimulus beyond the duration of the stimulus itself. Motor planning is thought to be mediated by the activation of neurons coding movement direction in advance of movement onset. Finally, decision processing is thought to be mediated by the modulation of motor planning signals as a function of the reward a movement is anticipated to produce.

The modulation of the timing or intensity of sensorimotor signals in parietal neurons associated with stage I cognition as defined here is illustrated in Figure 1. In the typical experiment, monkeys direct their gaze to a central target on a video monitor while visual stimuli are briefly presented in peripheral vision (Fig. 1a). (The position of the stimulus is randomly selected from the circular array shown). After a delay, monkeys move their eyes or hand toward the remembered position of the visual target (Fig. 1b; the arrow indicates the delayed movement of the eyes or the hand on a trial in which the movement target had been presented at the 270° posi-

tion). Separating the period of visual stimulation and movement initiation in time makes it possible to determine whether neurons are transiently activated by sensory or motor events. Some posterior parietal neurons possess retinocentric receptive fields (Fig. 1a; shaded circle) and are activated by the presentation of the visual target. Other parietal neurons possess movement fields (Fig. 1b; shaded circle) and are activated just before movement initiation. In either case, neural activity is spatially tuned. The magnitude of the neural signal varies systematically as a function of stimulus position (Fig. 1a; lower plot) or movement direction (Fig. 1b; lower plot). Each neuron has a preferred position or direction associated with the peak in the spatial tuning function (Fig. 1a, b). These spatially tuned visual and motor signals in parietal neurons comprise the fundamental sensorimotor representations upon which the following instances of stage I cognition are built.

Visual attention as a stage I cognitive process can be achieved by adjusting the amplitude of spatially tuned visual activity in parietal neurons (Fig. 1c). If the neural signal is larger when the monkey directs covert spatial attention toward the stimulus (Fig. 1c; heavy black line) than when it directs attention elsewhere (Fig. 1c; broken black line), the neuronal response can provide a cellular basis for visual attention in the brain. Working memory as a stage I cognitive process can similarly be achieved through an equally simple modification of the activity of a visual neuron in parietal cortex. If a neuron transiently activated by the appearance of a visual stimulus in its receptive field (Fig. 1d; broken black line) acquires the capacity to sustain its activity at an elevated level after the visual stimulus disappears (Fig. 1d; heavy black line), the neuronal response can provide a cellular basis for working memory. Motor planning as a stage I cognitive process can be achieved by a simple modification of movement-related signals in the brain. For example, if a neuron that is typically activated immediately before the animal initiates a movement into the neuron's movement field (Fig. 1e; broken black line), the time of movement onset is indicated by the vertical broken red line), acquires the capacity to initiate this activation earlier, at longer intervals in advance of movement onset (Fig. 1e; heavy black line), the neuronal response can provide a cellular basis for motor planning. Finally, a decision as a stage I cognitive process can be implemented by varying the intensity of motor planning activity as a function of the value of the planned action, or reward the movement is expected to yield. For example, if a neuron that is activated

when the monkey plans to make a movement into its movement field (Fig. 1f; broken black line) is more intensely activated when the same movement is anticipated to yield a larger reward (Fig. 1f; heavy black line), the neuronal response can provide a cellular basis for decision processing in the brain. Thus attention, working memory, motor planning, and decision processing are all cognitive processes presently thought to be implemented within parietal cortex by modulating either the amplitude or duration of sensorimotor signals. The ability to modulate the timing and intensity of sensorimotor signals seems a first step in the evolution of intelligent sensorimotor control systems. I refer to these instances of cognition as “stage I” to capture the fact that the neural signals responsible for them are still tightly coupled to the attributes of specific stimuli or particular movements (that is, neural signals that mediate stage I cognitive processing as defined above retain their spatial tuning for stimulus position or movement direction). In the following sections I consider some of what we know about the neural correlates of stage I cognition in parietal cortex in greater detail.

Gain modulation of visual sensory signals and the intention/attention debate.

Since the start of neurophysiological investigation into the functions of the posterior parietal cortex in the 1970s, the so called intention / attention debate has ensued as to whether the activity of parietal neurons codes the spatial direction of a planned movement (motor intention), as initially suggested by Mountcastle and colleagues (Mountcastle et al. 1975), or the locus of attended visual stimuli, as alternatively suggested by Goldberg and colleagues (Robinson et al. 1978; Bisley and Goldberg 2003). The question is difficult to resolve because neural activity coding the position of a visual target before a movement is made toward it could, with equal plausibility, reflect either the intention to make the movement, or the state of directing spatial attention toward the target in advance of the movement. Covert spatial attention and motor intention are frequently coupled. For example, shifts of covert spatial attention often precede overt saccadic eye movements (Godijn and Pratt 2002), and electrical stimulation of saccade-related motor areas of the prefrontal cortex can transiently enhance visual processing around movement targets (Moore and Fallah 2001). Thus, it is intrinsically difficult to be certain whether neural activity in parietal cortex codes motor intention, spatial attention, or both. In line with this uncertainty, after Mountcastle and colleagues published their landmark paper (Mountcastle

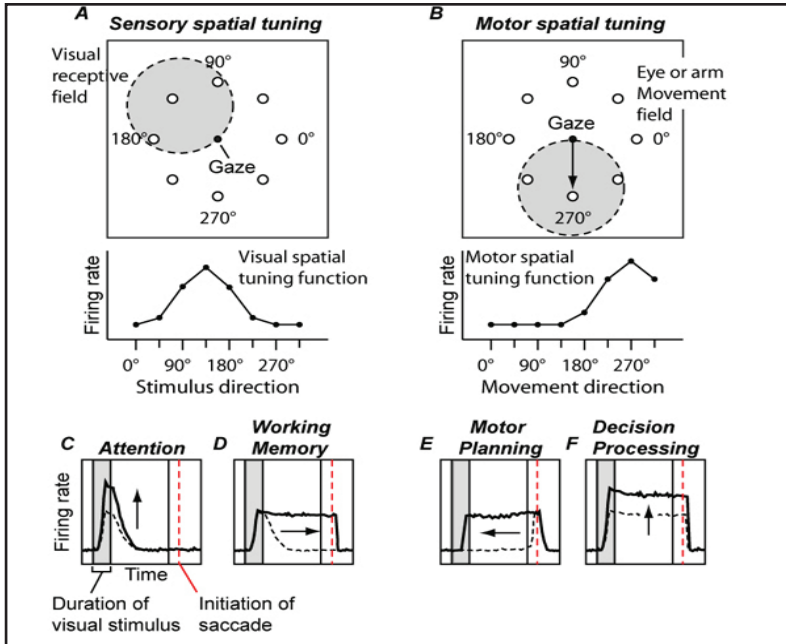


Figure 1. Spatial tuning of sensory and motor signals in parietal neurons, and the modulation of these signals to mediate *stage I* cognitive processes. **A.** Stimulus array used in the typical sensorimotor experiment. Visual targets are presented in a circular array surrounding a central visual target where monkeys hold their gaze. The circular shaded region indicates the retinocentric visual receptive field of a parietal neuron. The plot below shows the spatial tuning function of this hypothetical visual neuron. Stimuli presented at the upper left (135°) direction, in the center of the receptive field, evoke the maximal response. **B.** Circular shaded region indicates the movement field of a different hypothetical parietal neuron, activated before eye (or arm) movements directed toward downward targets. The plot below shows the spatial tuning function of this movement related activity. The maximal response occurs before movements are made in the preferred 270° direction. **C.** Modulation of the amplitude of a phasic visual response to mediate visual attention. The response is stronger when the monkey directs covert attention toward the stimulus (heavy black line) than when it directs attention elsewhere (broken black line). The duration of the visual stimulus is indicated by gray shading. **D.** Modulation of the duration of a phasic visual response to mediate spatial working memory. The duration of the typically transient visual response (broken black line) is extended beyond the duration of the visual stimulus and sustained throughout a subsequent delay period (heavy black line). **E.** Modulation of the duration of a phasic motor response to mediate motor planning. The onset of the typically transient motor response (broken black line) is shifted earlier relative to movement initiation (vertical broken red line), so that activity is sustained during the delay period preceding movement onset (heavy black line). **F.** Modulation of the amplitude of motor planning activity to mediate decision processing. Sustained activity coding a planned movement is stronger when the movement is expected to produce a large reward (heavy black line) than a small reward (broken black line). (Chafee)

et al. 1975) emphasizing the role of parietal cortex in motor control, Robinson and colleagues (Robinson et al. 1978) proposed that activation of posterior parietal neurons prior to movement was due in fact to the visual stimulus presented as the movement target. This emphasized the role of parietal cortex in spatial vision, and additional experimental observations by this group carefully documented the fact that the intensity of the neuronal response to visual stimulation differed as a function of whether the monkey directed covert attention toward the stimulus or not. For example, visual responses in parietal neurons are enhanced when covert spatial attention is directed toward the visual stimulus (Bushnell et al. 1981), and parietal neurons represent only the most behaviorally salient visual stimuli in the environment, leading to the suggestion that parietal cortex provides a salience map of the visual world (Gottlieb et al. 1998; Kusunoki et al. 2000; Gottlieb et al. 2005; Goldberg et al. 2006). In one recent study, Bisley and Goldberg recorded neural activity in parietal cortex of monkeys as monkeys were presented with visual saccade targets and distractor stimuli (Bisley and Goldberg 2003). They demonstrated that the spatial position represented by the activity of LIP neurons corresponded to a region of enhanced visual sensitivity consistent with this activity coding the locus of covert spatial attention. This was true whether the LIP activity was evoked by a saccade target, and the monkey planned a saccadic eye movement, or by a distractor stimulus that drew attention but did not require a saccade (Bisley and Goldberg 2003). Neurophysiological studies in an adjoining parietal area, area 7a, have documented that neuronal activity is modulated by the locus of covert spatial attention, but in a different manner. The visual responses of 7a neurons are suppressed by covert attention. That is, the response of 7a neurons to a visual stimulus is smaller if attention is directed toward the stimulus (Steinmetz et al. 1994; Steinmetz and Constantinidis 1995; Constantinidis and Steinmetz 2001). This has been interpreted as indicating that area 7a neurons command shifts of covert spatial attention toward their receptive fields. (If covert attention is already directed toward the visual receptive field of an area 7a neuron when the visual stimulus appears, the stimulus does not produce a shift of covert attention, accounting for the reduced neuronal response). Though distinct neural mechanisms have been identified, these studies clearly indicate that the neural representation of visual space in parietal areas LIP and 7a is modulated by covert spatial attention. Moreover, the neural mechanisms of covert

attention identified in parietal cortex conform to features of a stage I cognitive process. In the studies described above, the activity of parietal neurons remained spatially tuned to the positions of visual stimuli (and therefore did not exhibit sensorimotor independence). Attention was implemented in the brain by modulating the amplitude of neuronal signals that were tightly coupled to the visual sensory input.

Temporal modulation of sensorimotor signals and working memory / motor planning.

Decoupling the timing of visual or movement-related signals in parietal neurons from the sensory and motor events they represent provides the basis of both visual working memory (Fig. 1d) and motor planning (Fig. 1e). This decoupling can be demonstrated in monkeys that have been trained to make memory-guided saccades toward visual targets several seconds after the targets themselves have disappeared. In order to provide spatial guidance for the delayed movement and perform the task successfully, the brain has to store the location of the visual target in a transient buffer for several seconds after it disappears, providing an operational definition of working memory. During this task, some parietal neurons exhibit sustained activity that outlasts the duration of the saccade target and persists until the monkey completes the memory-guided saccade (Gnadt and Andersen 1988; Chafee and Goldman-Rakic 1998). This population of parietal neurons is functionally diverse, with sustained activity in some neurons coding the position of the prior stimulus (Gottlieb and Goldberg 1999), and in others the direction of the pending saccade (Mazzoni et al. 1996a). Therefore parietal neurons participate in both spatial working memory and motor planning. However, both working memory or motor planning appear to be implemented by modulating the duration of physiological signals in parietal neurons that are tightly coupled to sensorimotor events. The neural signals in question are spatially tuned to stimulus position or movement direction, and do not exhibit sensorimotor independence. This is the basis for identifying working memory and motor planning as stage I cognitive processes.

Gain modulation of motor planning signals as the neural basis for decision processing.

Platt and Glimcher found that LIP neurons were more strongly activated during the delayed saccade task when the saccade a monkey planned to make would yield a larger reward with greater probability (Platt and Glimcher 1999). This suggested that parietal neurons

implemented an oculomotor decision process, as follows. A decision can be understood as the resolution of a competition between populations of neurons representing alternative actions, with the action represented by the most active population winning the competition. The fact that the strength of neural signals coding movement direction in parietal cortex varies as a function of expected reward is consistent with these signals participating in a competitive decision process. The strongest signals will code the action expected to produce the greatest reward, and tend to win the competition. This and similar studies have led to a very active area of research establishing further links between neural activity in parietal cortex and decision variables. For example, Sugrue and colleagues recently characterized neural activity in parietal area LIP of monkeys performing a free-choice task in which they autonomously decided to saccade toward one of two simultaneously presented targets. The computer controlling the experiment assigned different reward probabilities to the two targets in blocks of trials, and within each block, monkeys selected each target with a frequency proportional to its reward probability. This “matching” behavior was well explained by a behavioral model in which the brain assigned values to targets by integrating over the recent reward history of each target. These authors discovered that the intensity of motor planning activity in area LIP varied with the value of the planned saccade so defined (Sugrue et al. 2004). A separate series of experiments investigated the relation of neural activity in parietal cortex to decision processing in a task that varied the perceptual strength of the visual stimulus instructing the delayed saccade. (Monkeys viewed a field of randomly moving dots in which a varying proportion moved in the same direction, and were trained to make a saccade in the predominant direction of perceived visual motion). Saccade planning activity in area LIP was more intense when the visual stimulus instructing the saccade was strong and perceptually unambiguous, and the monkey could be more certain about the direction of the instructed saccade (Shadlen and Newsome 2001; Huk and Shadlen 2005). However, in each of these behavioral contexts, the neural activity found to vary with decision variables (whether reward magnitude, reward probability, action value, or perceptual certainty) coded the direction of a forthcoming saccade. Neural correlates of decision processing as defined by the above studies in nonhuman primates therefore do not exhibit sensorimotor independence and as such mediate a stage I cognitive process.

“STAGE II” COGNITION: SENSORIMOTOR INDEPENDENCE AND THE EMERGENCE OF ABSTRACT REPRESENTATIONS IN PARIETAL CORTEX

The term “stage I cognition” is used above to refer to attention, working memory, motor intention and decision processing in order to convey the fact these comparatively simple though fundamental forms of cognition are likely to be built upon comparatively direct modifications (of either timing or amplitude) of sensorimotor signals in the brain. Stage II cognition in contrast, is introduced to identify a set of cognitive processes equated with neural signals that encode abstract information that no longer bears any direct relation to particular stimuli or specific movements. The capacity for abstraction is central to human intelligence, and it is an important advance in our understanding of human intelligence as a biological phenomenon that recent experiments (described below) have identified and characterized physiological correlates of stage II cognitive processes at a cellular level in the brain. As a group, stage II cognitive processes compute, derive, or generate neural representations that can provide the basis for intelligent action without relating to the attributes of any single stimulus or movement. For example, concepts such as “gravity” or “before” have no direct or singular external correlate. They are abstractions that describe or predict the behavior of a potentially infinite set of objects or events. As such these concepts generalize – they hold true across a wide range of sensorimotor particulars, and they are likely to equate to patterns of neural activity in the brain that similarly generalize across a wide range of stimulus and motor conditions. This highlights the distinction between neural signals that mediate stage I and stage II cognitive processes. Stage I processes are mediated by modulated patterns of neural activity that code the unique features of specific objects or particular actions. Stage II processes are mediated by patterns of neural activity that instead exhibit sensorimotor independence – that code abstract information, such as a rule or concept, which can be logically related to the selection of an intelligent response in a given circumstance without relating to the features of the specific objects or particular actions involved.

Nonspatial Stage II cognition in parietal cortex.

Recent neurophysiological research in the nonhuman primate cortex over the past decade has revealed numerous examples of neural

representations that meet the above criteria for neural correlates of a stage II cognitive process. A very compelling example was provided by Miller and colleagues who trained monkeys to match visual displays based on the number of items they contained. These authors were able to show that the activity of neurons in prefrontal and also posterior parietal cortex varied systematically as a function of the number of items present (Nieder and Miller 2004) apart from any specific physical attribute of the items in question (such as their size or position). Individual neurons were tuned to numerosity and different neurons had different preferred numbers. Parietal and prefrontal neurons that code numbers are comparably activated by visual displays that contain either each neuron's preferred number of items or by a symbol that represents that number (Diester and Nieder 2007). This shows that neural signals coding a given number generalize across a very diverse set of visual displays that connote the number in question. In addition to coding numbers, parietal neurons can also code abstract rules. For example, Snyder and colleagues (Stoet and Snyder 2004) trained monkeys to make different responses to the same stimulus depending on which of two abstract rules was in effect. (Depending on the rule, the correct response was instructed either by the color or contrast of the stimulus). These authors found that neural activity in area LIP varied as a function of which rule was in force, regardless of the visual properties of the stimuli presented or the directions of the pending movements. The representation of a number, or a rule, as an abstract mental construct, by neural signals in parietal cortex that exhibit sensorimotor independence, is evidence that parietal neurons participate in stage II cognitive processing. Parietal neurons code sensory and motor variables directly, modulate these signals to mediate stage I cognitive processing, and also are capable of coding abstract variables to mediate stage II cognitive processing. The existence of this hierarchy of neural representation within parietal cortex, a sensorimotor area of the cerebral cortex, suggests that cognition is mediated by a set of information processing operations that are embedded within the sensorimotor systems and circuits of the cerebral cortex, and may ultimately derive from sensorimotor experience.

Spatial Stage II cognition in parietal cortex.

In order to mentally solve demanding spatial problems, the brain may generate and manipulate neural representations of space that exhibit sensorimotor independence, reflect abstract spatial principles, do not encode the features of any particular visual stimulus or

movement, and as such meet the definition of a stage II cognitive process as set out above. Relational spatial concepts such as “above” or “nearer” for example are intrinsically abstract and neural signals coding these constructs would be expected to exhibit sensorimotor independence. In addition, the brain may compute a position that provides a solution to a spatial problem, without the position in question representing the position of a stimulus or the target of a movement. To investigate the possibility that neurons in inferior parietal cortex may participate in stage II cognitive processing specifically in the spatial domain, Georgopoulos and colleagues trained monkeys to solve comparatively complex spatial problems, and characterized the neural representation of space within parietal cortex as the brain computed the spatial solution (Crowe et al. 2004a, b; Chafee et al. 2005; Crowe et al. 2005; Chafee et al. 2007).

In a first series of experiments, this group trained monkeys to mentally solve visual mazes. Monkeys maintained their gaze fixated on a central fixation target as a large maze stimulus (30° in diameter) was presented on a visual display. The maze stimulus was octagonal in outline and contained a set of randomly generated lines delineating maze paths and path segments, each of which could turn but did not branch. At the center of the maze was located a start box from which a single, straight main path extended in one of eight radial directions. The main path either reached an opening at the maze perimeter (an “exit” maze) or a blind ending within the maze (a “no-exit” maze). The monkey’s task was to press one of two response pedals to report whether the main path reached an exit or a blind ending (the total number of maze exits was constant in either case). The task was intended to recruit a covert spatial analysis of the maze, by which the brain would analyze the main path, possibly following it from the start box outward toward the maze perimeter, in order to determine whether the path reached an exit or a blind ending. Neural activity was recorded within parietal area 7a during maze solution to detect neural correlates of the required spatial cognitive processing.

Neurons in parietal area 7a were robustly activated during the solution of visual mazes, increasing their activity when the maze stimulus appeared. This was not surprising in itself given the demonstrated role of parietal cortex in spatial visual processing. However, the activity of many area 7a neurons was spatially tuned to the radial direction of the maze path that monkeys covertly analyzed (Crowe et al. 2004b). There were two possible interpretations of this spatial tuning. For one, the spatial tuning of neural activity

could reflect the operation of a covert spatial cognitive process that followed the main path from the center of the maze outward. This would reflect a stage II cognitive process because path direction was an abstract variable, not related either to the position of a discrete visual stimulus or direction of a movement (the main path was embedded in a field of orthogonal line segments filling the central 30° of vision). Alternatively, the spatial tuning could reflect known sensory or motor properties of parietal neurons. To determine which of these provided the best account the authors compared the activity of the same neurons when monkeys solved visual mazes and when they performed sensorimotor control tasks in which they passively viewed spot visual stimuli, or planned and executed saccadic eye movements towards these stimuli. Visual stimuli and saccade targets in the sensorimotor tasks were placed at the same radial directions relative to the central gaze fixation target as the main paths in the maze task. If spatial tuning during maze solution reflected the stimulation of visual receptive fields by the maze stimulus, or the planning of saccadic eye movements which the monkey did not execute, then single neurons should exhibit similar spatial tuning during the maze task and the sensorimotor control tasks. This was not the case. Instead, most neurons that were spatially tuned during maze solution were not spatially tuned during the sensorimotor tasks. The minority of neurons that were activated during the performance of both the maze and sensorimotor control tasks exhibited uncorrelated spatial tuning under the two conditions. That is, it was not possible to predict the spatial preference (the preferred direction) of a neuron during maze solution on the basis of its spatial tuning during the sensorimotor tasks (Crowe et al. 2004b). This suggested that parietal cortex generated a spatial representation of path direction that was unique to maze solution, and did not reflect the basic sensory or motor properties of parietal neurons tested under simpler conditions. That conclusion was supported by the additional finding that in a naïve monkey that had not been trained to solve visual mazes, presentation of the same maze stimuli failed to elicit robust spatial tuning for path direction in parietal area 7a (Crowe et al. 2004b).

The hypothesis that the spatial tuning of neural activity for path direction reflected a type II spatial cognitive process, and not sensorimotor processing, was further substantiated by an analysis of neural activity in area 7a when monkeys solved visual mazes in which the main path contained a 90° turn. If the monkey covertly

followed the main path from the center of the maze outward, the neural representation of path direction should rotate at the point in the covert analysis that the monkey mentally negotiated the 90° turn, and in addition, the rotation should be in the direction of the turn. To test this prediction, the authors computed the average path direction represented by the population of active neurons in area 7a in successive 10 ms time bins, and found that the path direction represented by population activity rotated in the direction of the turn in the main path several hundred milliseconds after the maze appeared (Crowe et al. 2005). This dynamic change in neural representation was consistent with a mental process following the main path from the center of the maze outward, and occurred in the absence of any concurrent change in sensory input or motor output. These data indicated that neural activity in parietal cortex coded a spatial variable (path direction), logically related to the solution of the problem posed by the task. Based on the sensorimotor independence of this spatial representation, we can conclude that neural activity during maze solution mediates a stage II spatial cognitive process. That is, during maze solution, parietal neurons generate a representation of space in order to solve an abstract spatial problem, and not to mediate sensorimotor control.

The involvement of parietal neurons in stage II spatial cognitive processing was substantiated in a second series of experiments by the same group. These experiments characterized the neural representation of space in parietal area 7a of monkeys performing an object construction task. In the object construction task, monkeys first viewed a model object consisting of a variable spatial arrangement of identical square “parts”, and had to remember the spatial arrangement. The monkey then saw a second “copy” of the model configuration, identical except that a single square part was missing. The task of the monkey was to replace the missing part in the copy to recreate the model configuration. (The monkey did this by selecting one of two choice squares sequentially presented at different locations flanking the copy object. They pressed a single response key to indicate their choice, so movement direction did not vary). The task was intended to recruit a covert spatial analysis of object structure, by which the brain would analyze the spatial relationships between the components of the object. Neural activity was recorded in area 7a of parietal cortex during the performance of the object construction task in order to characterize neural correlates of the spatial cognitive processing required.

Neurons in parietal area 7a were robustly activated during the construction of visual objects. Some neurons increased their activity when the model object was presented, others when the copy object was presented. The second group of neurons was particularly interesting because their activity coded the spatial location of the part missing from the copy object (Chafee et al. 2005). In effect, the brain filled in the missing piece. Single neurons exhibited a spatial preference for a given missing square position, and were activated only when the missing square was on a particular side or at a particular height within the object. This was an intriguing neural representation of space for several reasons. First, the spatial information coded by this neural activity did not correlate with the spatial position (or configuration) of a visual stimulus. Notably, neural activity evoked by the copy object varied as a function the missing square location across trials in which the configuration and retinal position of the copy object did not vary. This excludes the visual sensory input associated with the copy object (relating to its position or form) as a factor controlling the neuronal response. Nor did the activity of neurons depend on the form of the model object considered alone. Rather, neurons were comparably activated by all pairs of model and copy objects in the set that jointly localized the missing square to each neurons preferred location.

To confirm that the neural representation of space during object construction did not reflect the direction of a planned but unexecuted saccade, the activity of the same neurons was compared as monkeys performed the construction task and a sensorimotor control task in which they executed delayed saccades to visual targets (Chafee et al. 2005). Saccade targets were placed at the same retinal positions as missing squares in the construction task. If the neural representation of space during object construction reflected saccade planning, neurons should exhibit the same spatial preference during object construction and the sensorimotor control task. As was found in the maze experiment, they did not. Rather, parietal neurons generated a representation of space that was unique to object construction. Most neurons active during object construction were inactive during passive visual stimulation or oculomotor planning (Chafee et al. 2005). Among the minority of single neurons activated during both object construction and sensorimotor control tasks, many neurons exhibited different spatial preferences under the two task conditions (Chafee et al. 2005).

Because the retinal positions of model and copy objects varied randomly across trials, it was possible to dissociate the object-centered position of the missing square from its viewer-centered (or retinal) position. For example, the missing square could be located on the left side of the copy object, but on the right or left side of viewer-centered space at random. The majority of neurons coding the position of the missing square did so in an object-centered spatial reference frame (Chafee et al. 2007). That is, these neurons were activated whenever the missing square was located on the relative left (or right) side of the copy object, regardless of whether the missing square and copy object were located to the left or right of the gaze fixation target (and therefore in left or right viewer-centered space). That is interesting from the perspective of a stage II spatial cognitive process, as it suggests that during object construction, neurons in inferior parietal cortex are capable of coding spatial relationships (e.g. ‘on the *left*’ with respect to the reference object), and this type of spatial representation can be likened to a spatial concept or principle that generalizes across a potentially infinite set of pairs of positions, so long as a preferred spatial relationship between them is maintained. The above observations indicate that the neural representation of space in parietal cortex observed during object construction exhibited sensorimotor independence, and therefore mediated a stage II spatial cognitive process. During object construction, parietal neurons generated a representation of space in order to solve an abstract spatial problem, and not to mediate sensorimotor control, much as they do during visual maze solution.

These data indicate that spatial representations that exhibit sensorimotor independence emerge within parietal cortex, a sensorimotor structure, in order to support stage II spatial cognitive processing. The crucial question is how this occurs. Do sensorimotor circuits generate abstract neural representations by transforming sensorimotor ones? An analysis of the time-varying information encoded by two groups of simultaneously active parietal neurons during object construction suggests that this is the case (Crowe et al. 2008). One group of parietal neurons active in this task coded the position of the missing square in retinal, viewer-centered coordinates. This representation was more closely tied to the visual sensory input. Another group of parietal neurons active in this task coded the position of the missing square in relative, object-centered coordinates. This representation exhibited sensorimotor indepen-

dence. Fluctuations in the strength of the two neural representations were correlated over time within each trial. Variation in the strength of viewer-centered representation led, and predicted variation in the strength of object-centered representation (Crowe et al. 2008). This neural dynamic is consistent with the hypothesis that more abstract spatial representations (of relative position) are generated by a transformation applied to more basic spatial representations (of absolute position). Obtaining more information to reveal the principles that govern such transforms from concrete to abstract neural representations may hold important clues as to how sensorimotor circuits acquire the capacity for abstraction through sensorimotor experience.

CONCLUSION

Several principles can be extracted from the findings provided by the research reviewed above. First, the same cortical areas that are involved in sensorimotor control mediate cognition. In fact correlates of cognition have been reported both in primary visual cortex (Roelfsema et al. 1998) and in primary motor cortex (Georgopoulos et al. 1989). It will be important to characterize the principles that govern the emergence of cognitive signals in sensorimotor circuits. With respect to this emergence, we can postulate the following general progression of information processing through a hierarchy of neural representation. At the most fundamental level, neural activity represents the features of stimuli and the parameters of movement. At the next level, we can imagine that neural signals mediating stage I cognitive functions emerge as these reflect relatively simple modulations in the timing and amplitude of sensorimotor signals. At the next level above this, we can imagine that neural signals mediating stage II cognitive functions emerge, at which point neural systems acquire the capacity for abstraction beyond sensorimotor representation. Perhaps the most mysterious link is the one between stage I and stage II processing. Understanding this progression in neural mechanistic terms will be essential to our understanding how mind emerges from brain.

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