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From visual affordances in monkey parietal cortex to hippocampo–parietal interactions underlying rat navigation

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SUMMARY

This paper explores the hypothesis that various subregions (but by no means all) of the posterior parietal cortex are specialized to process visual information to extract a variety of affordances for behaviour. Two biologically based models of regions of the posterior parietal cortex of the monkey are introduced. The model of the lateral intraparietal area (LIP) emphasizes its roles in dynamic remapping of the representation of targets during a double saccade task, and in combining stored, updated input with current visual input. The model of the anterior intraparietal area (AIP) addresses parietal–premotor interactions involved in grasping, and analyses the interaction between the AIP and premotor area F5. The model represents the role of other intraparietal areas working in concert with the inferotemporal cortex as well as with corollary discharge from F5 to provide and augment the affordance information in the AIP, and suggests how various constraints may resolve the action opportunities provided by multiple affordances. Finally, a systems-level model of hippocampo–parietal interactions underlying rat navigation is developed, motivated by the monkey data used in developing the above two models as well as by data on neurones in the posterior parietal cortex of the monkey that are sensitive to visual motion. The formal similarity between dynamic remapping (primate saccades) and path integration (rat navigation) is noted, and certain available data on rat posterior parietal cortex in terms of affordances for locomotion are explained. The utility of further modelling, linking the World Graph model of cognitive maps for motivated behaviour with hippocampal–parietal interactions involved in navigation, is also suggested. These models demonstrate that posterior parietal cortex is not only itself a network of interacting subsystems, but functions through cooperative computation with many other brain regions.

1. INTRODUCTION

Gibson (1966) observed that the pattern of optic flow, the movement of features across the retina from moment to moment, contained valuable information that could be used to guide navigation through the environment without prior recognition of objects. Gibson's term *affordances* is adopted in this paper for parameters for motor interactions signalled by sensory cues without the necessary intervention of 'high-level processes' of object recognition. Neurological data relate human parietal function not only to impairment of a variety of affordances but also to impairment of 'cognitive maps'. Bilateral parietal lobe damage often yields 'global spatial disorientation' (Kase *et al.* 1977), a symptom complex that involves the three systems whose parietal roles are modelled in this paper: the control of eye movements, the control of the grasping of objects, and the use of cognitive maps in navigation. Some of these deficits can also be seen in relatively pure isolated form.

In short, the parietal cortex is a complex system involved in a great diversity of subfunctions. More specifically, the inferior parietal lobule (IPL) of the parietal cortex in the monkey receives visual inputs from occipitotemporal areas as well as from the visual field periphery of V3 and V2 (Andersen 1987; Baizer *et al.* 1991). The IPL is functionally subdivided into several areas buried in the intraparietal sulcus, including the lateral (LIP), ventral (VIP), and anterior (AIP) intraparietal areas, as well as areas 7a and 7b and the secondary somatosensory area (SII). These areas have specific sensorimotor functions, including those for saccadic eye movements (LIP), ocular fixation (7a), reaching (VIP and 7b) and grasping (AIP). A similar modular organization is seen in the motor sector of the frontal lobe.

This paper outlines biologically based neural-network models for the role of the LIP in remapping during a double saccade task, and for the interactions of the AIP with the premotor cortex during the control of grasping. It is thus demonstrated how visual areas of the posterior parietal cortex process the affordances such as those involved in looking and grasping; other areas may be involved in more purely visual functions, such as shape extraction and motion extraction. On this basis, a systems-level model for the hippocampo–parietal interactions underlying navigation in the rat is outlined.

2. PARIETAL CORTEX AND DYNAMIC REMAPPING OF SACCADE TARGETS

Dominey & Arbib (1992) modelled the interaction of various brain regions in the execution of voluntary saccades in primates. This section focuses on the putative role of the LIP in the double saccade experiment. The monkey is seated in a primate chair with its head fixed and eyes free to move. Illuminated fixation points and saccade targets are presented on a visual screen in front of the primate; and the monkey has been trained not to move its eye while the fixation point remains on. In the double saccade task, following offset of the initial fixation point (F), targets A and B are successively presented in less than the time required to initiate the first saccade. Reward is contingent on successive saccades from F to A and then to B. In the double saccade, target B is not visible during or after the saccade to A. Thus, the representation of target B in a motor error map must be remapped to represent where B would appear were it still visible after the saccade to A. The double saccade task, then, is used to study the dynamic remapping of target representations to compensate for intervening movements.

Mays & Sparks (1980) detected a class of 'quasi-visual (QV)' cells in the intermediate layers of the superior colliculus (SC) that, before the second saccade in the double saccade task, were active in loci related to the second saccade, even though a visual stimulus with this retinal error did not appear in the receptive field of these cells. However, it appears that the QV property is not intrinsic to SC, but instead depends on a prominent direct projection from the LIP (Lynch *et al*. 1985). Indeed, Gnadt & Andersen (1988) found 'QV-like' cells in the LIP that code for the second eye movement although a visual stimulus never falls in the cells' receptive field, and Goldberg & Bruce (1990) found similar cells in frontal eye fields (FEF). Where does this dynamic remapping occur? It may well be computed 'independently' in several regions, with the regions interconnected to calibrate their computations. However, Dominey & Arbib (1992) hypothesize that the primary remapping occurs in the LIP, and model the LIP by two connected arrays of cells: PP, which is driven by retinal input, and PPqv, 'posterior parietal cells with QV-like activity', which drives both SCqv and FEFvis to yield the dynamic remapping in these regions.

To model the shifting activity in an array of QV-like cells, Droulez & Berthoz (1991) used an eye velocity signal to shift a 'mountain' of activity on a two-dimensional map of motor error. To date, a representation of eye velocity has not been recorded in the posterior parietal cortex. Dominey & Arbib (1992) thus developed an alternative model, which uses two eye-position signals, one a delayed version of the other, as the input for dynamic remapping. The difference between the two position signals is used to modulate two types of interneurones. Type r neurones implement *recurrent* self-excitation of the PPqv cells when the eye position signals are equal, which is reduced when the eyes are moving. Type S interneurones gate the lateral *shift* of activation between neighbouring cells as a function of the difference between the two position inputs. In a leftward saccade, the difference between the delayed signal and the original signal (calculated by S) is positive, so activity shifts from left to right.

The model also involves a projection from PP to PPq v, which ensures that when retinal input is available, it will eventually predominate over the 'memory map'. This projection allows the brain to combine stored, updated target information with current visual input.

3. PARIETAL CORTEX AND OBJECT GRASPING

In monkeys trained to grasp objects requiring different types of grip, about half the AIP neurones related to hand movements fired almost exclusively during one type of grip, with precision grip being the grip type most represented (Taira *et al*. 1990; Sakata *et al*. 1992). Some cells demonstrate specificity toward the size of the object to be grasped; some demonstrate independence from the size of the object. A small number of cells show modulation based on the object's position and/or orientation in space. In summary, it can be said that the visual responses of these cells provide a distributed code for affordances for grasping. Most neurones in AIP also show phasic activity related to the motor behaviour. The identifiable phases in the paradigm used by Sakata to study these cells are: set (key phase), preshape, enclose, hold (object phase), and ungrasp. Cells participate in varying degrees during different phases of the movement, but are usually most highly active during the preshape and enclose phases of movement. Very importantly, once a cell becomes active, it typically remains active until the object is released.

The area of monkey agranular frontal cortex involved in grasping is called F5 (Rizzolatti *et al.* 1988) and forms the rostral part of inferior area 6. Its main anatomical connections are with the AIP and the hand field of the precentral motor area (Muakkassa & Strick 1979; Matelli *et al*. 1985). Rizzolatti *et al.* (1988) described various classes of F5 neurones that discharge during specific hand movements (e.g. grasping, holding, tearing, manipulating). The largest class is related to grasping. The temporal relations between neurone discharge and grasping movements vary among neurones.

There now follows an outline of the FARS (Fagg–Arbib–Rizzolatti–Sakata) model of the grasping process, implemented in terms of simplified but biologically plausible neural networks Fagg 1996; Fagg & Arbib 1998). For example, given visual input from an object, the AIP computes—according to the model—the affordances corresponding to the various ways in which it may be grasped (as distinct from recognizing *what* the object is). The corresponding set of grasps is passed to F5. As a function of task or other information, F5 selects one of the specified grasps, and is responsible for unfolding the grasp in time. F5 activity is broadcast back to the AIP, strengthening the affordance that corresponds to the selected grasp. Motor responses in the AIP are explained as corollary discharges from F5, and the AIP provides an active memory for the grasp, which is continuously updated. This is similar to the dynamic remapping seen in the study of saccades (above), in which motor afference updated a map of targets of potential eye movements.

The location of target objects is represented in the VIP (Colby *et al*. 1993) by means of a broadly tuned population code. This affordance is passed to F4, which represents the arm goal position. Because grasp programming affects arm movements, the model modulates F4 with information from the AIP specific to the affordance–grasp pair selected by the AIP–F5 system.

A neighbouring region, the posterior intraparietal area (PIP), codes object-centred information (H. Sakata, personal communication) concerning different shapes presented to the monkey. In the model, the PIP codes the shape and size of the object to be grasped. An affordance derived from the PIP maps an object configuration to one possible grasp for that object. Castiello *et al*. (1991) studied impaired grasping in a patient (AT) with a lesion impairing the pathway V1→PP, and found evidence for a mapping from object identity to affordances that is effective whenever the nature of the object merits such a mapping. The model thus includes a corresponding path PIP→IT→AIP.

Figure 1 outlines the interaction between AIP and F5 populations during execution of the Sakata paradigm. Three AIP units are shown: a visual-related cell that recognizes objects that require a precision pinch, a motor-related cell of the same type, and a visual-related cell that recognizes objects requiring power grasps. Each F5 unit shown fires during a different phase of the programme. At each programme phase, the state is reported back to the AIP motor-type population. The full model also includes the role of SII in creating and monitoring haptic expectations, the role of the dorsal premotor cortex (F2) in the association of arbitrary stimuli with motor programme preparation, and the role of area 46 as a working memory in tasks requiring information to be held during a delay period. However, these details (and the presentation of simulation results) are beyond the scope of the present paper. It is stressed, however, that the circuitry controlling F5 programmes in the model is more complex than is shown in figure 1: the *effective connections* between programme states are not coded within F5 but are managed by the combined action of the portion of the supplementary motor area known as pre-SMA (F6) and the basal ganglia (BG).

In summary, the FARS model introduces not only the affordances for grasping in the AIP but also those for reaching in the VIP. It also shows that parietal areas need not be restricted to computing affordances: the PIP extracts object shape and size information that is as useful to the object recognition in inferotemporal cortex (IT), as it is to the AIP's determination of affordances. The concept has also moved from the 'self-contained' study of a parietal region, accorded LIP in the Dominey–Arbib model of dynamic remapping of saccades, to a 'cooperative computation' model of AIP in which its computation of visual affordances is complemented by corollary discharge from F5, which in the model is hypothesized to resolve multiple potential grasps by information on task constraints (from F6), working memory (from area 46) and instruction stimuli (from F2). As a result, the AIP can function as an active memory in which a set of affordances, not all of which need be activated by visual input, are updated as the plan of action unfolds. The IT gives a broadly tuned coarse code for affordances when object knowledge is appropriate for this, and when visual input to the AIP is available, the AIP can refine or replace IT input with a more finely tuned coarse code for affordances. Finally, action generally involves plans that take advantage of, but are not wholly driven by, current affordances; the FARS model thus addresses the role of the pre-SMA and BG in sequence management.

4. PARIETAL CORTEX AND NAVIGATION

The above models of the roles of the parietal cortex in saccades and grasping are firmly grounded in data from monkey neurophysiology, and comprise networks of biologically plausible neurones implemented on computers, yielding many simulation results. By contrast, the following model of the role of the parietal cortex and hippocampus of the rat in navigation is conceptual. A simulation study of parts of the model is provided by Guazzelli *et al*. (1998). It addresses data from rat neurophysiology, but is strongly motivated by data from primate neurophysiology whose implications for analogous properties of the rat brain have yet to be tested.

(*a*) *Cognitive maps and the hippocampus*

To use a road map, we must locate (the representations of) where we are and where we want to go, and then find a path that we can use as we navigate towards our goal. We use the term *cognitive map* for a mental map together with these processes for using it. Thus the 'place cells' found in CA3 and CA1 regions of rat hippocampus (O'Keefe & Dostrovsky 1971) provide only a 'you are here' signal, not a full cognitive map. Moreover, a given place cell will have a 'place field' in a highly familiar environment with up to 70% probability. This suggests that the hippocampus is dynamically tuned to a 'chart' of the current locale, rather than providing a complete 'atlas' with a different place cell for every place in the rat's 'entire world'. This suggests two alternatives (at least): (i) the different 'charts' are stored elsewhere, and must be 'reinstalled' in the hippocampus as dictated by the current task and environment; (ii) the cells of the hippocampus receive inputs encoding task and environment, which determine how sensory cues are used to activate a neural representation of the animal's locale.

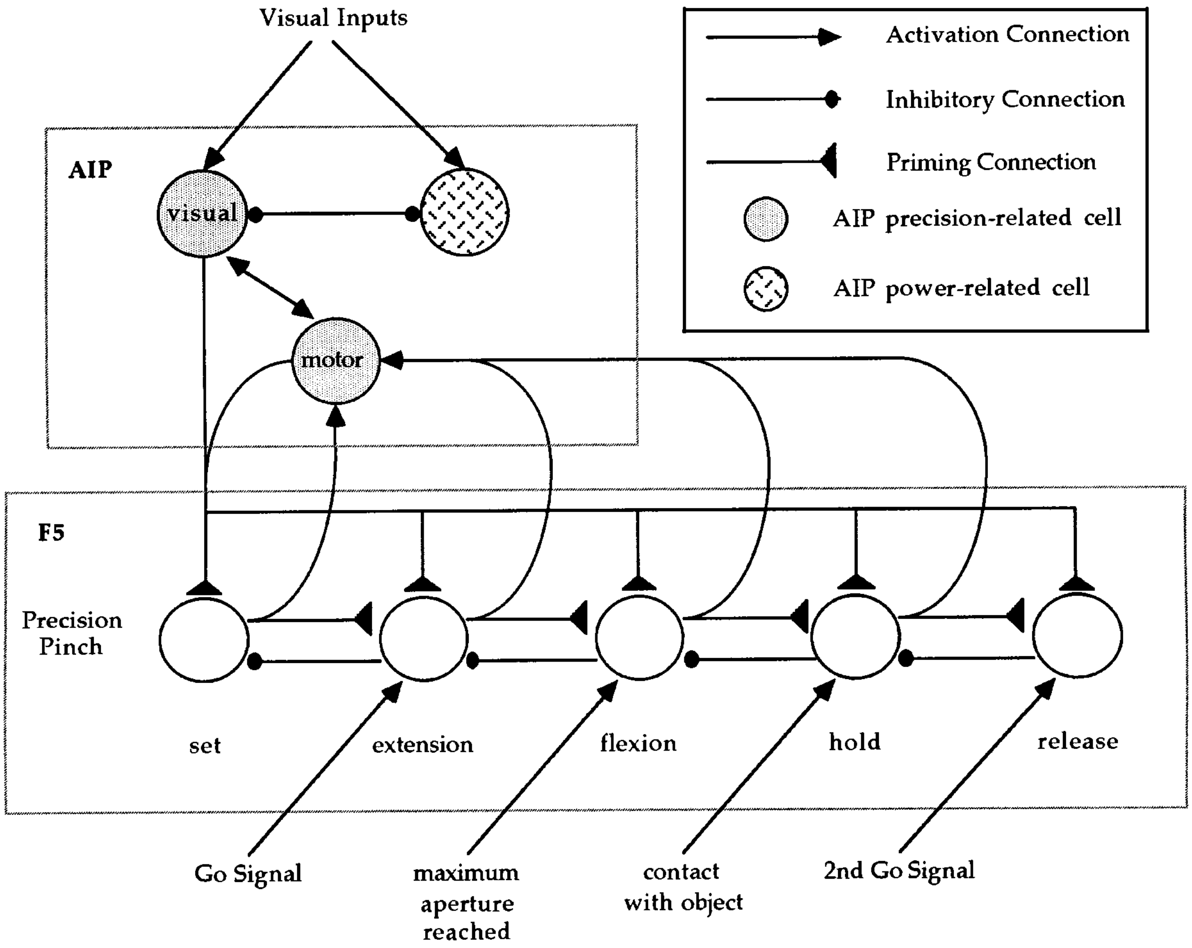

Figure 1. FARS model of interaction between AIP and F5 populations (circles) during execution of the preshape–grasp–hold programme. Activity within F5 cascades from left to right as the programme is executed. Each phase primes the next phase (which must await further activation to control motor output) and inhibits the preceding phase. At each programme phase, the state is reported back to the AIP motor-type population.

In either case, it is clear that these charts are highly labile. Noting the importance of parietal systems in representing the personal space of humans, we seek to understand cognitive maps in a framework that embraces the parietal cortex as well as the hippocampus.

Although some hippocampal cells fire when rats drink water or approach water sources (Ranck 1973), O'Keefe & Conway (1978) did not find the role of food or water to be markedly different from other cues that identify the location of a place field. Eichenbaum *et al.* (1987) recorded from rats repetitively performing a sequence of behaviours in a single odour discrimination paradigm, and found *goal-approach* cells, which fired selectively during specific movements, such as approach to the odour port or to the reward cup. Despite these and related findings, there is still no evidence that the hippocampus proper can simultaneously encode the rat's current location and the goal of current navigation.

(*b*) *Taxon and locale systems: an affordance is not a map*

O'Keefe & Nadel (1978) distinguished the *taxon* (behavioural orientation) system for route navigation (a taxis is an organism's response to a stimulus by movement in a particular direction) and the *locale* system for map-based navigation, and proposed that the locale system resides in the hippocampus. The present author and colleagues have already qualified the latter assertion, showing how the hippocampus may function as *part of* a cognitive map. Here taxis will be related to the notion of an affordance. Just as a rat may have basic taxes for approaching food or avoiding a bright light, for example, so does it have a wider repertoire of affordances for possible actions associated with the immediate sensing of its environment. Such affordances include 'go straight ahead' for visual sighting of a corridor, 'hide' for a dark hole, 'eat' for food as sensed generically, 'drink' similarly, and the various turns afforded by, for example, the sight of the end of the corridor. Because the rat's behaviour depends more on smell than on vision, 'olfactory affordances' should be added, but relevant data are sparse.

Both normal and hippocampal-lesioned rats can learn to solve a simple T-maze in the absence of any consistent environmental cues other than the T-shape of the maze. If anything, the lesioned animals learn this problem faster than normals. After criterion was reached, probe trials with an eight-arm radial maze were interspersed with the usual T-trials. Animals from both groups consistently chose the side to which they were trained on the T-maze. However, many did not choose the 90° arm but preferred either the 45° or 135° arm, suggesting that the rats had solved the T-maze by learning to rotate within an egocentric orientation system at the choice point through approximately 90°. This leads to the hypothesis of an orientation vector being stored in the animal's brain but does not give any information as to where or how the orientation vector is stored. One possible model would employ coarse coding in a linear array of cells, coded for turns from $-180°$ to $+180°$. From the behaviour, one might expect that only the cells close to the preferred behavioural direction are excited, and that learning 'marches' this peak from the old to the new preferred direction. However, it requires a simpler learning scheme to 'unlearn' $-90°$, say, by reducing the peak there, while 'building' a new peak at the new direction of $+90°$. If the old peak has 'mass' $p(t)$ and the new peak has 'mass' $q(t)$, then as $p(t)$ declines towards 0 while $q(t)$ increases steadily from 0, the centre of mass $(-90)p(t)+90q(t)/p(t)+q(t)$ will progress from -90 to $+90$, fitting the behavioural data.

The determination of movement direction is easily modelled by 'ratification' of the Arbib & House (1987) model of frog detour behaviour. There, prey were represented by excitation coarsely coded across a population, and barriers were encoded by inhibition whose extent closely matched the retinotopic extent of each barrier. The sum of excitation was passed through a winner-take-all circuit to yield the choice of movement direction. As a result, the direction of the gap closest to the prey, rather than the direction of the prey itself, was often chosen for the frog's initial movement. The same model serves for behavioural orientation once the direction of the prey (frog) is replaced by the direction of the orientation vector (rat); the barriers correspond to the absence of affordances for movement (see Guazzelli *et al.* (1998) for further details).

(*c*) *Hippocampal–parietal interactions in navigation*

McNaughton *et al.* (1989) found cells in the posterior parietal cortex of the rat with location specificity that were dependent on visual input for their activation. Of these cells, 40% had responses discriminating whether the animal was turning left, turning right, or moving forward (here called MLC cells in honour of the co-authors McNaughton, Leonard and Chen). Some cells required a conjunction of movement and location; for example, one parietal cell fired more for a right turn at the western arm of a cross-maze than for a right turn at the eastern arm, and these firings were far greater than for all left turns. Another parietal cell fired for left turns at the centre of the maze but not for left turns at the ends of the arms, or for any right turns. Turn-direction information was varied, with a given cell responding to a particular subset of vestibular input, neck and trunk proprioception, visual-field motion, and (possibly) efference copy from motor commands.

McNaughton & Nadel (1990) offered a model of rat navigation with four components (figure 2*a*) as follows; B, a spatiosensory input; A, in hippocampus, provides a place representation; L, posited to be parietal, outputs a movement representation; AL provides a place–movement representation, by means of the parietal MLC cells. In the model, A both transforms visual input from B into place-cell activity, and responds to input from AL by transforming the neural code of (prior place, movement) into that for the place where the rat will be after the movement. However, this model becomes untenable because MLC cells are *not* place–movement cells in the sense of 'place' in

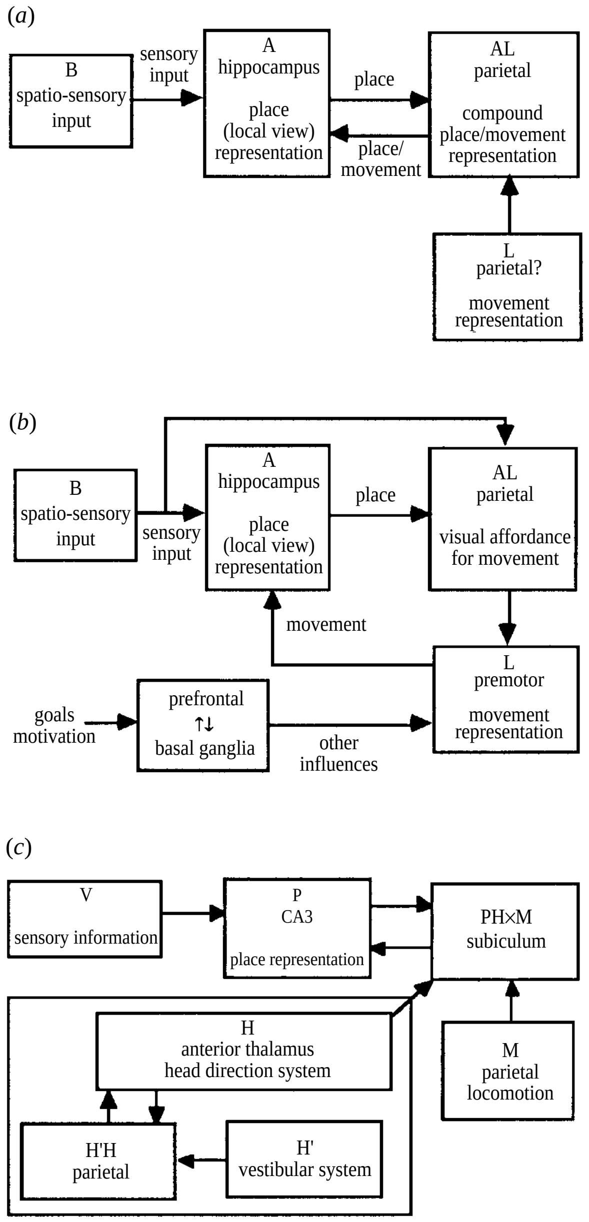

Figure 2. (*a*) A systems view of the role of the hippocampus in spatially guided navigation (adapted from McNaughton & Nadel 1990). (*b*) A recasting of the systems view of (a) which makes explicit that parietal cortex provides 'affordances' rather than explicit place information (Arbib *et al.* 1997). (*c*) The McNaughton *et al.* (1996) systems-level view of the role of the hippocampus in navigation, redrawn from the perspective of (*a*).

'place cells'. Examples of such a cell's place–movement field are 'left turn at end of arm' or 'move ahead along arm'.

To proceed, analogies with monkey parietal cortex are pursued. It is first hypothesized (for future experimental testing) that the parietal cortex of the rat also contains affordance cells for locomotion and navigation, akin to those documented in the monkey for reaching and grasping. Figure 2*b* thus has the cells in AL (parietal cortex) code for affordances, and includes a direct link from B to AL that is absent from figure 2*a*. Because 'grip affordance cells' in the AIP project to 'grip premotor cells' in premotor region F5, it is postulated analogously (figure 2*b*) that L is premotor and driven by AL. Once again, the current place is encoded in A, but it is now posited that movement information from L enables A to compute the correct transformation from current place to next place. In either model, then, the loop via AL can, in the absence of sensory input, update the place representation in A, with the cycle continuing until errors in this *expectation* accumulate excessively.

Figure 2*b* also adds links from brain areas involved in goals and motivation: the navigation of a hungry rat is different from that of a sated rat. In analogy to the monkey, it posits (without further analysis) that interactions between the prefrontal cortex and basal ganglia *choose* the rat's next movement on the basis of its current position relative to its goal. This is discussed further with reference to the World Graph model (below).

Let us now return to the MLC cells. Some fire before the rat's execution of a turn, and correspond to the affordance cells of figure 2*b*, but others do not fire until the turn commences. These, then, are not signalling affordances; a supplementary circuit is now described (P. Rothemund, USC term paper, Spring 1996) which includes the above model of these cells. To ground this circuit, reports are referred to from the *monkey* literature, of neurones that detect optic flow and have traces similar to those for MLC cells whose responses start at the initiation of a turn. These include medio-temporal sulcus (MST) neurones selective for expansion, contraction, and rotation (Graziao *et al.* 1994). Sakata *et al.* (1994) reported rotation-sensitive neurones of the posterior parietal association cortex which, unlike MST neurones (which seem specific for rotation in a frontoparallel plane), were mostly sensitive to rotation in depth.

A neurone responding to a focus of expansion could code for straight ahead and a neurone encoding translational flow or rotation in depth could code for a turn. Some of the MLC cells that fire at a turn require head orientation in addition to visual input. It is here suggested that 'parietal left turn' neurones combine input from an 'MST left turn' neurone with vestibular input, efference copy, or somatosensory input. Such a 'parietal left turn' neurone can thus function in the dark, but does not code place as well as movement. A neurone that does code for a 'place-specific left turn' might be constructed from a 'parietal left turn' neurone and hippocampal input. It is here postulated that, although it is based on monkey data, this circuitry will (with different anatomical loci) be instantiated in rat brain as well.

McNaughton *et al.* (1996) have proposed a new systems-level model, which incorporates head-direction information in the implementation of an angular path-integrator module. Note that head direction here is *not* absolute but is established with respect to sensory (e.g. visual) cues. It can be maintained moderately well if the animal moves in the dark, but will be changed if the sensory cues are rearranged. Figure 2(*c*) presents this model redrawn to emphasize its similarity with figure 2(*a*). Box PH × M, previously P × M and assumed to be parietal, is now assumed to be implemented by the subiculum, based on the report by Sharp & Green (1994) that some cells in the subiculum and dorsal presubiculum have broad, but significant, directional tuning in situations where directionality is absent from hippocampal cells.

McNaughton *et al.* (1996) view head direction as a point on a circle centred on the rat, and assign each head-direction cell a location on this circle. This head-direction ring (H) has local Gaussian excitatory connections from a cell to its neighbors. Another layer of neurones (H′H) receives information about the current location from H and information about rotational motion from the vestibular system and other sources of such information (H′). These cells encode the interaction between current location and the sign of rotation and feed this information to cells on the appropriate side of the current focus of activity in the direction circle. Cells with these response properties have been observed in the posterior parietal cortex of the rat (Chen *et al.* 1994*a*,*b*). The posterior parietal cortex is now assumed to implement the H′H system, which is almost identical with the dynamic remapping module postulated for LIP in the Dominey–Arbib model described above.

(*d*) *World graphs as cognitive maps for motivated behaviour*

Lieblich & Arbib (1982) model the building of a cognitive map based on their notion of a *world graph*, a set of nodes connected by a set of edges, where the nodes represent recognized places or situations, and the links represent ways of moving from one situation to another. A crucial notion is that a place encountered in different circumstances may be represented by multiple nodes, but that these nodes may be merged when the similarity between these circumstances is recognized. They model the process whereby the animal decides where to move next, on the basis of its current drive state (hunger, thirst, fear, etc.). The emphasis is on spatial maps for guiding locomotion into regions not necessarily currently visible, rather than retinotopic representations of immediately visible space, and yields exploration and latent learning without the introduction of an explicit exploratory drive. The model shows: (i) how a route, possibly of many steps, may be chosen that leads to the desired goal; (ii) how short cuts may be chosen; and (iii) through its account of node-merging why, in open fields, place-cell firing does not seem to depend on direction. Current work in the author's laboratory is addressed to a neurally realized updating of the model, which takes account of a large body of neural data.

5. DISCUSSION

This analysis of the role of the hippocampus and parietal cortex in the rat has been informed both by analysis of the monkey parietal cortex and by a broader systems view of the components of a cognitive map that go beyond signalling 'you are here'. In reviewing the distinction between the taxon and locale system, it was noted that affordances: (i) generalize taxes and enable the rat to navigate in novel circumstances; and (ii) may refine plans inferred on the basis of a cognitive map by providing explicit information on actions possible in the current environment. A parallel is noted here with the way in which the AIP may use current input to refine general grasp strategies that IT may outline on the basis of general object characteristics.

The McNaughton–Nadel model (figure 2*a*) was rejected by observing that MLC cells do not strongly encode place information. However, by analysing data from *monkey* parietal cortex, it was possible to hypothesize *two* systems in *rat* parietal cortex: one detecting affordances (corresponding to cells that fire in preparation for a movement), and one based on optic flow and vestibular cues during the movement. This latter information corresponds in part to a new model by McNaughton *et al*. (1996), which pays attention to vestibular, but not optic-flow, information, and posits a parietal system for 'direction integration', updating the animal's estimate of head direction in a fashion remarkably similar to the dynamic remapping for saccades in the LIP of the monkey. It is noted here that Touretzky & Redish (1996) have developed the CRAWL model of rodent navigation, which gives a functional non-biological analysis of the path-integration mechanisms for spatial position (as distinct from head position) that underlie the ability of animals to find a direct path home after a complex outward trajectory. However, in more complex environments, a direct path is seldom adequate to reach home or some other goal. The World Graph theory offers key ideas for analysis of motivated behaviour in complex environments. In moving *beyond* path integration—selecting a complex path rather than constructing a straight path home—we may expect to encounter the problems of 'sequence management' which, in the study of primate grasping discussed above, were suggested to be the domain of interactions between pre-SMA and the basal ganglia.

With this is established the fruitfulness of a 'cooperative computation' model, which (i) sees many parietal subregions as specialized for computing specific classes of affordances; (ii) stresses the interaction between these subregions as well as the dynamic interaction of parietal cortex with other neural systems; (iii) learns from cross-species comparisons, and (iv) points up the importance of neural architectures that may implement related schemas (functional units such as dynamic remapping and path integration) in different species and, perhaps, within different brain regions in a given brain.

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