

A Neuroethological Framework for the Representation of Minds

Leslie Brothers and Brian Ring

UCLA Brain Research Institute

and

Sepulveda VA Medical Center

Abstract

■ The cognition that constructs mental features such as intention, disposition, and character is an aspect of theory of mind. This aspect of representation of minds, which inherently has valence, is viewed from cognitive, evolutionary, and neural perspectives. It is proposed that this cognition is modular, and that it normally operates in association with a valence-free

cognition able to represent mental states such as belief. Examples of neural activity capable of supporting the social representations macaque monkeys are believed to possess (understanding of affective displays, purposeful movement, and elemental social interactions) are presented. ■

INTRODUCTION: THEORY OF OTHER MINDS

That mental states are intentional is a philosophical notion meaning they are “about” something. Beliefs and desires are prototypic mental states that necessarily are about things (one believes that **p**, one desires that **p**), as discussed for example by Dennett (1987). The proposal that a human or animal mind has first-order intentionality—in other words, is characterized by such states as beliefs and desires—can be accepted simply as providing the most economical description of the behavior patterns observed in such creatures.

Second-order intentionality is the ascription by an intentional being of intentionality to another being: as a second-order intentional being, I may have a mental state that is about the mental state of another. The fact that the existence of second-order intentionality in human beings is so easy to demonstrate should give us pause. What is remarkable is not so much that humans under normal circumstances are able to have what has been termed a “theory of other minds” (Premack & Woodruff, 1978): it is that we engage automatically and effortlessly in building theories about the inner states of those around us.

A comprehensive framework for the neural and cognitive substrates of representations of other minds must embrace two aspects of the underlying mental activity. The core cognitive achievement under the first aspect might be designated by placing emphasis on the word

“other” in the phrase “theory of other minds.” Our understanding of this aspect of second-order intentionality is due in large part to the observations of primatologists (Premack & Woodruff, 1978; Premack, 1988; Cheney, Seyfarth, & Smuts, 1986; Cheney & Seyfarth, 1990; Whiten & Byrne, 1988) and to the cognitive framework offered by developmentalists (Astington, Harris, & Olson, 1988). A key notion, proposed by Leslie (1987), is that of meta-representation, a cognitive capacity that decouples descriptions of mental states such as belief from descriptions of the external world. Along this “cold” cognitive dimension of theory of mind, there appears to be emerging a coherent phylogenetic and developmental account, in which concepts of “agency” and “goal” emerge early while concepts such as “belief” appear later (Leslie, 1992).

Another dimension of the representation of minds concerns the social and emotional significance for the observing subject of the intentions of the observed. Phylogenetically, this aspect develops much earlier than the dimension described above, appearing, for example, in the elaborate system of social displays and responses observed in macaque monkeys (see below). To illustrate the distinction between “cold” and “hot” aspects of representation of mind, consider the following story, which concerns deception:

The chancellor Nicolas Rolin dies: the duke is left in ignorance of his decease. Yet he begins to suspect

it and asks the bishop of Tournay, who has come to visit him, to tell him the truth. "My liege, says the bishop—in sooth, he is dead, indeed, for he is old and broken, and cannot live long.—Déa! says the duke, I do not ask that. I ask if he is truly dead and gone.—Hà! my liege—the bishop retorts, he is not dead, but paralysed on one side, and therefore practically dead.—The duke grows angry.—Vechy merveilles! Tell me clearly now, whether he is dead. Only then says the bishop: "Yes, truly, my liege, he is really dead." (Huizinga, 1949)

In order for the duke to understand the bishop, the duke must be able to represent the bishop as possessing knowledge that he, the duke, does not possess, and as withholding it. But this is not enough. The duke must also understand the intentions of the bishop, as directed at himself. Here, it is implied that the duke understood the bishop's motivation as a benevolent one, an attempt to spare him from painful knowledge. Thus, while this episode of deception frustrates the duke's desire for information, it is not a basis for enmity, for the bishop is implicitly signaling friendly intentions. The cognition that supports an understanding that another person possesses knowledge is independent of valence; the cognition that supports an understanding of another's intentions toward oneself, on the other hand, has valence attached to it inescapably.

Both forms of cognition are ordinarily called into play in interpreting others' actions, as illustrated above. Especially in the sphere of social interactions, psychological models of others tend to be richly imbued with the valence attached to their intentions. We seek to resolve whether another is disposed toward ourselves in a friendly or unfriendly way; we conclude that another has helpful inclinations, or is secretly jealous, or is ambitious, or in love, or resentful, and so forth. Interactions of others that have nothing to do with us directly become compelling by virtue of these qualities. Soap operas, diplomacy, academic politics, and other forms of intrigue are all compelling by virtue of our tendency to conduct continuous hypothesis testing regarding others' plans and dispositions in the social sphere.

Below, we offer an account of this cognition as the outcome of a particular stream of processing, which takes as its inputs features of the social environment. Evidence from neurologic syndromes and from experimental primate models will be presented, showing that specific brain regions participate in encoding high-level, psychological representations of other individuals.

A COGNITIVE MODULE

In *The Intentional Stance*, Dennett wrote, "It is easy for us, constituted as we are, to perceive the patterns that are visible from the intentional stance—and only from

that stance" (Dennett, 1987, p. 39). How we are constituted, in Dennett's sense, is the question to be addressed in what follows. In the remainder of the discussion, we will focus on representation of minds under the aspect of valence.

The criteria for a module of cognition include an evolutionary account, evidence for a stereotyped developmental sequence, the existence of innate deficits or accentuation of the cognition, the possibility of a selective deficit following damage to neural structures, a defined domain of inputs, automatic processing, and at least a proposal for core cognitive operations (Jackendoff, 1987; Fodor, 1983; Gardner, 1983). Only a few of these criteria will be addressed here. Some of what follows has been outlined previously by Brothers (1990).

The central proposal, as regards human representation of mind under the aspect of valence, is that the lowest level sensory inputs to the module are features of animate beings, such as faces, hands, and voices. Jackendoff (in press) similarly proposes that faces, voices, visual affect, and auditory affect are input modules to a faculty of social cognition. In our view, the highest representation is not of a mental state—although the construct may be extracted—but of a "person," where person is a human being with psychological features including a set of attitudes and propensities that have valence for the observer. We will attempt to show that it is not only a being with a mental life that is constructed from lower level inputs, but a person who is classified as, for example, a "mensch," or a knave (Harré, 1984; Carrithers, 1991). The highest level of representation, therefore, has reference to a social order. [The evolutionary significance of cooperativity, thus, of a social order, in the history of human cognition has been discussed by a number of authors (Premack, 1990; Cosmides, 1989; Axelrod & Hamilton, 1981).]

Automaticity and Acquired Deficits

The association of particular neurologic lesions with disordered language is critical evidence for the existence of a language module grounded in a neural subsystem. We shall call on readers' familiarity with disorders of language to point out analogous defects in the processing of information about persons, also associated with neurological lesions. Physical stimuli in this domain, such as faces and voices, are analogous to phonemes or graphemes in the language domain; person-representations are analogous to the semantic aspects of words.

In an input processing sense, faces, aspects of bodies, and voices are automatically processed in relation to persons as phonemes are processed in relation to words: just as one obligatorily hears words when listening to a speech stream in a language one understands, and not the speech sounds themselves, one obligatorily constructs persons from biological stimuli such as faces and

voices. This proposition receives support from a study of face recognition demonstrating that target faces are subsequently better recalled when observers make judgments regarding personality characteristics than when they make judgments about physical features of the face (Patterson & Baddeley, 1977), results suggesting that representations of psychological traits have privileged cognitive links with representations of faces. Bruce (1988, p. 31) has written:

It seems that face perception invokes attributional processes which go far beyond the information given. Shown only a face, we are prepared to judge a person's emotional state, personality traits, probable employment, and possible fate.

Bruce has designated these attributions "visually derived semantic coding," in distinction to other types of coding that faces are also hypothesized to elicit, namely, pictorial and structural visual coding, and linguistic processing of facial speech signals. Faces may act as inputs to each of these streams of processing; Bruce proposes that performance on various face recall tasks may depend on how the test conditions conform to the processing mode that subjects initially used when first exposed to an unfamiliar face. Visually derived semantic coding includes both psychological features attributable to persons, such as personality traits, and identity. Interestingly,

Instructing subjects to form personality impressions from faces (the "trait" condition) is likely to maximize visually derived semantic coding. (Bruce, 1988, p. 67)

Pictures of faces can provide access to representations of traits such as "helpfulness," even when relevant semantic memories are unavailable to consciousness. The following experiment was conducted by A. Damasio on the profoundly amnesic patient "Boswell." Several of the patient's caretakers undertook to be systematically generous and friendly toward him for a period of time, while several others conducted themselves in a negative and withholding manner. Although Boswell has no sense of familiarity or recall when exposed to a set of photographs of his caretakers, he was shown such a set and asked to indicate which faces belonged to persons likely to be "helpful." In indicating which persons he felt had that trait, he correctly chose the individuals who had behaved generously toward him in previous interactions. (A preliminary account of this experiment is given in Damasio, Tranel, and Damasio, 1989.)

Unfortunately for cognitive accounts of this aspect of face processing,

the framework (proposed by Bruce and colleagues for processing faces) provides no route whatsoever for a face to be judged as "honest". . . All we can

say is that such judgements are made in the cognitive system. (Bruce, 1988, p. 87)

We now turn to clinical evidence showing that the processes of deriving identity, and of deriving a person qua mental being, may become dissociated.

Automaticity of input processing, which has been proposed as a general feature of cognitive modules (Jackendoff, 1987), can be disrupted in the case of faces and persons, as happens in Capgras syndrome. The syndrome may occur as a result of diffuse neurologic insult (Bouckoms, Martuza, & Henderson, 1986; Fishbain & Rosomoff, 1986); however, in one case it was found to occur in a patient with a circumscribed parasitic cyst located in the left temporal lobe (Ardila & Rosseli, 1988) and in another in a patient with no demonstrable lesion except for a CT scan finding of bilateral atrophy of the temporal lobes (Joseph, 1985). Patients with Capgras syndrome are able to identify faces. They experience at the same time a failure to perceive the psychological entity, or person, which should be associated with the face. This failure is associated with a primary conviction of strangeness: sufferers are unable to override the affective immediacy of this conviction, which prevents them from inferring that it must after all be the person in question. A rather uncanny perception results, which may be conveyed as follows: "There is a person in my house who looks exactly like my husband, but I just know it is not my husband. It must be an imposter." The face remains associated with an abstract, verbal representation of the entity "my husband" (identity), but the sense of experiencing the person's presence is not accessed via physical stimuli such as face and voice. This suggests that processing a face for identity can remain intact while processing it for psychological attributes fails. A well-known science fiction film, "The Invasion of the Body Snatchers," evokes the experience of this dissociation in viewers.

Prosopagnosia, conversely, is the inability to retrieve relevant memories about a person's identity when the person's face is used as visual input (Damasio, Damasio & Van Hoesen, 1982). That the representation of the person as a psychological entity is nevertheless intact is demonstrated by the fact that the representation can be accessed by stimuli in other modalities, such as voice (Etcoff, Freeman, & Cave, 1991). Prosopagnosia is in this way analogous to alexia, a condition in which the central representation of a word is intact but cannot be accessed using the printed letters as visual input. In contrast, to use another analogy from language, Capgras syndrome parallels so-called semantic satiation (Amster, 1964), a state in which a word's sound becomes dissociated from its meaning, usually as a result of prolonged repetition. In both Capgras syndrome and semantic satiation, a higher level representation normally available to consciousness becomes unavailable in the presence of its lower level inputs.

Core Operations

To understand the core cognitive operations involved in constructing such psychological features as intention and disposition in others, we must adopt an ethological mode of thought. Classically, displays emanating from one individual act as releasers for complementary behaviors in the observer. For example, a threat display on the part of a dominant male macaque, which involves forward head movement, raised eyebrows, and open mouth, elicits withdrawal and submissive lipsmacking in a subordinate. A facial expression and mouth movements indicating intent to copulate in a male macaque trigger presentation by the female. Generally, mammalian responses to social displays encompass alterations in body movement, facial expression, and autonomic activity as indicated, for example, by piloerection and pupillary dilatation.

From the perspective of these externally observable physical responses, we may say that a computation of the significance of the eliciting gesture has occurred, as manifested by the response. The neural processes that link the sensory input (expressive display) to the motor output of the responder are equivalent to the computation of the gesture's significance (Mead, 1934; von Uexküll, 1982). Observed from a standpoint within the animal's experience, we may add that a feeling such as fear or arousal is the subjective aspect of the computation.

The core cognitive operation that underlies the representation of others' intentions and dispositions is exactly the computation of the gesture's significance for the receiver, which is felt subjectively as a social affect. Thus, separation distress (a social affect) is the core of the percept of a companion's intention to go away. Loneliness is the subjective aspect of the computation of others' determination to isolate one from the group. Fear is the subjective aspect of the computation of a dominant's tendency to attack. Jealousy is the subjective aspect of the computation of a special friend's attachment to a rival, and so on. These social affects, in other words, refer to the significance of an action or display for the observer. Brothers (1990) has proposed that the computations that give rise to these affects are the nuclei of cognitive constructs of others' intentions and dispositions. Thus, they form the core of the module that processes "hot" aspects of representation of mind. As Dennett (1987, p. 39) has written,

These patterns (of behavior generated by intentional minds) are objective—they are there to be detected—but from our point of view they are not out there entirely independent of us, since they are patterns composed partly of our own "subjective" reactions to what is out there.

The central nervous system organization that generates social affects by processing the relevant behavior of others is a legacy of the complex social groups in which

primates, including hominids, evolved. Such cognition presumably also includes computations of others' actions and intentions whether directed at the viewing subject or elsewhere.

The proposal that humans possess an innate cognitive "alphabet" representing ethologically significant actions of others is supported by observations made in patients undergoing electrical stimulation of limbic structures. In this setting, subjects experience a variety of discrete social affects as the accompaniments of mnemonic fragments depicting actions or mental attitudes of others directed at themselves (Gloor, 1986). Examples of such affects include a sense of being criticized or scolded, and a sense of being socially isolated or ostracized. Finally, the psychiatric syndrome paranoia is well explained as the hyperactivity of this core cognition. A paranoid person feels beset by "intentions," while the agents may remain poorly specified ("People are trying to hurt me," or "It's like someone is blaming me for something, saying it's all my fault").

A NEURAL CODE

Candidate Brain Structures

We now turn our attention to brain structures and neural processes that support the core cognitive operations sketched above. Evidence from lesions in both humans and nonhuman primates suggests that the processing of social information depends on intact limbic structures, notably, the amygdala, and orbital frontal cortex, with which the amygdala is interconnected (Price, Russchen, & Amaral, 1987). Damasio and Van Hoesen (1983), in a review of clinical syndromes associated with damage to the limbic frontal lobes, noted that patients with orbital frontal lesions classically display a lack of appreciation for social rules. Patient EVR (Eslinger & Damasio, 1985), following damage to orbital and lower mesial frontal lobes, developed an incapacity to make appropriate social judgments in real life situations despite a preserved intellectual ability to solve social problems presented in abstract, verbal form. A number of his difficulties could be explained as arising from failure to accurately assess the character and motivations of other persons. Reminiscent of the social disinhibition associated with orbital frontal lesions is the inappropriateness described in a patient with bilateral congenital calcifications of the amygdala (Tranel & Hyman, 1990). In macaque monkeys, experimental lesions of the amygdala, orbital frontal cortex, and temporal pole have been shown to produce alterations of social behavior including withdrawal, decreased aggression, and failure of maternal behavior (Butter, Snyder, & McDonald, 1970; Steklis & Kling, 1985; Bachevalier, 1991; Kling & Brothers, 1992). It thus appears that, in both humans and macaque monkeys, limbic lesions interrupt pathways that ordinarily produce automatic, correct responses to social stimuli.

In addition to the interconnection with orbital frontal cortex, the amygdala receives a significant portion of its inputs from higher order association cortices of all modalities. As well as projecting back to these cortices, the amygdala sends efferents to the hypothalamus and to brainstem centers controlling heart rate and respiration (Harper, Frysinger, Trelease, et al., 1984; Kapp, Gallagher, Frysinger, et al., 1981). The direct link between polymodal sensory information on the one hand, and autonomic effectors on the other, may account for the phenomena of emotional experience associated with amygdala function (for review of emotional phenomena, see Gloor, 1992). Because of evidence for its role in both social and emotional behavior, we have focused on neural activity in the amygdala in our search for elements of the representations of others' intentions and dispositions.

An Animal Model

In what follows, we present data obtained from studies of awake macaque monkeys observing socially relevant stimuli. Macaques live in complex social groups and use a large array of social signals (Bertrand, 1965; Chevalier-Skolnikoff, 1974; Kaufman & Rosenblum, 1966). While we believe that a macaque theory of other minds differs greatly from that of a human, we may expect macaques to have an understanding of affective display, of basic social interactions occurring between other animals, and perhaps of simple agency. We assume, furthermore, that there is a phylogenetic continuity between macaques and humans in the organization of brain tissue that produces percepts of others' meaningful actions. The existence in an animal model of neural activity that encodes features such as the purpose or emotional state of another suggests there is a definable neural substrate for the proposed cognitive module. Below, we offer evidence for such neural activity in monkeys.

Interpreting Single Neuron Data

It is sometimes mistakenly believed that saying a neural structure plays an important role in processing social information is equivalent to saying it is dedicated to processing only that domain of environmental stimuli. In fact, a number of studies have shown that "face" cells in temporal cortex are selective for, but not dedicated only to, faces, in that they may respond weakly to other visual stimuli as well (Bruce, Desimone, & Gross, 1981; Perrett, Rolls, & Caan, 1982; Desimone, Albright, Gross, & Bruce, 1984; Baylis, Rolls, & Leonard, 1985; Leonard, Rolls, Wilson, & Baylis, 1985). In discussing the neural data below, we will not be interested in showing to what degree certain neurons are selective for social as opposed to inanimate or abstract stimuli. Instead, we will assume a priori that the capacity for social perception in primates has been subjected to considerable selection

pressure, such that there exist neural ensembles that are very good at performing social evaluations. Whether they also participate in other perceptual tasks is not our focus here.

(It may be that in primates, cognition evolved for social tasks has formed the scaffolding for the subsequent development of logically analogous processing of nonsocial stimuli. Deficits in processing certain classes of nonsocial stimuli, such as those observed in some prosopagnosics (Eccoff, Freeman, & Cave, 1991), would be expected by this account, which does not, however, imply that all nonsocial objects are equivalent, cognitively, to social ones. The existence in monkeys of the ability to perform certain logical operations in the social domain but not in nonsocial ones (Cheney & Seyfarth, 1990) supports such an evolutionary primacy of social cognition in primates.)

It is necessary to specify a general framework in which to place single-neuron activity, since we believe encoding takes place at the ensemble level. Single neurons may participate in an ensemble in a narrowly tuned manner, such that they respond strongly to a particular combination of features, and weakly or not at all to any one of those features. Such a neuron would have the response profile associated with a "grandmother cell," but this would arise by virtue of its sensitive participation in a particular type of ensemble. The same ensemble may also contain cells of a different class, namely, cells that respond to a number of different aspects of the environment. The latter would be considered to be broadly tuned with respect to dimensions of the social environment. Combined with the activity of neurons possessing different discriminative profiles, such broadly tuned neurons could contribute to a quite specific representation at the ensemble level. While we expect to find both narrowly and broadly tuned units using social stimuli as probes, only the former may be cited as evidence for the existence of an ensemble coding for a particular high-level feature of the environment. That is, a cell that appears to be highly specific in its stimulus selectivity is evidence for the activity of an ensemble with at least that level of specificity.

To accept a neuron as participating in the encoding of a high-level feature, we expect it to show a response across a range of pictures with varying visual features whose implicit higher level content remains invariant, compared to pictures with the same or similar features but a different higher level content. Alternatively, when the lower level features of a stimulus are recombined so as to generate a new higher level meaning, a cell's activity should change correspondingly, in order for it to be considered as encoding at the higher level.

Let us now ask what feature-responsive characteristics we would expect in neurons that encode representations of others' mental states. A classification of socially responsive cells into viewer-centered, object-centered, and goal-centered categories has been put forward by Perrett

and his colleagues (Perrett, Harries, Bevan, Thomas, Benson, Mistlin, Chitty, Hietanen, & Ortega, 1989; Perrett, Harries, Benson, Chitty, & Mistlin, 1990b; Perrett, Harries, Mistlin, & Chitty, 1990a) as a framework for observations made on neural activity in the superior temporal sulcus and inferotemporal cortex. Of particular interest for the present proposal are their data on neurons in area TEa, which are responsive to hand-object interactions (Perrett, Mistlin, Harries, & Chitty, 1989). (An understanding of hand-object interactions by infants has been demonstrated by Leslie, 1984.) Such neurons may fire in response to views of a hand plucking or tearing an object, for example, but cease to fire when the action is carried out in a slightly different plane from the position of the object, such that contact with the object is not made. Some of these cells are selective for particular actions on objects. Since the neurons Perrett et al. describe appear to respond to purposeful interactions with objects, they can be considered components of a system encoding another's intention.

Another example of a goal-centered neuron, described by Perrett, is shown in Figure 1. The cell's activity is best characterized as responsive to the experimenter's motion toward the outside door. It is an alternative possibility that the cell is encoding the social significance of the movement for the animal—in this case, the probability of being left alone. The latter may be the core computation underlying a representation of the experimenter's purposeful action.

We propose that in a brain region that processes social stimuli, one should find neurons in the following general response categories: (1) neurons selective for low-level visual features of conspecifics, such as limb movements or body parts; (2) neurons coding at an intermediate level, for features such as direction of movement or category of action; and (3) neurons selective for high-level features such as expressive content, goal-directed activity, or category of social interaction. The degree of selectivity, or breadth of tuning, of a neuron at any of these levels might vary.

RESULTS

Low- and Intermediate-Level Encoding

We have previously (Brothers, Ring, & Kling, 1990) described a neuron, located in the medial amygdala of an adult stump-tail macaque, that fired in response to views of swinging limb movements typical of locomotion. The response of this neuron to pictures of locomoting vs. stationary animals is shown in Figure 2 (for a description of experimental design and controls, see section on Methods below). As reported previously, the stimuli also included a sequence of an animal trotting, in which locomotion was obvious due to the movement of the background and the alternating motion of the animal's shoulders, but the limbs were out of the camera's view. The cell responded only weakly to this stimulus, com-

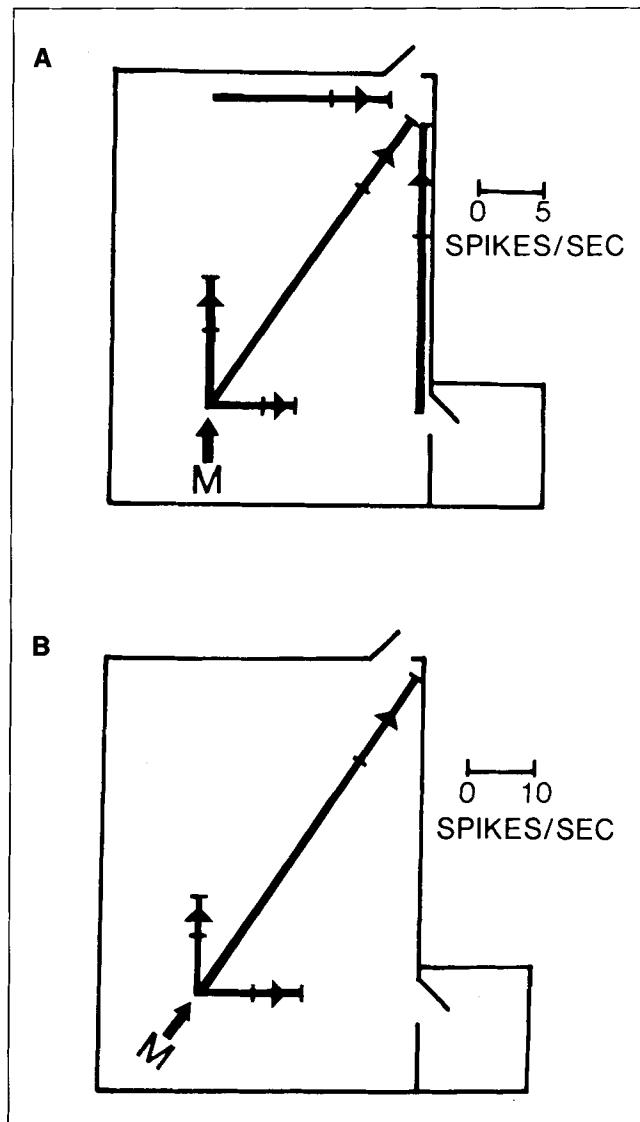


Figure 1. Diagram of cell response from laboratory of D. I. Perrett (diagram and following description reproduced by permission). (A) Neuronal response to the sight of an actor walking in different directions in the laboratory. The length of each line represents the magnitude of neuronal response (mean \pm 1 SE for 5 trials) for one direction of movement. The external boundary of the figure gives the plan view of the laboratory with an indication of the position of the external door and an internal door to a small preparation room. The direction of walking is given by the filled arrowheads and the starting position by the origin of the lines. The vantage point and orientation of the monkey (M) are given by the short arrow at the base of the figure. From a starting position close to the monkey, movement toward the external door produces a significantly larger response ($p < .05$ each comparison) than the other two directions of movement [$F(2,8) = 16.6, p < .01$]. (B) The same conventions as in A, but the monkey's orientation (short arrow) in the room was modified. With the monkey's vantage point changed the cell still gave a significantly larger response ($p < .01$ each comparison) to movement toward the external door than to other directions [$F(2,8) = 19.8, p < .01$] (see Perrett, Harries, Benson, Chitty, & Mistlin, 1990).

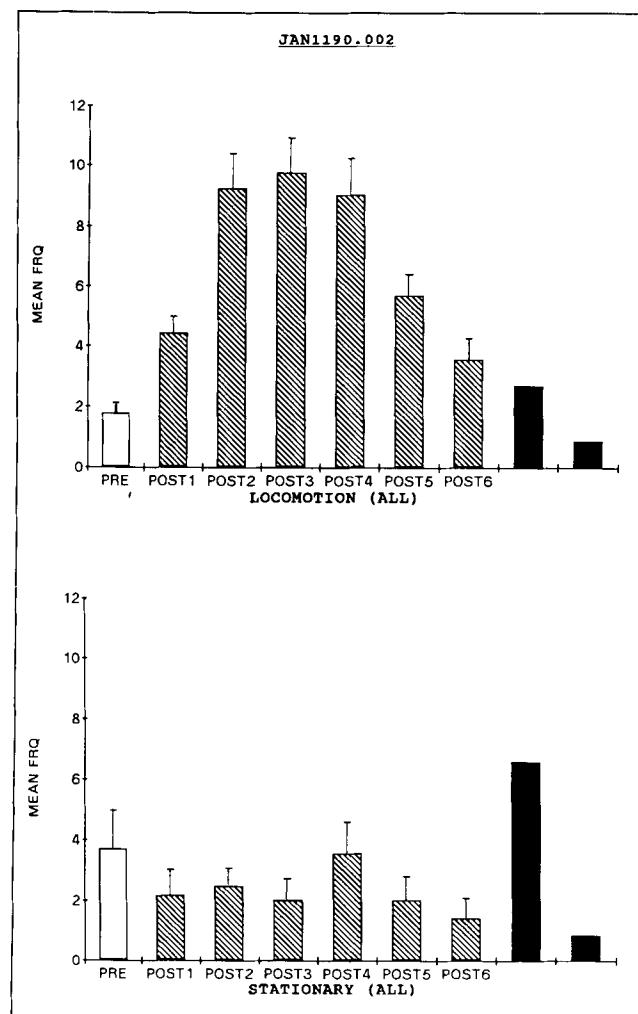


Figure 2. Response of cell Jan11.002, located in the medial amygdala, to all segments depicting locomotion ($n = 43$) and all segments depicting stationary animals ($n = 13$). The latter category included many segments in which there was motion of the head; thus, the two categories were distinguished by presence or absence of limb movement. The average firing rate prior to stimulus onset is shown as "Pre." Post1 is the 500-msec epoch beginning at stimulus onset. Post2-6 are subsequent 500-msec epochs. Stimulus offset occurs during Post5. Black bars at right show frequency needed in order to achieve significant excitation or inhibition during stimulus presentation at $p < .005$. The sight of locomotion produced significant excitation in this cell; stationary views of animals produced no significant change in firing.

pared to those in which legs were well visualized, a finding similar to informal observations reported by Bruce, Desimone, and Gross (1981) on neurons in the superior temporal sulcus, in which screening the lower part of a walking person eliminated activity otherwise elicited by walking movements.

While this cell responded to locomotion either in a forward or reverse direction, it was more responsive to forward ("feet follow the nose") than to reverse sequences. In all five cases where locomotion in various directions on the horizontal plane (that is, walking or

trotting on the ground) were shown in both normal and reverse directions, the excitation produced by the reverse sequences was less, ranging from 28 to 58% of the rate for the corresponding forward sequence. One instance of vertical motion, that is, climbing up, elicited as strong a response as horizontal motion: like the locomotion pairs in the horizontal plane its reverse counterpart (climbing down) produced a diminished firing rate (36%) compared to the forward motion. Whereas walking backward is somewhat unusual compared with walking forward, and trotting backward definitely so, climbing down and climbing up are equally probable events in the real world. The relative decrement in firing rate produced in this cell when the feet did not "follow the nose" is therefore most likely due to a bias on the cell's part in favor of forward motion, rather than to a bias favoring conventional over unconventional types of locomotion. Thus, although this cell codes for a relatively low level feature, limb movement in locomotion, its activity is affected by a higher level feature, namely, forward-goingness.

Recently we have recorded from a cell that responded with a markedly different pattern to a sequence of an animal climbing up compared to the same frames played in reverse (Figures 3A and B). In contrast to the cell described above, which invariably responded with significant excitation to reverse locomotion, although with rates lower than those to forward movement, this cell responded with excitation to one direction of movement, and inhibition to the other. The stimulus sequence shows apparent motion, but almost no actual translation with respect to the observer, since the animal's body is kept centered in the camera's view throughout most of the segment. Thus, "up" and "down" are object-centered percepts that have to be derived from the pictures shown. The reverse (down) segment is very slightly slower than the forward segment (up); in all other respects it is identical except for the order in which the frames are shown. Note that the stimulus-long pattern of excitation and inhibition is substantially different in the two cases. This cell did not respond to three different segments depicting forward locomotion on the ground; therefore, it does not appear to be selective for the general condition "feet following the nose." If we except possible effects of the slight difference in speed, it would appear that this cell participates in encoding the percepts "animal going down" and "animal going up." An alternative and possible interpretation is that the cell encodes different rates of movement with different firing patterns.

High-Level Encoding

We have also found neurons that appear to code for high-level aspects of others' activities. Previously we described a cell that responded to two different sequences, in each of which a pair of animals circled and rotated about each other, but in different directions and ori-

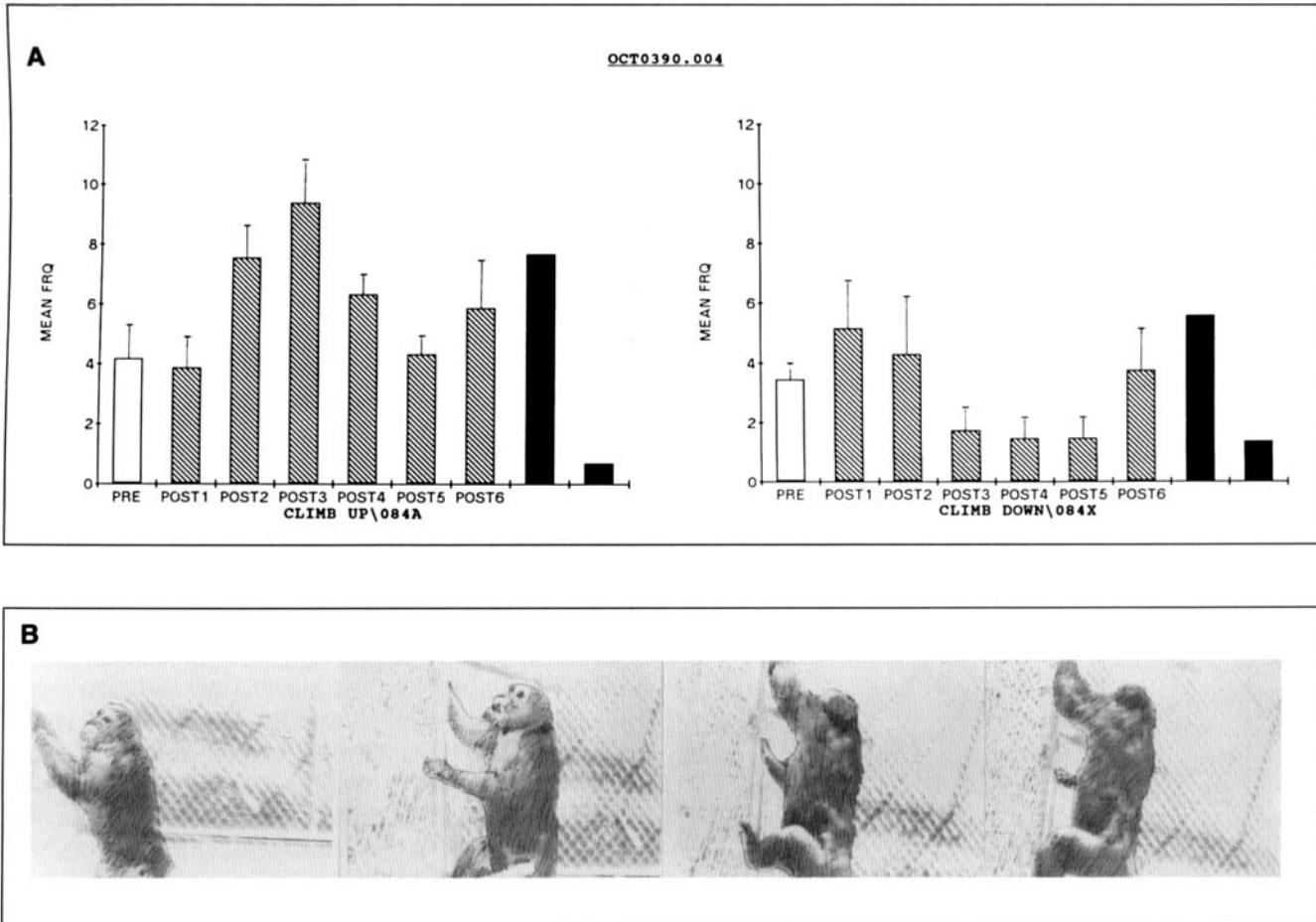


Figure 3. (A) Response of cell Oct0390.004, located in the region of the amygdala, to two segments. The average firing rate prior to stimulus onset is shown as "Pre." Post1 is the 500-msec epoch beginning at stimulus onset. Post2–6 are subsequent 500-msec epochs. For "Climb Up," stimulus offset occurs during Post5; for "Climb Down" offset occurs during Post6. Black bars at right show frequency needed in order to achieve significant excitation or inhibition during stimulus presentation at $p < .005$. Average stimulus-long firing rates for the two stimulus conditions was significantly different at $p < .01$. (B) Sample frames taken from Post1–4 near the beginning of each epoch are shown for "Climb Up." Note that the animal's body is centered in the viewing frame during most of the stimulus, thus, there is almost no spatial translation with respect to the viewer. "Climb Down" consisted of exactly the same frames, but shown in reverse order (that is, as if the strip were read from right to left). The pattern of cell firing was markedly different to these two sequences, even though all visual features except perceived direction, and to a small degree speed of movement (reverse being slightly slower), were common to both sequences. See text for additional discussion.

tations in the two segments. The content in both cases was a bid by one to approach the other for a desired piece of fruit. Control sequences of one of the subjects eating the fruit by herself, of each of the individuals, or of other monkeys moving about in the same manner by themselves, and of pairs of animals sitting together, were ineffective in driving the cell. We concluded that this cell responds to the basic interaction "Approach." A tendency to perceive certain dyadic interactions as depicting social intentions has been described in children by Dasser, Ulbaek, and Premack (1989): the activity of this neuron may reflect the presence of similar cognition in macaques.

Here we describe the response profile of a neuron recorded in a current experiment that is also being carried out in the region of the amygdala. As illustrated in

Figure 4, the cell responded to several categories of faces and heads. The segments that are grouped as "Look and Pause," "Face-Eye Signals," and "Face Movements" were pictures of macaques in natural settings, seen predominantly from the shoulders up. The group of segments that elicited the strongest response was that which included staring, usually in the form of pauses punctuating ongoing head or face movement ("Look and Pause"). A stare is a mild form of facial threat. This category contained six different segments, each presented multiple times, for a total of 28 presentations.

Also effective in eliciting an excitatory response were faces with eyebrow movement, a signal indicative of aggressive intent in macaques. This set, labeled "Face-Eye Signals," contained four different segments presented a total of 17 times.

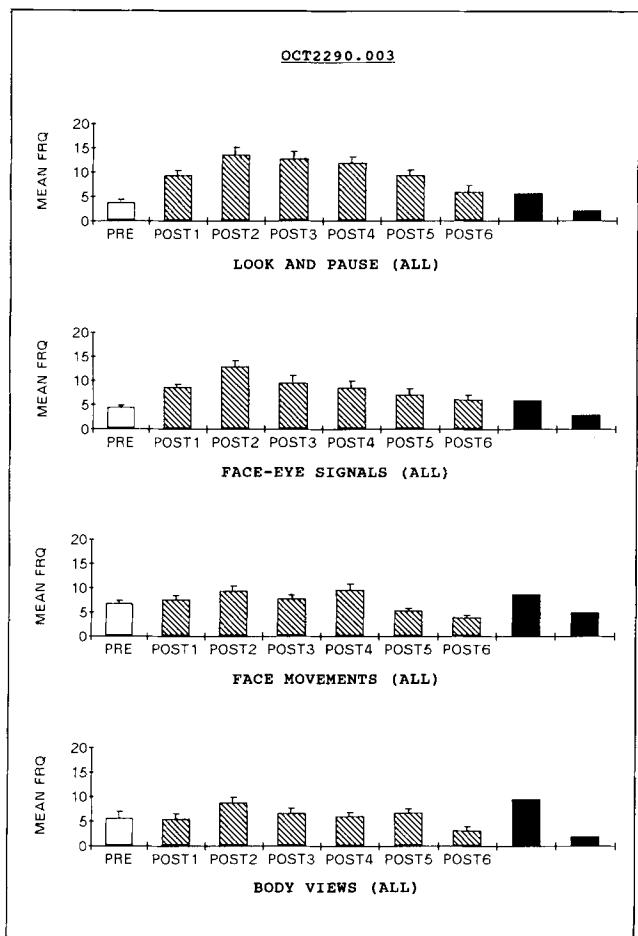


Figure 4. Response to Cell Oct2290.003 to four categories of stimuli (see text for full description). The average firing rate prior to stimulus onset is shown as “Pre.” Post1 is the 500-msec epoch beginning at stimulus onset. Post2–6 are subsequent 500-msec epochs. Stimulus offset occurs during Post5. Black bars at right show frequency needed in order to achieve significant excitation or inhibition during stimulus presentation at $p < .005$. Faces with threatening or agonistic displays (top two sets) were more effective in driving the cell than were similar views of faces performing other movements, or views of bodies. The profile of activity suggests the cell is responsive to the agonistic component of facial movements.

In contrast, as Figure 4 shows, heads that moved and looked about, and faces with nonagonistic facial movements such as chewing or calling, failed to produce significant excitation. Such movements were also present in the “Look and Pause” category; however, in the latter category the movements were punctuated by stares while the “Face Movements” category did not contain stares. “Face Movements” contained seven different segments, shown a total of 39 times. Various views of moving bodies were also ineffective in driving the neuron (6 segments; 24 presentations). The profile of the cell’s response suggests it is selective for the agonistic component of facial movements.

That the cell’s response was merely a reflection of arousal elicited in the animal subject is unlikely, since

many of the segments, particularly those of moving bodies, are of intrinsic interest to the subject as evidenced by her intent visual fixation on them; however, these did not produce increased firing activity. Furthermore, juice rewards administered occasionally during the session failed to produce increased firing in this neuron.

DISCUSSION

We have put forward an outline for human cognitive processes involved in constructing representations of persons from sensory inputs such as faces. We suggested that, side-by-side with a recently evolved cognitive capacity for representing minds as independent loci of beliefs, there is a second, complementary aspect of representation of minds. This latter aspect, which necessarily possesses valence, has its phylogenetic origins first in simple responses to affective displays and, more recently, in the assignment of social traits within a cooperative social order. Evolutionarily speaking, there should be a premium on the accurate assignment of qualities such as “helpful,” “generous,” “selfish,” and “untrustworthy” to other individuals. The experiment conducted by Damasio and co-workers shows that representations of this kind are robust even in a severely amnesic patient.

Single neuron data obtained in monkeys observing the actions of other monkeys were presented in support of a neural basis for the macaque version of representation of minds. These data revealed neural selectivity for intermediate-level features of the behavior of others, such as object-centered direction of movement, and for high-level features such as “aggressive tendency” and “approach.”

In contrast to research on visual processing of inanimate features and objects, there is a dearth of models for how high-level representations of a social nature are formed. Studies of biological motion and face perception at the neural level have sometimes invoked a “specialized neural system,” without further elaboration. Notable exceptions are accounts offered by Perrett (Perrett et al., 1989, 1990a, b, c; Harries & Perrett, 1991) and Leslie and Johnson (1992). There are several obstacles to the construction of detailed cognitive models of representation of mind. While rigorously obtained data from visual psychophysics have been essential in guiding the development of neural models for processing visual features of objects, the perceptual data necessary for guiding neural models of primate social cognition are both disparately scattered across several fields, and methodologically uneven. The chief difficulty for a realistic neural model embracing human social cognition, however, is the infamous plasticity of social judgments and responses based on cultural learning and social experience (Dweck & Lloyd, 1990). Accounting for this very plasticity should be required of future candidate neural models of social cognition.

METHODS

The methods used in these experiments have been described in detail elsewhere (Brothers et al., 1990). Standard techniques for isolating and recording from single neurons in awake, behaving macaque monkeys, and for marking and reconstructing the locations of responsive cells, were used. We will describe here the stimulus set and methods of data analysis.

To create the stimulus set, we videotaped a group of outdoor-housed bonnet (*M. radiata*) and stump-tail macaques (*M. arctoides*) extensively. We attempted to obtain exemplars of all possible body views, all directions of movement and gait, close-ups of body parts (such as fur, hands, eyes, ears, feet), and many instances of typical activities such as eating, playing, copulating, grooming, and sleeping. A large variety of affective facial and postural displays were also taped. Editing yielded 15 min of tape for each of the two species (50,400 frames total). The edited tapes were transferred to laser disks, allowing computer-controlled presentation of arbitrarily defined moving segments. Animal subjects viewing these segments display responses indicating perception of content, e.g., fear grimace in response to pictured threat stare or dominant approach.

Files composed of the "addresses" (start frame) and special instructions regarding audio and speed of stimulus segments are stored on disk. Each segment is approximately 2 sec in duration. A few examples of the numerous files containing such sets of segment addresses are "Juveniles," "Yawns," "Blinks," "Rear Ends," and "Eating." The definition of each segment and each file of segments is flexible. Software based on laser disk driver codes (Allen Communications) has been developed to permit the rapid redefinition of both segments and files during a recording session by changing the instructions for accessing the images on the laser disks. Frame number records for new stimulus events, together with any new files, are catalogued and stored as they are created. Thus, visual segments may be shown with and without accompanying vocalization, and they may be shown in reverse, slow-motion, or as a freeze-frame. Likewise, files containing sets of these segments may be created, or repeatedly altered, during recording sessions.

Data acquisition is carried out as follows. Isolated units are observed for responses to visual, auditory, and tactile input. Unit activity is collected every 2 msec for 500 msec prior to stimulus onset, throughout the stimulus, and for 1 sec following stimulus offset. Counts are assigned to 10 msec bins and saved on computer disk. On-line graphics (customized ASYST, Integrated Scientific Resources) consist of the peristimulus histogram for each stimulus event, the cumulative histogram for the cell's responses to all identical events, and a display of eye position and pupil size. Eye information is obtained using a video imaging system originally developed by Barbur (1987). A raster pattern for unit activity is printed for each stim-

ulus presentation, creating a record of the order in which individual stimulus events were shown. To test for responses to specific visual stimuli, a screening file ("Chinese menu") composed of each of the major classes of stimulus segment is presented to the subject. More narrowly defined files are then selected and their contents presented as dictated by the emerging profile of a cell's response. All stimuli are presented in pseudorandom order. Units are considered responsive only if no habituation occurs over multiple stimulus presentations, the minimum being six.

Since most of the stimuli are visually complex, consisting of various textures, shapes, movements, amounts of contrast, and so forth, the critical task is to select and present necessary controls once a response is identified. For example, during the presentation of a screening set, we detected responsiveness to a segment of an animal "walking" upside down by gripping the fencing material that formed the roof of her enclosure. We then switched to the "Upside Down" file, which revealed that static upside down views of animals in the pen did not drive the cell. Views of animals seen from other unusual perspectives were also ineffective, as were views of the same individual in other activities. By proceeding in this fashion, through files such as "Climbing," "Walking," "Running," "Walking-Reverse," and "Swaying," we were able to identify the stimulus sets that maximally drove the cell, namely, locomotion involving alternating limb movements as in walking, trotting, or climbing as described above. We were also able to eliminate from consideration many of the features that were present in the original effective stimulus, since these were common to ineffective segments. Effective segments are shown repeatedly, interspersed with other segments, to ensure that the response is maintained over multiple presentations.

The composition of the set of "locomotion" pictures, which were taped under a variety of light conditions and from different perspectives and distances, precludes interpreting the cell's response as due to a common incidental visual feature such as texture or contrast boundary. Presenting an array of complex visual sequences that are similar in behavioral content, but that differ radically at the level of simple visual elements, allows us to discriminate between responses to incidental visual features and responses to higher level content. An alternative procedure for evaluating a unit's response is the systematic alteration of temporal features of an effective segment, as in the forward and reverse presentations described above. This is a converse kind of control to that just described, in that all visual features are held constant while the temporal sequence alone is changed—thus changing the meaning of the depicted action.

Statistical analysis is performed as follows. To ascertain whether a response to a given stimulus is significant, cell firing counts are pooled into 500 msec bins. The first bin is the 500 msec prior to stimulus presentation; the

second bin begins 150 msec after stimulus onset and spans the next 500 msec. Succeeding bins span sequential 500-msec intervals. Bin counts are combined across all presentations of a given stimulus to a cell, yielding average firing rates, which are converted to counts/sec. We measure the level of activity of the cell in the 500-msec period prior to stimulus onset and compute a mean and a 99.5% confidence interval about that mean using a two-tailed *z*-statistic. A significant change in firing rate is considered to have occurred if the firing frequency lies outside the confidence interval in any of the four bins following stimulus onset. A 99.5% criterion was selected to allow for the fact that four response bins are tested. Figure 2 illustrates such an analysis.

A second form of analysis is used to compare responses of a neuron to different classes of stimuli. All stimuli that have been presented to a cell may be grouped into several categories (e.g., rear ends, faces with threats, faces with neutral expressions, faces vocalizing, etc.). Total counts for the 2 sec after stimulus onset are converted to counts/sec for each individual response and pooled for each group. When analysis of variance comparing within- and between-group means is significant at the .05 confidence level, the Duncan multiple range test for nearly equal *ns* is carried out (Bruning & Kintz, 1968). The activity of cells depicted in Figure 4 was analyzed using this method. Alternatively, if stimuli are divided into only two classes (e.g., monkeys vs. humans) a *t* test is used to compare mean firing rates, for the 2 sec of stimulus duration, between the two groups.

Acknowledgments

This work is supported by the Department of Veterans Affairs. We thank A. Leslie for helpful comments and discussions, D. Perrett for permission to reproduce Figure 1, and A. Damasio, A. Fridlund, and J. Rubin for comments on an earlier version of this paper.

Reprint requests should be sent to Leslie Brothers, UCLA-Sepulveda VA Medical Center, Office of Research-151, 16111 Plummer Street, Sepulveda, CA 91343.

REFERENCES

- Amster, H. (1964). Semantic satiation and generation: Learning? Adaptation? *Psychological Bulletin*, 62, 273-286.
- Ardila, A., & Rosseli, M. (1988). Temporal lobe involvement in Capgras syndrome. *International Journal of Neuroscience*, 43, 219-224.
- Astington, J., Harris, P., & Olson, D. (Eds.). (1988). *Developing theories of mind*. Cambridge: Cambridge University Press.
- Axelrod, R., & Hamilton, W. D. (1981). The evolution of cooperation. *Science*, 211, 1390-1396.
- Bachevalier, J. (1991). An animal model for childhood autism: Memory loss and socioemotional disturbances following neonatal damage to the limbic system in monkeys. In C. A. Tamminga & S. C. Schulz (Eds.), *Advances in neuropsychiatry and psychopharmacology*, Vol. 1, *Schizophrenia research* (pp. 129-140). New York: Raven Press.
- Barbur, J. L., Thomson, W. D., & Forsyth, P. M. (1987). A new system for the simultaneous measurement of pupil size and two-dimensional eye movements. *Clinical Vision Sciences*, 2, 131-142.
- Baylis, G., Rolls, E. T., & Leonard, C. M. (1985). Selectivity between faces in the responses of a population of neurons in the cortex in the superior temporal sulcus of the monkey. *Brain Research*, 342, 91-102.
- Bertrand, M. (1969). The behavioral repertoire of the stump-tail macaque. *Bibliotheca Primateologica*, no. 11.
- Bouckoms, A., Martuza, R., & Henderson M. (1986). Capgras syndrome with subarachnoid hemorrhage. *Journal of Nervous and Mental Disorders*, 174, 484-488.
- Brothers, L. (1990). The social brain: A project for integrating primate behavior and neurophysiology in a new domain. *Concepts in Neuroscience*, 1, 27-51.
- Brothers, L., Ring, B., & Kling, A. (1990). Response of neurons in the macaque amygdala to complex social stimuli. *Behavioural Brain Research*, 41, 199-213.
- Bruce, C., Desimone, R., & Gross, C. G. (1981). Visual properties of neurons in a polysensory area in superior temporal sulcus of the macaque. *Journal of Neurophysiology*, 46, 369-384.
- Bruce, V. (1988). *Recognising faces*. East Sussex, U.K.: Lawrence Erlbaum.
- Bruning, J. L., & Kintz, B. L. (1968). *Computational handbook of statistics*. Glenview IL: Scott Foresman.
- Butter, C. M., Snyder, D. R., & McDonald, J. A. (1970). Effects of orbital frontal lesions on aversive and aggressive behaviors in rhesus monkeys. *Journal of Comparative and Physiological Psychology*, 72, 132-144.
- Carrithers, M. (1991). Narrativity: Mindreading and making societies. In A. Whiten (Ed.), *Natural theories of mind: Evolution, development and simulation of everyday mind-reading* (pp. 305-317). Oxford: Blackwell.
- Cheney, D. L., & Seyfarth, R. M. (1990). *How monkeys see the world: Inside the mind of another species*. Chicago: University of Chicago Press.
- Cheney, D. L., Seyfarth, R., & Smuts, B. (1986). Social relationships and social cognition in nonhuman primates. *Science*, 234, 1361-1366.
- Chevalier-Skolnikoff, S. (1974). The ontogeny of communication in the stump-tail macaque (*M. arctoides*). In *Contributions to primatology* (Vol. 2, pp. 1-174). Basel: S. Karger.
- Cosmides, L. (1989). The logic of social exchange: Has natural selection shaped how humans reason? Studies with the Wason selection task. *Cognition*, 31, 187-276.
- Damasio, A., Damasio, H., & Van Hoesen, G. (1982). Prosopagnosia: Anatomic basis and behavioral mechanisms. *Neurology*, 32, 331-341.
- Damasio, A., Tranel, D., & Damasio, H. (1989). Amnesia caused by herpes simplex encephalitis, infarctions in basal forebrain, Alzheimer's disease and anoxia/ischemia. In F. Boller & J. Grafman (Eds.), *Handbook of neuropsychology* (Vol. 3). Amsterdam: Elsevier.
- Damasio, A., & Van Hoesen, G. (1983). Emotional disturbances associated with focal lesions of the limbic frontal lobe. In K. Heilman & P. Satz (Eds.), *Neuropsychology of human emotion* (pp. 85-110). New York: Guilford Press.
- Dasser, V., Ulbaek, I., & Premack, D. (1989). The perception of intention. *Science*, 243, 365-367.
- Dennett, D. C. (1987). *The intentional stance*. Cambridge, MA: MIT Press.
- Desimone, R., Albright, T. D., Gross, C. G., & Bruce, C. (1984). Stimulus-selective properties of inferior temporal neurons in the macaque. *Journal of Neuroscience*, 4, 2051-2062.
- Duveen, G., & Lloyd, B. (Eds.). (1990). *Social representations and the development of knowledge*. Cambridge: Cambridge University Press.
- Eslinger, P. J., & Damasio, A. R. (1985). Severe disturbance

- of higher cognition after bilateral frontal lobe ablations: Patient EVR. *Neurology*, 35, 1731–1741.
- Etcoff, N. L., Freeman R., & Cave, K. R. (1991). Can we lose memories of faces? Content specificity and awareness in a prosopagnosic. *Journal of Cognitive Neuroscience*, 3, 25–41.
- Fishbain, D. A., & Rosomoff, H. (1986–7). Capgras syndrome associated with metrizamide myelography. *International Journal of Psychiatry and Medicine*, 16, 131–136.
- Fodor, J. A. (1983). *The modularity of mind: An essay on faculty psychology*. Cambridge, MA: MIT Press.
- Gardner, H. (1983). *Frames of mind: The theory of multiple intelligences*. New York: Basic Books.
- Gloor, P. (1986). Role of the human limbic system in perception, memory, and affect: Lessons from temporal lobe epilepsy. In B. K. Doane & K. E. Livingston (Eds.), *The limbic system: Functional organization and clinical disorders* (pp. 159–169). New York: Raven Press.
- Gloor, P. (1992). Role of the amygdala in temporal lobe epilepsy (pp. 505–538). In J. Aggleton, (Ed.), *The amygdala*. New York: Wiley, in press.
- Harper, R. M., Frysinger, R. C., Trelease, R. B., Marks, J. D. (1984). State-dependent alteration of respiratory cycle timing by stimulation of the central nucleus of the amygdala. *Brain Research*, 306, 1–8.
- Harré, R. (1984). *Personal being: A theory for individual psychology*. Cambridge, MA: Harvard University Press.
- Harries, M. H., & Perrett, D. I. (1991). Visual processing of faces in temporal cortex: Physiological evidence for a modular organization and possible anatomical correlates. *Journal of Cognitive Neuroscience*, 3, 9–24.
- Huizinga, J. (1949). *The waning of the middle ages* (pp. 52–53). New York: St. Martin's Press.
- Jackendoff, R. (1987). *Consciousness and the computational mind*. Cambridge, MA: MIT Press.
- Jackendoff, R. Is there a faculty of social cognition? In R. Jackendoff (Ed.), *Languages of the mind*. Cambridge, MA: MIT Press, in press.
- Joseph, A. B. (1985). Bitemporal atrophy in a patient with Freigoli syndrome, syndrome of intermetamorphosis, and re-duplicative paramnesia. *American Journal of Psychiatry*, 142, 146–147.
- Kapp, B. S., Gallagher, M., Frysinger, R. C., Applegate, C. D. (1981). The amygdala, emotion, and cardiovascular conditioning. In Y. Ben-Ari (Ed.), *The amygdaloid complex* (pp. 355–366). New York: Elsevier.
- Kaufman, I. C., & Rosenblum, L. A. (1966). A behavioral taxonomy for *Macaca nemestrina* and *Macaca radiata*: Based on longitudinal observation of family groups in the laboratory. *Primates*, 7(2), 205–244.
- Kling, A., & Brothers, L. (1992). The amygdala and social behavior (pp. 353–377). In J. Aggleton (Ed.), *The amygdala*. New York: Wiley, in press.
- Leonard, C. M., Rolls, E. T., Wilson, F. A. W., & Baylis, G. C. (1985). Neurons in the amygdala of the monkey with responses selective for faces. *Behavioural Brain Research*, 15, 159–176.
- Leslie, A. (1984). Infant perception of a manual pick-up event. *British Journal of Developmental Psychology*, 2, 19–32.
- Leslie, A. (1987). Pretense and representation in infancy: The origins of "theory of mind." *Psychological Review*, 94, 412–426.
- Leslie, A. (1992). In preparation.
- Leslie A., & Johnson, M. (1992). In preparation.
- Mead, G. H. (1934). *Mind, self and society: From the stand-point of a social behaviorist*. Chicago: University of Chicago Press.
- Patterson, K. E., & Baddeley, A. D. (1977). When face recognition fails. *Journal of Experimental Psychology*, 3, 406–417.
- Perrett, D. I., Harries, M. H., Bevan, R., Thomas, S., Benson, P. J., Mistlin, A. J., Chitty, A. J., Hietanen, J. K., & Ortega, J. E. (1989). Frameworks of analysis for the neural representation of animate objects and actions. *Journal of Experimental Biology*, 146, 87–113.
- Perrett, D. I., Harries, M. H., Mistlin, A. J., and Chitty, A. J., (1990a). Three stages in the classification of body movements by visual neurones. In H. B. Barlow, C. Blakemore, & M. Weston-Smith (Eds.), *Images and understanding* (pp. 94–107, 377–378). London: Cambridge University Press.
- Perrett, D. I., Harries, M. H., Benson, P. J., Chitty, A. J., & Mistlin, A. J. (1990b). Retrieval of structure from rigid and biological motion: An analysis of the visual responses of neurones in the macaque temporal cortex. In T. Troscianko & A. Blake (Eds.), *AI and the eye* (pp. 181–200). Chichester: Wiley.
- Perrett, D. I., Mistlin, A. J., Harries, M. H., & Chitty, A. J. (1989). Understanding the visual appearance and consequence of hand actions. In M. A. Goodale (Ed.), *Vision and action: The control of grasping* (pp. 163–180). Norwood, NJ: Ablex.
- Perrett, D. I., Rolls, E. T., & Caan, W. (1982). Visual neurons responsive to faces in the monkey temporal cortex. *Experimental Brain Research*, 47, 329–342.
- Premack, D. (1988). 'Does the chimpanzee have a theory of mind?' revisited. In R. W. Byrne & A. Whiten (Eds.), *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes, and humans*. Oxford: Clarendon Press.
- Premack, D. (1990). The infant's theory of self-propelled objects. *Cognition*, 36, 1–16.
- Premack, D., & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *Behavioral and Brain Sciences*, 1, 515–526.
- Price, J. L., Russchen, F. T., & Amaral, D. G. (1987). The amygdaloid complex. In L. W. Swanson, A. Bjorklund, & T. Hokfelt (Eds.), *Handbook of chemical neuroanatomy*, Vol. 5: 279–388. New York: Elsevier.
- Steklis, H. D., & Kling, A. S. (1985). Neurobiology of affiliative behavior in nonhuman primates. In M. Reite & T. Field (Eds.), *The psychobiology of attachment and separation* (pp. 93–129). New York: Academic Press.
- Tranel, D., & Hyman B. (1990). Neuropsychological correlates of bilateral amygdala damage. *Archives of Neurology*, 47, 349–355.
- von Uexküll, J. (1982). The theory of meaning. *Semiotica*, 42, 1–87.
- Whiten, A., & Byrne, R. W. (1988). Tactical deception in primates. *Behavioral and Brain Sciences*, 11, 233–273.