The Cognitive Neuroscience of Social Behaviour

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1 Introduction: What is social cognitive neuroscience (SCN)?

Nathan J. Emery and
Alexander Easton

Understanding the neural mechanisms of cognitive processes, such as thought, perception, and language, or *cognitive neuroscience*, has been a rapidly progressing discipline for the last two decades. This expansion has been driven primarily by significant advances in the development of technology to observe the activity of the living human brain in action. Revolutionary techniques such as positron emission tomography (PET), event-related potentials (ERP), and functional magnetic resonance imaging (fMRI) have been at the heart of this revolution, and we now know much about how the human brain processes sensory information, plans and controls movement, perceives and produces speech, and experiences emotions.

Although we know infinitely more about the neural basis of human psychology than we did 20 years ago, the problems facing us in the future are immense. We highlight two main problems. First, the questions themselves are huge. For example, visual processing is a relatively minor component in the overall story of how the brain functions to give rise to complex human cognitive processes, but, in itself, vision is a horrendously complicated process involving over 50 cortical areas, and billions of neurons. Therefore, major advances must be made before we can even contemplate solving relatively "simple" processes, such as perception. Second, not all aspects of traditional psychology can be easily combined with the tools of cognitive neuroscience. This second problem applies especially to *social cognitive neuroscience* (SCN).

SCN is the study of the neural mechanisms of social cognition and social interactions in humans and animals, particularly nonhuman primates. It is also concerned with deficits of sociocognitive processes in humans, particularly those which have a dedicated neural basis, such as autism, schizophrenia, sociopathy, and depression. This branch of cognitive neuroscience is directed towards understanding complex aspects of social behaviour, such as mentalizing (understanding another's mental states), empathy, attractiveness, self-awareness, moral reasoning, intentionality, and imitation. As such, it is slightly different from *social neuroscience*, or the study of the neurobiology of social behaviour from a comparative perspective. This branch of neuroscience is concerned with the neurobiology of motivational systems, such as aggression, sexual and parental behaviour, and play. These behaviours appear to be controlled by the interaction of neural and endocrine systems, particularly the amygdala, hypothalamus, brainstem, and basal ganglia, and are largely devoid of cognitive processing. These behaviours are displayed by virtually all vertebrates, from amphibians and reptiles to birds and mammals. In contrast, the topics covered by SCN are restricted to higher-order cognitive processes, which are 1. mainly controlled by association cortical areas, such as the prefrontal cortex, 2. not under the influence of hormones, 3. party to disruption by psychopathological disorders or discrete brain lesions, and 4. found almost predominantly (although not exclusively) in human and nonhuman primates.

Traditional social psychology is inferential or relies on pseudo-natural experimental situations, neither of which lend themselves to the tools of cognitive neuroscience, which requires tightly controlled variables. There are also other problems in applying the techniques of cognitive neuroscience to social psychology. For example, functional imaging studies (which are a common tool of cognitive neuroscientists) are difficult to apply in situations that require interaction between subjects. Such studies are very much in their infancy. Similarly, animal studies which may shed light on the neural basis of social behaviour can be problematic because human social behaviour is extremely complex, very much more so than in any of the animals that might be used in such experiments. Indeed, those animals that most closely resemble humans, the great apes, cannot be used for invasive research. Therefore, SCN has been slow to get started (see below). However, in the last few years, there has been a sudden and dramatic increase in the number of studies in the field, and technological problems are finally not only being addressed, but are also being overcome.

In this introductory chapter, we will attempt to introduce the field of SCN, first from a historical perspective, focusing particularly on the recent development of the field and its specialization within cognitive neuroscience. Then we discuss what we predict might be the major research themes of the future, and finally we address Adolphs' (2003) 10 questions for SCN, putting it into context.

A brief history of SCN

The field of SCN has had a long gestation with two parents—cognitive neuroscience and social psychology. Attempts to understand the neural basis of cognition have a history longer than modern cognitive neuroscience, with their foundation in studies of brain-lesioned patients, such as soldiers sustaining gunshot wounds to the head during battle. However, the development of cognitive neuroscience as an experimental science was dependent on the invention of a new methodology—functional neuroimaging. Developed in the 1980s, these techniques, particularly PET and the subtraction method, provided researchers with the capability of localizing function to specific brain areas. These early studies were crude, largely replicating simple cognitive experiments in the scanner; however, the technology has become more complex, using sophisticated experimental designs to remove noise from the system. The formation of cognitive neuroscience was therefore driven primarily by improvements in technology rather than producing an entirely new theoretical approach.

Within cognitive neuroscience, studies in nonhuman primates were more sophisticated and elegant than those performed in humans. Of particular relevance to SCN was the finding, in the early 1980s, that neurons in the anterior temporal cortex of rhesus monkeys are selectively responsive to biologically important stimuli, such as faces (Bruce, Desimone, & Gross, 1981; Perrett, Rolls, & Caan, 1982). Later studies revealed that different neurons in this region are responsive to facial expressions, facial identity, gaze direction, facial movements, walking, and even intentional actions (for reviews, see Emery & Perrett, 2000; Jellema & Perrett, this volume).

Perhaps the most significant paper in the establishment of SCN as a tangible field of study was "The Social Brain: A Project Integrating Primate Behaviour and Neurophysiology in a New Domain" by Leslie Brothers (1990). This paper introduced the idea that it was possible to investigate the neurobiology of social interaction by integrating studies of neurophysiology, behaviour, and psychopathological disorders which specifically affect social behaviour, such as autism. What was particularly significant about this paper was the focus on a specific neural circuit essential to processing social information, which Brothers called the "social brain". This circuit included the anterior temporal cortex and temporal pole, the nuclei of the amygdala and the orbitofrontal cortex. As we will discover throughout this book, these areas and others connected to them play a central role in social behaviour.

A fundamental process which functions during social interaction is the ability to read another individual's mental states ("theory of mind" [ToM]). This "mind-reading" ability develops in human infants around 3–4 years of age, and is affected strikingly in various psychopathological disorders, such as autism, Asperger's syndrome, and schizophrenia. The first functional neuroimaging studies to address this issue of social problem solving were focused specifically on the neural basis of mental attribution (Baron-Cohen, Ring, Moriarty, Schmitz, Costa, & Ell, 1994; Fletcher, et al., 1995). These two studies found that different parts of the prefrontal cortex were activated during a story-comprehension ToM task. We now know that ToM is a suite of abilities (Emery, this volume) that are likely to be based on the integration of different neural systems (Heberlein & Adolphs, this volume). From the seeds sown by these two neuroimaging studies, similarly complex aspects of social interaction are now being investigated by this technique, such as self-knowledge, moral behaviour, empathy, stereotyping, gender or racial biases, attractiveness, and humour appreciation.

Earlier in this section, we made the claim that perhaps the most significant paper in the history of SCN was that of Brothers (1990). To investigate the claim that SCN has developed primarily in the years since this paper, we searched the PubMed on-line citation reference database (MEDLINE; www.ncbi.nlm.nih.gov/PubMed/) from 1990 to 2003, using the keywords "social" AND "brain". This produced a total of 5645 documents. As many of these papers were either not related to SCN or reported studies in social neurobiology, a more refined search using the keywords "social" AND "cognitive" AND "brain" was performed, producing 1013 documents. The titles and abstracts of the papers in the second search were examined for the following criteria. The papers were either theoretical, review, or experimental. The experimental papers used traditional methods of cognitive neuroscience (neuroimaging, lesion analysis, transcranial magnetic stimulation, and electrophysiology) and reported research performed on humans and nonhuman primates. The theoretical focus of the papers included the neurobiology of social interaction, ToM, imitation, empathy, facial attractiveness, self-awareness, moral cognition, cooperation, deception, humour, and gaze processing. Papers on the processing of emotion, including facial expressions, were not included if they did not focus on the role of social communication. Papers on language and face perception (with respect to visual processing) were not included. Finally, papers on disorders of social cognition were included only if they addressed both the social aspects of the disorder and the neural basis. Additional searches using other related criteria ("social" AND "amygdala"; "social" AND "prefrontal cortex"; "empathy" AND "brain"; "imitation" AND "brain", etc.) were also performed to determine whether any papers had failed to be selected with the search terms of the earlier searches.

We found a total of 312 documents that fulfilled these criteria. These documents were sorted by date, and the totals for each year from 1990 to 2003 are represented in Figure 1.1. As can be seen in Figure 1.1, throughout the 1990s, research in SCN was slowly increasing; however, there was an explosion of research at the beginning of the twenty-first century.

There are many possible explanations for this explosion of interest in the neural basis of social interaction. We make three suggestions. First, mental health has become a research priority for funding councils and government agencies. This increase in funding has grown steadily across the 1990s, the so-called Decade of the Brain. Second, cognitive neuroscience has become mainstream, using sophisticated methods for observing the brain in action, and techniques for extracting the huge amounts of information produced. Third, cognitive neuroscientists and social psychologists have started talking to one another, and they are now collaborating. This final point is crucial. For SCN to work, it is vital that there is collaboration between cognitive scientists (such as linguists, computer scientists, philosophers, and cognitive psychologists), neuroscientists, ethologists, and social psychologists. The requisite skills for the successful completion of projects in this area can be achieved only by a strong interdisciplinary approach.

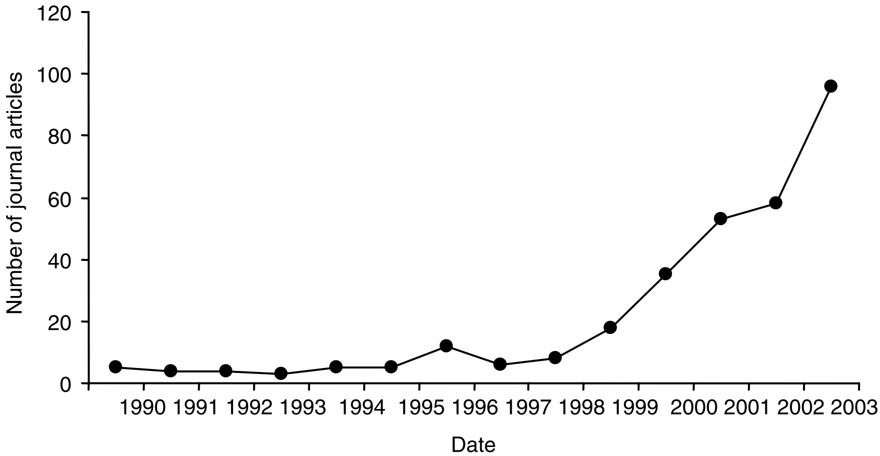

Figure 1.1 Number of journal articles directly related to social cognitive neuroscience (SCN) published every year between 1990 and 2003. Results were produced by an on-line PubMed (MEDLINE) and PsychInfo search, initially using the search criteria "social" AND "brain", and then "social" AND "cognitive" AND "brain". The titles and abstracts were studied to determine whether the papers were relevant to SCN. Other more refined searches were then made, using more specific search criteria, such as "empathy", "theory of mind", "self-awareness", "imitation", etc. There has been a steady increase in the number of papers published, with a dramatic increase after 2000.

What are the methods of SCN?

Although SCN was founded on work performed in animals, particularly nonhuman primates, is there still a place for this type of research? As will be seen in Chapters 2–5, animal studies remain vitally important to the neurobiology of social interaction. We see three main reasons why animal research is still essential. First, functional neuroimaging technology, although greatly advanced in the last 10 years, is still limited in how it can be applied to situations in which two or more protagonists are physically interacting. At present, our investigations are based on how individuals (constrained within a scanner or attached to electrodes) respond to static or moving video images of faces, hands, and bodies, and on questionnaires and self-report. Neuropsychological studies in human patients are equally constrained by the presentation of "simple" social stimuli, rather than involvement in real-life social scenarios. There are fewer methodological constraints with nonhuman animals. Animals can be observed during social interactions, or socially relevant cognitive tests can be presented after or during invasive manipulation. Techniques such as selective neurotoxic and reversible lesions, multiunit electrophysiology, microdialysis, psychopharmacology, and genetic knockouts have been used successfully for a number of years, providing a level of analysis currently impossible in studies of human beings. Some of these techniques, such as experimental lesions and genetic knockouts, can be used only in animals.

Second, a comparative approach to SCN may inform us about the evolutionary history of social interaction, and how certain neurocognitive processes may function similarly to or differently from those in humans. For example, there is increasing convergent evidence that western scrub-jays may possess an avian analogue to human ToM (Emery & Clayton, 2001). This is particularly striking because the common ancestor of scrub-jays and humans lived over 300 million years ago, and the brains of birds and mammals are completely different in structure. The medial prefrontal cortex appears to be the primary structure involved in the attribution of mental states in humans (Heberlein & Adolphs, this volume); however, birds do not have a prefrontal cortex (Emery & Clayton, 2003). Understanding the neural basis of "ToM" in corvids by using neurophysiology, lesions, and network models may inform us about whether understanding another's mental states is dependent on similar neural circuitry in terms of efficiency of coding, or whether completely different mechanisms are employed in distantly related species.

Third, the development of behavioural tests in nonhuman animals may be used in human populations which are impaired in their use of language, such as preverbal infants, patients with aphasia, the mentally handicapped, or autistics.

The physical and analytical techniques currently employed in human SCN studies are increasing in complexity. fMRI, in particular, may be the most revolutionary method available to help us understand the human brain. However, with respect to SCN, there are still many problems and limitations in applying these techniques to understand social behaviour. First, social behaviour involves the interaction of two individuals. Although presentation of images on a monitor provides us with information about how we perceive and categorize social stimuli, into different facial expressions, races, or genders, the interactive component essential to social cognition is missing. Currently, a number of laboratories have developed methods by which an individual interacts with either another person or a computer in a cooperative game (McCabe, Houser, Ryan, Smith, & Trouard, 2001; Rilling, Gutman, Zeh, Pagnoni, Berns, & Kilts, 2002), or two individuals in two separate MRI scanners interact in various deceptive games while their brains are scanned simultaneously (Montague et al., 2002). In both cases, the participants cannot see one another; however, with the implementation of web cams and the Internet, this does not seem too difficult to implement. Outside the realms of science fiction and portable MRI scanners, this new technology appears to have incredible potential, if the equipment is made available through collaborative effort.

These newly developed technologies should bring about unique opportunities to investigate previously difficult or impossible problems. As we described earlier, it has been impossible to investigate the neurobiology of human social interaction with the technology currently available, so that we rely instead on studies of social perception, particularly responses to facial stimuli. In the future, we see extensive use of video images (live and pre-recorded) to present social stimuli, possibly with the use of "actors". This advance would directly utilize the methods of social psychological research. In this instance, images with sound could be presented as scenarios in the "real world" (for example, from popular soap operas), or live images of an actor in an adjacent room, or facial images of another individual also in a scanner by hyperscanning (Montague et al., 2002).

The future of SCN will be driven by advances not only in technology but also in sociocognitive theory. Most studies in SCN, to date, have focused on: 1. social perception, resulting from electrophysiological studies of face-responsive neurons in rhesus monkeys; 2. ToM, resulting from studies on autism; 3. social emotions. What is starting to occur, as will be highlighted in Chapters 6 and 7, is explicit collaboration between cognitive neuroscientists and social psychologists to investigate particular problems in social cognition, such as social exclusion (Eisenberger, Lieberman, & Williams, 2003), self-conscious emotions (Beer, Heerey, Keltner, Scabini, & Knight, 2003), social evaluation (Cunningham, Johnson, Gatenby, Gore, & Banaji, 2003), self-knowledge (Kelley, Macrae, Wyland, Caglar, Inati, & Heatherton, 2002), and social versus object knowledge (Mitchell, Heatherton, & Macrae, 2002).

Addressing Adolphs' 10 questions

In a recent review paper, Adolphs (2003) attempted to define the field of SCN within a framework of 10 questions to be addressed if it is to be taken seriously. In this section, we will discuss these questions, and try to provide some instances where they have been addressed in the literature.

1. How can we measure social behaviour?

It is incredibly important to be able to quantify social interactions, so that the components of such interactions can be correlated with the activity of specific patterns of neural activation. Is it sufficient to establish an ethogram of human social behaviour along similar lines to those established for nonhuman animals? Cross-cultural ethological studies of human social behaviour have been attempted, most notably by Eibl-Eibesfeldt (1970) and Morris (1967), but were largely problematic in their unusual interpretations and lack of appreciation of contextual variables. This is not to say that an ethogram of human social behaviour is not possible, but only that it needs careful consideration of the multiple factors involved. The complexity inherent in the components of any ethogram of human behaviour may be essential for correlating with specific neural activity, such as found in studies of nonhuman primate social behaviour; however, this complexity may also make this an impossible endeavour.

2. How should social stimuli be categorized?

Adolphs (2003) suggests that social stimuli are currently classified either by their physical properties (such as different facial expressions) or by a priori specified categories derived from a particular social psychological theory with high ecological validity (such as untrustworthy faces). As Adolphs suggests, it is almost impossible not to begin a study without having classified stimuli into some prior category—for example, classifying faces as category 1 and cars as category 2.

Recent work on human facial expressions has found that even traditional categories are sometimes blurred. For example, Young, Rowland, Calder, Etcoff, Seth, & Perrett (1997) (see also Calder, Young, Rowland, & Perrett, 1997) used computer morphing techniques to morph two facial expressions together with different intensities of each expression; for example, 50% fear and 50% disgust. When presented with a series of faces with different levels of intensity of each emotion (such as 10% disgust and 90% fear, and then 20% disgust and 80% fear, etc.), subjects were asked to state which emotion they saw in each morph. This study is a clear example of the problems involved in classifying complex biological stimuli, even those based on a priori categories.

3. How can we best use data to guide theory?

Adolphs also raised an important issue that is not specific to SCN, namely, whether we should include nonsignificant data as well as significant data in the interpretation of experiments, and particularly in the formulation of new theories. This may be particularly relevant to studies on social behaviour, where it may be impossible to eliminate all irrelevant variables without disrupting the main effects. Certainly, reporting only effects where $p<0.05$ may be meaningless. Adolphs makes the useful suggestion that reporting effect sizes, confidence intervals, or even raw data rather than significance based on an arbitrary choice of alpha level may overcome some of these problems.

4. What is the most appropriate way to interpret the data?

There may be many nonsignificant results in studies of SCN because there are many factors affecting social behaviour that cannot be controlled (see above). This may have particularly significant effects in lesion and neuroimaging studies where the intent is to localize a particular function to a specific brain area.

5. How can we best establish the reliability and generalizability of our results?

Of vital importance is the convergence of findings from different studies using different techniques: neuropsychological studies (lesions) in humans, experimental lesions in animals, and neuroimaging. A good example of where this approach has been successful is the social evaluation of trustworthy faces. Adolphs, Tranel, & Damasio (1999) presented a series of 50 faces which had been previously rated by normal control subjects as trustworthy, and a series of 50 faces rated as untrustworthy, to patients with bilateral amygdala lesions, patients with other brain lesions, and normal controls. The normal subjects and patients with other brain lesions rated the two sets of faces appropriately, whereas the amygdalectomized patients rated all faces as trustworthy. In a similar study using functional neuroimaging, the amygdala of normal people was activated when viewing untrustworthy faces, independently of emotional expression, gaze direction, and gender (Winston, Strange, O'Doherty, & Dolan, 2002). These two studies suggest that the amygdala is essential for making judgements about the social attributes of faces. Convergent evidence for this finding comes from a study of amygdala lesions in rhesus monkeys (Emery, Capitanio, Mendoza, Mason, Machado, & Amaral, 2001). When normal adult, male rhesus monkeys meet for the first time, they either fight or remain at a distance from one another, evaluating the other's strengths and weaknesses. This distance is reduced over time. Emery et al. (2001) found that monkeys with amygdala lesions directed high levels of affiliative behaviour towards novel monkeys on their first encounter. This suggests that the monkey amygdala is also essential for the appropriate evaluation of faces.

6. How theoretical should SCN be?

Is it too early to produce a theory of how the brain computes social problems from current knowledge? There is abundant evidence that a distinct neural circuit, including the anterior temporal lobes, the nuclei of the amygdala, and the medial/orbital prefrontal cortex, functions in perceiving social stimuli and producing appropriate behavioural responses. Although other brain areas have been included in this circuit (see Heberlein & Adolphs, this volume), consistent activation in response to social stimuli has been reported in these three brain areas. Although we know little about how these areas are functionally related, this preliminary theory is a useful starting point for framing future research questions. It may be premature to produce theories of more complex aspects of social cognition, such as a sense of self or moral reasoning, but it is likely that such theories will have to be derived from current states of knowledge concerning "simpler" neurocognitive systems.

7. What should be the language of SCN?

As SCN is the child of cognitive neuroscience and social psychology, what should be its language? Should it use a proprietary vocabulary which has been developed specifically for SCN; should it use an existing one, say, from experimental social psychology; or should it be bilingual? This is an especially important issue when we use terms which are exclusively related to a particular field, such as terms used in social psychology (for example, "trustworthy", "dominance", or "empathy"), or terms which are used only in relation to the brain, such as anatomical areas. One additional problem is that social psychology relies on the discussion of domain-specific processes, such as schemata, attitudes, scripts, and stereotypes, whereas cognitive psychology is based on general processes which can be social or nonsocial in nature, such as perception, memory, and attention. It may be possible to reconcile these differences only by training the next generation of social cognitive neuroscientists in both languages.

8. Are social cognitive processes reducible to nonsocial processes?

This is perhaps the most fundamental question facing SCN. Are there neural systems which are specialized for the processing of social stimuli or the production of social behaviour, or can general neural systems be cajoled into processing both social and nonsocial stimuli? For example, what is the evidence (if any) that the temporal-amygdala-prefrontal circuit described earlier is involved exclusively in processing social stimuli?

For example, in this book, we have restricted our view of sociality to processes that are not based primarily on emotion (unless the emotions are social and interact with cognitive processes). There is an intimate relationship between emotion and social behaviour, and between emotion and cognition. One function of facial expressions of emotion, for example, may be in social communication; to inform others of one's current emotional state. Facial expressions may also be inhibited or produced voluntarily with the purpose of deceiving others about one's true emotional state (Ekman, 2003). An alternative explanation for the evolution of facial expressions may be that they are by-products of the output of neural systems involved in the emotion that is currently being experienced. For example, contorting the facial muscles after eating something which tastes disgusting may produce the classic facial expression of disgust. This expression may then have evolved into the expression associated with experiencing disgust in other contexts, such as viewing disgusting images. There is abundant evidence that the amygdala processes facial expressions of fear (Heberlein & Adolphs, this volume); however, what is not clear is whether the amygdala is performing a perceptual role (processing the physical attributes of fear expressions) or an evaluative role (processing the emotional-communicative attributes of fear expressions). It is very unlikely that the former explanation is true, as this would mean that the amygdala is an extremely specialized perceptual processor, rather than one involved in the experience of emotion (as the large majority of contemporary evidence suggests). Therefore, when answering the question of whether specific neural circuits process social stimuli independently of nonsocial stimuli, we need to be certain of what we mean by social.

This question may also welcome an evolutionary approach. The "social intelligence hypothesis" (see Emery, this volume) states that the enhanced intelligence of primates evolved to solve social problems (rather than physical problems, such as finding and extracting food). Some theorists have suggested that sociocognitive processes may be an adaptive specialization to social living in some species, particularly those which live in large social groups (e.g. Bond, Kamil, & Balda, 2003), whereas other theorists have suggested that animals in complex societies will generally perform better in both social and nonsocial tasks (e.g. Humphrey, 1980). Therefore, one possible line of research is to test closely related social and solitary (or less social) species on the same social and nonsocial tasks. The adaptive specialization view predicts that the social species will outperform the nonsocial species only on the social tasks, whereas the social intelligence view predicts that social species will outperform the nonsocial species on both social and nonsocial tasks.

A different approach to the question is to ask whether all social processes are just specialized cases of nonsocial processes, such as memory, attention, or perception of complex stimuli. Perhaps the best-known research on this is the neural basis of face perception, and whether the "fusiform face area" (FFA) really responds only to facial stimuli, or whether it is involved in the categorization of all perceptually salient learned stimuli (such as "greebles"; Tarr & Gautier, 2000). There is no space here to discuss this question in detail. However, one issue which should be addressed is that neurobiological studies of face processing in monkeys have used techniques which are infinitely more subtle than those currently used in humans, and this may have clouded the issue somewhat. Neuroimaging still suffers from the problem of localizing activation to the same level of specificity as single- or multiunit electrophysiology uses in animals. Therefore, the presentation of faces and objects may both appear to activate the same area of the human fusiform gyrus; however, this does not mean that the activity for each category of visual stimuli is not specific to a particular area within the fusiform gyrus. This issue may be resolved only after refinement of scanner resolution.

9. How will we be able to understand a future SCN?

What will an understanding of the neural basis of social behaviour actually tell us that we do not already know from our "folk psychology" of how and why others behave the way they do? If such information is at odds with our folk psychology, where does this leave us? We think that the problem which Adolphs is addressing here is not what is the ultimate benefit of SCN to society, as this is clear with respect to understanding and treating psychopathological or neurological disorders of social cognition, but rather the more fundamental issue of whether this information will change the way we interpret one another's behaviour in our day-to-day lives. This problem may be related to question 7, in that we already use a language to describe one another's behaviour and intentions, but we are unlikely to adopt explanations of their behaviour and intentions based on knowledge of the underlying neural mechanisms. Many folk psychological concepts which are currently being investigated, such as moral cognition, self-awareness, and ToM may never map onto distinct neural systems, largely because we still do not know precisely what these concepts actually mean, but only what our intuitive sense tells us. This may be akin to recent attempts to study the neural basis of consciousness, without actually knowing what consciousness is and what it is not.

10. How integrative should SCN be?

What studies should be included as SCN? Earlier, we suggested that studies of the neurobiology of socially motivated behaviour (social neuroscience), such as aggressive, sexual, and parental behaviour, should not be included in SCN, but SCN should include analysis at all three levels—social, cognition, and neuroscience (Ochsner & Lieberman, 2001)—and so studies on only motivated behaviour are not likely to include the cognitive component. The question becomes more difficult when discussing emotion. However, if we follow Ochsner and Lieberman's criteria, only studies of the neurobiology of social emotions or facial expressions used within a social context should be included. The case for including studies on the neural basis of language is perhaps the most difficult because it includes all three levels of analysis. We would argue that the study of language is covered by a specific area of cognitive science, with its own vocabulary, which may be alien to those outside the field, and so difficult to integrate with other areas of SCN.

Overview of the book

This book attempts to review some of the main areas in which SCN has progressed over the last few years. In Part I, we are shown how understanding specific aspects of emotion (Chapter 2), memory (Chapter 3), and vision (Chapter 4) can provide fascinating insights into the mechanisms that are required to function normally in a social environment. All of these have led us to understand more fully what the neural basis of social behaviour might be.

Chapter 2 outlines studies that have been carried out on socioemotional processing in animals, with particular emphasis on the amygdala and orbitofrontal cortex. When these structures are surgically disrupted in monkeys, their emotional behaviour changes and they typically become tamer and less fearful. There is an intrinsic link, however, between emotion and social behaviour; therefore, animals with these changes in emotional behaviour also show abnormal social interactions. Recent studies have linked the tools of cognitive neuroscience with sophisticated behavioural methods used in primatology that are beginning to show how damage to these structures affects animals within social situations.

Chapter 3 explores recent work on the way in which the frontal cortex interacts with temporal lobe visual areas in retrieving visual memories. In this model, the frontal cortex is seen to play a part in the recall of memories (and the implementation of behaviour) only in circumstances where there is no fixed reward outcome for a learning condition. This is very similar to social situations in which the outcome of behaviour is not fixed, but, rather, depends on the social context in which it is carried out. Therefore, the cognitive neuroscience investigation of memory can also lead us to an understanding of the processes involved in social behaviour.

Chapter 4 examines the way in which studies of visual processing are also providing insights into the neural basis of social behaviour. To understand how to interpret the social world (in order to interact with others, or make decisions), we need to understand the aims and intentions of other people. For most of us, this requires interpreting the visual world, and Chapter 4 presents a series of studies in which specific aspects of visual processing give a clear insight into how we interpret others' goals.

Although social psychology is a difficult issue to apply the tools of cognitive neuroscience to, Part I shows us that social behaviour is just the result of combining lots of different processes in the brain. When we interact with one another, we need to understand the sensory world around us (to interpret the social situation we are in), we need memories of past situations that are similar, and we need to have emotive responses to those situations in order to guide our behaviour appropriately. Therefore, the first step in SCN is to understand how we can apply the research of many different areas of cognitive neuroscience to problems in social psychology.

Of fundamental importance to the SCN approach is the integration of cognitive neuroscience with social cognition. At the heart of this endeavour is research aimed to understand the neural basis of our intuitive *folk psychology*, which is used to categorize individuals into social categories (stereotyping), predict another's intentions, beliefs, and desires (ToM), form predispositions to evaluate people favourably or unfavourably (attitudes), categorize the actions of others (person perception), and determine self-knowledge (Ochsner & Lieberman, 2001).

Understanding others' mental states (ToM) is a high-level cognitive process which appears to depend on the same network of brain regions described in the preceding chapters; that is, the anterior temporal cortex, amygdala, and prefrontal cortex. As with the discovery of the important role of these brain areas in social behaviour, the concept of ToM was derived, from work not in humans, but in nonhuman primates (Premack & Woodruff, 1978). Chapter 5 reviews and evaluates the wealth of comparative evidence that nonhuman primates, dogs, and corvids may possess some appreciation of mental states in other beings, for example, their intentions, visual perspectives, knowledge states, and beliefs.

Chapter 6 covers the neurobiology of social cognition from the perspective of cognitive neuroscience. It covers a wide range of studies in the cognitive neuroscience of human social behaviour from the attribution of intentions to objects and people, emotional states, personality, and ToM. In so doing, Heberlein and Adolphs provide clear evidence for the importance of the temporal-amygdala-prefrontal neural circuit in human social behaviour, as in that of nonhuman primates (Chapter 2).

Chapter 7 approaches the neurobiology of social cognition from the perspective of social psychology, specifically whether an understanding of the self can be illuminated by an understanding of others, particularly the role of the self within a social group. This chapter differs quite significantly from the others in its approach, providing a framework for investigating some of the major questions concerned with the neurobiology of the self.

Part III of this book deals with human disorders of social behaviour or social cognition, and how the understanding of the mechanisms outlined in Parts I and II can allow us to understand these disorders and produce appropriate treatments.

Chapter 8 discusses the neural basis of autism, a developmental disorder that results in complex changes in cognition, including poor social interaction and knowledge. The hypothesis is outlined that empathy is required in order to have good social interaction, and that this is dysfunctional in autistic subjects. Much of our understanding of the neural basis of such dysfunction comes from work such as that outlined in Chapter 2 showing that monkeys with damage to the amygdala can superficially resemble human children with autism. Humans with damage to the amygdala also show problems with ToM and empathy, problems that seem so crucial in autism, and so strongly support a link between amygdala dysfunction and the social behavioural impairments in autistic subjects.

Chapter 9 outlines recent work on depression. Although depression is not normally considered a disorder relating to social behaviour or cognition, this chapter presents the hypothesis that social cognition, and in particular self-perception, is crucial to the pathogenesis of the disorder. Dysfunction in the pathways discussed in detail in Chapter 7, therefore, could provide crucial insights into the neural basis of depression.

Finally, Chapter 10 discusses the neural basis of psychopathy and antisocial behaviour. With increasing concern about antisocial behaviour in society, understanding the neural basis of this behaviour is of the utmost importance, but the issue is a complex one. Not only are there different types of antisocial behaviour, but there also appear to be different neural mechanisms for these different types. Such disorders, then, provide one of the greatest challenges to SCN, but Chapter 10 outlines how many differences between hypotheses are now starting to be integrated into a coherent understanding of a complex set of disorders.

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