From SCAN to Neuropolitics

Darren Schreiber

University of California, San Diego

All political behavior is reflected in the brain, yet the brain has been treated largely as a black box by political science because of the previous limitations on our ability to make useful inferences about it. Despite being a very young field, social cognitive and affective neuroscience (SCAN) has already converged on a set of consistent results that have been verified though a variety of methods. Neuropolitics can advance the agenda of political science by founding our theories in modern notions of human nature that are in harmony with our sibling disciplines and advance the agenda of neuroscience by providing the context that drove the evolution of the human brain.

A common misconception about research into the neural correlates of social phenomena is that it entails the presumption of a form of biological determinism. This seems to stem from a fear that neuroimaging either might reveal the soul to be an illusion or firmly resolve a nature/nurture debate in favor of nature (Wolfe 1996). Unless one assumes a rather unusual version of dualism, the presumption is that all mental activity is at least reflected in the brain. Thus, one can give a central role to individual agency or to the influence of culture and context, while still considering how those would alter and be altered by the structure and function of the brain.

A study a few years ago asked people who were experts in either classical ballet or the Brazilian martial art of capoeira and non-experts to view video clips of people performing similar moves from either style (Calvo-Merino et al. 2005). People who had developed expertise in a style of movement had higher levels of activity in brain regions associated with movement when they viewed clips of their own style than when viewing the other style. The most logical inference from this experiment is not that some people are born to be ballet dancers and some are

born to be capoeira dancers because their brains differ, rather it is that learn these movement styles alters the function of the brain.

This inference is further supported by a study where a group of students was taught to juggle and then asked to practice each day for three months, then asked not to juggle for another three months (Draganski et al. 2004). Structural brain images were generated for the students before training, after the practice period, and after the interval with no practice. The neo-cortex in portions of the mid-temporal area increased in size as subjects learned to juggle and then atrophied slightly as they ceased practice. As these two examples show, engaging in the world alters the function and structure of the brain. Our biology (as reflected in our brains) responds to our environment.

Demonstrating the effect of individual agency on the brain is far more complex experimentally (see e.g. Maye et al. 2007), but again, if one believes that brain activity is correlated with mental life then neuroimaging may reflect the consequences or even components of individual agency. Data showing brain activity in regions known to be involved in auditory perception does not by itself tell us whether the person is intentionally imagining a voice, actually hearing a voice, or having an hallucination of a voice (see Sommer et al. 2008). In this manner, neuroimaging data is like all other data, it can constrain our explanations, but we should neither fear nor hope that it will resolve metaphysical debates.

We should also be careful about the kind of inferences we expect imaging data to support. Merely showing that a part of the brain has heightened activity during a task, does not demonstrate that this brain region is a "module" for that task nor that the task is "localized" in that region (van Eijsden et al. 2009). Having a brain region respond to the sound of a piano, does not tell us that this is the "piano" region of the brain. While the brain may exhibit specialization

or task localization under some circumstances, it is also highly integrated and able to adapt to utilize other resources when important function are disrupted. A sighted subject who is blindfolded for five days will learn to read Braille using canonically visual regions of the brain, but when the blindfold is removed, it takes less than 24 hours for the Braille reading to be diverted to another part of the brain (Merabet et al. 2008). Attempts to describe the contribution of a brain region to mental function must be understood in this context and must not be misconstrued at neophrenology.

Neuroimaging may provide us evidence that the same region of the brain that enables us to feel pleasure from the spiritual ecstasy of silent prayer (Schjodt et al. 2008) is involved when we punish people who violate social norms (de Quervain et al. 2004) or when we desire a sports car (Erk et al. 2002). While this data may allow us to make a number of interesting inferences about the pleasurable nature of each of these activities, it does not tell us about the existence of God, the value of a particular social norm, or true quality of the car. Taking the results of neuroscience seriously does not require us to reject free will (Mele 2009) and may even necessitate the rejection of a merely reductionist project (Mitchell 2009). The hard questions of political science will remain the hard questions as neuropolitics develops. However, our field of potential answers will likely be narrowed a bit by the data that this approach generates.

Why neuropolitics?

With an explosive amount of research taking place in SCAN, what can political science gain that will help to refine our theories? Political science has long been built on theories about the nature of social cognition and affect, but the disconnect between our theories and the results obtained by SCAN is problematic. Political science is built on founding assumptions about how individuals process their world and make choices in it.

Debates are currently raging about the relevance of neurophilosophy (Churchland 2007), neuroeconomics (Clithero, Tankersley, and Huettel 2008), and neurolaw (Rosen 2007) to each of their non-neuro counterparts. Each of these fields, like political science, has longstanding traditions about the appropriate modes of inquiry, but also has assumptions and provisional answers that the fields hold sacrosanct. Regardless of whether data from neuroimaging confirms, refutes, or is ambiguous about these prior beliefs, that data constrains the set of explanations we are able to give.

While it might still be reasonable to treat the mind as a black box, it is certainly no longer reasonable to treat the brain that way. The many meta-analyses cited in this chapter are demonstrating that even in the very early years of SCAN we have sets of results that appear to be at least somewhat robust, if not precise or conclusive. Traditions that dichotomized affect and cognition have been consistently undermined; whereas traditions that claimed a distinctly social character for interpersonal interactions (as opposed to interactions with objects) have been consistently supported.

When I attended the very first meeting of the SCAN movement at the start of the millennium, I noted the predominance of gray hair and the domain specificity of the knowledge of the participants. These older luminaries in their disciplines were like the scattered people after Babel. The economists needed to have the neuroscience explained. And, the primatologists did not know what an ultimatum game was.

As the decade closed and I attended later incarnations of the SCAN meetings, I was struck by the fact that most of the attendees were well under 30 and cross-trained in a variety of disciplines, often under the tutelage of the same luminaries I had met at the first meeting. The neuroeconomists knew their neuroanatomy, were collaborating on primate experiments, and

could easily converse with other neuro- scholars trained in mash of psychology, molecular biology, neuroscience, ethology, philosophy, and law. NY Times columnist David Brooks (2009) shared my impression of this community and notes that a search for "social cognitive neuroscience" on Google in 2001 yielded on 53 hits, whereas a search now yields a million and a half more.

The common set of questions discussed by this agglomeration of scholars sit at the heart of political science. Is there a human nature and what is it? How do we value our choices and why do we decide the way we do? How do our biology and our experience? And, how do our experiences shape our biology?

However, dominant paradigms in political science such as rational choice theory and behaviorism do a poor job at integrating with the insights being developed at the nexus where SCAN resides. A series of experiments has consistently shown that people make will choose to route a train away from a track where it would have killed six people and thus sacrifice the one person sitting on the track the train is switched to. However, subjects are typically unwilling to push a person off a bridge if that would stop an out of control trolley and save the six people down the track (Greene et al. 2001). Rational choice theory does not do good job at accounting for this discrepancy, nor for the facts that lesions to the medial prefrontal cortex increase (Koenigs et al. 2007) and that cognitive task load decreases (Greene et al. 2008) the likelihood of the utilitarian judgment in the trolley/train dilemma. Similarly behaviorism is at a loss when identical gambling patterns arise from the neurologically distinct mental processes of Republicans and Democrats (Schreiber et al. 2009).

There are a variety of approaches to neuropolitics (Lieberman, Schreiber, and Ochsner 2003), ranging from bringing political science into the scanner (e.g. replicating political tasks

like attitudinal response or economic games), bringing results from the scanner to political science methods (e.g. testing implications using survey experiments), or re-evaluating scanning work in light of political science theories (e.g. using classic psychological tasks and their neurocorrelates to distinguish party members). I also contend that many SCAN researchers are running experiments that could easily become relevant to central questions of political science with the addition of only a few variables that would likely clarify the experimental results.

Neuropolitics is an opportunity for political science to connect with a broader conversation that is taking place across a wide range of disciplines about human nature. The amazing variety of methods reflected in SCAN are already bearing fruit and yielding results that parallel very old lines of argument (e.g. moral iniquity, utilitarianism vs. deontology, theory of moral sentiments) that have swayed political discourse. There are low cost routes for political scientists to engage in this conversation and generate theories that are more commensurable with work beyond our own field. But first, it is important to have a basic understanding of how SCAN makes it's claims.

SCAN's Methods

One of the challenges that neuropolitics faces as a subfield is that many of the tools employed by SCAN are unfamiliar to political scientists. This unfamiliarity leads us to then be poor consumers of the results, over-reacting to methodological controversies (e.g. Vul et al. 2009) or believing spurious results merely because there is a pretty brain picture attached (McCabe and Castel 2008). This section provides a brief overview of the variety of methods that SCAN researchers have been employing, providing relevant examples for each of the methods. I also provide a more detailed discussion of the most commonly used method, fMRI.

The study of the alterations to the structure of the brain that accompany learning juggling was done with structural magnetic resonance imaging (MRI). In MRI, a subject is placed in the center of a large superconducting magnetic field and pulsed with a sequence of radio waves that alter the alignment of the subatomic particles that comprise the subject's brain and body. The resonance of this signal varies widely depending on the composition of the matter, thus allowing the differentiation of skull from soft tissue, but also allowing for more fine grained distinctions among the grey matter (neural cell bodies and other structures) and white matter (sheathed nerve fibers). The technique to image the structure of the brain with MRI is essentially the same as imaging a persons' knee (although pulse sequences will vary). The insight in the juggling study, however, relied upon the use of a statistical technique known as voxel-based morphometry (VBM) that detects subtle changes in the composition and thickness of brain regions (Draganski et al. 2004).

Another technique for investigating the structural differences among people's brains is diffusion tensor imaging (DTI). DTI is another creative use of the MRI signal, this time to investigate the diffusion of water molecules in the brain. Because water will more easily diffuse within a neuron rather than across the cellular membrane, we can use DTI to generate maps of neural connections within a living, healthy person. One recent DTI study demonstrated that lower levels of neural connectivity within Broca's area (a brain region involved in language processing) in healthy subjects corresponded to poorer abilities at learning a new grammar (Floel et al. 2009). And, another DTI study recently showed that learning to juggle also alters the white matter in the brain that facilitates neural connections (Scholz et al. 2009).

I will discuss functional MRI (fMRI) in more depth at the end of this section, but it relies on roughly the same technology that underpins structural MRI. When an fMRI study is

conducted, a high-resolution structural MRI image is first acquired of the subject so that the functional data may be overlaid upon it. The essential difference with fMRI is that a sequence of images is acquired over a period of time (a typical scanning sequence lasts from 5-10 minutes), which allows inferences about the change in the flow of blood through the brain.

Positron Emission Tomography (PET) scanning also investigates the flow of blood in the brain to make inferences about mental processes. In PET imaging, the subject is injected with radioactive sugar water[1], which is metabolized by neural tissue. Since the radioactive molecule has a short-half life, it will quickly decay and emit an antimatter particle (a positron). When the positron collides with an electron (its matter counterpart), they annihilate each other and produce photons that are picked up by the detector surrounding the person's head. PET scanning is useful because the data it generates enables far more direct inferences about metabolic processes in the brain and provides an absolute metric (whereas the value of the MRI signal has no absolute baseline and is only meaningful in relative changes). While fMRI has exploded in use, PET (despite the radiation risks) has been particularly valuable in the investigation of phenomena like the resting state networks that will be discussed later in this chapter (e.g. Raichle et al. 2001).

Another pair of imaging techniques that provide far greater temporal resolution, but sacrifice on spatial resolution, are electroencephalography (EEG) and magnetoencephalography (MEG). In EEG, a web of electrodes is placed on the participants' scalp and millisecond scale readings are taken of the electrical activity at each node. With a larger number of nodes, one can make increasingly accurate inferences about the spatial location of the origin of the electrical activity in neural tissue. MEG uses a series of superconducting quantum interference devices

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[1] Having volunteered for a PET study, I can attest that it is odd to feel the warmth of the radiation as it follows up one's veins.

(SQUIDs) to similarly measure the changes in electrical signals in the brain, but provide a much better spatial resolution, while preserving the millisecond temporal resolution of EEG. A study of conflict processing in liberals and conservatives relied upon EEG to make inferences about how potential differences in basic cognitive processing might be associated with political ideology (Amodio et al. 2007).

One of the oldest, and yet most important tools for studying brain function has been the study of people with unhealthy brains, typically known as lesion studies. The most famous lesion patient is Phineas Gage who had metal rod shoot through the frontal lobe of his brain in 1848 as the result of an explosion while he was tamping down gunpowder (Sanfey, Hastie et al. 2003). Gage miraculously survived the accident, but many of the social aspects of his personality were drastically altered. Antonio and Hanah Damasio pioneered the more systematic study of lesions with a database mapping out lesions in a large number of patients who could then be included in experiments to see what cognitive deficits pertained to particular focal brain lesions (see Glascher et al. 2009; Damasio and Damasio 1989). The study of autism patients in particular has been illuminating in understanding the social nature of the brain because some people with autism are so high functioning in other forms of intelligence but have tremendous difficulty navigating the social world (Frith and Frith 1999). The blindfolded Braille readers study described above used the transcranial magnetic stimulation (TMS) technique of electro-magnetic pulses that briefly disrupt neural function in order to verify when the visual areas of the brain were being recruited for reading Braille (Merabet et al. 2008). TMS is a relatively non-invasive way of conducting lesion studies in healthy subjects.

The final approach involves the study of animals to develop insight into political intelligence (e.g. the chapter in this volume by Proctor and Brosnan.) For instance, by designing

experiments that provide parallel tasks to both human infants and chimpanzees, researchers have looked at the contrasts between social and technical intelligence (Herrmann et al. 2007), the tendency toward altruistic acts (Warneken and Tomasello 2009), and a wide range of other cognitive tasks (Premack 2007). By comparing the neuroanatomical differences and the cognitive differences between humans and chimpanzees we can also make inferences about the linkages between structure and function (Premack 2007).

While each of the methods briefly described above are important for the particular kinds of insights they can facilitate about social and political mental processes, the real explosion in SCAN has been propelled by fMRI (Friston 2009). The reason for fMRI's transformation of neuroscientific research is that it filled a gap in their toolkit.[2] Functional MRI allows for studies with a temporal resolution between fractions of a second and hours, a spatial resolution between millimeters and the full size of the brain, and a very small level of invasiveness. The technique takes advantage of the fact that oxygenated and deoxygenated hemoglobin have different magnetic properties and generates a blood oxygen level dependent (BOLD) MRI signal that is believed to correspond to changes in neural activity.[3]

While brain is constantly active, an increase in cognitive effort requiring specific mental processes increases neural activity in the regions important for those mental processes. Since the metabolic rate of the neurons supporting that increased activity goes up, additional oxygenated blood flows into the region to support the additional workload. That shift in the ratio of oxygenated to deoxygenated hemoglobin alters the BOLD MRI signal slightly (typically on the

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[2] Viewing the 1988 version of the famous mapping of neuroscientific tools on a log/log plot of temporal and spatial resolution one can easily see the deficit in methods that the next coming decade's development of fMRI was to fill (Churchland and Sejnowski 1988).

[3] Spezio and Adolphs (2007) note many of the challenges involved in properly interpreting the results from the BOLD signal analysis.

order of a fraction of a percent) and those slight changes are then used to make inferences about the change in neural activity. While there are an incredible number of interactions and variables between the neural activity and the measurement of the BOLD signal, the relationship between the two is essentially linear, which is what allows fMRI to function as well as it has.

While experimenters have crafted far more ingenious paradigms for exploiting the properties of the BOLD signal, the two basic designs are the block and event-related. In the block design, a stimulus (e.g. a photo) is provided for an extend period of time (e.g. 20 seconds) with the hope that this will provoke a more easily detectable sustained response to the stimulus. If a tone is played for a period and then ceases, we might expect to observe that brain areas involved in the perception of the one will be very active during the tone and then cease activity when it ceases. Two central limitations of the block design are the limited number of repeated stimuli one can fit into a scanning session and the tendency of the brain to habituate quickly to a stimulus. In the event-related design, the analysis of the BOLD is timed to an event such as the subject pressing a button in response to a task. Initially, block designs were more common, but as statistical methods and experimental results have accumulated the event-related design has become the more prevalent. An example of a more interesting experimental design involved having subjects merely watch a video clip and then looking for common patterns of brain activity as subjects received the same stimulus (Hasson et al. 2004).

During a typical fMRI scanning session, data is repeatedly acquired at intervals that typically range from a second to four seconds (constrained by a number of tradeoffs between temporal and spatial resolution) with about 50,000 voxels (cubic millimeter measurements) collected during each acquisition. This generates gigabytes of data per participant that is subjected to noise from head movement, breathing, signal drift over time, and a wide range of

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other artifacts. Further complicating the analysis of this 4D data is that each of the 50,000 time series are not independent, but probably correlate with each other in complicated ways.

Preprocessing fMRI data entails registering it to the structural image collected for that participant and then warping that participant's brain onto a common reference brain so that data from a number of participants can be compared. Algorithms are used to identify portions of the data that are not brain so that they can be removed from the statistical analysis. And, one must compensate for standard problems like the flow of air into the sinus cavities that causes artifacts in the magnetic signal. Data is typically smoothed, filtered, and normalized to compensate for known issues with the fMRI signal, such as its lack of a natural baseline.

After the preprocessing stages, the data is often analyzed with general linear model applied, treating each voxel of the brain as an independent time series. The pattern of experimental stimuli is used as the basis for the model and each voxel is analyzed for how well its time series fits a prediction based upon the timing of the onset of each instance of the stimulus and knowledge of the typical hemodynamic response function that is reflected in the BOLD fMRI signal. If an individual participant is scanned multiple times, the data analysis from each of the runs is statistically aggregated into a 3D image summarizing the level of fit of the model at each voxel in the brain. Typically, a group-level result is generated by using the analyses of the individual participants and fitting a hierarchical model that either identifies the common patterns of brain activity in the group or identifies contrasts between groups.

There are a wide variety of ways of analyzing fMRI data and presenting the results, so the consumer of such results must take care to actually note what the exact data display is representing. Often, the result is a map of the fit of the model at each voxel in the brain in terms of z-scores. Positive z-scores (typically indicating higher neural activity during the task

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condition) are conventionally marked with colors in the hotter range of the color spectrum (e.g. yellow, orange, red) while negative z-scores (often either neural activity below a resting baseline or below a control condition) are colored with cooler colors. In order to focus attention on only the brain regions that are most likely to be actually responding to the task, a variety of approaches are taken to thresholding the data. Since a whole brain scan typically involves tens of thousands of active voxels, researchers will often set a number of contiguous voxels that must have z-scores above a certain value in order for a cluster of activations to be considered significant, or they will use assumptions from Gaussian random field theory to identify clusters that are most likely to be truly responding to the task based upon the spatial extent and the intensity of response to the stimulus, or they will set a false discovery rate (the expected proportion of false positives among voxels above a threshold).

It is important to emphasize that images typically displayed in articles using fMRI are not of a single subject, rather they represent the responsiveness of a the brains of a group of subjects warped into a common space. The images also do not represent the intensity of the BOLD fMRI signal, since that signal has an arbitrary value. Rather, the activity level indicated in the images is usually a thresholded map of the z-score for the model at each particular voxel, with only statistically significant voxels colored in.

Often the z-scores are represented on a slice through the brain. Axial slices view the brain as if looking down on a person's head; sagittal slices view the brain from the side of a person's head; and coronal slices render the image as if looking faces to face. Because neuroimaging developed as an interdisciplinary field merging varying intuitions, it is important to note that occasionally the images are flipped so that left is on the right and right is on the left. The uneven use of this radiological convention combined with the fact that the "Analyze" data

format did not specify the orientation of the image caused frequent problems in the past, but these have been resolved with the adoption of the Neuroimaging Informatics Technology Initiative (NIfTI) format.

In addition to representing data on slices, occasionally volume rendering or surface rendering are used. To help with visualization of the location of the activation, sometimes an entire head is represented with wedges removed and the data displayed on the remaining interior spaces. Surface rendering is used when the relevant activity is in the neo-cortex. The wrinkles of the neo-cortex allows the skull to enclose a much larger surface area of grey matter than it otherwise would be able to contain. The compression of this large surface yields a series of gyri (hills) and sulci (valleys) that can be flattened out in order to visualize activity patters that might be difficult to notice when looking only at a volumetric rendering. In these images, the gyri are typically colored lighter and the sulci are colored darker.

Another common approach to analyzing fMRI data is the use of a set of regions of interest (ROIs) from which the fMRI data is extracted and analyzed. If one has theoretic reasons to believe that a particular brain region is involved in a task then it often makes sense to simply analyze that specific region, rather than testing the hypothesis against the whole brain. This avoids many of the multiple comparison problems faced with whole brain analysis. ROI's are usually defined either anatomically (e.g. expecting the amygdala is responding to a threatening stimulus) or functionally (e.g. expecting that the portion of the fusiform gyrus that responds to faces will respond more strongly to familiar faces than unfamiliar faces.) While identifying the anatomical ROIs poses some difficulty due to natural variability in the structure of the brain, many of the fMRI data analysis software packages now have built-in tools for identifying the anatomy based on standardized atlases. The functional ROIs, however, require a localizer task to

identify the region (Saxe, Brett, and Kanwisher 2006). The fusiform face area (FFA) is a classic example of a functional ROI since its location in the fusiform guys varies person by person. The FFA is not an anatomically defined region and it can only be identified by the intensity and specificity of the voxels' responsiveness to human faces.

The use of functional ROI's has gained some sensational and negative publicity recently and led to claims of "voodoo correlations" in neuroimaging (Vul et al. 2009). The problem that these authors pointed to in this meta-analysis was that the same data used by researchers to identify the area responding to the task was then used to identify the relationship between neural activity and the behavior. This issue is familiar to political scientists as selecting on the dependent variable. However, in neuroimaging the problem can be even subtler. Selecting voxels based on their responsiveness to task A and then comparing the responsiveness to task B can simultaneously over-estimate the effect from task A and under-estimate the effect from task B. Another issue is that the ROI analyses were often done using only a single peak voxel (rather than an average of a cluster of voxels), effectively choosing the most responsive case out of 50,000. Despite the hype that this critique of data analysis methods in neuroimaging received in the press, there are numerous correctives that are easily applied, as the authors note.

Basic Results

Although SCAN is a very new field, researchers have already converged on a set of consistent results that demonstrate the role of a relatively small set of brain regions in a wide variety of social behavior. In this section, I review a few brain regions and their role in important social cognition functions. I then detail the mental functions that have been frequently studied with fairly consistent results.

As mentioned above, the fusiform face area (FFA) is a region of the fusiform gyrus in the temporal lobe that responds specifically to faces. Other regions known to be heavily involved in the processing of faces include the amygdala, the occipital face area (OFA), superior temporal sulcus (STS), and the premotor face area. If the human brain has evolved for social cognition (Schreiber 2007) and given that faces convey a tremendous amount of information about affect and intention (Capella and Schreiber 2006), then having brain regions with functional specialization for processing faces would be a valuable way of aiding efficient social cognition. And, deficits in the FFA and other face processing regions appear to correlate with the impaired social cognition attendant to autism (Kleinhans et al. 2008).

The FFA appears to be involved in perceiving gender characteristics, although the subjective ascription of gender appears to rely more on the prefrontal cortex (Freeman et al. 2009). Similarly, the FFA is involved in processing cues about racial identity and higher levels of activity there appear to be correlated with increased ability to recognize people of the same race (Golby et al. 2001). In fact, it may be that the FFA has greater specialization for facial identity and that other areas like the superior temporal sulcus (Winston et al. 2004) and the amygdala are reacting to the affective status of the face (Vuilleumier et al. 2003).

The amygdala is a small, almond shaped region and is often discussed as being involved in the processing of fear (LeDoux 2000; LeDoux 2007). However, the story is far more complex and claims have been made for the involvement of the amgydala in positive emotions (Holland and Gallagher 2004) and social cognition (Adolphs 2003). Research showing the amygdala as connected to implicit racial attitudes has been particularly prominent (Phelps et al. 2000; Lieberman et al. 2005)

A meta-analysis of 385 functional brain imaging studies with a total of 5,307 individual subjects confirms that the role of the amygdala in fear processing appears to be robust (Costafreda et al. 2008), but also shows that disgust seems to just as likely to activate the amgydala. While fear and disgust consistently activated the amgydala, so did other negative emotions like sadness and anger and some positive emotions surrounding humor and sexuality, although negative emotions seemed to provoke stronger reactions than positive emotions and happiness provoked the lowest responses. A second meta-analysis concluded that positive emotions were able to elicit as strong of responses from the amgydala (Sergerie, Chochol, and Armony 2008). Meta-analysis (Costafreda et al. 2008) also demonstrates that explicit attention to stimuli was significantly less likely to activate the amgydala than was passive experience, a result consistent with the theory that the amygdala is related to automatic processing (Lieberman, Schreiber, and Ochsner 2003). Of particular interest, is the strong result showing that amgydala responses can be attenuated by intentional repression of emotion.

The down-regulation of the amygdala as a result of conscious processing has been shown in the context of racial (Lieberman et al. 2005) and emotional processing (Taylor et al. 2008). This interaction between more automatic amygdala processes and more controlled frontal lobe processes are important for clarifying the nature of implicit attitudes, especially in the context of race. Some have treated such automatic attitudes as if they reveal 'true' attitudes (e.g. Kristof 2008), rather than recognizing the individuals have both automatic and controlled attitudes that have distinct cognitive, affective, behavioral, and neural components (Dovidio et al. 1997; Lieberman, Schreiber, and Ochsner 2003).

While the role of the amygdala in racial processing has been robustly demonstrated, its role is nuanced. Because other race faces morphed with the face of the participant deactivate the

amygdala, some have argued that the amygdala is computing an interaction of personally and socially relevant characteristics (Platek and Krill 2009). Consistent with this theory, as individuals become more familiar with foreigners, amygdala activity diminishes (Derntl et al. 2009). It is also worth noting that dark skin tones of are more likely to activate the amygdala, regardless of race (Ronquillo et al. 2007)

Another brain region important to social and affective processing is the insula, a thumb-sized region that runs laterally along the sides of the brain and is located a couple of centimeters above the ear and a few centimeters into the interior of the brain. Because the insula has been implicated in such a wide variety of interesting social phenomena, its function is being intensely researched (Blakeslee 2007). The human insula is particularly interesting because it appears to have a very different structure than in many of our primate cousins and even has a particular type of neuron (the von Economo or spindle cell neuron) which appears to occur only in animals with complex sociality. The evolutionarily older part of the insula is closer to the back of the brain and responds to physiological stimuli like pain or temperature. The anterior insula, which is closer to the front of the brain, in contrast, appears to integrate the objective stimulus with our perceptions of it. Thus, while activity in the posterior insula increases with objective increases in a burning temperature, the activity in the anterior insula increases with the painful perception of temperature increase (Craig 2009). Others have argued that the insula is integrating representations of current and future perceptual states into a general subjective feeling state (Singer, Critchley, and Preuschoff 2009).

The notion that the insula plays a primary role in interoception, the perception of internal physiological states, is supported by its activity during pain, temperature, and itch perception (Craig 2002). While the posterior portion of the insula responds to the sensation of pain in

ourselves, it has been observed that the anterior insula responds to the experience of pain in ourselves and in others (Singer et al. 2004). The engagement of the anterior insula in empathic responses has been supported by a number of studies (Singer and Lamm 2009; Craig 2009). Intriguingly, activity in and thickness of the gray matter in the anterior insula corresponded with heightened interoceptive awareness (Critchley et al. 2004) and interoceptive awareness has been shown to be related to empathic ability (Singer, Critchley, and Preuschoff 2009). However, a proposed simulation role for the insula is undermined by recent findings that the anterior insula appears to be engaged even when a patient who is congenitally unable to experience pain is observing pain in others (Danziger, Faillenot, and Peyron 2009).

Some evidence suggests that the insula not only is active during our own physical pain or observation of physical pain in others, but also in the pain from social exclusion (Eisenberger, Lieberman, and Williams 2003) and the perception of social suffering in others (Immordino-Yang et al. 2009). The insula is often ascribed a role in the processing of disgust, whether experienced in the individual or perceived in others (Wicker, Keysers et al. 2003), however more recent work suggests that only a certain type of disgust activates the insula (Borg, Lieberman, and Kiehl 2008). Other studies show a role for the anterior insula when a person rejects unfair offers in the ultimatum game (Sanfey, Rilling et al. 2003). It is unclear whether the responsiveness of the insula in such cases is due to violations of social norms or to expectations of risk (Knutson and Bossaerts 2007). The complex pattern of activity in the insula strongly suggests that the insula plays a role in integrating our own feelings and experiencing the states of others, but the details of its role in social cognition have yet to be fully articulated.

Most of the work on empathy has studied connections for negative emotions like pain or disgust, but a greater affinity for a person also increases our experience of personal reward when

we see that person benefiting and is related to greater activity in the ventral striatum (Mobbs et al. 2009). The striatum is the largest component of the basal ganglia, which also includes the globus pallidus and substantia nigra. The striatum itself is comprised of the caudate, putamen, and nucleus accumbens. The most interesting function of the basal ganglia for social science is its role in reward, and thus decision-making and learning.

The basal ganglia have been well established as being involved in reward processing (Delgado 2007). Activity in these regions have been shown for both basic physical pleasures like food and more socially complex pleasures like giving either as charity or taxation (Harbaugh, Mayr, and Burghart 2007) or witnessing the suffering of an envied person (Takahashi et al. 2009). Neuroscientists have described hedonic "liking" processes that appear to be distinct from motivational "wanting" processes, but both appear to involve subcomponents of the basal ganglia (Walter et al. 2005; Smith et al. 2009). The basal ganglia are thus implicated in decision making (Balleine, Delgado, and Hikosaka 2007), but their role does not require conscious awareness. When subjects are subliminally flashed a symbol of a higher monetary value, their behavior can subconsciously respond as their striatum react (Pessiglione et al. 2007). In fact, direct neural recording shows that specific neurons will respond preferentially to the expected value of a choice (Samejima et al. 2005). Of particular interest, however, is that social phenomena like cooperating with a person appears to cause higher levels of activity than merely cooperating with a computer (Rilling et al. 2002; Rilling et al. 2004).

Because of their roles in valuation, reward, and decision-making, the basal ganglia are often implicated in neuro-economic studies. When individuals make decisions in the face of uncertainty (Platt and Huettel 2008; Rushworth and Behrens 2008), express socially relevant preferences (Fehr and Camerer 2007), encode value (Seymour and McClure 2008), play

economic games (Sanfey 2007; Krueger, Grafman, and McCabe 2008), build a reputation

(Izuma, Saito, and Sadato 2008), and compute the value of present versus future rewards

(Rangel, Camerer, and Montague 2008; Doya 2008; Kalenscher and Pennartz 2008) the basal

ganglia are typically involved. However, complicating matters is the clear evidence that distinct

neural systems underpin particular types of decision making, be they automatic or deliberative,

conscious or unconscious, fast or slow, associative or rule based, or affective or cognitive

(Sanfey and Chang 2008). There are multiple reward pathways through the basal ganglia

connecting to a variety of regions such as the amygdala, insula, prefrontal cortex, and anterior

cingulate. There is not a single place in the brain representing value and multiple circuits may be

involved in decision making that are even outside of the traditional reward pathways

(Rushworth, Mars, and Summerfield 2009).

Another brain region with important implications for decision-making is the anterior

cingulate cortex (ACC). The cingulate gyrus is a part of the limbic system and runs along the

midline of the brain below the neocortex. The portion closer to the forehead is known as the

anterior cingulate and has been shown to have an important role in both decision-making and the

detection of mental conflict. It has been described as an alarm system in the brain, notifying the

executive functions of the frontal lobe that a problem is worth conscious attention (van Veen and

Carter 2002; Carter and van Veen 2007). The ACC then is processing the decisions and

potential conflicts regardless of conscious attention. In fact, it appears to function with the insula

when an approaching an effortless coordination game, in contrast to the effortful dominance

solveable games (Kuo et al. 2009).

By attending to conflicts in mental states, decisions, and outcomes, the ACC plays a key

role in decision making (Botvinick 2007) as well as generating potential choices (Rushworth et

al. 2007). Single neuron recording studies demonstrate the role of neurons in the ACC

integrating choices and rewards (Williams et al. 2004). And, lesions in the ACC do not appear to

impair error detection, but do impair the integration of choices and consequences (Walton et al.

2007). In a related vein, the ACC also appears involved in cognitive dissonance and the

dissonance reduction attendant to attitude change (van Veen et al. 2009).

The ACC also activates in a number of social contexts (Dichter et al. 2009; Rudebeck,

Bannerman, and Rushworth 2008), as when we detect errors in the actions of others. The

intensity of the ACC activity when we detect other's errors appears to be modulated by whether

we feel affiliation with them (Newman-Norlund et al. 2009). The ACC also seems to be active

when we feel threatened by political candidates and do not vote for them (Spezio et al. 2008).

Similarly, while the pain of social exclusion activates the ACC (Eisenberger, Lieberman, and

Williams 2003) that activity is heightened when we are excluded by someone of the same race

(Krill and Platek 2009).

The change in ACC function by social salience is consistent with its role in a "salience

network" along with the fronto-insular cortex. This salience network is suggested as modulating

brain function between an attentional "central executive network" and the "default mode

network" (Sridharan, Levitin, and Menon 2008). Others have suggested that the rostral portion

of the ACC is particularly synchronized with the default mode network (Margulies et al. 2007).

This default mode network (DMN) was identified by Marcus Raichle after the insight of

looking for task independent deactivations (Gusnard and Raichle 2001; Raichle et al. 2001).

Rather than only looking to see what areas increased in activity when the brain went from being

at rest to focusing on a particular cognitive task, Raichle's innovation was to look for parts of the

brain that were very active during rest and then did little regardless of which task the brain was

engaged in. The discovery of the network, its robustness, and the intensity of its metabolic activity led to a well over a hundred subsequent investigations (Raichle and Snyder 2007).

Of particular interest was that the parts of the DMN actually did function as a network. Activity in the posterior cingulate (Fransson and Marrelec 2008) and the medial prefrontal appeared to be functionally connected and later investigation would show this corresponded with structural connectivity as well (Damoiseaux and Greicius 2009; Greicius et al. 2009). While the network can be consistently identified in subjects even after long periods of time (Meindl et al. 2009; Shehzad et al. 2009), it is subject to disruption. Deep sleep, for instance, decouples the DMN (Horovitz et al. 2009), even though it still maintained coherence under anesthesia (Martuzzi et al. 2010). More importantly, its function appeared to suffer under a variety of different mental disorders (Broyd et al. 2009), for instance autism (Iacoboni 2006; Kennedy, Redcay, and Courchesne 2006) and even in the induced stress from a catastrophic earthquake (Lui et al. 2009).

The dysfunction during autism and the fact that the DMN appeared only to truly activate during social tasks (Iacoboni et al. 2004; Rilling et al. 2008) has led to suggestions that the network is centrally important in social cognition (Schreiber 2007; Schilbach et al. 2008). Other suggestions have been that the DMN is important for sense of self (Gusnard et al. 2001; Wicker, Ruby et al. 2003), mind wandering (Mason et al. 2007), free will (Goldberg, Ullman, and Malach 2008), and moral judgment (Greene et al. 2001; Moll et al. 2007). One particularly nice experiment demonstrated the DMN activating (the social moral judgment task), at rest, and deactivating (the cognitively demanding Stroop task)(Harrison et al. 2008). Other work has shown that the DMN is engaged during sophisticated political judgment (Westen et al. 2006), but

deactivated during when political novices try to do the same task (Schreiber 2005; Fowler and Schreiber 2008).

While the posterior cingulate is now best known for its role in the DMN (Immordino-Yang et al. 2009), the medial prefrontal cortex (mPFC) has been known to be important for social cognition for quite a while. The disruption of Phineas Gage's social behavior (Macmillan 2000) when his medial prefrontal lobe was damaged (Ratiu et al. 2004) was an early clue. But early imaging work suggested a particularly important role for contemplating the mental states of others (Frith and Frith 1999; Frith and Frith 2006) and showed that people strategized about the choices of other people using the mPFC (McCabe et al. 2001). Other work showed the role of the mPFC in a variety of moral and ethical judgments (Greene et al. 2001; Cunningham et al. 2003; Heekeren et al. 2003). In particular, interpersonal connection appeared to discount purely utilitarian judgment (Greene et al. 2001) unless there was damage to the mPFC (Ciaramelli et al. 2007). Dehumanizing others diminishes the function of the region (Harris and Fiske 2006, 2007) and considering your place in an unstable social hierarchy activates it (Zink et al. 2008). It has been suggested that it is the anterior rostral portion of the mPFC that is particularly focused on both attending to our own mental states and those of others, while the posterior portion monitors the our actions and the orbital portion monitors the outcomes of choices (Amodio and Frith 2006). Others contend that the role of the mPFC in valuation can be contrasted with the role of the dorsolateral prefrontal cortex (DLPFC) in self-control (Hare, Camerer, and Rangel 2009).

More generally, the DLPFC is known for its role in executive function and making choices in the midst of conflicting considerations (Mansouri, Tanaka, and Buckley 2009; Wittfoth et al. 2009), for example in mixed strategy games (Barraclough, Conroy, and Lee 2004). The region is involved in deciding to punish others for their violations of social norms

(Sanfey, Rilling et al. 2003) and holding them responsible for those violations (Buckholtz et al. 2008). In a potentially related function, the DLPFC activates during self criticism, in contrast to the ventrolateral prefrontal cortex's (VLPFC) activation during self assurance (Longe et al. 2009).

This emotional regulation function of the VLPFC has been demonstrated in the context of tamping down amygdala activity in response to racial stimuli (Lieberman et al. 2005). The down regulation of the amygdala by the VLPFC is related to the degree of psychosocial resources a person has (Taylor et al. 2008). The interplay between the VLPFC and amygdala appears in a variety of different contexts (Lee and Siegle 2009).

In fact, it is important to keep in mind that contrary to a naïve modularity hypothesis, the brain regions described above are all involved in a series of sometimes overlapping networks. In addition to the DMN, there are at least eight other coherent networks that are functionally connected during rest, most of which have established structural connections as well (van den Heuvel et al. 2009). Much of our previous knowledge about this connectedness depended on dissection and animal models, but with techniques like DTI it is now possible to model structural connections in the same healthy subjects that are participating in the functional studies. And, although prior analysis of the functional data was biased by statistical models that had localization implicit in the design, more statistical approaches that model functional connectivity are being utilized. So while it is useful to attempt to discern the patterns in types of mental functions that recruit particular brain regions, it is also important to keep in mind that the brain is networked on both the micro and macro scales (van den Heuvel et al. 2008; Modha and Singh 2010).

The Nature of the Human Animal

Aristotle contended that we are, by nature, political animals. This assessment continues to be born out as SCAN develops our understanding of the human brain. We observe politics, however, in a wide variety of animals (see the Proctor and Brosnan chapter) and the deeper question of precisely what kind of political animal we are remains. Neuropolitics has the potential to aide in our answering that question. Exploring the function of the brain will reveal more about the mind and illuminate the political context it operates in.

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