SOCIAL COGNITIVE & AFFECTIVE FUNCTION: BEHAVIOR AND BRAIN SYSTEMS

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People are social animals. They play, work, eat, and compete with one another. Yet people differ greatly from one another in the number of relationships they form and maintain. In the smallest social circles people maintain between 6 and 20 emotionally close relationships (Dunbar and Spoors, 1995). In larger circles, composed of relatively weaker relationships in which people still individually know each network member, they may maintain between 100 and 300 relationships (Hill and Dunbar, 2003). The size of social networks has been shown to decrease with age (Fung et al., 2001; McPherson et al., 2006) and increase with level of education (Roberts et al., 2008), emotional intelligence (Austin et al., 2005), self-monitoring (Mehra et al., 2001), and propensity to connect with others . Yet contrary to what might be expected, there is no clear and consistent link between measures of personality, like extraversion, and social network size (Austin et al., 2005; Roberts et al., 2008).

For humans, larger social networks confer benefits. Individuals who participate in more relationships experience positive health outcomes, such as a lower susceptibility to the common cold (!!! INVALID CITATION !!! (Cohen, 2004; Cohen, et al., 1997)), whereas those who are more socially isolated are more susceptible to health problems . Although there are demonstrable benefits for belonging to larger social networks, forming and managing more relationships requires investing more cognitive and emotional resources. Indeed social network size seems to be constrained by limits in cognitive capacity (Stiller and Dunbar, 2007) and the emotional demands of each relationship (Roberts et al., 2010).

Social information is multifaceted, dynamic, and ambiguous. To cultivate social relationships people must monitor and detect social signals from one another that provide clues to their internal states and future behaviors, remember these for future reference, and generate interpersonal behavior accordingly. As we learn more about social function, it is becoming clear that multiple types of cognitive and affective processes contribute to social behavior.

As in other domains of cognition, social information processing relies initially on attending to, perceiving, and decoding relevant cues. Again as with other types of information, the nature and importance of social information is then determined by rapid, automatic emotion-driven mechanisms. Social information is further processed via more conscious and controlled mechanisms, involving reasoning about others' thoughts, emotions and intentions, while using acquired knowledge about social concepts and common sequences of behavior that typically occur in social interchanges. After perceiving and interpreting social information, a behavioral response is selected and enacted, often requiring executive and regulatory processes. This syllabus will provide a brief overview of fundamental social cognitive functions and their neuroanatomical correlates.

How do we detect and interpret socially-relevant information?
Sensory perceptual systems

The exchange of information between individuals—social signals—necessarily engages multiple sensory systems involved in detecting and interpreting this information. In humans, the detection of socially-relevant information relies heavily on visual and auditory processes, in addition to somatosensory and olfactory processes subserved by sensory systems. Ultimately, this sensory information converges on limbic cortical and subcortical structures that determine the relevance of social signals in the context of past experience and current and future goals.

In the visual domain, a number of cortical regions in humans and non-human primates appear specialized for the processing of specific types of social information. The fusiform gyrus contains a region called the "fusiform face area" that is engaged by a variety of types of visual information but more robustly by faces. The "extrastriate body area" in the lateral occipitotemporal cortex responds most robustly to images of parts of the body. The direction and movement of another person's eye gaze and so-called "biological movement" (such as postures and gait) are processed by the superior temporal sulcus. Once this information is detected in these occipitotemporal regions it is further processed along more rostral areas of the temporal cortex and prefrontal cortex in order to

more fully interpret its meaning and relevance. The amygdala plays a central role in further processing social visual information, receiving input from many of these regions as well as subcortical structures such as the superior colliculus, which may process some of this visual information in a rapid and potentially unconscious fashion.

Besides visual systems, other sensory systems are also critical to the processing of social signals. Auditory cortical regions—particularly unimodal and heteromodal regions in the superior temporal gyrus and sulcus bilaterally—respond more robustly to the sound of human voices than other sounds. Prosodic elements of speech perception appear to be processed by right temporal auditory regions. The touch of another person is processed not only by somatosensory cortices but also insular cortex, and the latter is particularly important for decoding somatosensory stimuli as pleasant or unpleasant. Although seemingly much less important in humans than many animals, the olfactory system also processes information relevant to social exchange.

Heteromodal association and paralimbic cortical regions in the anterior temporal lobe and medial and orbital prefrontal cortex perform important integrative operations on this sensory information, decoding its meaning based on emotion, general knowledge (semantic memory), and past experience (episodic memory), as well as the present context, needs, and goals (see the next sections). This information is then integrated and used to make decisions and take action.

How do we use sensory information in order to understand other people's minds?
Mirroring and theory of mind
A number of investigators have discussed the potential importance of "mirroring" or simulating other people's actions in our own minds as a means of communication. Some behavioral displays convey another person's intended goals while others convey their feelings. Observing someone else's emotion or pain typically causes a "mirroring" reaction that is thought to duplicate their experience within oneself, extending in some cases to automatic mimicry of the other person's facial expression and/or body posture. Anatomically, the anterior insula and the anterior cingulate cortex (ACC) are involved in our own experiences of emotion and in viewing others' emotions; the inferior frontal gyrus and inferior parietal lobule are involved in both our own movements and in simulating others' motor movements, including their facial displays. Some investigators believe that these systems provide a substrate for empathy via shared representations. This instinctive aspect of empathy, which can be seen in various forms in many other species, is thought to be supplemented in humans by additional higher cognitive abilities important for communication, including consciously taking another person's emotional perspective and making inferences about it—so-called theory of mind.

Theory of mind (ToM) refers to the awareness that other people have their own mental representations that are distinct from one's own. Distinguishing others' thoughts from one's own is partly subserved by the right temporoparietal junction (TPJ, the junction of the inferior parietal cortex and posterior temporal cortex), which attributes internal or external agency to an intention. Additionally, the medial prefrontal cortex (MPFC) is engaged in both self-referential thinking as well as imagining the perspective of others. Within the MPFC, a dorsal region is involved in taking another's cognitive perspective and in representing their typical behavior traits, while a ventral MPFC region, which is highly interconnected with limbic structures, represents and reasons about others' emotions.

How do we determine the relevance of this information?
Calculation of salience and value
In many situations including social interactions, we rapidly process sensory information and attempt to determine what other people are thinking, feeling, or intending to do. With all of this information, how do we quickly determine what is most relevant? The determination of the salience of information depends on a network of limbic subcortical and cortical structures including the insula and ACC, orbitofrontal cortex, amygdala, ventral striatum, and brainstem structures.

The lateral orbitofrontal cortex and amygdala are thought to receive sensory information about social and emotional stimuli from temporal cortex visual areas, update the reinforcement value of these cues according to the social context, and subsequently guide attention to gather more information from the environment (Rolls, 2007). Electrophysiological recording studies in monkeys for example demonstrate neurons in the amygdala, lateral orbitofrontal cortex, and temporal lobe visual areas responsive to facial identity (Rolls, 1984; Leonard et al., 1985; Hasselmo et al., 1989; Rolls et al., 2006; Rolls, 2007) and changeable aspects of faces like expressions, eye gaze, and lip movement (Baylis et al., 1985; Hasselmo et al., 1989; Haxby et al., 2002; Rolls, 2007), which all serve as signals for social communication. Task-based fMRI studies in humans demonstrate a similar topography of brain responses to socially salient features in the human face such as facial expressions (Morris et al., 1996; Phillips et al., 1997; Allison et al., 2000; Haxby et al., 2000; Winston et al., 2003), eye gaze (Kawashima et al., 1999; George et al., 2001; Richeson et al., 2008), facial identity (Iidaka et al., 2003; Schwartz et al., 2003;

Pourtois et al., 2005; Gobbini and Haxby, 2006; Wright and Liu, 2006), racial or group identity (Hart et al., 2000; Phelps et al., 2000; Phelps, 2001; Cunningham et al., 2004; Freeman et al., 2010), and trustworthiness (Winston et al., 2002; Engell et al., 2007; Todorov et al., 2008; Todorov and Engell, 2008; Said et al., 2009; Bzdok et al., 2011).

      Primary processing of sensory information is tuned by the salience system: for example, increased visual acuity is linked to enhanced activity in the amygdala (Lim et al., 2009) and visual cortex including area V1 (Padmala and Pessoa, 2008), where the amygdala might directly modulate visual cortex responses to relevant stimuli.

      The representation of value or salience is further performed by structures including the insula and orbitofrontal cortex. The insula is specifically involved in representing information about the "internal mileu" of the body at a given moment, thereby enabling the relevance of information to be determined in relation to a person's current needs.   The orbitofrontal cortex also contributes to the interpretation of information in the current context. In addition to representing the positive (rewarding) or negative (aversive) value of information, the orbitofrontal cortex continuously updates this value based on the outcome of actions. Many other structures are involved in approach and avoidance behavior, including the nucleus accumbens (reward) and fear or threat (amygdala).

How do we know how to behave in different situations?
Social episodic and semantic memory
Like all experience, we learn about social concepts from our own experience and from the collective experiences or normative rules. Episodic memory systems are critical for learning and remembering information about other people and the contexts in which we have encountered them. The hippocampus and other medial temporal lobe structures are critical for episodic memory for both social and non-social information. Semantic memory systems are essential for learning about societal rules, etiquette, and how to interpret others' social signals. Anterior and ventrolateral temporal cortices, as well as medial and lateral prefrontal cortices, are critical for these forms of memory.

How do we make decisions about social actions and carry them out?
Regulation of comportment and social decision making
Ultimately, all of the processing power that is used to understand other people is then put to use when we make decisions about how to act. In certain situations, substantial executive control and response inhibition may be necessary in order to regulate behavior appropriately for the context. Dorsolateral prefrontal cortex and ventrolateral prefrontal cortex are key regions that are critical to the regulation of emotion and play important roles in the execution of appropriate social behavior. Anterior cingulate cortex is also important for monitoring conflicts and errors and for response inhibition.

      Several investigators have recently developed highly consistent neurobehavioral models that implicate many of these structures in social judgment and decision-making (Moll et al., 2005a; Sanfey, 2007; Rilling et al., 2008; Moll and Schulkin, 2009; Rilling and Sanfey, 2011). These neural models for social judgment and decision-making were derived primarily from lines of human neuroimaging and neuropsychological work examining the neural correlates of social interaction and morality. This body of work demonstrates a partial separation in the neural correlates of social affiliative and avoidant judgments and decisions.

      Some regions associated with reward are responsive to pictures of loved ones and positive social feedback (e.g. complimentary peer reviews or cooperation from a partner) that elicit prosocial sentiments (e.g. compassion or empathy) and in turn motivate decisions to behave altruistically and cooperate (e.g. donation to charities or repaying trust in kind). For example, in neuroimaging studies when people look at pictures of their own babies or romantic partners the ventral tegmental and striatal areas (Bartels and Zeki, 2004; Aron et al., 2005) as well as the amygdala (Leibenluft et al., 2004) demonstrate increased activity. Stimuli and scenarios that elicit prosocial sentiments like compassion, guilt, pity, gratitude, and pride also activate structures within the social affiliation network including the ventromedial prefrontal cortex, subgenual anterior cingulate cortex, ventral striatum, as well as septal and hypothalamic areas (Takahashi et al., 2004; Moll et al., 2007; Zahn et al., 2009a; Zahn et al., 2009b). Similarly, receiving fair treatment from other people in simulated social interactions or positive peer evaluation evokes neural responses in ventromedial prefrontal and mesolimbic structures (Izuma et al., 2008) as well as the amygdala (Tabibnia et al., 2008). These regions also demonstrate increases in activity when people make prosocial decisions such as choosing to treat others fairly or cooperate with them during simulated social interactions (Rilling et al., 2002; Rilling et al., 2004; Delgado et al., 2005; King-Casas et al., 2005; Li et al., 2009) or when deciding to donate money to charitable causes (Moll et al., 2006; Harbaugh et al., 2007; Izuma et al., 2009).

In contrast, regions associated with aversive behavior are responsive to untrustworthy-appearing faces and negative social feedback (e.g. disapproval or violations of trust) that elicit sentiments of social aversion (e.g. disgust or contempt) and in turn motivate decisions to defect cooperation or disengage from a group. For example, the amygdala is consistently activated when participants view faces that appear untrustworthy (Winston et al., 2002; Engell et al., 2007; Todorov et al., 2008; Todorov and Engell, 2008; Willis et al., 2010). Stimuli or scenarios that elicit sentiments of social aversion like disgust, contempt, and anger or indignation preferentially activate some of these areas (Phillips et al., 1998; Rizzolatti et al., 2003; Decety et al., 2004; Moll et al., 2005b; Moll et al., 2007; Buckholtz et al., 2008; Zahn et al., 2009b). Similarly, negative social feedback activates the caudal anterior cingulate cortex and ventral anterior insula (Klucharev et al., 2009), and participants who exhibit the greatest increases in caudal anterior cingulate cortex activity change their behavior most in response to the negative social feedback. Similarly, activity in the ventral anterior insula, which is elicited by unfairness (Sanfey, 2007), social exclusion (Eisenberger et al., 2003), and unreciprocated cooperation (Rilling et al., 2008) predicts the likelihood that participants will reject cooperation with someone who has treated them unfairly in a previous simulated interaction (Sanfey et al., 2003). The caudolateral orbitofrontal cortex and neighboring ventral anterior insula display activation when participants decide not to donate to charitable causes (Moll et al., 2006). In addition, recent neuroimaging studies reveal that in addition to pain responsive areas in the caudal anterior cingulate cortex and anterior thalamus, dorsal and posterior sectors of the insula and its neighboring parietal operculum, which includes the secondary somatosensory cortex, also demonstrate responses to second hand pain, actual pain, and the pain of social rejection (Decety et al., 2006; Eisenberger et al., 2006; Cheng et al., 2007; Kross et al., 2007; Moriguchi et al., 2007; Benuzzi et al., 2008; Cheng et al., 2008; Decety and Lamm, 2008; Akitsuki and Decety, 2009)

Further Reading
Adolphs, R. (2009). The social brain: Neural basis of social knowledge. *Annual Review of Psychology, 60*, 693-716.
Dickerson BC (2015) Dysfunction of social cognition and behavior. Continuum (Minneap Minn) 21:660-677.
Frith, C. D. (2008). Social cognition. *Philosophical Transactions of the Royal Society of London.Series B, Biological Sciences, 363*(1499), 2033-2039.
Lieberman, M. D. (2007). Social cognitive neuroscience: A review of core processes. *Annual Review of Psychology, 58*, 259-289.
Sollberger, M., Rankin, K. P., & Miller, B. L. (2010). Social cognition. *Continuum Lifelong Learning Neurol, 16*(4), 69-85.

Detailed bibliography

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(!!! INVALID CITATION !!! (Cohen, 2004; Cohen, et al., 1997)).
Akitsuki Y, Decety J (2009) Social context and perceived agency affects empathy for pain: an event-related fMRI investigation. Neuroimage 47:722-734.
Allison T, Puce A, McCarthy G (2000) Social perception from visual cues: role of the STS region. Trends Cogn Sci 4:267-278.
Aron A, Fisher H, Mashek DJ, Strong G, Li H, Brown LL (2005) Reward, motivation, and emotion systems associated with early-stage intense romantic love. J Neurophysiol 94:327-337.
Austin EJ, Saklofske DH, Egan V (2005) Personality, well-being and health correlates of trait emotional intelligence. Personality and Individual Differences 38:547-558.
Bartels A, Zeki S (2004) The neural correlates of maternal and romantic love. Neuroimage 21:1155-1166.
Baylis GC, Rolls ET, Leonard CM (1985) Selectivity between faces in the responses of a population of neurons in the cortex in the superior temporal sulcus of the monkey. Brain Res 342:91-102.
Benuzzi F, Lui F, Duzzi D, Nichelli PF, Porro CA (2008) Does it look painful or disgusting? Ask your parietal and cingulate cortex. J Neurosci 28:923-931.
Buckholtz JW, Asplund CL, Dux PE, Zald DH, Gore JC, Jones OD, Marois R (2008) The neural correlates of third-party punishment. Neuron 60:930-940.
Bzdok D, Langner R, Caspers S, Kurth F, Habel U, Zilles K, Laird A, Eickhoff SB (2011) ALE meta-analysis on facial judgments of trustworthiness and attractiveness. Brain Structure & Function 215:209-223.
Cheng Y, Yang CY, Lin CP, Lee PL, Decety J (2008) The perception of pain in others suppresses somatosensory oscillations: a magnetoencephalography study. Neuroimage 40:1833-1840.
Cheng Y, Lin CP, Liu HL, Hsu YY, Lim KE, Hung D, Decety J (2007) Expertise modulates the perception of pain in others. Curr Biol 17:1708-1713.

Cunningham WA, Johnson MK, Raye CL, Chris Gatenby J, Gore JC, Banaji MR (2004) Separable neural components in the processing of black and white faces. Psychol Sci 15:806-813.

Decety J, Lamm C (2008) Is the extrastriate body area (EBA) sensitive to the perception of pain in others? Cerebral Cortex 18:2369-2373.

Decety J, Jackson PL, Brunet E, Meltzoff AN (2006) Empathy examined through the neural mechanisms involved in imagining how I feel versus how you feel pain. Neuropsychologia 44:752-761.

Decety J, Jackson PL, Sommerville JA, Chaminade T, Meltzoff AN (2004) The neural bases of cooperation and competition: an fMRI investigation. Neuroimage 23:744-751.

Delgado M, Frank R, Phelps E (2005) Perceptions of moral character modulate the neural systems of reward during the trust game. Nature neuroscience 8.

Dickerson BC (2015) Dysfunction of social cognition and behavior. Continuum (Minneap Minn) 21:660-677.

Dunbar RIM, Spoors M (1995) Social Networks, Support Cliques, and Kinship. Human Nature-an Interdisciplinary Biosocial Perspective 6:273-290.

Eisenberger NI, Lieberman MD, Williams KD (2003) Does rejection hurt? An FMRI study of social exclusion. Science 302:290-292.

Eisenberger NI, Jarcho JM, Lieberman MD, Naliboff BD (2006) An experimental study of shared sensitivity to physical pain and social rejection. Pain 126:132-138.

Engell AD, Haxby JV, Todorov A (2007) Implicit trustworthiness decisions: automatic coding of face properties in the human amygdala. J Cogn Neurosci 19:1508-1519.

Freeman JB, Schiller D, Rule NO, Ambady N (2010) The neural origins of superficial and individuated judgments about ingroup and outgroup members. Hum Brain Mapp 31:150-159.

Fung HH, Carstensen LL, Lang FR (2001) Age-related patterns in social networks among European Americans and African Americans: Implications for socioemotional selectivity across the life span. International Journal of Aging & Human Development 52:185-206.

George N, Driver J, Dolan RJ (2001) Seen gaze-direction modulates fusiform activity and its coupling with other brain areas during face processing. Neuroimage 13:1102-1112.

Gobbini MI, Haxby JV (2006) Neural response to the visual familiarity of faces. Brain Res Bull 71:76-82.

Harbaugh WT, Mayr U, Burghart DR (2007) Neural responses to taxation and voluntary giving reveal motives for charitable donations. Science 316:1622-1625.

Hart AJ, Whalen PJ, Shin LM, McInerney SC, Fischer H, Rauch SL (2000) Differential response in the human amygdala to racial outgroup vs ingroup face stimuli. Neuroreport 11:2351-2355.

Hasselmo ME, Rolls ET, Baylis GC (1989) The role of expression and identity in the face-selective responses of neurons in the temporal visual cortex of the monkey. Behav Brain Res 32:203-218.

Haxby JV, Hoffman EA, Gobbini MI (2000) The distributed human neural system for face perception. Trends Cogn Sci 4:223-233.

Haxby JV, Hoffman EA, Gobbini MI (2002) Human neural systems for face recognition and social communication. Biol Psychiatry 51:59-67.

Hill RA, Dunbar RIM (2003) Social network size in humans. Human Nature-an Interdisciplinary Biosocial Perspective 14:53-72.

Iidaka T, Terashima S, Yamashita K, Okada T, Sadato N, Yonekura Y (2003) Dissociable neural responses in the hippocampus to the retrieval of facial identity and emotion: an event-related fMRI study. Hippocampus 13:429-436.

Izuma K, Saito DN, Sadato N (2008) Processing of social and monetary rewards in the human striatum. Neuron 58:284-294.

Izuma K, Saito DN, Sadato N (2009) Processing of the incentive for social approval in the ventral striatum during charitable donation. J Cogn Neurosci 22:621-631.

Kawashima R, Sugiura M, Kato T, Nakamura A, Hatano K, Ito K, Fukuda H, Kojima S, Nakamura K (1999) The human amygdala plays an important role in gaze monitoring. A PET study. Brain 122 (Pt 4):779-783.

King-Casas B, Tomlin D, Anen C, Camerer CF, Quartz SR, Montague PR (2005) Getting to know you: reputation and trust in a two-person economic exchange. Science 308:78-83.

Klucharev V, Hytonen K, Rijpkema M, Smidts A, Fernandez G (2009) Reinforcement learning signal predicts social conformity. Neuron 61:140-151.

Kross E, Egner T, Ochsner K, Hirsch J, Downey G (2007) Neural dynamics of rejection sensitivity. J Cogn Neurosci 19:945-956.

Leibenluft E, Gobbini MI, Harrison T, Haxby JV (2004) Mothers' neural activation in response to pictures of their children and other children. Biol Psychiatry 56:225-232.

Leonard CM, Rolls ET, Wilson FA, Baylis GC (1985) Neurons in the amygdala of the monkey with responses selective for faces. Behav Brain Res 15:159-176.

Li J, Xiao E, Houser D, Montague PR (2009) Neural responses to sanction threats in two-party economic exchange. Proc Natl Acad Sci U S A 106:16835-16840.

Lim SL, Padmala S, Pessoa L (2009) Segregating the significant from the mundane on a moment-to-moment basis via direct and indirect amygdala contributions. Proc Natl Acad Sci U S A 106:16841-16846.

McPherson M, Smith-Lovin L, Brashears ME (2006) Social isolation in America: Changes in core discussion networks over two decades. American Sociological Review 71:353-375.

Mehra A, Kilduff M, Brass DJ (2001) The social networks of high and low self-monitors: Implications for workplace performance. Administrative Science Quarterly 46:121-146.

Moll J, Schulkin J (2009) Social attachment and aversion in human moral cognition. Neuroscience and Biobehavioral Reviews 33:456-465.

Moll J, Zahn R, de Oliveira-Souza R, Krueger F, Grafman J (2005a) Opinion: the neural basis of human moral cognition. Nat Rev Neurosci 6:799-809.

Moll J, Krueger F, Zahn R, Pardini M, de Oliveira-Souzat R, Grafman J (2006) Human fronto-mesolimbic networks guide decisions about charitable donation. Proceedings of the National Academy of Sciences of the United States of America 103:15623-15628.

Moll J, de Oliveira-Souza R, Moll FT, Ignacio FA, Bramati IE, Caparelli-Daquer EM, Eslinger PJ (2005b) The moral affiliations of disgust: a functional MRI study. Cogn Behav Neurol 18:68-78.

Moll J, de Oliveira-Souza R, Garrido GJ, Bramati IE, Caparelli-Daquer EMA, Paiva MLMF, Zahn R, Grafman J (2007) The self as a moral agent: Link-ling the neural bases of social agency and moral sensitivity. Social Neuroscience 2:336-352.

Moriguchi Y, Decety J, Ohnishi T, Maeda M, Mori T, Nemoto K, Matsuda H, Komaki G (2007) Empathy and judging other's pain: an fMRI study of alexithymia. Cereb Cortex 17:2223-2234.

Morris JS, Frith CD, Perrett DI, Rowland D, Young AW, Calder AJ, Dolan RJ (1996) A differential neural response in the human amygdala to fearful and happy facial expressions. Nature 383:812-815.

Padmala S, Pessoa L (2008) Affective learning enhances visual detection and responses in primary visual cortex. J Neurosci 28:6202-6210.

Phelps EA (2001) Faces and races in the brain. Nat Neurosci 4:775-776.

Phelps EA, O'Connor KJ, Cunningham WA, Funayama ES, Gatenby JC, Gore JC, Banaji MR (2000) Performance on indirect measures of race evaluation predicts amygdala activation. J Cogn Neurosci 12:729-738.

Phillips ML, Young AW, Scott SK, Calder AJ, Andrew C, Giampietro V, Williams SC, Bullmore ET, Brammer M, Gray JA (1998) Neural responses to facial and vocal expressions of fear and disgust. Proc Biol Sci 265:1809-1817.

Phillips ML, Young AW, Senior C, Brammer M, Andrew C, Calder AJ, Bullmore ET, Perrett DI, Rowland D, Williams SC, Gray JA, David AS (1997) A specific neural substrate for perceiving facial expressions of disgust. Nature 389:495-498.

Pourtois G, Schwartz S, Seghier ML, Lazeyras F, Vuilleumier P (2005) Portraits or people? Distinct representations of face identity in the human visual cortex. J Cogn Neurosci 17:1043-1057.

Richeson JA, Todd AR, Trawalter S, Baird AA (2008) Eye-gaze direction modulates race-related amygdala activity. Group Processes & Intergroup Relations 11:233-246.

Rilling J, Gutman D, Zeh T, Pagnoni G, Berns G, Kilts C (2002) A neural basis for social cooperation. Neuron 35:395-405.

Rilling JK, Sanfey AG (2011) The Neuroscience of Social Decision-Making. In: Annual Review of Psychology, Vol 62, pp 23-48.

Rilling JK, King-Casas B, Sanfey AG (2008) The neurobiology of social decision-making. Curr Opin Neurobiol 18:159-165.

Rilling JK, Sanfey AG, Aronson JA, Nystrom LE, Cohen JD (2004) Opposing BOLD responses to reciprocated and unreciprocated altruism in putative reward pathways. Neuroreport 15:2539-2543.

Rizzolatti G, Wicker B, Keysers C, Plailly J, Royet JP, Gallese V (2003) Both of us disgusted in My Insula: The common neural basis of seeing and feeling disgust. Neuron 40:655-664.

Roberts SGB, Wilson R, Fedurek P, Dunbar RIM (2008) Individual differences and personal social network size and structure. Personality and Individual Differences 44:954-964.

Rolls ET (1984) Neurons in the cortex of the temporal lobe and in the amygdala of the monkey with responses selective for faces. Hum Neurobiol 3:209-222.

Rolls ET (2007) The representation of information about faces in the temporal and frontal lobes. Neuropsychologia 45:124-143.

Rolls ET, Critchley HD, Browning AS, Inoue K (2006) Face-selective and auditory neurons in the primate orbitofrontal cortex. Exp Brain Res 170:74-87.

Said CP, Baron SG, Todorov A (2009) Nonlinear amygdala response to face trustworthiness: contributions of high and low spatial frequency information. J Cogn Neurosci 21:519-528.

Sanfey AG (2007) Social decision-making: insights from game theory and neuroscience. Science 318:598-602.

Sanfey AG, Rilling JK, Aronson JA, Nystrom LE, Cohen JD (2003) The neural basis of economic decision-making in the Ultimatum Game. Science 300:1755-1758.

Schwartz CE, Wright CI, Shin LM, Kagan J, Whalen PJ, McMullin KG, Rauch SL (2003) Differential amygdalar response to novel versus newly familiar neutral faces: a functional MRI probe developed for studying inhibited temperament. Biol Psychiatry 53:854-862.

Stiller J, Dunbar RIM (2007) Perspective-taking and memory capacity predict social network size. Social Networks 29:93-104.

Tabibnia G, Satpute AB, Lieberman MD (2008) The sunny side of fairness: preference for fairness activates reward circuitry (and disregarding unfairness activates self-control circuitry). Psychol Sci 19:339-347.

Takahashi H, Yahata N, Koeda M, Matsuda T, Asai K, Okubo Y (2004) Brain activation associated with evaluative processes of guilt and embarrassment: an fMRI study. Neuroimage 23:967-974.

Todorov A, Engell AD (2008) The role of the amygdala in implicit evaluation of emotionally neutral faces. Soc Cogn Affect Neurosci 3:303-312.

Todorov A, Baron SG, Oosterhof NN (2008) Evaluating face trustworthiness: a model based approach. Soc Cogn Affect Neurosci 3:119-127.

Willis ML, Palermo R, Burke D, McGrillen K, Miller L (2010) Orbitofrontal cortex lesions result in abnormal social judgements to emotional faces. Neuropsychologia 48:2182-2187.

Winston JS, O'Doherty J, Dolan RJ (2003) Common and distinct neural responses during direct and incidental processing of multiple facial emotions. Neuroimage 20:84-97.

Winston JS, Strange BA, O'Doherty J, Dolan RJ (2002) Automatic and intentional brain responses during evaluation of trustworthiness of faces. Nat Neurosci 5:277-283.

Wright P, Liu Y (2006) Neutral faces activate the amygdala during identity matching. Neuroimage 29:628-636.

Zahn R, de Oliveira-Souza R, Bramati I, Garrido G, Moll J (2009a) Subgenual cingulate activity reflects individual differences in empathic concern. Neuroscience Letters 457:107-110.

Zahn R, Moll J, Paiva M, Garrido G, Krueger F, Huey ED, Grafman J (2009b) The Neural Basis of Human Social Values: Evidence from Functional MRI. Cerebral Cortex 19:276-283.

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