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The role of facial expressions in social interactions

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Computation of emotions in man and machines

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Abstract

The expressions we see in the faces of others engage a number of different cognitive processes. Emotional expressions elicit rapid responses, which often imitate the emotion in the observed face. These effects can even occur for faces presented in such a way that the observer is not aware of them. We are also very good at explicitly recognising and describing the emotion being expressed. A recent study, contrasting human and humanoid robot facial expressions, suggests that people can recognise the expressions made by the robot explicitly, but may not show the automatic, implicit response. The emotional expressions presented by faces are not simply reflexive, but also have a communicative component. For example, empathic expressions of pain are not simply a reflexive response to the sight of pain in another, since they are exaggerated when the empathiser knows he or she is being observed. It seems that we want to people to know that we are empathic. Of especial importance among facial expressions are ostensive gestures, such as the eyebrow flash, that indicate the intention to communicate. These gestures indicate first, that the sender is to be trusted, and second, that that any following signals are of importance to the receiver.

Key words: Emotion, face, awareness, communication

1. Multiple systems of emotion recognition

It has become increasingly apparent, initially from studies of neurological patients with circumscribed brain damage, that much, if not most, information processing occurs in the brain without any accompanying conscious experience. The final products of this information processing often become available to consciousness, but in many cases these unconscious processes can control behaviour without any need for awareness. The most dramatic example of this is blind sight (Weiskrantz & Warrington, 1975). In such cases patients have damage to primary visual cortex, which renders them blind in the associated part of the visual field. Nevertheless, if a stimulus is rapidly moved, for example, across this blind field, the patient is able to 'guess' the direction of this movement considerably better than chance. Another example is patient DF who, as a result of damage to inferior temporal cortex is also effectively blind, since, she is unable to recognise of objects from their shape (Goodale, Milner, Jakobson, & Carey, 1991). In spite of this problem, when she reaches for an object, she shapes her hand to match the shape of the object. In her case information about the shape of objects is available to achieve appropriate grasping behaviour, but does not enter consciousness.

Subsequent to these demonstrations, the same phenomena have been demonstrated in healthy volunteers. Behavioural studies have demonstrated that we are aware of far less of the visual world than we realise (e.g. change blindness (Rensink, Oregan, & Clark, 1997) and inattentional blindness (Mack & Rock, 1998). Furthermore, we make accurate reaching and grasping movements *before* we become aware of the stimuli that are eliciting these movements (Castiello, Paulignan, & Jeannerod, 1991; Pisella *et al.*, 2000) and can be influenced by the meanings of words that we are not aware of having seen (Marcel, 1983). Brain imaging studies have also confirmed that stimuli of which volunteers are unaware, nevertheless elicit activity in the brain (e.g. Beck, Rees, Frith, & Lavie, 2001) and that this activity can be observed up to and including those areas associated with the processing of meaning (e.g. Dehaene *et al.*, 1998).

These results reveal that there are at least two processes through which sensory signals can be converted into behaviour: one of which is associated with consciousness while the other is not. These processes seem to occur in parallel, rather than the unconscious

processing being the early stage of a route to consciousness. Different kinds of information seem to be extracted by the two routes. For example, when reaching and grasping I need information about the shape of the object I am planning to grasp, but this information requires an egocentric perspective. The precise nature of the reach and grasp depends on the precise spatial relationship between me and the object. In contrast, when I recognise an object from its shape I need information about the shape of the object that is independent of my current viewpoint, so that the object can be identified even from an unusual view (Schenk, 2006). Thus these two perceptual routes seem to have have different functions.

It is, of course, an oversimplification to suggest that there are just two independent routes to action. There are likely to be many routes and, furthermore, there will be interactions between these routes (see, for example, Braddick et al, 2000). However, there remains the important distinction between those routes that lead to conscious awareness and those that do not (Frith et al., 1999). The question as to why only some routes are associated with consciousness is a subject of great interest, but will not be addressed in any detail in this paper. Our intuition is that consciousness has a very important role in our behaviour, but it is surprisingly difficult to define precisely what this role might be. It is certainly not the case that processing that leads to consciousness is, in some sense, better than processing that does not lead to consciousness. Some tasks are better learned without awareness (e.g. Fletcher et al., 2005). Introspection about the sources of our behaviour can be very misleading (e.g. Johansson et al., 2005). In the social domain, as we shall see later is this essay, the same signal can have very different effects depending upon whether or not it reaches consciousness. The role of consciousness in our response to emotions is equally complex and poorly understood.

In contrast the role of unconscious processes are perhaps slightly better understood. Unconscious routes to action seem to apply when responses need to be made with great rapidity. For example, the two routes are engaged by stimuli that induce fear (LeDoux, 2000). I will jump out of the way of the snake-like object in the path before I become aware that it is only a bent stick. In this case there is a clear survival advantage for responding rapidly to a signal of danger, even when the signal has been incorrectly interpreted. In the rest of this paper I shall be concerned with the use of various kinds of

facial expressions as signals, which can also be processed with and without consciousness.

2. Emotional contagion: the covert imitation of facial expressions

Social interactions depend upon complex signals in many modalities. For human interactions, however, spoken language plays such an important role that we often forget about the importance of non-verbal signals. Among these non-verbal signals, facial expressions have a major part in social interactions (Adolphs, 1999; but see de Gelder, this volume). I shall first consider the facial signals that are processed without awareness. The sight of a human face expressing fear elicits fearful responses in the observer, as indexed by increases in autonomic markers of arousal (Ohman & Soares, 1998) and increased activity in the amygdala (Morris *et al.*, 1996). This effect occurs even when the observer is unaware of the expression on the face because it has been *masked* (see Pessoa, 2005 for review). The process by which the sight of a fearful face elicits fear in the observer is an example of a more general effect known as mirroring or contagion, whereby an observer tends to covertly and unconsciously mimic the behaviour of the person being observed. This effect occurs for a whole range of behaviours: facial expressions (Dimberg, Thunberg, & Elmehed, 2000), limb movements (Kilner, Paulignan, & Blakemore, 2003), gestures (Chartrand & Bargh, 1999) and many aspects of speech (Pickering & Garrod, 2004). Although, as will be discussed below, the magnitude of this automatic mimicry is modulate by a number of factors including the social context and the relationship between the observed and the observer (Bourgeois & Hess, 2008)

There are many advantages from this mirroring behaviour. In the case of speech, the mirroring creates a greater alignment of the communicants, in terms of vocabulary and grammar, which facilitates communication. Experiments on the imitation of gestures during conversations show that the person imitated feels more friendly towards to the other speaker and subsequently behaves in a more prosocial manner (e.g. is more likely to give money to a charity van Baaren, Holland, Kawakami, & van Knippenberg, 2004).

However, these effects probably only occur when the person is unaware of the imitation (Lakin & Chartrand, 2003). This in an interesting case where the effect of the signals

seem to be very different depending on whether or not they are consciously perceived.

Ideas about the advantages accruing from the unconscious imitation of facial expressions are more speculative. The sight of a fearful face is likely to be a cue that there is something to be afraid of and that the observer should therefore be vigilant. Furthermore, the facial expression of fear enhances vigilance: the widening of the eyes increases the size if the visual field, while the widening of the nostrils increases inspirational capacity and enhances the sense of smell (Susskind *et al.*, 2008). Thus, by imitating the expression of fear we increase our sensitivity to sensory signals and become more vigilant. In contrast, the expression of disgust is a cue that there is some noxious substance to be avoided. The facial expression of disgust has the opposite effect to that of fear. The eyes are narrowed, reducing the size of the visual field, and the nose is wrinkled, narrowing the nasal passages and reducing the exposure to smells. By imitating the expression of disgust we reduce the impact of potential noxious stimuli.

A problem in need of further research concerns the mechanism by which people can covertly recognise facial expressions of emotion in masked faces that they are not aware of seeing (Dimberg *et al.*, 2000). There is some evidence that such recognition depends upon subcortical pathways to the amygdala (via superior colliculus and pulvinar) that bypass primary visual cortex (Morris, Ohman, & Dolan, 1999). This idea is supported by the demonstration that a patient (GY) with severe damage to left occipital cortex can, nevertheless, recognise (i.e. make better than chance guesses) emotional facial expressions in his blind visual field (de Gelder, Vroomen, Pourtois, & Weiskrantz, 1999). Further evidence for this speculation comes from studies of the role of different spatial frequencies in face recognition. Vuilleumier et al (2003) showed that activity in the fusiform cortex was linked with facial identity with high spatial frequency presentation, while amygdala activity was linked with facial emotion with low spatial frequency presentation. Recognising the expression of masked faces via a subcortical route may therefore depend upon signals about the face carried by low spatial frequencies. One interesting possibility is that the critical sign of a fearful face is the area of white round the eye, which is greater when the eyes are opened wide. Whalen et al (Whalen *et al.*, 2004) showed that amygdala activity was elicited by masked fearful faces even when all information, but the eye whites, was removed. It remains to be shown how this sign can

be so rapidly extracted from the visual signal in the absence of cortical processing.

It is not only facial expressions of emotion that are processed rapidly and without awareness. Gaze direction is another important facial cue when observing the behaviour of others. We are very sensitive to eye gaze direction and can discover the target of the gaze with great accuracy (Anstis, Mayhew, & Morley, 1969). This ability enables us to discover who or what people are looking at and may reveal their interests and intentions. Eye gaze direction has been used as a cue on the covert attention tasks. In these tasks, volunteers must detect a target that appears briefly to the left or right of fixation. Prior to the presentation of the target, a central cue is presented, for example, an arrow pointing left or right. The reaction time to detect the target is modulated by this cue, being faster when the cue is congruent with the target location and slower when it is incongruent. Typically congruent cues are presented on 80% of trials and incongruent cues on 20% of trials. If a face with eyes gazing left or right is used as the cue the same congruency effect is found (Driver *et al.*, 1999). Strikingly, however, this congruency effect occurs even if the eyes gaze consistently in the wrong direction. Bayliss & Tipper (2006) used a series of faces as cues in a covert attention task. The eye gaze direction in some faces was always congruent with the location of the following target, while other faces always looked in the incongruent direction. The effect of gaze on time to detect targets was unaffected by the identity of the faces. In other words, the volunteers attended in the direction indicated by the eye gaze even for the faces of individuals who consistently looked in the wrong direction. This result suggests that our tendency to follow the gaze direction of others is automatic and difficult to suppress. On the other hand, volunteers did learn something about the individuals. The faces that consistently gave invalid cues were rated as less trustworthy.

3. Explicit recognition of expressions

In parallel with the unconscious face processing route there is a conscious route, which is engaged, for example, when volunteers are explicitly asked to identify facial identities or facial expressions. Evidence that these two routes are indeed parallel comes from the study of patients who have acquired the inability to recognise faces (prosopagnosia) as the result of brain injury, usually to the right temporal lobe (Calder & Young, 2005). Such patients usually have difficulty identifying facial expressions also. However, there

is evidence that these patients still show covert recognition of faces. For example, Tranel et al. (1988) describe four patients with prosopagnosia resulting from occipito-temporal lesions, who all showed covert recognition in terms of larger SCRs for familiar faces. In other words, although they were unable to identify familiar faces, presentation of these faces elicited an emotional response. Further evidence for the two routes comes from patients with Capgras syndrome. This syndrome can occur both in psychiatric conditions and as a result of structural brain damage. Capgras patients are able to identify a familiar person's face. However, they believe that highly familiar people have replaced by impostors, doubles or aliens, and they often hold this belief with extreme conviction (Ellis & Lewis, 2001). Ellis & Young (1990) suggested that Capgras syndrome is the result of damage to an affective route to face recognition and is thus the mirror image of prosopagnosia. They recognize the face of a familiar person but do not experience the emotional response that normally accompanies such recognition. As a result the face does not 'feel' right. In agreement with this idea it has been shown that Capgras patients do not show enhanced SCR responses to familiar faces (Ellis, Young, Quayle, & De Pauw, 1997).

My colleagues, led by Thierry Chaminade have recently completed an imaging study in which volunteers were shown a variety of dynamic facial expressions displayed by a person or by a robot (humanoid robot WE-4RII, Takanishi lab). This robot incorporates a simplified version of the facial Action Units identified by Ekman & Friesen (1978) and can display anger, joy and disgust. Our volunteers had no difficulty in recognising the expressions made by the robot. The neural activity elicited by the facial expressions of this robot remain to be determined. An interesting possibility is that activity in areas such as the amygdala, which are associated with emotional responses, will not be elicited by robots. Such a pattern of responses would have obvious parallels with the case of Capgras syndrome discussed above. Here the patient sees a human face and recognize identities and expressions, but feels no emotional resonance. In many cases the patient believes that the person in question has been replaced by a robot (Ellis & Lewis, 2001). It may turn out the phenomenology described by the patient is correct in the sense that the experience is indeed like that elicited by observing a robot.

This speculation suggests that the observation of robots may not automatically elicit the

contagious mimicry that occurs when we observe other people. There is some evidence in favour of this speculation. As mentioned above, Kilner et al. (2003) showed that observation of a another person's incompatible movements interfered with the subject's own movements. However, this interference did not occur when the incompatible movements were made by a robot arm. On the other hand there is evidence that automatic alignment increases when we interact with artificial agents just as it does when we interact with people. Oviatt, Darves & Coulston (2004) showed that childrens' speech reliably and flexibly converged in terms of a number of acoustic and prosodic features with the speech of the artificial agent they were conversing with. In this the convergence might have been promoted by the need to interact with the agent rather than simply observe it. As we shall see in the next section the contagious effects of observation are considerable enhanced when we are social contact with the person we are observing (e.g. Kilner, Marchant & Frith, 2006).

4. Emotions as communicative signals

So far I have presented facial expressions as an example of public information (Danchin, Giraldeau, Valone, & Wagner, 2004). Public information is a cue inadvertently produced by the behaviour of one animal that is useful to another animal. Many animals take advantage of such cues. Starlings, for example, locate likely sources of food by observing the foraging success of other members of the flock (Templeton & Giraldeau, 1995). Facial expressions are another example of public information. Such expressions are also cues that are produced inadvertently and can be useful to observers. The appearance of an expression of fear is a signal to be vigilant since there may something dangerous nearby. However, once emotional expressions become signals of value to observers, then it also becomes possible for these signals to be used deliberately as acts of communication (Parkinson, 2005). The key characteristic of these communicative signals is that the communicator is aware that she is sending a signal and is also aware that her signal is being observed. As a result, the presence of an audience can alter the intensity of emotional expressions. An experiment by Bavelas et al. (1986) provides one of a number of examples of this effect. A volunteer sat in a waiting room unaware that she is being filmed. Two actors enter the room carrying a heavy object which is then dropped, apparently injuring one of the actors. The observing volunteer mimics the expression of pain shown by the injured actor. This is a typical 'mirror'

response. However, the pained expression in the observer is greatly intensified if the actor is in eye contact with the observer. The pained expression shown by the observer is now a communicative act, signalling 'I recognise your pain and I sympathise' and/or' I am a caring person'.

So far I have talked about situations in which one person responds to the facial expression of another, i.e. the observer responds to expression of the actor. This an example of open-loop behaviour. However, communications are more typically two-way interactions. In a two-way interaction, after the observer has responded to the expression of the actor, the actor then responds to the changed expression of the observer, thereby closing the loop. An example of an interactive sequence of emotions in which the communication loop is closed comes from an analysis of the expression of embarrassment by Keltner & Buswell (1997). Embarrassment is complex emotion, which, like guilt and shame, is concerned with reputation in the eyes of others. In particular, Keltner & Buswell suggest that embarrassment can be seen as an act of appeasement, whereby a loss of reputation can be mitigated. The interactive sequence could be described as follows: The actor commits a social *faux pas*. This elicits surprise and anger in the observers, communicating their disapproval. The actor expresses embarrassment, communicating that he is ashamed, apologetic and unhappy. This appeases the observers, who express compassion communicating forgiveness. This elicits happiness in the actor indicating that he recognises that he has been forgiven.

These deliberate emotional signals can also be deliberately deceptive. The person signals embarrassment in order to appease observers may not actual feel the emotion.

5. Ostensive signals

If the same cue can be produced inadvertently or as a deliberate signal, then it is important to be able to distinguish between such causes of cues. Inadvertent signals are less likely to be deceptive, while deliberate signals may require an answer. In many situations a special cue (an ostensive signal) is produced to indicate that the signalling is deliberate. The production of an ostensive signal indicates two things: first, that the person wishes to initiate communication and, second, that the signal that follows will relevant to the interests of the receiver (Sperber & Wilson, 1995).

The most direct way of initiating a communication is to call someone's name. However, facial gestures are also used such as making eye contact, often accompanied a brief raising of the eyebrows (the eyebrow flash Eibl-Eibesfeldt, 1972). Kampe et al (2003) scanned volunteers while they received ostensive signals either in the auditory modality (their name) or in the visual modality (prolonged eye contact). Activity common to both types of signal was observed in medial prefrontal cortex and temporal poles. These are regions that are frequently activated when subjects have to think about mental states (Frith & Frith, 2006; Mitchell, Banaji, & Macrae, 2005). Making inferences about the mental states of the other is a key requirement for communicative interactions, since these are essentially about transferring knowledge and beliefs from one mind to another. The results of Kampe et al suggest that the ostensive signal causes the receiver to prepare for mentalising.

An ostensive signal indicates that the signals that follow are deliberately communicative and will provide useful and relevant information the observer. Belief in this promise is nicely demonstrated in the behaviour of infants in a study by Senju & Csibra (2008). In this experiment the infants, aged 6 months, observed an adult who directed her gaze towards on object on the left or an object on the right. The experimenters tested whether or not the infant would follow the gaze of the adult. The results clearly showed that the infants followed the gaze only when it had been preceded by an ostensive signal; eye contact with eye brow flash or infant directed speech (motherese). The implication is that they understand that these ostensive signals indicate that eye gaze that follows is intended to point to something of interest.

What is the origin of these ostensive signals? Calling someone's name is a straight forward way of attracting some one's attention, but why should the eyebrow flash have acquired this role? Watt et al (2007) have shown that raising the eyebrows, as happens with the eyebrow flash, increases the distance at which it is possible for an observer to detect gaze direction. Watt et al suggest that this means that the eyebrow flash allows the observer to be more easily able to see that the actor is making eye contact with them. I speculate that the eyebrow flash may also be a signal of relevance.

There is good agreement among observers that some peoples' faces look more trustworthy than others (e.g. Winston, Strange, O'Doherty & Dolan (2002); Todorov, Baron, & Oosterhof, 2008), although there is no evidence that these judgements have any validity. Todorov et al have identified four facial features that drive the perception of trustworthiness. One of these is the height of the inner eyebrow. Faces with high inner eyebrows look trustworthy. Those with low inner eyebrows look untrustworthy. These differences can be interpreted on the basis of the results of Watt et al. Trustworthy people have raised eyebrows so that observers can see where they are looking. Untrustworthy people have lowered eyebrows so that observers have more difficulty in seeing where they are looking. Given these observations we can interpret the eyebrow flash as a signal that the sender is to be trusted. The raised eyebrows enable eye gaze direction be seen more easily thereby helping to reveal the intentions of the sender. As an ostensive gesture the eyebrow signals that the message that follows will be relevant and true.

6. Conclusions

The study of facial expressions illustrates very nicely how a behaviour can evolve into a sophisticated communication system. At first, the facial expression of fear has direct behavioural advantages for the actor since widening the eyes, for example, increases the visual field thereby increasing the likelihood of detecting signals of danger. This expression then becomes public information that observers can use as a signal to be vigilant. In the next step, the actor becomes able to control the sending of a signal that was previously emitted inadvertently. Through such control he can express sorrow and embarrassment as a means of appeasing aggression in others. Finally, both actor and receiver become aware that they are exchanging signals and that these can be used for deliberate communication. At this stage the signals need no longer be tied to their original behavioural function. They can be arbitrarily related to meaning making possible the development of language.

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References

Adolphs, R. (1999). Social cognition and the human brain. *Trends Cogn Sci, 3*(12), 469-479.

Adolphs, R. (2002). Neural systems for recognizing emotion. *Current Opinion in Neurobiology, 12*(2), 169-177.

Anstis, S. M., Mayhew, J. W., & Morley, T. (1969). The perception of where a face or television "portrait" is looking. *Am J Psychol, 82*(4), 474-489.

Bavelas, J. B., Black, A., Lemery, C. R., & Mullett, J. (1986). I Show How You Feel - Motor Mimicry as a Communicative Act. *Journal of Personality and Social Psychology, 50*(2), 322-329.

Bayliss, A. P., Paul, M. A., Cannon, P. R., & Tipper, S. P. (2006). Gaze cuing and affective judgments of objects: I like what you look at. *Psychon Bull Rev, 13*(6), 1061-1066.

Beck, D. M., Rees, G., Frith, C. D., & Lavie, N. (2001). Neural correlates of change detection and change blindness. *Nature Neuroscience, 4*(6), 645-650.

Bourgeois, P. & Hess, U. (2008). The impact of social context on mimicry. *Biological Psychology*, 77, 343-352.

Braddick, O.J., O'Brien, J.M., Wattam-Bell, J. Atkinson, J. & Turner, R. (2000). Form and motion coherence activate independent, but not dorsal/ventral segregated, networks in the human brain. *Curr Biol.*10(12), 731-734.

Calder, A. J., & Young, A. W. (2005). Understanding the recognition of facial identity and facial expression. *Nat Rev Neurosci, 6*(8), 641-651.

Castiello, U., Paulignan, Y., & Jeannerod, M. (1991). Temporal dissociation of motor responses and subjective awareness. A study in normal subjects. *Brain, 114 (Pt 6)*, 2639-2655.

Chartrand, T. L., & Bargh, J. A. (1999). The chameleon effect: the perception-behavior link and social interaction. *J Pers Soc Psychol, 76*(6), 893-910.

Danchin, E., Giraldeau, L. A., Valone, T. J., & Wagner, R. H. (2004). Public information: from nosy neighbors to cultural evolution. *Science, 305*(5683), 487-491.

de Gelder, B., Vroomen, J., Pourtois, G., & Weiskrantz, L. (1999). Non-conscious recognition of affect in the absence of striate cortex. *Neuroreport, 10*(18), 3759-3763.

Dehaene, S., Naccache, L., Le Clec, H. G., Koechlin, E., Mueller, M., Dehaene-Lambertz, G., van de Moortele, P. F., & Le Bihan, D. (1998). Imaging unconscious semantic priming. *Nature, 395*(6702), 597-600.

Dimberg, U., Thunberg, M., & Elmehed, K. (2000). Unconscious facial reactions to emotional facial expressions. *Psychol Sci, 11*(1), 86-89.

Driver, J., Davis, G., Ricciardelli, P., Kidd, P., Maxwell, E., & Baron-Cohen, S. (1999). Gaze perception triggers reflexive visuospatial orienting. *Visual Cognition, 6*(5), 509-540.

Eibl-Eibesfeldt, I. (1972). Similarities and differences between cultures in expressive movements. In R. A. Hinde (Ed.), *Non-verbal communication* (pp. 297-311). Cambridge: Cambridge University Press.

Ekman, P., & Friesen, W. V. (1978). *The facial action coding system*. Palo Alto, Calif: Consulting Psychologists Press.

Ellis, H. D., & Lewis, M. B. (2001). Capgras delusion: a window on face recognition. *Trends Cogn Sci, 5*(4), 149-156.

Ellis, H. D., & Young, A. W. (1990). Accounting for delusional misidentifications. *Br J Psychiatry, 157*, 239-248.

Ellis, H. D., Young, A. W., Quayle, A. H., & De Pauw, K. W. (1997). Reduced autonomic responses to faces in Capgras delusion. *Proc Biol Sci, 264*(1384), 1085-1092.

Fletcher, P.C., Zafiris, O., Frith, C.D., Honey, R.A., Corlett, P.R., Zilles, K. & Fink, G.R. (2004) On the benefits of not trying: brain activity and connectivity reflecting the interactions of explicit and implicit sequence learning. *Cereb Cortex*. 15(7), 1002-1015.

Frith, C., Perry, R. & Lumer, E. (1999) The neural correlates of conscious experience: an experimental framework. *Trends Cogn Sci*, 3(3),105-114.

Frith, C. D., & Frith, U. (2006). The neural basis of mentalizing. *Neuron, 50*(4), 531-534.

Goodale, M. A., Milner, A. D., Jakobson, L. S., & Carey, D. P. (1991). A neurological dissociation between perceiving objects and grasping them. *Nature, 349*(6305), 154-156.

Johansson, P., Hall, L., Sikström, S. & Olsson, A. (2005) Failure to detect mismatches between intention and outcome in a simple decision task. *Science*, 310(5745):116-119.

Kampe, K. K., Frith, C. D., & Frith, U. (2003). "Hey John": signals conveying communicative intention toward the self activate brain regions associated with "mentalizing," regardless of modality. *J Neurosci, 23*(12), 5258-5263.

Keltner, D., & Buswell, B. N. (1997). Embarrassment: its distinct form and appeasement functions. *Psychol Bull, 122*(3), 250-270.

Kilner, J. M., Paulignan, Y., & Blakemore, S. J. (2003). An interference effect of observed biological movement on action. *Curr Biol, 13*(6), 522-525.

Kilner, J.M., Marchant, J.L. & Frith, C.D. (2006) Modulation of the mirror system by social relevance. *Soc Cogn Affect Neurosci* **1**, 143-148.

Lakin, J. L., & Chartrand, T. L. (2003). Using nonconscious behavioral mimicry to create affiliation and rapport. *Psychol Sci, 14*(4), 334-339.

LeDoux, J. E. (2000). Emotion circuits in the brain. *Annu Rev Neurosci, 23*, 155-184.

Mack, A., & Rock, I. (1998). *Inattentional Blindness*. Cambridge, MA: MIT Press.

Marcel, A. J. (1983). Conscious and unconscious perception: Experiments on visual masking and word recognition. *Cognitive Psychology, Vol 15*(2), 197-237.

Mitchell, J. P., Banaji, M. R., & Macrae, C. N. (2005). General and specific contributions of the medial prefrontal cortex to knowledge about mental states. *Neuroimage, 28*(4), 757-762.

Morris, J. S., Frith, C. D., Perrett, D. I., Rowland, D., Young, A. W., Calder, A. J., & Dolan, R. J. (1996). A differential neural response in the human amygdala to fearful and happy facial expressions. *Nature, 383*(6603), 812-815.

Morris, J. S., Ohman, A., & Dolan, R. J. (1999). A subcortical pathway to the right amygdala mediating "unseen" fear. *Proc Natl Acad Sci U S A, 96*(4), 1680-1685.

Ohman, A., & Soares, J. J. (1998). Emotional conditioning to masked stimuli: expectancies for aversive outcomes following nonrecognized fear-relevant stimuli. *J Exp Psychol Gen, 127*(1), 69-82.

Oviatt, S., Darves, C. & Coulston, R. (2004) Toward adaptive conversational interfaces: Modelling speech convergencewith animated personas. *ACM Tranactions on Computer-Human Interacion 11*(3), 300-328.

Parkinson, B. (2005). Do facial movements express emotions or communicate motives? *Pers Soc Psychol Rev, 9*(4), 278-311.

Pessoa, L. (2005). To what extent are emotional visual stimuli processed without attention and awareness? *Curr Opin Neurobiol, 15*(2), 188-196.

Pickering, M. J., & Garrod, S. (2004). Toward a mechanistic psychology of dialogue. *Behav Brain Sci, 27*(2), 169-190; discussion 190-226.

Pisella, L., Grea, H., Tilikete, C., Vighetto, A., Desmurget, M., Rode, G., Boisson, D., & Rossetti, Y. (2000). An 'automatic pilot' for the hand in human posterior parietal cortex: toward reinterpreting optic ataxia. *Nature Neuroscience, 3*(7), 729-736.

Rensink, R. A., Oregan, J. K., & Clark, J. J. (1997). To see or not to see: The need for attention to perceive changes in scenes. *Psychological Science, 8*(5), 368-373.

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annu Rev Neurosci, 27*, 169-192.

Schenk, T. (2006). An allocentric rather than perceptual deficit in patient D.F. *Nat Neurosci, 9*(11), 1369-1370.

Senju, A., & Csibra, G. (2008). Gaze following in human infants depends on communicative signals. *Curr Biol, 18*(9), 668-671.

Sperber, D., & Wilson, D. (1995). *Relevance: Communication and cognition* (2 ed.). Oxford: Blackwell.

Susskind, J. M., Lee, D. H., Cusi, A., Feiman, R., Grabski, W., & Anderson, A. K. (2008). Expressing fear enhances sensory acquisition. *Nat Neurosci, 11*(7), 843-850.

Templeton, J. J., & Giraldeau, L.-A. (1995). Patch assessment in foraging flocks of European starlings: evidence for the use of public information. *Behav. Ecol., 6*(1), 65-72.

Todorov, A., Baron, S. G., & Oosterhof, N. N. (2008). Evaluating face trustworthiness: a model based approach. *Soc Cogn Affect Neurosci, 3*(2), 119-127.

Tranel, D., & Damasio, A. R. (1988). Non-conscious face recognition in patients with face agnosia. *Behav Brain Res, 30*(3), 235-249.

van Baaren, R. B., Holland, R. W., Kawakami, K., & van Knippenberg, A. (2004). Mimicry and prosocial behavior. *Psychol Sci, 15*(1), 71-74.

Vuilleumier, P., Armony, J. L., Driver, J., & Dolan, R. J. (2001). Effects of attention and emotion on face processing in the human brain: an event-related fMRI study. *Neuron, 30*(3), 829-841.

Vuilleumier, P., Armony, J. L., Driver, J., & Dolan, R. J. (2003). Distinct spatial frequency sensitivities for processing faces and emotional expressions. *Nat Neurosci, 6*(6), 624-631.

Watt, R., Craven, B., & Quinn, S. (2007). A role for eyebrows in regulating the visibility of eye gaze direction. *Q J Exp Psychol (Colchester), 60*(9), 1169-1177.

Weiskrantz, L., & Warrington, E. K. (1975). Blindsight - Residual Vision Following Occipital Lesions in Man and Monkey. *Brain Research, 85*(1), 184-185.

Whalen, P. J., Kagan, J., Cook, R. G., Davis, F. C., Kim, H., Polis, S., McLaren, D. G., Somerville, L. H., McLean, A. A., Maxwell, J. S., & Johnstone, T. (2004). Human amygdala responsivity to masked fearful eye whites. *Science, 306*(5704), 2061.

Winston, J.S., Strange, B.A., O'Doherty, J. & Dolan, R.J. (2002) Automatic and intentional brain responses during evaluation of trustworthiness of faces. *Nat Neurosci* **5**, 277-283.