

Electrophysiology and brain imaging of biological motion

Aina Puce^{1*} and David Perrett²

¹*Centre for Advanced Imaging, Department of Radiology, West Virginia University, PO Box 9236, Morgantown, WV 26506-9236, USA*

²*School of Psychology, University of St Andrews, St Andrews, Fife KY16 9JU, UK*

The movements of the faces and bodies of other conspecifics provide stimuli of considerable interest to the social primate. Studies of single cells, field potential recordings and functional neuroimaging data indicate that specialized visual mechanisms exist in the superior temporal sulcus (STS) of both human and non-human primates that produce selective neural responses to moving natural images of faces and bodies. STS mechanisms also process simplified displays of biological motion involving point lights marking the limb articulations of animate bodies and geometrical shapes whose motion simulates purposeful behaviour. Facial movements such as deviations in eye gaze, important for gauging an individual's social attention, and mouth movements, indicative of potential utterances, generate particularly robust neural responses that differentiate between movement types. Collectively such visual processing can enable the decoding of complex social signals and through its outputs to limbic, frontal and parietal systems the STS may play a part in enabling appropriate affective responses and social behaviour.

Keywords: biological motion; event related potentials; functional magnetic resonance imaging; humans; single-unit electrophysiology; animals

1. INTRODUCTION

Primates, being social animals, continually observe one another's behaviour so as to be able to integrate effectively within their social living structure. At a non-social level, successful predator evasion also necessitates being able to 'read' the actions of other species in one's vicinity. The ability to interpret the motion and action of others in human primates goes beyond basic survival and successful interactions with important conspecifics. Many of our recreational and cultural pursuits would not be possible without this ability. Excellent symphony orchestras exist not only owing to the exceptional musicians, but also their ability to interpret their conductors' non-verbal instructions. Conductors convey unambiguously not only the technical way that the orchestra should execute the piece of music, but modulate the mood and emotional tone of the music measure by measure. The motion picture industry owes much of its success today to its silent movie pioneers, who could entertain with their non-verbal antics. The world's elite athletes rely on the interpretation of other's movements to achieve their team's goals successfully and foil opponents.

2. HUMAN BEHAVIOURAL STUDIES OF BIOLOGICAL MOTION PERCEPTION

The perception of moving biological forms can rely on the ability to integrate form and motion but it can also

rely on the ability to define form from motion (Oram & Perrett 1994, 1996). The latter is evident in the ingenious work of Johansson who filmed actors dressed in black with white dots attached to their joints on a completely black set (Johansson 1973). With these moving dots human observers could reliably identify the walking or running motions, for example, of another human or an animal (figure 1). This type of stimulus is known as a Johansson, point light or biological motion display.

A number of important observations have emerged from the human behavioural biological motion perception literature. First, the perceptual effect of observing an individual walking or running is severely compromised when the display is inverted (Dittrich 1993; Pavlova & Sokolov 2000). Second, while biological motion representing locomotory movements is recognized the most efficiently, social and instrumental actions can also be recognized from these impoverished displays (Dittrich 1993). Third, biological motion can be perceived even within masks of dots (Perrett *et al.* 1990a; Thornton *et al.* 1998). Fourth, the gender of the walker (and even the identity of specific individuals) can be recognized from pattern of gait and idiosyncratic body movements in these impoverished displays (Cutting & Kozlowski 1977; Kozlowski & Cutting 1977). Fifth, there is a bias to perceive forward locomotion, at the expense of misinterpreting the underlying form in time-reversed biological motion films (Pavlova *et al.* 2002). Finally, observers can discern various emotional expressions from viewing Johansson faces (Bassili 1978).

In very low light conditions many animals are efficient at catching prey or evading predators. In such conditions the patterns of articulation (typical of biological motion) may be more discernible than the form of stationary ani-

* Author for correspondence (apuce@hsc.wvu.edu).

One contribution of 15 to a Theme Issue 'Decoding, imitating and influencing the actions of others: the mechanisms of social interaction'.

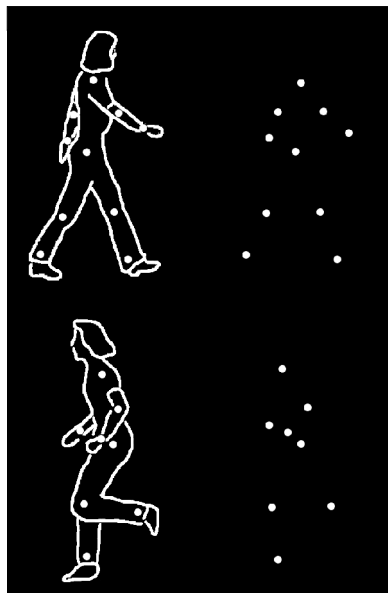


Figure 1. An example of a biological motion stimulus. (Adapted from Johansson (1973), with permission from *Percept. Psychophys.*)

imals. Indeed, in behavioural experiments it is evident that point light displays are sufficient for cats to discriminate the pattern of locomotion of conspecifics (Blake 1993). In an ingenious behavioural study in cats, a forced choice task where selection of a biological motion display (of a cat walking or running) was rewarded with food resulting in the animals performing significantly above chance. A series of foil stimuli showing dots changing their spatial location provided a set of tight controls in this experiment (Blake 1993).

Evidence for the existence of specialized brain systems that analyse biological motion (and the motion of humans and non-humans) comes from neuropsychological lesion studies. Dissociations between the ability to perceive biological motion and other types of motion have been demonstrated. Several patients who are to all intents and purposes 'motion blind' can discriminate biological motion stimuli (Vaina *et al.* 1990; McLeod *et al.* 1996). The opposite pattern, i.e. an inability to perceive biological motion yet have relatively normal motion perception in general, has also been reported (Schenk & Zihl 1997).

3. BIOLOGICAL MOTION PERCEPTION IN NON-HUMANS

One brain region known as the STP area in the cortex surrounding the STS has been the subject of considerable scrutiny ever since cells selective for the sight of faces were characterized in this region in monkeys (Perrett *et al.* 1982; Desimone 1991). This STS brain region is known to be a convergence point for the dorsal and ventral visual streams. The STP area derives its input from the MST area in the dorsal pathway and the anterior inferior-temporal area in the ventral pathway (Boussaoud *et al.* 1990; Felleman & Van Essen 1991). The cortex of the STS has connections with the amygdala (Aggleton *et al.* 1980) and also with the orbitofrontal cortex (Barbas 1988), regions implicated in the processing of stimuli of social and emotional significance in both human and non-

human primates (reviewed in Baron-Cohen 1995; Brothers 1997; Adolphs 1999).

In addition to having face-specific cells, the cortex of the STS has other complex response properties. It has emerged that visual information about the shape and posture of the fingers, hands, arms, legs and torso all impact on STS cell tuning in addition to facial details such as the shape of the mouth and direction of gaze (Desimone *et al.* 1984; Wachsmuth *et al.* 1994; Perrett *et al.* 1984, 1985a; Jellema *et al.* 2000). Motion information presumed to arrive from the dorsal stream projections arrives in the STS some 20 ms ahead of form information from the ventral stream (figure 2a), but despite this asynchrony, STS processing overcomes the 'binding problem' and only form and motion arising from the same biological object are integrated within 100 ms of the moving form becoming visible (Oram & Perrett 1996). Indeed, STS cell integration of form and motion is widespread and there are numerous cell types specializing in the processing of different types of face, limb and whole body motion (Perrett *et al.* 1985b; Carey *et al.* 1997; Jellema *et al.* 2000, 2002; Jellema & Perrett 2002).

While most STS cells derive sensitivity to body movement by combining signals about the net translation or rotation of the body with the face and body form visible at any moment in time, a smaller proportion (20%) of cells are able to respond selectively to the form of the body defined through patterns of articulation in point light displays (Perrett *et al.* 1990a,b; Oram & Perrett 1994, 1996; figure 1). These cells tuned to biological motion are selective for the sight of the same action visible in full light and when depicted in point light displays.

Cells responding to whole body motion exhibit selectivity for direction of motion and view of the body: most respond preferentially to compatible motion with the body moving forward in the direction it faces, though some are tuned to backward locomotion with the body moving in the opposite direction to the way it faces (Perrett *et al.* 1985b, 1989; Oram & Perrett 1996; figure 2b). This cellular tuning bias for forward locomotion may underlie the forward bias found in perceptual interpretation of locomotion depicted in point light displays (Pavlova *et al.* 2002).

Responses to purposeful hand object actions such as reaching for, picking, tearing and manipulating objects have also been characterized in the STS (Perrett *et al.* 1989, 1990c; Jellema *et al.* 2000). These STS cells are sensitive to the form of the hand performing the action, and are unresponsive to the sight of tools manipulating objects in the same manner as hands. Furthermore, the cells code the spatio-temporal interaction between the agent performing the action and the object of the action. For example, cells tuned to hands manipulating an object cease to respond if the hands and object move appropriately but are spatially separated. This selectivity ensures that the cells are more responsive in situations where the agent's motion is causally related to the object's motion. The STS cell populations coding body and hand actions appear to be exclusively visual, although information from the motor system does affect other STS cell populations (Hietanen & Perrett 1996) and modulates STS activity in humans (Iacoboni *et al.* 2001; Nishitani & Hari 2001).

Information defined by the visual characterization of

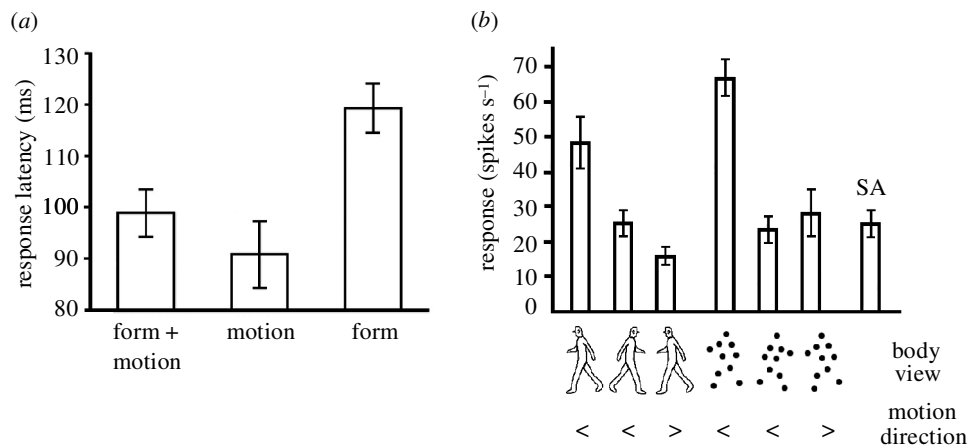


Figure 2. Some response properties of primate STP area neurons elicited by biological motion stimuli. (Adapted from Oram & Perrett (1994, 1996), with permission.) (a) Average response latencies for neurons with different response properties. (b) An example of a neuron that does not differentiate between real human motion and biological motion. Also, the strongest response is in the motion direction compatible with direction of the body.

actions in the STS appears to be relayed via parietal systems (Gallese *et al.* 2002) to frontal motor planning systems. In frontal and parietal areas a neural system has recently been found to respond selectively both during the execution of hand actions, and (like STS cells) during the observation of corresponding actions performed by others. The frontal region of primate cortex had long been known to be somatotopically organized for the representation and control of movements of the mouth and arm (Rizzolatti *et al.* 1988). Neurons within area F5 of the monkey premotor cortex have now been labelled 'mirror' neurons, because they discharge when monkeys perform or observe the same hand actions (di Pellegrino *et al.* 1992; Rizzolatti *et al.* 1996*a,b*; Gallese *et al.* 1996). An F5 cell selective for the action of grasping would respond for example when the monkey grasps an object in sight or in the dark (thereby demonstrating motoric properties). The visual properties of such an F5 cell are strikingly similar to those described in the STS: both F5 and STS cells will respond when the monkey observes the experimenter reaching and grasping an object, but not to the sight of the experimenter's hand motion alone or the sight of the object alone. These conjoint properties have led Rizzolatti *et al.* (1996*a,b*) and Gallese *et al.* (1996) to postulate that the F5 neurons form a system for matching observation and executing actions for the grasping, manipulation and placement of objects. Because the cells additionally respond selectively to the sound of actions (Kohler *et al.* 2002), the mirror system may provide a supra-modal conceptual representation of actions and their consequences in the world. Crucially the properties of the frontal mirror system indicate that we may understand actions performed by others because we can match the actions we sense through vision (and audition) to our ability to produce the same actions ourselves.

The actions of others are not always fully visible, for example someone may become hidden from our sight as they move behind a tree, or their hands may not remain fully in view as they reach to retrieve an object. The similarity of STS and F5 systems in processing of actions has become more apparent in experiments investigating the nature of processing during these moments when actions

are partially or totally occluded from sight. Within the STS it is now apparent that specific cell populations are activated when the presence of a hidden person can be inferred from the preceding visual events (i.e. they were witnessed passing out of sight behind a screen and have not yet been witnessed re-emerging into sight, so they are likely to remain behind the screen; Baker *et al.* 2001). In an analogous manner, F5 cells may respond to the sight of the experimenter reaching to grasp an object. The same cells are active when the experimenter places an object behind a screen and then reaches as if to grasp it (even though the object and hand are hidden from view (Umiltà *et al.* 2002)). The sight of equivalent reaching when there is no reason to believe an object is hidden from sight fails to activate the F5 cells. Thus F5 and STS cells code the sight of actions on the basis of what is currently visible and on the basis of the recent perceptual history (Jellema & Perrett 2002; Jellema *et al.* 2002).

The manner in which temporal STS and frontal F5 systems interact is not fully clear, but appears to involve intermediate processing steps mediated by parietal areas (Nishitani & Hari 2000, 2001; Gallese *et al.* 2002). While STS and F5 cells have similar visual properties they may subserve distinct functions; the frontal system perhaps serves to control the behaviour of the self particularly in dealing with objects (Rizzolatti *et al.* 1996*a,b*), whereas the STS system is specialized for the detection and recognition of the behaviour of others (Perrett *et al.* 1990*c*; Mistlin & Perrett 1990; Hietanen & Perrett 1996).

4. HUMAN NEUROIMAGING AND ELECTROPHYSIOLOGICAL STUDIES OF BIOLOGICAL MOTION PERCEPTION

The first suggestion that humans may possess specialized biological motion perception mechanisms came from a point light display depicting a moving body designed to investigate the response properties of medial temporal/V5, a region of occipito-temporal cortex known to respond to motion. In this fMRI study activation was observed in MT/V5 as well as areas of superior temporal cortex. This was regarded at that time as surprising, as the activation

appeared to lie in brain regions traditionally regarded as participating in auditory speech processing (Howard *et al.* 1996). Localization of primary auditory cortex was not performed in this visual stimulation study. In a PET study published in the same year Johansson displays of body motion (depicting a person dancing), hand motion (depicting a hand reaching for a glass and bringing it to a mouth), object motion (depicting a three-dimensional structure rotating and pitching) and control conditions, consisting of either random dot motion or a static display of randomly placed dots, were shown to a group of healthy subjects (Bonda *et al.* 1996). The human motion conditions selectively activated the inferior parietal region and the STS. Specifically, the body motion condition selectively activated the right posterior STS, whereas the hand motion condition activated the left intraparietal sulcus and the posterior STS (Bonda *et al.* 1996). In a more recent fMRI study, a Johansson display depicting a walker was used and the activation contrasted to control conditions that included a dot display with non-random motion and a gender discrimination task with real images of faces (Vaina *et al.* 2001). Biological motion differentially activated a large number of dorsal and ventral regions, most notably the lateral occipital complex, but the STS was not preferentially activated in this study.

Grossman and colleagues found that biological motion stimuli depicting jumping, kicking, running and throwing movements produced more right STS activation than control motion irrespective of the visual field in which the biological motion display was presented. Conversely, the control motion, including scrambled biological motion displays, activated MT/MST areas and the lateral-occipital complex (Grossman *et al.* 2000). Moreover, the STS region could also be activated by *imagining* Johansson stimuli, although the size of the activation was small (Grossman *et al.* 2000). While the most robust STS activation was elicited by viewing upright Johansson displays, a smaller STS activation signal was also seen to viewing inverted Johansson displays.

While biological motion clearly activates the STS region in humans, the function of the region may be more general in performing a visual analysis of bodies based on either the characteristic patterns of articulation that comprise biological motion or information about bodies that can be derived from static images (Downing *et al.* 2001); hence the term 'extrastriate body area' has been applied to one cortical region within the STS complex.

5. BIOLOGICAL MOTION PERCEPTION VERSUS HUMAN MOTION PERCEPTION

As in non-human primates, responsiveness to Johansson-like displays of facial motion is present in STS regions that also respond to real images of facial motion, e.g. non-linguistic mouth movements (Puce *et al.* 2001), although the per cent magnetic resonance signal change to the Johansson-like face was smaller than that observed to the natural facial images. In parallel to the neuroimaging data, direct measures of neural activity in humans, in the form of scalp ERPs, are elicited to Johansson-like and real images of faces (Thompson *et al.* 2002*b*), with a prominent negativity occurring at *ca.* 170 ms post-motion onset

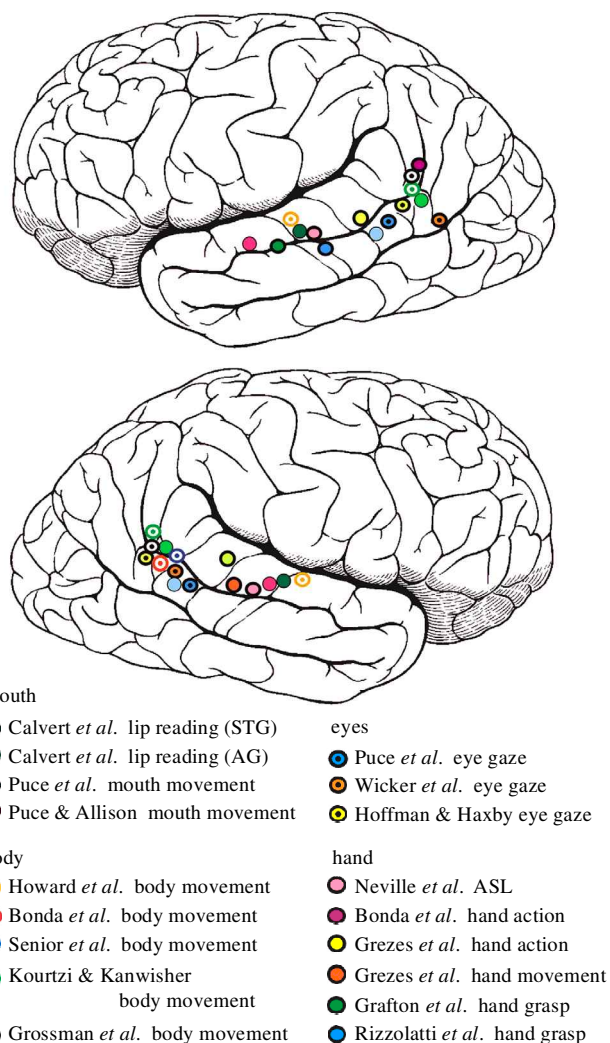


Figure 3. Centres of activation to viewing the face, hand and body movements of others obtained from a series of PET and fMRI studies. (Adapted from Allison *et al.* (2000), with permission.)

(N170) over the bilateral temporal scalp. This activity is significantly greater than that seen to motion controls.

Over the latter half of the 1990s, a series of PET and fMRI studies examining activation to viewing the motion and actions of others have pointed to the existence of cortical networks that preferentially process certain attributes of these high-level visual displays (reviewed by Allison *et al.* 2000; Blakemore & Decety 2001). Figure 3 displays activation observed in these studies, lying along the posterior extent of the STS and its ascending limb in inferior parietal cortex in response to observing movements of the body, hands, eye and mouth. Activation in these regions can also be elicited to imagining the motion of others (Grossman *et al.* 2000), and additionally to viewing static images of implied motion (Kourtzi & Kanwisher 2000).

Interestingly, differences in activation patterns can occur when subjects view compatible versus incompatible motion of the head or body (Thompson *et al.* 2002*a*). Specifically, the bilateral posterior lateral temporal cortex is active when viewing compatible motion. By contrast, viewing incompatible motion activates the right posterior lateral temporal cortex, left anterior temporal cortex, left

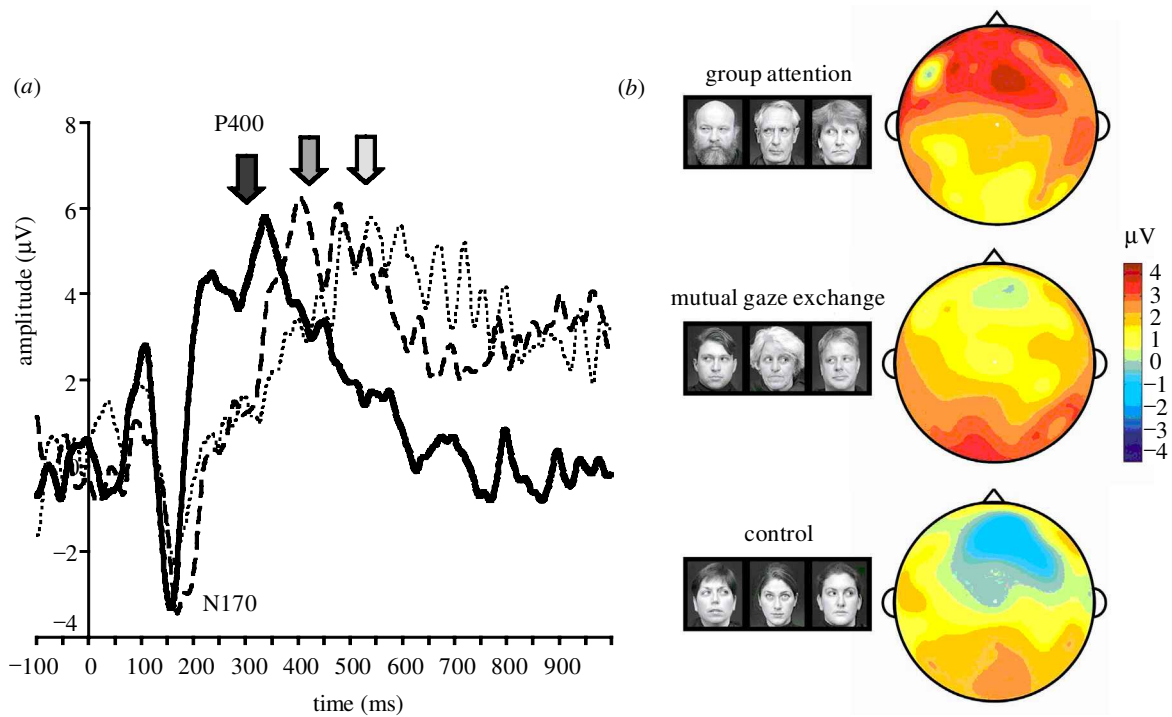


Figure 4. ERPs elicited to a social attention task. (a) ERP waveforms elicited to three conditions: solid line, group attention; dashed line, mutual gaze exchange; dotted line, control. The arrows indicate a late peak of ERP activity that follows the N170 ERP (P400), which changes its latency as a function of viewing condition. (b) Voltage maps for the three viewing conditions generated at the peak of P400 activity for the group attention condition (black arrow in (a)). The group attention condition shows fronto-temporal positivity, whereas the other two conditions show small posterior positivities.

temporoparietal junction and left precentral gyrus. This extended network of activation might be due to the novelty or salience of the incongruent body and head motion stimuli (Downar *et al.* 2002). The differential experience with compatible and incompatible motion may explain STS cell sensitivity to the compatibility of motion direction and body view during the locomotion described above.

What is unique about the motion of animate beings? Animals and humans possess articulated joints, enabling the movement of body parts without having to maintain a constant spatial relationship in space relative to each other. This results in the ability to produce a limitless set of movements. Man-made objects, such as utensils and tools, in general do not have this capability. Beauchamp *et al.* (2002) investigated the differences in brain activation to these different types of high-level motion stimuli. Interestingly, observing human motion stimuli activated the STS and observing the motion of tools/utensils activated cortex ventral to the STS, on the MTG. In another fMRI experiment in this same study, stimuli depicting articulated and non-articulated human motion were presented. The STS responded to the articulated human motion and the MTG to non-articulated motion, indicating that these high-order processing mechanisms process selectively the higher-order motion type (Beauchamp *et al.* 2002).

Grezes *et al.* (2001) also reported activation differences between observing rigid and non-rigid motion. Specifically, they observed an anterior–posterior gradient of activation in the STS regions, with non-rigid motion producing the most anterior activation. Additionally, they observed activation in left intraparietal cortex to non-rigid

biological motion (Grezes *et al.* 2001). The magnitude of the activation in the STS to biological motion, and indeed in other cortical regions, can be coloured by the task requirements and the attention that the observer places on the ‘human’ quality of the motion (Vaina *et al.* 2001). Additionally, attention to the displayed emotion enhances fMRI activation in the STS, whereas increased activation to facial attributes *per se*, such as identity or isolated features, increased activation in all known face-sensitive cortical regions (Narumoto *et al.* 2001).

(a) Social cognition

The limbic system, in conjunction with the orbitofrontal cortex and the STS, is thought to form a network that is involved in social cognition (Baron-Cohen 1995; Brothers 1997; Adolphs 1999). One important aspect of social cognition is the identification of the direction of another’s attention from their direction of gaze or head view (Perrett *et al.* 1985a, 1992; Kleinke 1986; Allison *et al.* 2000; Emery 2000). Indeed, the existence of an eye direction detector has been postulated in this hierarchical system of social cognition, which at its top level allows us to ‘mind-read’ and infer the intentions of others (Baron-Cohen 1995; Baron-Cohen *et al.* 1997). While there is evidence for cell populations coding for eye and attention direction within STS (Perrett *et al.* 1985a, 1992), the populations are not anatomically grouped in such a way that scalp evoked potentials are necessarily linked to a given eye direction (Bentin *et al.* 1996; Eimer 1998; Taylor *et al.* 2001). Our attention and behaviour can be modified when confronted with a face with averted gaze. A peripheral target stimulus is detected by normal subjects more

efficiently when it lies in the direction of gaze of a central stimulus face (Friesen & Kingstone 1998; Driver *et al.* 1999; Hietanen 1999, 2002; Langton & Bruce 2000). Moreover, patients with unilateral neglect are less likely to extinguish a contralesional target stimulus when it lies in the gaze path of a stimulus face (Vuilleumier 2002). Following the attention direction of someone's gaze may be such an over-learned response that it needs little conscious awareness.

(b) *Gaze perception*

Neuroimaging studies involving gaze perception indicate that there is an active cortical network involving occipito-temporal cortex (fusiform gyrus, inferior temporal gyrus, parietal lobule and bilateral middle temporal gyri) when subjects passively view gaze aversion movements (Wicker *et al.* 1998). One prominently active region to viewing eye movements (gaze aversion and also eyes looking at the observer) is the cortex around the STS, particularly in the right hemisphere, and this same region is active also to viewing opening and closing movements of the mouth (Puce *et al.* 1998). Thus, as is evident from the single cell responses, the STS region contains neural populations representing multiple aspects of the appearance of the face (including gaze) and body and their motion; the STS should not be considered exclusively an 'eye detector' or 'eye processor'. The STS is more activated during judgements of gaze direction than during judgements of identity, whereas the fusiform and inferior occipito-temporal activation is stronger during judgements of identity than gaze direction (Hoffman & Haxby 2000). Intracranial ERP recordings from these structures indicate that the STS responds to facial motion, whereas the ventral-temporal cortex responds more strongly to static facial images (Puce & Allison 1999). This is not surprising if one considers that eye gaze direction changes are transient and their detection might require motion processing systems, whereas identity judgements can be made independently of facial movements. Indeed, the processing of dynamic information about facial expression and the processing of static information about facial identity appear neuropsychologically dissociable (Campbell 1992; Humphreys *et al.* 1993).

(c) *Lip reading*

Lip reading, an important function for both hearing and deaf individuals, can be neuropsychologically dissociated from face recognition (Campbell *et al.* 1986), in a somewhat similar manner to gaze perception. Normal lip reading uses cortex of the STG in addition to other brain regions such as the angular gyrus, posterior cingulate, medial frontal cortex and frontal pole (Calvert *et al.* 1997). The STG and surrounding cortex activate bilaterally when subjects view face actions that could be interpreted as speech (Puce *et al.* 1998; Campbell *et al.* 2001), while some regions of the posterior right STS activate for the sight of speech and non-speech mouth movements (Campbell *et al.* 2001). Centres of activation to visual speech appear to overlap those associated with hearing speech (Calvert *et al.* 1997), indicating that these regions receive multimodal inputs during speech analysis (Kawashima *et al.* 1999; Calvert *et al.* 2000). Further evidence for this multimodal integration is a phenomenon

known as the McGurk effect (McGurk & MacDonald 1976), where what observers hear when listening to speech sounds is altered by simultaneously viewing mouth movements appropriate to a different speech utterance. Indeed, magnetoencephalographic recordings of neural activity to speech stimuli show sensitivity to auditory-visual mismatch (Sams *et al.* 1991) with activity 200 ms post-stimulus augmented when the visual speech does not correspond to the accompanying auditory speech.

(d) *The mirror neuron system and action observation/execution*

The existence of a mirror neuron system in humans has been investigated during the manipulation of objects (Rizzolatti *et al.* 1996*a,b*; Binkofski *et al.* 1999*a,b*). The activation in fronto-central regions, seen when subjects observe and/or execute grasping behaviours, is accompanied by activity in the parietal cortex and STS (Jeannerod *et al.* 1995; Iacoboni *et al.* 1999, 2001; Rizzolatti *et al.* 2001; Gallesse *et al.* 2002), paralleling the mirror neuron system in non-human primates.

Additionally, the secondary somatosensory cortex, SII, located in the temporal operculum is postulated to analyse the intrinsic properties of the graspable object while activation observed in the cortex in the intraparietal sulcus was thought to be related to kinaesthetic processes (Binkofski *et al.* 1999*b*), although strictly speaking it is not part of the mirror neuron system.

The neuroimaging data mesh well with reported disturbances in executing grasping movements in the neuropsychological lesion literature. For example, Jeannerod and colleagues have reported a case with bilateral posterior parietal lesions of vascular origin where there was no difficulty in reaching toward the location of the object; however, a profound deficit in executing the anticipatory grasping movement with the fingers occurred to nondescript objects (cylindrical dowels). Interestingly, there was no deficit in grasping behaviour when well-known recognizable objects were used in the same test (Jeannerod *et al.* 1994). Mental imagery of hand and finger movements was found to be impaired in patients with unilateral parietal lesions, who had difficulties in producing movements with their hands and fingers (Sirigu *et al.* 1996). It has been reported that patients with unilateral parietal lesions have more difficulty in imitating gestures involving their own bodies relative to movements involving external objects, particularly if the lesion is in the left hemisphere (Halsband *et al.* 2001).

The human STS in its posterior extent has been found to be active not only to the hand and body movements of others (see figure 3; Allison *et al.* 2000), but also to faces (Puce *et al.* 1998). Interestingly, ERP recordings indicate that neural activity can differentiate between types of facial movements (Puce *et al.* 2000). Viewing mouth opening movements produces larger N170 responses relative to viewing mouth closing movements. A similar N170 response gradient is seen for observing eyes averting their gaze away from the observer relative to eyes focusing their gaze on the observer. Augmented neural responses to eye aversion movements may be a powerful signal that the observer is no longer the focus of another's attention. Similarly, larger N170s to mouth opening movements might be important for recognizing the beginning of an

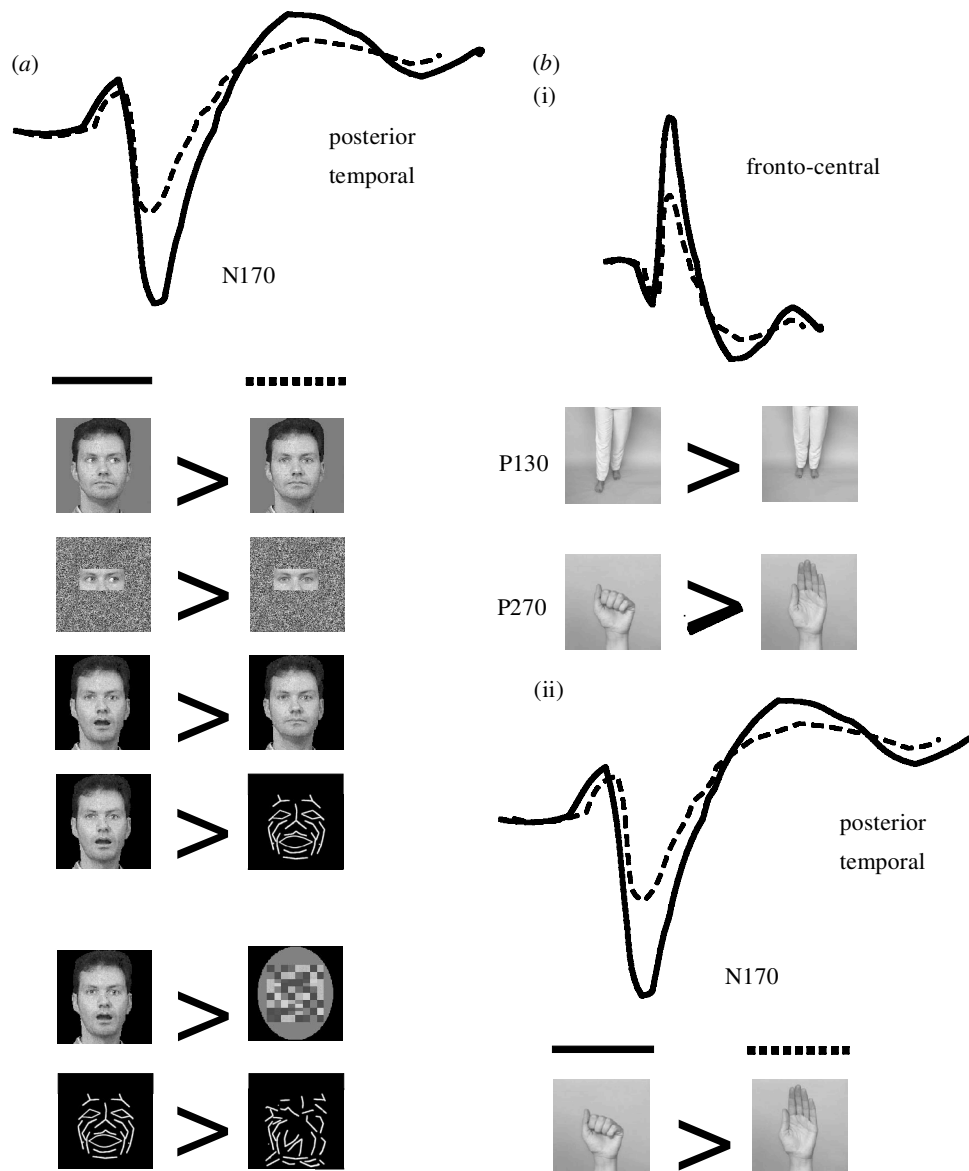


Figure 5. Schematic summary of ERP waveforms elicited in response to observing human motion. (a) Posterior temporal N170 (solid line) to conditions listed in the left column is larger relative to N170 (dashed line) elicited to conditions listed in the right column. (b)(i) Frontocentral ERPs show larger P130 and P270 components across body and hand motion conditions shown in the left and right columns (solid versus dashed line). (b)(ii) Posterior temporal N170 (solid line) is larger to hand closure relative to hand opening (dashed line).

utterance (Puce *et al.* 2000). With recording electrodes sited in the STS of epilepsy surgery patients, selective responses to mouth opening have been elicited (see Allison *et al.* 2000, box 1). No responses were observed to mouth closing movements or eye deviations, indicating that these regions might be responsive during lip reading (or the sight of gestures and emotional expressions in which the mouth opens, e.g. during eating and surprise). The Talairach coordinates of these electrode positions are comparable to sites of fMRI activation in lip reading (Calvert *et al.* 1997).

If eye aversion movements are given a context, late ERPs that differ as a function of the social significance of the aversion movement can be elicited (figure 4; A. Cooper and A. Puce, unpublished data). This was demonstrated in a visual task where two permanently gaze-averted flanker faces were presented with a central face that changed its

gaze direction. The central face could look in the same direction as both flanker faces, setting up an apparently common focus of attention off to the side ('group attention'). Alternatively, if the central face looked away from the observer in the opposite direction to the other two faces, a mutual gaze exchange between the central face and one of the flankers became apparent ('mutual gaze exchange'). Finally, the central face could look away from the observer and the other two flanker faces by looking up ('control'). An N170 ERP to the gaze aversion of the central face was elicited, and its characteristics did not change as a function of condition (see also Puce *et al.* 2000). A later positive ERP, elicited between 300 and 500 ms post-motion onset (P400) was seen to differentiate in latency as a function of viewing condition: group attention produced the shortest latency response, followed by the mutual gaze exchange condition and then the control condition.

Our non-verbal and verbal facial movements usually do occur in an affective context, and preliminary ERP data indicate that our brains are very sensitive to these gesture–affect blends. If facial movements (either non-verbal or verbal) are combined with different types of affect, temporal scalp N170 peak latency and the amplitude of later ERP activity can be altered as a function of affect type (Wheaton *et al.* 2002*b*). If gesture–affect combinations are incongruous, as shown by increased reaction time to classify affect in behavioural data, late ERP activity from 300 to 975 ms post-motion onset is modulated as a function of not only affect or gesture but also their combination (Wheaton *et al.* 2002*a*). These preliminary data indicate that the processing of inconsistencies in others' behaviour can be detected physiologically.

ERPs, in the form of N170 negativities occurring over bilateral temporal scalp regions, have been elicited not only to facial movements but also to hand and body movements (Wheaton *et al.* 2001). The N170 activity was larger for observing hand clenching movements relative to hand opening movements. In addition, ERP activity was also observed to hand and body motion over the central scalp. Interestingly, ERP activity was larger to observing a body stepping forward than to a body stepping back (paralleling the cellular bias for forward or compatible direction of locomotion; Perrett *et al.* 1985*b*; Oram & Perrett 1994). Taken together, the ERP differentiation in the hand and body movements might indicate a stronger neural signal for potentially threatening movements (Wheaton *et al.* 2001). When fMRI activation to these movement types is compared, there is a robust signal within the temporoparietal cortex to all of these motion types (Wheaton *et al.* 2002*c*). Figure 5 summarizes the main findings from the ERP studies (Puce *et al.* 2000; Wheaton *et al.* 2001; Thompson *et al.* 2002*b*), and indicates that processing between movement types begins before 200 ms post-motion onset not only in the posterior temporal cortex but also in the frontocentral regions, which would be expected from the distribution of action processing evident in fMRI and cell recording.

(e) Gesture and action processing: implications for disorders of social communication

The processing of non-verbally presented messages, in the form of face and hand gestures, is crucial for social primates to be able to interact with one another—and there are considerable similarities in the high-level biological motion processing systems in human and non-human primates. The importance of comprehending actions of others may also be evident when such comprehension is impaired in clinical conditions. Disorders such as autism, Asperger syndrome, and schizophrenia are characterized by the inability to form or maintain social relationships. This can be difficult if the sufferer cannot process incoming social messages communicated by the bodily and facial actions of others, or sends inappropriate social reactions to such signals (e.g. Williams *et al.* 2001). Further neuroimaging and neurophysiological studies of healthy subjects and those with impairments of human motion processing may shed light on the interactions between the various components of these high-level biological motion processing systems.

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GLOSSARY

- ERP: event-related potential
fMRI: functional magnetic resonance imaging
MST: medial superior temporal
MTG: mid-temporal gyrus
PET: positron emission tomography
STG: superior temporal gyrus
STP: superior temporal polysensory
STS: superior temporal sulcus