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The Role of Social Cues in the Involuntary Attribution of  
Intentionality

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## Abstract

Predicting the behavior of others is crucial in social interactions and requires sophisticated cognitive mechanisms with which to do so. In order to make a more informed prediction, it is necessary to integrate information about the mental state and intentions of the actor with the perception of the action itself. The aim of this thesis was to investigate in what way social cues that convey another person's goals and intentions contribute to an observer's anticipation of that person's actions.

The first three experiments used a representational momentum paradigm to test the hypothesis that judgments of how far another agent's head has rotated are influenced by the perceived gaze direction of that agent. Participants observed a video-clip of a face rotating  $60^\circ$  towards them starting from the left or right profile view. The gaze direction of the face was either congruent with, ahead of, or lagging behind the angle of rotation. Following this, two static faces, at varying angles of rotation with respect to the end-point angle of the face in the video-clip, were presented simultaneously. The task of the participants was to decide which of the two heads was at an angle best resembling the angle of the end-point of the moving face. The critical test condition consisted of one test face oriented at  $10^\circ$  before, and the other at  $10^\circ$  after the end-point.

In experiment 1 the gaze-lagging condition elicited a significant underestimation of the rotation compared to the 'congruent' and 'ahead' gaze conditions. Participants did not exhibit similar biases when judging the rotation of several non-face control stimuli with visual features that mimicked different aspects of gaze direction, in particular the configuration of black and white components and the directional information it conveys. In experiment 2, the stimuli were spatially inverted to disrupt the integration of gaze direction and head rotation. Under these circumstances there was no effect of social cues on action anticipation, while presentation in an upright orientation replicated the effect observed in experiment 1. In experiment 3 the effect of gaze persisted when the actor expressed an

avoidance motivation (fear, disgust) but not when expressing an approach motivation (happiness, anger). As the goal of an action that moves toward the observer with an avoidance expression is ambiguous but is unambiguous when expressing approach, it is concluded that the use of gaze as a cue to the end-point of the action is flexible and depends on the perceived ambiguity of the agent's behavioural intentions.

Experiment 4 assessed the role that social cues have in attributing the intentions of an individual. Furthermore, it looked at whether this capacity is related to individual differences in empathising, systemising and the extent to which participants possess autistic-like traits. Participants completed a gaze cueing experiment in which a centrally presented gaze averted to the left or right preceded the appearance of a target in either the gazed at location (valid) or on the opposite side of the screen (invalid). The difference in target detection times between valid and invalid trials is a measure of how quickly an observer is able to orient their attention in the direction that someone is looking. The speed with which participant's oriented attention in response to the gaze direction was expected to depend on the intentions attributed to the identity. Participants initially completed a learning phase in which the three identities were presented. The gaze and expression of the identities was such that one conveyed a prosocial intention, one conveyed an antisocial intention and one was spatially predictive of target location. It was found that those with high empathising skills and few autistic traits showed a smaller cueing effect in response to the gaze of the antisocial identity than the prosocial identity. Those with more autistic traits and systemising skills showed a larger cueing effect in response to the gaze of the predictive identity. This suggests that both groups were able to orient attention in response to gaze direction, but that they prioritised different aspects of the gazers intentions. Those who are more sensitive to social information learnt the social intentions of the individual and this decreased the cueing effect in response to a negative identity. Those less sensitive to social information but more sensitive to spatial regularities learnt that one identity was spatially predictive and consequently increased the cueing effect in

response to the gaze direction of that identity.

Overall, these studies suggest that social cues are automatically integrated in the representations of the perceived actions of others, and contribute to anticipations of how they will behave in the immediate future. This plays a crucial role in Theory of Mind and in enabling us to successfully interact with others.

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## **Chapter 1. The role of social cues in the involuntary attribution of intentionality**

Humans inhabit large and complex social groups, and such social complexity requires a level of cognitive complexity with which to manage the social information regarding the interactions of oneself and others (e.g. Brune & Brune-Cohrs, 2006; Dunbar, 1992, 1995, 1998). It is important to understand the behaviour of others, and to interpret the mental states that govern and dictate their actions. Theory of mind (ToM, also referred to as perspective taking, folk psychology, empathising, mentalising) is the ability to conceptualise the internal mental states of oneself, and to recognise and represent the mental states held by others. These mental states encompass the perceptual experience, attention, desires, emotions, beliefs, knowledge and thoughts of others (Flavell, 2004). ToM is defined as the ability to represent not only one's own mental state (1<sup>st</sup> order intentionality) but also those of others (2<sup>nd</sup> order intentionality). It is necessary to know that the mental states of oneself and others are subjective and are not necessarily the same, nor that they are the same as the real state of the environment. Moreover, the behaviour of oneself and that of others is determined by these subjective states of mind (Gallagher & Frith, 2003; Tomasello & Rakoczy, 2003). As a consequence, the behaviour of others can be predicted and manipulated based upon what one knows about the others persons emotional and epistemic mental state. Tests of these abilities, such as the false belief task or that of 2<sup>nd</sup> order perspective taking consistently show the age of acquisition of belief/reality discrimination to be between 3-5 years of age (Flavell, 2004). From here on further advances are made in terms of the complexity of mental state attributions, such as the recognition of social faux pas at between 9-11 years of age (Baron-Cohen, O'Riordan, Stone, Jones, & Plaisted, 1999).

There are several schools of thought regarding the cognitive mechanisms underpinning mental state attribution. Simulation Theorists (ST) propose that understanding and predicting what, why, and how another person will act is achieved by

the same means as envisaging the nature and outcome of one's own actions (Flavell, 1999). That is, by imagining what one's own mental state and behaviour would be in the same situation, and then attributing the same to the other person (Currie & Ravenscroft, 1997). In contrast, theory theorists (TT) propose that, as mental states are intangible and cannot be directly perceived, the individual must therefore literally theorise as to their content. These theories are either supported and persist, or are modified and refined to account for anomalous findings (Gopnik, 2003). Some authors argue that such theorising is a domain general ability that is also used to understand other non-social domains such as the biological and physical world as well (e.g. Gopnik, 2003). However, others propose that ToM is a domain specific capacity only employed to understand other people. Leslie (1994) argues that ToM is rooted in a core neurocognitive architecture that selectively confines the inputs it receives to just the social domain. This serves to maintain the high level of innateness necessary for such a complex domain specific ability, whilst enabling enough flexibility to allow for developmental learning and plasticity (Scholl & Leslie, 1999). Baron-Cohen (1995, 2005) and Leslie (1994) have both proffered models based on this core neurocognitive architecture they call the Theory of Mind Mechanism (ToMM). The role of the ToMM is two-fold. Firstly, to represent the mental states held by others. Secondly, to merge these into a workable theory as to the causative relation between an observable action and the mental states that brought it about (Baron-Cohen, 1995). Baron-Cohen (2005) proposes that the ToMM works in tandem with a second domain specific module he calls The Empathising System (TESS), the task of which is to instil an appropriate emotional reaction in the observer that compels the individual to act. In this way, theory of mind is less a passive observer, and takes a more proactive role in the creation of adaptive pro-social behaviour.

Several authors point to evidence both for and against the different models of ToM and suggest that the role of simulation and theory in social cognition is not so much an either/or debate, but more an integration of the two processes (Apperly, 2008; Mitchell,

2005). For example, Keysers and Gazzola (2006, 2007) propose that simulation processes enable the automatic and implicit attribution of another's emotion, sensation and intentionality, and that these form a 'primary representation' of another person's bodily state. A subsequent theory based process then uses these 'primary representations' to form 'secondary representations' of another person's knowledge and beliefs through explicit conscious reflection. In this way, simulation informs the formation of subsequent theories. Lieberman (2003) has extended this dual process system by proposing that simulation mechanisms form part of a reflexive X system and that Theory of Mind forms part of a reflective C system. The X system is engaged pre-attentively to generate expectancies based on perceptual input. The outputs of these processes are mediated and/or overridden by the consciously controlled C system when necessary (e.g. when X system outputs are erroneous). The dichotomy between the X and C systems is not discrete but reflects two ends of a processing spectrum. Furthermore, novel situations that necessitate the C system will, through repeated encounters, become more automatic and be governed by the X system (Satpute & Lieberman, 2006). Others have argued that simulation processes encompass reflective as well as reflexive mechanisms in that it can be disembodied, conscious and voluntary (Coricelli, 2005). Uddin (2007) points to evidence that reflecting on the mental state of others employs the same mechanisms as when reflecting on one's own mental state. This implies the presence of shared circuits for the explicit representation of the mental states of oneself and others. Overall, the evidence in favour of either TT or ST is equivocal and the more pertinent question is in what circumstances one is employed over another and why (Mitchell, 2005).

Neurophysiological data implicate the frontal lobes in tasks necessitating the attribution of another person's mental state (Frith & Frith, 2003). For example, inferring the knowledge and beliefs that another person has elicits activity in the medial prefrontal cortex (Gallagher & Frith, 2003), medial frontal gyrus (Fletcher et al., 1995; Ruby & Decety, 2003) and also in the anterior cingulate cortex (Vogeley et al., 2001). Impairments

in ToM tasks are evident in patients with lesions to the frontal lobes (Rowe, Bullock, Polkey, & Morris, 2001; Stuss, Gallup, & Alexander, 2001). Two studies have specified the location of medial prefrontal cortex activity during mental state attributions to the anterior paracingulate cortex, a border region between the ACC and MFG (Gallagher, Jack, Roepstorff, & Frith, 2002; McCabe, Houser, Ryan, Smith, & Trouard, 2001). This area is also active in tasks involving the attempted deception of others (Langleben et al., 2002). However, the attribution of emotional states of mind has been shown to activate more ventral areas of the mPFC (Adolphs, 1999; Saxe, 2006) and the orbito-frontal cortex (Hynes, Baird, & Grafton, 2006). This suggests a dissociation between different aspects of mental state attributions, that of the cognitive and the emotional, each recruiting separate cortical areas (Blair, 2005; Saxe, 2006), which corroborates the modular separation between ToMM and TESS proposed by Baron-Cohen (2005). This is further corroborated by the finding that a task requiring the detection of a social faux pas, which necessitates the attribution of a social emotion, elicits activity in the orbitofrontal cortex (Baron-Cohen et al., 1994). Those with lesions to this area are unable to do so, but retain their ability to pass tasks of 2<sup>nd</sup> order mental state attribution (Stone, Baron-Cohen, & Knight, 1998).

Despite the divergent views as to the nature of how mental states are attributed there is a consensus that ToM is the product of less complex, prerequisite cognitive abilities. Tomasello and Rakoczy (2003) propose that the ability to form an abstract representation of knowledge and beliefs is ultimately an auxiliary capability to a prerequisite, and more important ability to recognise that others are intentional agents in the first place, whose behaviour is determined by more basic psychological states such as goals, desires, attention and emotion. These can be derived from a perceptual analysis of their behaviour that Tomasello and Rakoczy (2003) refer to as 'scratching the surface' of immediately observable behaviour. That is, because mental states cannot be observed directly, they must be inferred from the behaviour of others through the analysis of their actions, which reveal the underlying motives. For them, this provides a foundation upon

which more complex socio-cognitive abilities can be built later in life. The ability to deduce basic psychological states from observable behaviour therefore emerges earlier in development. Furthermore, it also acts as an evolutionary precursor to ToM and may account for the socio-cognitive abilities of non-human primates.

### *Action perception*

By necessity, the individual must first distinguish between biological and non-biological objects. That is, to recognise the distinction between stimuli which are animate and whose behaviour is caused by its goals and intentions, and those stimuli which are inanimate and incapable of internal mental processes. The spontaneous nature of such classifications necessitates an efficient and automatic cognitive system with which to do so (Hassin, Bargh, & Uleman, 2002). For example, attention is automatically allocated to biological stimuli, such as images of human bodies, but not to other stimuli (Downing, Bray, Rogers, & Childs, 2004; New, Cosmides, & Tooby, 2007; Thornton & Vuong, 2004). Baron-Cohen (1995, 2005) encapsulates this ability in a domain specific module called the 'Intentionality Detector' (ID), the task of which is to identify agentive motion through the amodal perception of self-propelled motion, and to interpret it as a product of basic intentional states such as desire or goal-directedness. Likewise, Leslie (1994) describes a module called the 'Theory of Bodies' (ToBy), a domain general ability involved in monitoring the spatio-temporal dynamics of all 3D objects, by which biological motion is similarly delineated by virtue of its difference from that of non-biological motion. Again, the primary differentiating factor is that of self-propulsion. Behavioural studies in infants have shown that these mechanisms are in place from birth (Simion, Regolin, & Bulf, 2008). They have also shown that, as well as self-propulsion, other facets of motion kinematics are necessary for an object to be perceived as agentive. These include reciprocal interaction with other agents (Johnson, 2000; 2003), and a trajectory and speed of movement that is



similar to one's own movement (Morewedge, Preston, & Wegner, 2007; Rakison & Poulin-Dubois, 2001).

However, neither Leslie (1994) nor Baron-Cohen (1995, 2005) provide a precise mechanism by which acknowledging that an agent's motion is mechanically distinct from that of non-agents leads to the attribution of desires and goals. That is, whilst the visual appearance of the motion itself is sufficient to set it apart from other objects, it seems a leap to assume that this in itself warrants the attribution of agency and intentionality, and does not preclude the possibility that its motion is purely mechanical. Rakison and Poulin-Dubois (2001) and Baldwin and Baird (2001) propose that biological motion shows structural regularities that coincide with the initiation and termination of goal-directed actions. Sensitivity to these regularities, especially when associated with the spatial context in which it occurs (Bach, Knoblich, Gunter, Friederici, & Prinz, 2005), is sufficient enough to be able to parse the constant flow of complex movement into discrete functional units of goal directed actions. The action is therefore perceived in terms of its end-point, and is encoded synonymously with the perception of the motor act itself (Hassin, Aarts, & Ferguson, 2005). The emergence of this ability by 10 months of age (Baldwin, Baird, Saylor, & Clark, 2001), and its evidence in Macaque monkeys (Rochat, Serra, Fadiga, & Gallese, 2008), indicates this to be a rudimentary foundation on which further advances in social cognition can be built.

However, adopting this 'teleological stance' (Csibra, 2003) is still one step removed from appreciating its psychological nature (Baldwin & Baird, 2001). That is, that the aim to achieve a goal through performing the action is the product of internal and unobservable intentional drives. Meltzoff (2005, 2007a, 2007b) bridges this gap by proposing that intentionality is ascribed to individuals through a process of self/other equivalence. From birth, the infant possesses an internal representation of its own body and is able to perceive its own movements (proprioception) that encompasses visual, auditory and tactile information. It is able to recognise that the kinematic regularities of its own movements

correspond to those it observes in others. The infant is therefore aware that some objects share mechanistic qualities with itself, and are labelled as 'like me'. Furthermore, because of its amodal nature, actions can be recognised that are visually unavailable, such as facial movements. The encoding of the goal of the action enables the observer to recall the concomitant intentional drives that accompany the action when oneself is performing it, thus providing a means by which intentional states can be associated with the observation of goal directed actions. A by-product of this process is that intentionality is often over-attributed to inanimate objects whose behaviour approximates the characteristics used to define agency (Baron-Cohen, 1995; Luo & Baillargeon, 2005). In such ambiguous situations where errors are likely, natural selection favours making the less costly error (Haselton & Buss, 2000). This over attribution may therefore be an adaptive cognitive bias to assign agency where there is none (false positive) rather than assume an intentional agent to be inanimate (false negative) (Haselton & Nettle, 2006).

### *Action anticipation*

Perceiving the behaviour of others in terms of their goal or end-state enables the actions to be predicted. Several studies have shown an anticipatory effect for biological motion. In such studies, participants typically view a biological action sequence, followed by a test stimulus of a static posture. The posture depicted in the test stimulus can vary in three ways with respect to the final posture of the action sequence. It can be either the same posture, it can be a posture that preceded the final posture, or it can be a posture that would have resulted had the action been allowed to continue. An anticipatory effect is evident as a processing asymmetry between postures that occur after the stopping point and those that occur before it, or are the same as it. This notion of asymmetric processing encompasses a number of different effects. For example, Verfaillie and Daems (2002) found that judgments of whether or not the test posture was anatomically possible or not

were faster for postures that were related to a previously observed action sequence. Crucially, such priming was greater for postures that occurred after the stopping point than those preceding it (which had actually been witnessed).

The most common method used to measure anticipation of biological motion is that of representational momentum (RM). Again, after watching an action sequence, participants view a static posture that is either after, the same as, or before the stopping point of the moving sequence. Participants are required to judge whether the test posture and the stopping point are the same or different. The proportion of same responses is higher for postures that occur after the stopping point than those occurring before the stopping point. Therefore, participants are less able to distinguish the end-point of an action from a posture that will naturally follow on from it, than from a posture that precedes the end-point. As such, the memory for the end-point of the action sequence is displaced further along the observed trajectory and this is taken as evidence that observers automatically anticipate how an observed action is most likely to unfold in the immediate future (please see Chapter 3 for a detailed review of the representational momentum literature and also its relationship with motion anticipation). This bias has been consistently demonstrated for a wide variety of biological motion stimuli, from simple linear movements of schematic animals (Freyd & Miller, 1992), to the more complex pattern of motion of point light stimuli (Graf et al., 2007; Jarraya, Amorim, & Bardy, 2005), and video-clips of real world scenes of people moving (Thornton & Hayes, 2004). It has even been observed for the motion of oneself, with a spatiotemporal forward displacement observed for the pattern of optic flow caused by egocentric motion (Thornton & Hayes, 2004).

#### *Neural basis for action anticipation*

The ability to perceive and predict the actions of others is underpinned by a comprehensive cortical system that encompasses both visual and motor areas. Cortical

regions in the ventral and dorsal visual streams have been shown to be either dedicated, or at least maximally active, to the perception of biological motion. Several areas in the posterior visual cortex exhibit category specific processing of body stimuli, and as such have been termed the Fusiform Body Area (FBA) and Extrastriate Body Area (EBA) (Downing, Chan, Peelen, Dodds, & Kanwisher, 2006; Peelen & Downing, 2007). The EBA, located in the inferior temporal sulcus, shows selective activation to the sight of bodies (Downing, Jiang, Shuman, & Kanwisher, 2001; 2007), and does not differentiate between the actions of others (Peigneux et al., 2000; Urgesi, Candidi, Ionta, & Aglioti, 2007) and those of oneself (Astafiev, Stanley, Shulman, & Corbetta, 2004). Furthermore, when presented with an action sequence, the EBA shows greater activation when frames were presented in an incoherent order than in the correct temporal sequence, suggesting its functional properties are more concerned with the form and structure of the body than with biological motion (Downing, Peelen, Wiggett, & Tew, 2006). Equivalent selectivity for body-like stimuli has been found in homologous areas in the macaque using both single cell (Desimone, Albright, Gross, & Bruce, 1984) and fMRI techniques (Pinsk, DeSimone, Moore, Gross, & Kastner, 2005). The FBA, in the mid-fusiform gyrus, is similarly active to body like stimuli (Morris, Pelphey, & McCarthy, 2006; Peelen & Downing, 2005; Schwarzlose, Baker, & Kanwisher, 2005). However, whereas the extent of FBA activity is greater in response to the whole body than to individual body parts, the EBA is more sensitive to the amount of the body presented, with activity increasing as the extent of visible body increases (Taylor, Wiggett, & Downing, 2007).

The EBA feeds into the Superior Temporal Sulcus (STS) (Giese & Poggio, 2003) which also shows activity to static images of bodies. However, whilst the EBA is most responsive to postures presented in a random order, the STS shows preferential activation when they are sequenced in a coherent temporal order (Downing, Peelen et al., 2006). This elucidates the functional role of the STS in processing biological motion. Single cell recording in the anterior portion of the STS of Macaques (corresponding to the posterior

STS in humans) have revealed that coding in the STS goes beyond that of recognition of general biological motion, to the coding of specific actions and postures (Jellema & Perrett, 2006). Furthermore, this can be accomplished when the information conveyed by the stimulus is impoverished. For example, accurate recognition of biological actions and STS activity in monkeys and humans is observed for motion cues alone in the absence of information regarding the form and structure of the stimulus, such as for point light walkers (Neri, Morrone, & Burr, 1998) and elicits STS activity in both monkeys and humans (Oram & Perrett, 1996; Pelphrey, Morris, Michelich, Allison, & McCarthy, 2005; Puce & Perrett, 2003). Activity is also observed in response to static images of bodies in which motion is implied by the articulation of body parts (Jellema & Perrett, 2003a; Perrett et al., 1989).

The visual properties of STS cells extend beyond that which is necessary for mere identification of particular actions (Jellema & Perrett, 2005). For example, cells selectively active to grasping actions will respond only to the sight of a valid interaction with an object, such that the absence of the object or its remoteness from the action will fail to elicit activation (Perrett et al., 1989). Activity in these cells is therefore reliant on the action being meaningful and goal-directed. Furthermore, repeated observation of specific actions enables associations to be made between postures that constitute part of the same action. This enables probabilistic inferences about the end-point of an action to be made based on previous experience (Giese & Poggio, 2003; Perrett, Xiao, Jellema, Barraclough, & Oram, 2006). For some cell populations, no discrimination is made between the action and its articulated end-point, in that they are coded for synonymously (Jellema & Perrett, 2003a). The activity of other neurons to a specific posture is conditional on it being the result of a specific action sequence (Jellema & Perrett, 2003b), whilst this sensitivity to perceptual history may allow other cell groups to code for an end-point after it has become occluded from view (Baker, Keysers, Jellema, Wicker, & Perrett, 2001; Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004). The integration of the spatial context in which an action occurs and its positioning within a temporal sequence allows for not only the compilation of biological

postures to be coherently processed, but for the end-state of the action to be encoded synonymously with the action itself during the perceptual process (Hassin et al., 2005). The goal of the action can then be derived and predicted on the basis of a purely visual analysis of its appearance (Jellema & Perrett, 2005, 2007). Thus, a mechanism is apparent for the analysis and parsing of the continuous inputs of biological motion into discrete units based on the (sub)goals of the action. The role of the STS is elevated beyond that of a visual description, to the parsing and comprehension of biological motion (Redcay, 2008).

Despite the complex perceptual properties of the STS, its processing remains confined to the purely mechanistic nature of biological motion (Jellema & Perrett, 2005, 2007). However, the STS projects to the intraparietal lobe (IPL) in the dorsal stream, which along with the ventral premotor cortex (vPFC), is also involved in the processing of biological motion. The role of these regions in motor coordination affords it a degree of processing capable of accessing the intentions underlying others actions. In macaques, these areas are involved in the preparation of making goal-directed actions and contain cells that fire immediately prior to the onset of the action (Rizzolatti, Fadiga, Fogassi, & Gallese, 1999). This enables an internal prediction to be made of how the action will proceed (forward model), and which can be compared to visual and somatosensory inputs during execution in order to make fine adjustments and increase efficacy (Blakemore & Decety, 2001; Miall, 2003; Wilson & Knoblich, 2005; Wolpert, Doya, & Kawato, 2003). However, some of the cell populations are also active to the sight of another individual performing the action. Neurons in the Macaque F5 that fire prior to the execution of a specific hand action will fire in response to the sight of another individual performing that action (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Such cells are called mirror neurons (MNs). A large proportion of these neurons do not code for specific motor commands, but are able to generalise across different actions if they share the same goal, such as grasping an object with the hand, mouth or even a tool

(Ferrari, Rozzi, & Fogassi, 2005). Conversely, two identical actions will elicit differential activity if the goal of the actions differ (Fogassi et al., 2005; Iacoboni et al., 2005), and will similarly persist in activity even if the end-point of the action is not visible (Umiltà et al., 2001).

It is not possible to use single cell recording techniques in humans to establish the presence of visuomotor neurons. Therefore, no studies have directly investigated if observed and executed actions share a common representation at the neuronal level, or whether they are encoded by separate neurons that are distributed within the same cortical area (Dinstein, Thomas, Behrmann, & Heeger, 2008). Nevertheless, neuroimaging using both PET and fMRI have revealed activity in the IPL and vPMC, as well as the STS, during action observation (Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Grezes, Armony, Rowe, & Passingham, 2003). Because MNs prepare an action for execution, responses to actions performed by others are restricted to those that are part of the observers motor repertoire, such as those which can be replicated (Buccino et al., 2004) and for those performed regularly in the past (Calvo-Merino, Grezes, Glaser, Passingham, & Haggard, 2006).

Several theorists have argued that MNs constitute the internal simulation of others behaviour that is necessary for ToM (Gallese & Goldman, 1998; Preston & de Waal, 2002; Wolpert et al., 2003). That is, embodied simulation of others actions provides access to their epistemic and emotional mental states. The transformation of an intention into an action can be operated in reverse when observing other people's actions, such that the intention can be inferred from the action. However, ToM is not evident in macaques for which MNs are also evident, or for any other species of primate. This suggests that MNs evolved for a different purpose that is common to both human and non-human primates (Brass & Heyes, 2005), that of understanding and predicting the complex sequence of actions performed by others (Jacob & Jeannerod, 2005), or 'motor empathy' (Blair, 2005). The recruitment of the 'forward model' during action observation serves an anticipatory

function as to the future course of an action through facilitating the recognition and categorisation of actions (Binkofski & Buccino, 2006), which in turn enables inferences to be made as to the goal or end-point of the action (Blakemore & Frith, 2005). This is supported by neurophysiological evidence showing that anticipating another person's action elicits activity in the vPMC, whereas the dPMC shows activity during preparation to act oneself (Ramnani & Miall, 2004). Further evidence from behavioural studies shows that anticipation of biological actions occurs only for actions that are anatomically possible and not for those that the observer cannot perform themselves, implicating a role for MNs in action prediction (Verfaillie & Daems, 2002). However, as noted above, the ability to encode the end-point of an action necessitates only a visual description that can be provided by the STS (Csibra, 2005). This has led to the proposal that the MNs functions to infer not only the goal of the immediately observable action, but in predicting the action most likely to follow it (Jeannerod, 2001). In this way, the current action can be placed within a temporal context of both the causative and consequential actions it enables, permitting the behaviour of others to be more richly understood (Csibra, 2005).

The ability to anticipate the behaviour of others relies on more than analysing the kinematics of observed behaviour, but also relies on other cues as to the intentions underpinning behaviour. Of particular importance in this respect is the face, and more specifically the social cues it provides such as direction of gaze and the expression. From these the observer can discern the other person's attentional state and emotions and ultimately their intentions. Furthermore, the morphology of these features has evolved to intentionally convey such information to others. Understanding the goals and intentions motivating an observed action and predicting its outcome is facilitated by integrating information derived from these cues with the action itself. This provides a means by which socio-cognitive processes go beyond the observable kinematics of an observed action, to the intentional dynamics that underpin and motivate its execution.



### *Face perception*

Faces present a complicated but informative stimulus in our environment, and there is evidence that they are afforded preferential processing in the human visual-cognitive system. Faces capture visual attention (Hershler & Hochstein, 2005; Theeuwes & Van der Stigchel, 2006), and when freely viewing natural scenes containing people, 80% of initial fixations are directed towards faces (Cerf, Harel, Einhaeuser, & Kock, 2007). Furthermore, when freely viewing faces alone, the spatial distribution of attention of humans and other primates is predominantly biased to the internal features (mouth, nose, eyes) rather than the external features, such as the hair and jaw line (Barton, Radcliffe, Cherkasova, Edelman, & Intriligator, 2006; Guo, Mahmoodi, Robertson, & Young, 2006; Guo, Robertson, Mahmoodi, Tadmor, & Young, 2003; Pelphrey et al., 2002).

The first order relations between the inner features are uniform across all faces (Maurer, Grand, & Mondloch, 2002), with the two eyes positioned above the mouth to form a triangle, with the nose at the centre (Barton, Zhao, & Keenan, 2003). Some studies suggest that humans are sensitive to this unique configuration from birth, with newborns gazing more at face-like stimuli than non-face-like stimuli (Pascalis & Kelly, 2009). This has led to the proposal that humans are born with an innate disposition to detect faces that has evolved as a result of the adaptive pressures placed on cognitive abilities to process social information (de Gelder & Rouw, 2001; Johnson, 2005; Morton & Johnson, 1991).

Repeated exposure to faces leads to greater sensitivity to facial configurations, and this drives the sophisticated face processing skills of adults, collectively known as face expertise. This includes the differentiation between identities, the recognition of familiar faces, and discerning age and gender. The origin of this sophisticated sensitivity to facial information has been proposed to derive from a unique ability to process the 2<sup>nd</sup> order relations between facial features. That is, whereas the first order relations define that the two eyes are placed above the nose, which in turn is above the mouth, the second order

relations refer to the relative spatial distances between these features, their size and position within the face contour, whilst retaining the same first order configuration (Maurer et al., 2002). The integrated whole therefore takes on additional properties not accounted for by the mere summation of its individual parts (Tanaka & Sengco, 1997). The prototype theory proposes a means by which configural information is measured (Anderson & Wilson, 2005; Leopold, O'Toole, Vetter, & Blanz, 2001; Leopold, Rhodes, Muller, & Jeffery, 2005; Rhodes & Jeffery, 2006). The configural information of all the faces one encounters are averaged and represented as a prototype. All individual faces are then assessed in terms of how much they deviate from the average, with increasing strength of any given social attribute represented by an increase in the distance from the prototype. Judgments of identity, gender, attractiveness and trustworthiness have all been correlated with how much the 2<sup>nd</sup> order relations between the facial features differ from that of an average face (Oosterhof & Todorov, 2008; Potter & Corneille, 2008; Todorov, Baron, & Oosterhof, 2008; Wallis, Siebeck, Swann, Blanz, & Bulthoff, 2008; Wilson, Loffler, & Wilkinson, 2002).

Further support for the contention that configural information is important for face processing comes from the effect of stimulus inversion. Detecting a change in the spatial relations between features (the distance between the eyes, or between the nose and mouth), is worse for inverted faces than for upright faces (Barton et al., 2003; Davies & Hoffman, 2002; Leder, Candrian, Huber, & Bruce, 2001; Leder & Carbon, 2006), more so than for detection of changes to individual features, for example their size or colour (Barton, 2001; Leder & Bruce, 2000; Rhodes, Brake, & Atkinson, 1993; Searcy & Bartlett, 1996). Detecting configural and featural changes in upright faces is correlated across individuals, whereas they are not for inverted faces, suggesting that the two processing types are dissociated from each other when processing inverted faces (Yovel & Kanwisher, 2008). This inversion effect appears to disrupt the processing of spatial relations on the vertical axis more than those on the horizontal axis (Goffaux & Rossion, 2007).

Processing the inter-individual variation in the 2<sup>nd</sup> order relations between features is necessary for discriminating between individuals, as well as their age and gender. Recognition of identity is less accurate and slower for inverted faces than for upright faces (Diamond & Carey, 1986; Dwyer, Mundy, Vladeanu, & Honey, 2009; Metzger, 2001; Nachson & Shechory, 2002; Teunisse & de Gelder, 2003). Judgments of age, gender, and attractiveness have also been found to be impaired for inverted faces, as well as personality judgments such as trustworthiness and intelligence (Baudouin & Humphreys, 2006; Bauml, Schnelzer, & Zimmer, 1997; Sangrigoli & de Schonen, 2004; Santos & Young, 2008). Furthermore, the second order relations between features also vary within individuals over time. Therefore, face inversion also impairs the perception of dynamic facial information such as lip reading (Rosenblum, Yakel, & Green, 2000) and emotional expressions (Aguado, Garcia-Gutierrez, & Serrano-Pedraza, 2009; Calder & Jansen, 2005; Goren & Wilson, 2006). Inversion has not been found to impair the processing of non-face stimuli, such as dot patterns, houses or textures (Husk, Bennett, & Sekuler, 2007; Tanaka & Farah, 1991), and an ambiguous stimulus elicits an inversion effect if perceived as a face but not if perceived as a Chinese character (Ge, Wang, McCleery, & Lee, 2006; McCleery et al., 2008). However, inversion effects have also been observed when discriminating between and identifying static body postures (Reed, Stone, Bozova, & Tanaka, 2003; Reed, Stone, Grubb, & McGoldrick, 2006), and when processing biological action sequences (Loucks & Baldwin, 2009; Pavlova & Sokolov, 2003). As such, the processing of social stimuli in general may require configural processing.

It must be noted, though, that the face inversion effect is defined as the decrement in performance in relation to that of upright faces. However, processing remains above chance. Furthermore, inversion also affects the processing of featural changes (Leder & Carbon, 2006; Riesenhuber, Jarudi, Gilad, & Sinha, 2004), but to a lesser extent than for configural changes, suggesting that inversion effects reflect a quantitative shift in

processing rather than a qualitative/categorical shift between processing styles (Sekuler, Gaspar, Gold, & Bennett, 2004).

As with the perception of biological motion, there is evidence to suggest that the face and its dynamic features exploit a distributed and dedicated processing system. Faces have been found to elicit a negative event related potential deflection that peaks at around 170ms (N170) and which is larger than in response to other types of stimuli (Bentin, Allison, Puce, Perez, & McCarthy, 1996; de Haan, Pascalis, & Johnson, 2002). This suggests that faces exploit a specific cortical system not exploited by non-face stimuli. Several areas in the lateral occipital complex have been shown to be selectively responsive to faces. Discrete regions of the inferior occipital cortex and middle fusiform gyrus exhibit greater activity in response to faces than to bodies without faces, places and other objects (Downing, Chan et al., 2006; Grill-Spector, Knouf, & Kanwisher, 2004; Kanwisher, McDermott, & Chun, 1997; Rossion, Schiltz, & Crommelinck, 2003; Schwarzlose et al., 2005). These have been termed the occipital face area (OFA) and the fusiform face area (FFA) respectively. A further area has been identified in the posterior Superior Temporal Sulcus (Allison, Puce, & McCarthy, 2000).

The distributed nature of these areas suggests some functional dissociation between them, with each area serving a specific facet of face processing (Haxby, Hoffman, & Gobbini, 2000, 2002). Several studies indicate that the OFA is sensitive to the physical features of the face whilst the FFA is sensitive to facial identity. FFA activity is higher when discriminating faces with equivalent physical structure but which differ in identity (Rotshtein, Henson, Treves, Driver, & Dolan, 2005), and only when the observer is consciously aware of these differences (Large, Cavina-Pratesi, Vilis, & Culharn, 2008). FFA activity is also sensitive to stimulus manipulations that modulate the ability to perceive identity, such as reversal of contrast polarity (George et al., 1999), stimulus inversion (Chen, Kao, & Tyler, 2007; Tong, Nakayama, Moscovitch, Weinrib, & Kanwisher, 2000; Yovel & Kanwisher, 2004) and deviation from an averaged prototype (Loffler, Yourganov,

Wilkinson, & Wilson, 2005). Face inversion is associated with decreased activity in the FFA (Goffaux, Rossion, Sorger, Schiltz, & Goebel, 2009; Mazard, Schiltz, & Rossion, 2006; Passarotti, Smith, DeLano, & Huang, 2007; Tong et al., 2000; Yovel & Kanwisher, 2004) and the magnitude of this decrease correlates with the extent to which inversion impairs face processing ability (Yovel & Kanwisher, 2005). The response of the OFA to inverted faces is less consistent, with both an insensitivity to face inversion and a reduction in activity being reported (Chen et al., 2007; Joseph et al., 2006; Yovel & Kanwisher, 2005), whilst the pSTS has been shown to increase activity (Leube et al., 2003).

Activity in OFA is not sensitive to identity changes but is higher when discriminating between two faces based on differences in their physical structure (Rotshtein et al., 2005), and this is evident in the absence of any conscious awareness of those differences (Large et al., 2008). Creating neuronal noise in the OFA by means of Transcranial Magnetic Stimulation (TMS) impairs the ability to detect featural changes in faces but not the 2<sup>nd</sup> order spatial relationships between those changes (Pitcher, Walsh, Yovel, & Duchaine, 2007). Putative homologues of these areas have been found in non-human primates. fMRI and single cell recordings have revealed face selective areas in the inferior temporal cortex (ITC) and anterior STS of macaques (Desimone et al., 1984; Perrett, Rolls, & Caan, 1982; Pinsk et al., 2005).

Haxby et al (2000, 2002) (see also Cohen & Tong, 2001; Kadosh & Johnson, 2007) proposed a model of face processing to account for the broad distinctions outlined above. The OFA performs an initial analysis of the physical structure of the face which projects in two parallel streams to the FFA for the purpose of identification and the pSTS to process the facial movement (see below). In this way, the OFA and FFA process static and invariant facial attributes, whilst the pSTS is motion sensitive. These constitute the core components of a distributed system of face processing, and interact with non-face specific areas (the extended system), to integrate the facial information with emotional (amygdala), semantic (anterior temporal regions), and spatial (intraparietal sulcus) information. Others

have elaborated on this model. The functional distinction between areas could be due to the constant attentional demands necessary when processing motion but not when perceiving invariant features (Calder & Young, 2005). O'Toole, Roark and Adbi (2002) propose that these areas interact rather than function in parallel, such as when recognising identity from facial movement, and Rossion et al (2003) suggest that face selective areas may be involved in several functions but at different stages of processing.

### *Are faces special?*

The nature of face processing outlined above suggests an innate predisposition to attend specifically to faces that employs a qualitatively different means of processing to that of other objects by a dedicated cortical system. This has led many to propose that faces are represented in the cognitive system differently to other stimuli and therefore represent a special stimulus (Fox, 2005; Liu & Chaudhuri, 2003). However, many have challenged this assumption. The innate tendency to orient to faces demonstrated by newborns has been proposed to reflect a generalised sensory bias to the low level visual properties of the face, such as the amplitude spectra of faces (Kleiner & Banks, 1987; Nelson, 2001) and the greater number of features in the upper half than the lower half (Simion, Cassia, Turati, & Valenza, 2001; Turati, 2004). Furthermore, these types of non-face patterns also elicit greater activity in the adult FFA (Caldara et al., 2006). This casts into doubt the specialisation of specific cortical areas for processing faces. However, whilst these areas do show some activity in response to non-face stimuli, it is significantly less than in response to faces, suggesting that the stimulus selectivity in these regions is relative rather than absolute (Spiridon & Kanwisher, 2002). Others maintain that so-called face specific cortical regions show no bias for faces at all, but subserve a generalised expertise process (Gauthier & Tarr, 1997). That is, where all exemplars of a stimulus share the same basic configuration, the FFA and OFA enable one to discriminate between them

at the subordinate level. For example, people trained to identify cars, birds or abstract stimuli show greater OFA and FFA activity in response to these categories, whereas those with no training do not (Gauthier, Skudlarski, Gore, & Anderson, 2000; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Rogers, Hocking, Mechelli, Patterson, & Price, 2005). However, this is not to say that faces do not preferentially activate these regions. Indeed, these areas may most frequently be employed for face stimuli, and the need to recognise individual faces may have been the initial adaptive pressure favouring the evolution of an expertise mechanism.

### *The role of the face in Theory of Mind*

Infants are more likely to interpret a stimulus as agentive if it has a face than if not (Johnson, Slaughter, & Carey, 1998; Johnson, 2003), and where a face is not present, its location will be inferred from the direction of movement (Johnson, Grossmann, & Farroni, 2008). As such, the presence of a face contributes to Baron-Cohen's (1995) notion of an Intentionality Detector in ascribing agency. However, the role of the face extends beyond conveying that a stimulus has intentions, but also specifies what those intentions are, and this is achieved primarily through facial movement (Yazbek & D'Entremont, 2006). Two crucial facets of facial dynamics are the changing direction of eye gaze and emotional expression. These two important components in social interactions will now be introduced in turn.

### *Gaze direction*

The gaze direction of another person denotes the focus of their attention, and as such is informative about the external world. Furthermore, an observer can also deduce aspects of the other person's internal mental state from gaze direction, such as their intentions towards the focus of attention, be it oneself or another object/individual. This can

subsequently enable the observer to anticipate and predict the nature of the other person's actions. The direction of another's attention can be discerned from the orientation of their torso, their head, or the direction of their gaze (cf. Perrett et al., 1989). However, the eyes offer the most specific and informative cue, and this is reflected in the preferential allocation of attention afforded to the eye region over other internal facial features (Bindemann, Scheepers, & Burton, 2009; Buchan, Pare, & Munhall, 2007; Hernandez et al., 2009). Indeed, this attention to the eyes has been proposed to facilitate face processing and the development of face expertise, as the eye region is important for the recognition of identity and expression (Gliga & Csibra, 2007). The computation of the exact direction of gaze has been proposed to be a function of the geometrical properties of the eye, with the position of the round iris within the oval sclera determining the gaze direction (Todorovic, 2006). This is facilitated by a sharp degree of contrast marking the boundary between the two features, known as the limbus. However, the degree of contrast itself is insufficient to discern gaze direction, as reversing the polarity (whilst maintaining the contrast), can impair judgments of gaze direction (Ricciardelli, Baylis, & Driver, 2000; Senju & Hasegawa, 2005), and can induce the perception that gaze is looking in the opposite direction (Sinha, 2000). Furthermore, reducing the contrast on one side of the eye can lead to a bias in perceiving the gaze to be averted in that direction (Ando, 2002, 2004). This suggests that, in addition to the geometrical configuration of the components, mechanisms for perceiving gaze direction are also sensitive to the relative contrast between them, with the dark part of the configuration indicative of where the eyes are directed.

However, the above studies assume the head to be oriented toward the observer, whereas gaze discrimination must also be possible when the head is averted, which alters the perceptual geometry of the eyes (Kluttz, Mayes, West, & Kerby, 2009; Todorovic, 2006). Discriminating gaze direction is impaired when the head is incongruently aligned with gaze direction, both in terms of accuracy and discrimination time (e.g. Todorovic,



2009). Discerning where someone is looking is therefore computed from adding the direction of head orientation to the direction of gaze (Kluttz et al., 2009; Todorovic, 2006). However, Ricciardelli and Driver (2008) observed that such interference was evident only when participants were required to discriminate gaze as quickly as possible, but not when no time limit was imposed, suggesting that when under pressure, participants will use easily identifiable cues such as head orientation as a proxy to gaze direction. Furthermore, George and Conty (2008) note that the effect of head orientation is stronger for averted gaze, but has less of an influence on direct gaze, possibly due to the greater social saliency of direct gaze (see below). However, these constitute what Bock et al (2008) refer to as 'sender-centric' processes, which contrast with 'receiver-centric' properties of gaze processing, such as the observers expectancies as to the gaze direction based on the environmental context. For example, perceptions of gaze direction can be erroneously biased towards the location of external objects (Lobmaier, Fischer, & Schwaninger, 2006).

#### *The social significance of direct and averted gaze*

Several distinctions between the different facets of gaze direction have been proposed based on the functions they serve and the cognition involved in their processing. Todorovic (2006) proposes three frames of reference in which gaze can be processed. Firstly, whether or not the other person is looking at you or not (mutual gaze or dyadic gaze direction), and secondly where they are looking with respect to oneself (averted gaze e.g. to the left right, down or up). The preferential fixation on the eye region is enhanced when the gaze direction is directed at the observer. For example, in visual search tasks, faces with direct gaze 'pop-out' of an array of faces with averted gaze, whereas no pop-out effect is observed for faces with averted gaze in an array of faces with direct gaze (Senju & Hasegawa, 2005; Senju, Kikuchi, Hasegawa, Tojo, & Osanai, 2008). Furthermore, disengagement of attention from a direct gaze is impaired compared to that of an averted

gaze (Senju & Hasegawa, 2005). As direct gaze enhances attention to the face, the processing of social information is also facilitated, with direct gaze improving recognition of gender and identity (Hood, Macrae, Cole-Davies, & Dias, 2003; Macrae, Hood, Milne, Rowe, & Mason, 2002; Vuilleumier, George, Lister, Armony, & Driver, 2005). There is evidence that discrimination of different gaze directions is possible early in life. Within 36 hours after birth the infant is able to discriminate between faces with eyes open and shut (Batki, Baron-Cohen, Wheelwright, Connellan, & Ahluwalia, 2000), and by 5 days old they look preferentially at faces with a mutual gaze than with an averted gaze (Farroni, Csibra, Simion, & Johnson, 2002).

Thirdly, a more complex process is to compute to what another person is looking at (joint attention or triadic gaze direction). The target of another's attention when their gaze is mutual is unambiguously oneself. However, when it is averted, their target of attention could be any number of external stimuli. To accomplish this, the observer must first follow their line of sight to the correct location (level 1 perspective taking). By inferring an outward bound line that originates from the eyes, an observer can determine to where another is looking with a high degree of accuracy, and can pinpoint the target of another's attention to  $2.81^\circ$  (Bock et al., 2008). Tomasello and Rakoczy (2003) proposes that these three abilities constitute merely a low level capacity to process gaze, and proposes an additional high level capacity in which the observer is able to comprehend what the other person is seeing. That is, once the other person's line of sight has been deduced, one can then infer what the object looks like from their perspective (level 2 perspective taking). The perspective oneself has of the scene (the spatiotopic map of the egocentric and allocentric coordinates) is reoriented to that of the other person, and thus enables the observer to imagine the perspective of the other person. The dissociable nature of level 1 and 2 perspective taking was demonstrated by Michelon and Zacks (2006). They found that the time taken to perform level 1 perspective taking increased as the distance between the other person and the target increased, and thus the length of the line of sight to be traced

increased. However, this was not affected by the extent to which the perspectives of the observer and the other person differed. Conversely, the opposite was found for level 2 perspective taking. The time taken to identify the perspective of a scene from another person's viewpoint increased as the difference between the two, and therefore the degree of mental transformation required, increased. However, this was not affected by the distance between the other person and the target objects. Furthermore, there is evidence that level 2 perspective taking is accomplished automatically. Participants viewed a scene in which another person was either absent or present. They were then required to identify the same scene from a different perspective. Such perspective transformations were facilitated if the viewpoint was that of the other person depicted rather than if the person was absent, suggesting that their viewpoint was automatically encoded (Amorim, 2003). Baron-Cohen (1995) proposed that these abilities are governed by an innate ability to detect the gaze direction of others that he calls the Eye Direction Detector (EDD). The module functions to detect eye-like stimuli and discern in which direction they are looking, and also to infer what they are seeing. The relationships that the EDD processes are dyadic, in that the other person's gaze direction is represented with respect to either the observer or to another object. However he, as well as Emery (2000), suggest that a full understanding of the social significance of another person's gaze direction requires the additional ability of knowing that you and another person are attending to the same stimulus ('shared attention mechanism').

#### *Neural basis of gaze perception*

The prominent role that gaze direction plays in social cognition is reflected in the extensive network of brain areas implicated in its perception, encompassing visual and semantic processing of the extrastriate and temporal cortices (Haxby et al's core system), as well as sub-cortical areas, the spatial orienting mechanisms of the parietal lobe and

higher level cognitive functions of the MPFC (Haxby et al's extended system). Haxby et al's (2000) distributed model of face perception proposes that dynamic facial information is predominantly processed by the STS, in keeping with its more general role in the perception of biological motion. Indeed, fMRI studies have revealed robust activation in the posterior STS in response to determining the direction of another's gaze (Hoffman & Haxby, 2000; Kuzmanovic et al., 2009; Materna, Dicke, & Thier, 2008). Furthermore, impairments in ascertaining direction of gaze have been observed in patients with lesions to the right Superior Temporal Gyrus (Akiyama et al., 2006), and lesions to the right Medial Temporal Lobe are associated with an inability to perform level 2 perspective taking (Lambrey et al., 2008). More specifically, several studies have suggested that different gaze directions are encoded by separate cell populations in the STS, as evidenced by both behavioural (Calder, Jenkins, Cassel, & Clifford, 2008; Duchaine, Jenkins, Germine, & Calder, 2009; Kloth & Schweinberger, 2008; Seyama & Nagayama, 2006) and fMRI adaptation studies Calder et al (2007). Furthermore, right pSTS activity is higher when gaze is directed at the observer than when looking into empty space (Pelphrey, Viola, & McCarthy, 2004). Single cell studies in macaques have found cell populations in the anterior STS (a proposed homologue of the human pSTS) selectively active to specific directions of gaze, head and torso orientation (Perrett et al., 1985). Many species of non-human primates engage in joint attention (Ferrari, Kohler, Fogassi, & Gallese, 2000; Tomasello, Call, & Hare, 1998) and exploit another's gaze direction in situations of food competition (Hare, Call, & Tomasello, 2001; Hare & Tomasello, 2004; Melis, Call, & Tomasello, 2006). This is in keeping with the shared selection pressures favouring the ability to process the social behaviour of others.

The STS is not the only area implicated in the processing of gaze direction. Because of the simplicity of the pattern formed by the eyes, Senju and Johnson (2009) have proposed that gaze direction can initially be processed by a rapid, but crude, sub-cortical route sensitive to low spatial frequencies. For example, bilateral amygdala activity is found

in response to gaze direction, with the right amygdala more responsive to direct than averted gaze, and the left amygdala equally responsive to both gaze directions (Kawashima et al., 1999) and lesions to the amygdala prevent normal gaze processing (Adolphs et al., 2005). Information regarding gaze direction from both cortical and sub-cortical areas then proceeds to other areas such as the intraparietal sulcus for the purpose of spatial orienting (Hoffman & Haxby, 2000; Mosconi, Mack, McCarthy, & Pelphrey, 2005; Pelphrey, Singerman, Allison, & McCarthy, 2003), and the mPFC for more higher level mental state attributions necessary for ToM (Calder et al., 2002; Kuzmanovic et al., 2009).

### *Emotional facial expressions*

When faced with a stimulus that either promotes or impairs the attainment of one's goals, an emotional response is often elicited in the form of changes in one's physiological, psychological and behavioural state. These prepare the organism for a particular course of action. Emotions are therefore thought to be an adaptive response to external stimuli that aid an organism's survival (Lang & Davis, 2006; Nesse, 1990). Different external stimuli require different behavioural responses, and as such elicit different emotional states. These emotional states are often displayed by the individual as expressions through movement of the facial musculature into distinctive configurations (Burrows, 2008), though emotions are also expressed via other means such as body posture and vocal intonation. Expressions are thought not to be a simple manifestation of an individual's internal state, but serve to intentionally communicate specific information to others. Therefore, an observer is well placed to obtain information regarding the stimulus that elicited the response, the expresser's internal physical and mental state, what their behavioural response will be, and the expected response of the observer to the sight of the expression (Ekman, 1997). Whilst expressions can be a consequence of a person's emotional state, they can also be strategically deployed in the absence of a felt emotion for other social

purposes (Blair, 2003; Griffiths, 2003; Hager & Ekman, 1983). Whilst the array of possible expressions and the emotions they convey is vast, Ekman (1999) proposed six basic emotions, along with their antecedent expressions. The basic expressions are sadness, anger, joy, disgust, fear and surprise. This is drawn from evidence that they appear early in life, are evident across different cultures, share homologies in non-human primates, and are characterised by distinct physiological and psychological changes. Furthermore, the expressions that accompany them are distinct from one another, with little overlap between them in terms of the patterns of facial movement (Smith, Cottrell, Gosselin, & Schyns, 2005), although there is individual variation in the quality and quantity of their production (Waller, Cray, & Burrows, 2008).

*Parallels between the processing of emotional expression and gaze direction*

Expressions are as vital a component in an observer's ability to anticipate another's behaviour as is gaze direction, and share a common social function in the information they convey. Emotional expressions can be delineated on the grounds of what behaviour or course of action the emotion prepares the individual to make. The experience of anger or happiness is associated with appetitive motivations and a disposition to approach the stimulus, whereas the experience of fear or disgust is associated with withdrawal motivations and a disposition to avoid the stimulus (Gray, 1994). The experience of these different behavioural motivations are characterised by hemispheric asymmetries in frontal and anterior temporal activity, with approach emotions showing greater activation in the left hemisphere and avoidance emotions greater activity in the right hemisphere (Davidson, Saron, Senulis, Ekman, & Friesen, 1990). The dissociation between approach and avoidance is also supported by the motor responses that different affective stimuli elicit. Participants are faster to pull their arm towards them (indicative of an approach response) in response to a positively valenced stimulus, and quicker to push their arm

away from them (indicative of an avoidance response) in response to a negatively valenced stimulus (Chen & Bargh, 1999). The influence of stimulus valence and motor response also works the other way, as moving the arm towards oneself in response to a neutral stimulus induces a more positive evaluation of that stimulus than when moving the arm away from oneself (Cretenet & Dru, 2008).

In this way, the behavioural inferences made on the part of an observer when seeing another's emotional expressions are comparable to those when seeing their gaze direction. As the target of another's attention is often indicative of what they want and the goal of their action, a direct gaze is synonymous with the tendency to approach, whereas an averted gaze is synonymous with a tendency to avoid. In support of this, viewing someone with a direct gaze increases neuronal activity in the left hemisphere, congruent with the motivation to approach, whereas viewing someone with an averted gaze increases neuronal activity in the right hemisphere, congruent with the motivation to avoid (Hietanen, Leppanen, Peltola, Linna-Aho, & Ruuhiala, 2008).

#### *The role of gaze direction in the perception and anticipation of goal directed actions*

The use of gaze as a cue to the attentional state of the observer can be integrated with the processing of the actions and with the location of external objects. This can derive from the relationship between their gaze and the location of environmental objects, and its relationship with other parts of the body, most notably head orientation. This contributes to the generation of expectancies as to how the other person will act in the immediate future. Comprehending the relationship between another's gaze direction and the location of objects enables anticipation of the potential actions that another can make on them. Action execution is guided by visual information, which places the action in an egocentric spatial frame of reference, and enables planning of the fine motor control of future movements (Bertenthal & Von Hofsten, 1998). Gaze is typically directed to the intended location of the

action in the immediate future (Land & Furneaux, 1997), either when reaching for an object (Land, Mennie, & Rusted, 1999), walking (Hollands, Patla, & Vickers, 2002), or steering a vehicle (Wilkie, Wann, & Allison, 2008). This intricate coupling of eye and head movement with other motor behaviours are initiated automatically and in parallel (Biguer, Jeannerod, & Prablanc, 1982), most likely subserved by the superior colliculus (Gorbet & Sergio, 2009). However, as orienting of the eyes is a quicker and more efficient means with which to focus visual attention, saccadic shifts will often precede movement of the head, resulting in an articulation of the eyes and the head, such that they are oriented in incongruent directions (Biguer et al., 1982; Freedman, 2008; Oommen, Smith, & Stahl, 2004).

In a perceptual sense, the expectancy that someone's gaze will be fixated at an object results in a bias to perceiving others gaze to be directed at a specific target rather than to open space (Lobmaier et al., 2006). Several studies have shown that observing someone simply look at an object influences one's own perception of the object. Seeing someone look at an object facilitates the subsequent detection, localisation or discrimination of the object (e.g. Driver et al., 1999) and this has been proposed to arise due to the observers spatial attention being automatically oriented in the direction that another person is looking. However, such orienting is greatest when the eyes and head of the other person are oriented in incongruent directions (Hietanen, 1999). As gaze movement often precedes movement of the head when orienting to a stimulus, this articulation of head and gaze direction conveys the impression that something has recently caught the attention of the agent and is indicative of the location of external objects (Conty, Tijus, Hugueville, Coelho, & George, 2006; Vuilleumier et al., 2005).

An observer can therefore use the relative orientation of another's gaze direction with that of their head orientation, or with the location of objects as an aid to inferring their goal and behavioural intentions. That is, because of the necessity of fixating on the goal of an action, an observer can use gaze direction as a probabilistic cue to the goal of the action and therefore anticipate its end-point. Children as young as 4 years old will infer that



another person wants or desires an object they are looking at (Baron-Cohen, Campbell, Karmiloff-Smith, Grant, & Walker, 1995; Lee, Eskritt, Symons, & Muir, 1998). Adults will similarly hold objects in a positive regard if they are looked at by another, either whilst they are reaching for it or merely looking at it (Bayliss, Paul, Cannon, & Tipper, 2006; Hayes, Paul, Beuger, & Tipper, 2008). Therefore, the gaze direction of others plays an important role in inferring their intentions towards the objects themselves. For this reason, the relationship between gaze direction and object location plays a role in action perception. In the same way that an actor's gaze is directed at the goal of his/her action, an observer will gaze at the goal of the actor's action as well (Flanagan & Johansson, 2003; Rotman, Troje, Johansson, & Flanagan, 2006) and this ability is evident as early as 12 months of age (Falck-Ytter, Gredeback, & von Hofsten, 2006). In addition, children will use gaze direction to determine whether or not an action was performed intentionally, or to understand an action whose goal is not clear (Call & Tomasello, 1998; Phillips, Baron-Cohen, & Rutter, 1992).

The same behaviours have also been observed in a variety of non-human primates, with orangutans and chimpanzees attributing intentionality to actions from gaze direction (Call & Tomasello, 1998). Diana monkeys expect the gaze of others to be congruent with the location of an object (Scerif, Gomez, & Byrne, 2004), and cotton-top tamarins expect an actor to grasp the object they are looking at, and show violation of expectancy behaviours (longer looking time) when an actor grasps the object not looked at (Santos & Hauser, 1999), although the same behaviour has not been observed in several other monkey species (Anderson, Kuroshima, Kuwahata, & Fujita, 2004).

Evidence for a role of gaze direction in action perception is evident in imitation studies. Reaching for and grasping an object is facilitated after observing someone else perform the same action. Such priming occurs even when the observer hasn't seen an overt action, but merely watches someone look at the object. No priming is observed when the other person is looking away from the object (Pierno et al., 2006). Furthermore, the

presence of a distracter object will interfere with the person's execution of an action toward a target object, and this interference will be similarly imitated by an observer (Frischen, Loach, & Tipper, 2009), but only when the other person is seen to look at the distracter and not when fixating only at the target (Castiello, 2003). Evidence suggests that infants as young as 6 months of age can use the relationship between gaze direction and object location when comprehending the goal directed reaching of others (Luo & Baillargeon, 2007; Luo & Johnson, 2009). Level 2 perspective taking, or an allocentric representation of what the other person is seeing, is therefore necessary when perceiving the actions of others. According to Becchio et al (2008), this enables a process of 'intentional imposition'. An object seen to be gazed at by another individual activates representations of its affective valance and the possible motor acts that can be performed on it. This leads to an attribution of the intentions of the person who is looking at it. This process does not occur for objects not looked at by another person.

Cortical areas previously shown to be involved in biological motion perception have been implicated in the integration of gaze direction and the actions of others. Jellema et al (2000) recorded the activity of single cells in the STS of Macaques and found a small population to respond selectively to reaching actions only when the actor's gaze was directed at the target of the reach, and not when directed away from it. STS activity was similarly observed by Pierno et al (2008; 2006) in adults using fMRI when observing someone reach for an object or merely observe the object, but not when looking away from the object. Furthermore, the same task also elicited activity in the premotor cortex and intraparietal cortex, which contain mirror neurons in monkeys and show mirror properties in humans.

As noted above, studies of RM using biological stimuli have suggested that the perception of biological motion entails a synonymous encoding of how the action is most likely to continue. This results in a distortion for the remembered final position of the action. As gaze direction is indicative of the goal or end-point of an action, it is plausible

that such memory distortions would be sensitive to the gaze direction of the actor. That is, that anticipating the end-point of an action would be facilitated through integration of information regarding the goal of the action from gaze direction. This hypothesis has so far never been explicitly tested, but several studies report related effects. Freyd and Miller (1992) observed a greater displacement effect for a schematic animal moving forward in the direction it was looking than when moving backwards. However, Thornton and Hayes (2004) found the opposite effect using video clips of real world crowd scenes, with a greater displacement for clips played backwards than forwards. It should be noted, however, that for both of these studies the movement itself was not the same across conditions, so the differences cannot be attributed solely to the variation in gaze direction. Jellema et al (2009) used static images of two characters depicted as running towards each other and asked participants to subsequently recall the distance between the two figures. They were remembered as being closer together if they were both looking in the direction of motion than if both were looking in the opposite direction (i.e. looking over their shoulder), despite their proximity being the same. Nummenmaa et al (2009) presented participants with an actor depicted as walking towards them with a mutual gaze, which necessitated a change in trajectory in order to avoid a collision. If the other person's gaze is averted to the left or right, the observer can anticipate that they will alter their path of motion in the direction they are looking. The observer will then choose to move to the opposite side. Finally, Adams et al (2006) presented participants with a face whose gaze was directed either to the left or right. The face then moved in a direction either congruent or incongruent with gaze direction, and participants were required to judge in which direction (left/right) the face had moved. Responses were quicker when the movement was congruent with gaze direction than when incongruent, suggesting that gaze direction enabled the observer to anticipate the direction the face was most likely to move. Interestingly, this effect was found to interact with the emotional expression of the stimulus. However, the motion itself could not be described as biological in nature, as the

picture was of a disembodied face and motion was induced through the presentation of two frames depicting the stimulus as shifting laterally across the screen, which is more reminiscent of the type of motion used in studies of non-biological stimuli (see Chapter 2).

### *Summary and aims*

Observing other people's behaviour is crucial in social interactions as it is revealing of the goals and intentions motivating their actions. This enables the observer to anticipate how the action will most likely continue in the immediate future. A visual description of the kinematics of another person's movement can be parsed into units of goal directed actions. The end-point of an action can therefore be encoded along with the perception of the action itself. Previous research has provided evidence for this by demonstrating that, after observing a biological action sequence, subsequent processing is biased for static postures that would have occurred after the end-point of the observed action than those occurring before the end-point. Furthermore, that this is underpinned by a distributed cortical system that shows selective activity to actions based on the goal of the action, and maps these onto one's own motor representation of those actions.

Attributing goals to actions is facilitated by integrating information obtained from their gaze direction. During the execution of a goal-directed action, visual attention is aimed at the target of the action. An observer can therefore use the gaze direction of another when observing their behaviour as a predictive cue to the end-state of the action. Therefore, encoding the end-point of an action, and predicting its future course, entails not only a representation of the mechanical kinematics of the action, but also integrates a representation of the dynamics underpinning the action, in terms of the actor's goals and intentions.

The aims of this thesis:

1. The aim of Experiment 1A is to establish if estimations of how far an action has proceeded are influenced by the gaze direction of the actor whilst performing the action. Participants should overestimate how far the action has progressed when the actor's gaze is directed at the goal of the action and underestimate how far it has progressed when the actor's gaze is directed in the opposite direction. A further aim was to ensure that the influence of gaze on action anticipation is due to inferences made by the observer with regards to the goals and intentions of the actor, and not to any non-social aspect of gaze direction, such as its visual appearance or directional meaning. The effect of gaze direction was therefore compared with several non-biological control stimuli (Experiments 1A and 1B).
2. The proposed effect of gaze direction on action anticipation assumes that intentional information from gaze direction is integrated with the perception of the action itself. The ability to process body parts in relation to one another (configural processing) has been found to be impaired when the stimulus is inverted. The aim of Experiment 2 is to disrupt this ability to integrate visual information by inverting the stimuli. It is predicted that gaze direction will have no effect on judgments of how far the action has proceeded when the stimuli are inverted.
3. The aim of Experiment 3 is to investigate how the role of gaze direction on action anticipation is affected by the presence of other social cues that serve a similar function in attributing goals to the actions of others, namely facial expressions of emotion. Different emotional expressions convey different information, and as such will influence the social meaning of gaze direction. It is therefore expected that the effect of gaze direction on action anticipation will be affected by the emotional expression of the actor.
4. Experiment 4 aimed to investigate how the contribution of social cues to intentional attribution goes beyond anticipating the end-point of actions that are immediately

observable (motor empathy) to predicting behaviour in a subsequent interaction. Specifically, that gaze direction and emotional expression enable an observer to infer whether that person is prosocial or antisocial, and that these inferences will affect how quickly the observer orients their spatial attention in response to the gaze direction of that individual. Participants should be quicker to follow the gaze of someone they infer to be prosocial and slower to follow the gaze of someone they infer to be antisocial.

5. A secondary aim of Experiment 4 is to investigate if the perception of gaze direction is uniform across the population or whether individuals differ in how such cues are interpreted. Those who are more sensitive to social information will be better able to attribute prosocial/antisocial intentions from gaze and expression and the effect of such attributions on gaze following will be larger in these individuals. Others are less sensitive to the social meaning of gaze direction and process it in a more mechanistic way. The effect of inferences based on gaze and expressions should be weaker for these individuals. However, a third identity was introduced whose gaze direction was spatially predictive of target location. Those who are more sensitive to the mechanistic properties of gaze direction should be more perceptive of the spatial congruency between gaze direction and target location and should be quicker to follow the gaze of the spatially predictive identity.

## **Chapter 2. The effect of gaze direction on anticipating the movement of biological stimuli**

Based on evidence that gaze direction plays a role in inferring the intentions of another's actions, and contributes to the anticipation of how they may act in the immediate future, the aim of the first experiment was to investigate if the anticipation of biological motion is modulated by the gaze direction of the actor. That is, different gaze directions lead observers to infer differing intentions underpinning the action, which will in turn modulate their anticipation of how the action will most likely proceed. This necessitates the integration of the perception of the movement itself with information regarding the dynamics underpinning the movement. Anticipatory memory displacements have been extensively observed for non-biological stimuli, which has been shown to be sensitive to cues regarding the physical causes and constraints acting upon the object's motion. This chapter will begin with a detailed review of the literature on the anticipation of movement for non-biological stimuli, both in terms of the methodologies used and the effects found. This will lead to the formulation of the central hypothesis that estimations of biological motion are influenced by the observed gaze direction of the agent.

### *Forward displacements in memory for the motion of non-biological stimuli*

Just as for biological stimuli, the memory for a non-biological stimulus (typically a geometric shape) is displaced further along the observed trajectory. Participants are less likely to detect the difference between the stopping point and a test stimulus positioned after the stopping point, than one positioned before it (Freyd & Finke, 1984), implying that the stopping point appeared as more similar to the 'after' than to the 'before' test stimulus. This forward displacement is evident over a number of different types of motion including rotations in the picture plane (Freyd & Finke, 1984), linear translations (Hubbard, 1997) and rotations in depth (Munger & Minchew, 2002; Munger, Solberg, Horrocks, & Preston,

1999). It has also proved robust despite differences in the quality of the depicted motion, ranging from the apparent motion created by presenting several frames in which the object is depicted as having moved a large amount between frames (e.g. Freyd & Finke, 1984), to the smooth motion created when the difference in the object's position between frames is too small to be noticed by the observer (e.g. Hubbard, 1995), and even for the implied motion depicted in static pictures of objects in motion (e.g. Freyd, 1983). Evidence of forward memory displacements is not confined to motion, but is also evident for other types of object transformations including changes in size and dimensions (Kelly & Freyd, 1987), and for auditory transformations, such as increases in pitch (Freyd, Kelly, & Dekay, 1990; Neuhoff, 1998, 2001).

The nature of the displacement has been shown to vary as a function of cues regarding the physical forces that underpin the movement. For example, increasing the speed of the object's motion results in a greater forward displacement (Finke, Freyd, & Shyi, 1986; Freyd & Finke, 1985; Freyd & Johnson, 1987). This effect seems to reflect a cognitive representation of momentum, whereby objects moving at a greater speed will cover more distance in a given time. In contrast, the magnitude of the displacement is decreased if the object is seen to travel along another surface, or to approach or break through a barrier, suggesting that the frictional forces implied by such contact are similarly represented and lead to an expectation that the object's motion will be impeded (Hubbard, 1995, 1998). Furthermore, a representation of the gravitational forces acting upon object motion has also been observed to affect memory displacements (Bertamini, 1993; Freyd, Pantzer, & Cheng, 1988). Objects moving from left to right show a displacement downwards as well as a displacement in the direction of motion (Hubbard, 1995, 1997). Objects moving downwards show a greater memory displacement in the direction of motion than objects moving upwards, presumably because the former is moving in the same direction as the pull of gravity, whereas the latter is moving against gravity (Hubbard, 1997, 1998; Nagai, Kazai, & Yagi, 2002). If the source of the object's motion is implied to



result from a collision with another moving object, the discrepancy between the remembered and veridical final positions may be less than if just the moving target is presented. Therefore, if the object's motion is self-propelled, it is subject to a greater displacement than if it is depicted to have no intrinsic means of movement (Hubbard, Blessum, & Ruppel, 2001; Hubbard & Favretto, 2003; Hubbard & Ruppel, 2002).

*Methodological issues relating to the displacement effect*

The magnitude of the displacement effect has been found to be susceptible to two major methodological factors. The first is that of the time delay between offset of the moving stimulus and onset of the test stimulus on which the similarity judgment must be made, also known as the retention interval (RI). Various RI lengths have been used throughout the literature, from 10 ms (Freyd & Johnson, 1987) through to 2000 ms (Finke, Freyd, & Shyl, 1985), with the most frequent being between 250 ms and 1000 ms. The extent of the memory displacement increases as a function of RI up to around 250 – 300 ms. RI lengths greater than this elicit either no further increases, or a slight decrease in the magnitude of the displacement effect. This relationship between RI length and memory displacement is quite robust when the extent of the memory displacement is derived by analyzing the proportion of errors made when judging the similarity between the stopping-point and the test stimulus positions. However, several studies have estimated the degree of memory shift by performing a quadratic regression on the data, and plotting this against RI. As with the previous method, the memory shift increases with RI's up to 250 – 300 ms. However, a sharp decrease is observed at RIs longer than this (Bertamini, 1993; Freyd & Johnson, 1987).

There have been few explicit tests of whether the memory distortion of biological motion is similarly subject to the length of RI. In the RM studies on biological motion described above, RI was varied between 100 ms and 1500 ms, and in the priming study of

Verfaillie and Daems (2002) the test postures were presented five minutes after observation of the priming action sequences. Graf et al (2007) found that the extent of displacement for a point light walker was greatest when the length of the RI corresponded to the temporal difference between the stopping point of the action and the particular test posture. That is, with an RI of 250 ms, displacement was greatest for test stimuli consisting of a posture that would have occurred 250 ms after the stopping point. However, no study has investigated if the presence of an RI is necessary to elicit a memory displacement for the motion of biological stimuli. Indirect evidence is provided by a priming study by Kourtzi and Shiffrar (1999). They presented participants with the static start and end-points of an action sequence. The participants then saw a posture that would have occurred either between the start and end-points or after the end-point. These two test stimulus types are equivalent to the before and after postures used in studies of motion anticipation. Given the literature described above, one would expect priming for the 'after' but not the 'before' posture. However the opposite was found, with processing facilitated for 'before' postures and not for 'after' postures. Crucially this study did not have an RI between the end-point and the test stimulus, suggesting that a temporal delay is necessary for the displacement of biological motion, as it is in the case of non-biological motion.

The second factor influencing the extent of displacement is that of the response mode. One method is to have the participant indicate by pressing one of two buttons whether the position of the test stimulus is the same or different as that of the stopping point (e.g. Freyd & Finke, 1984). A second method is to have the participant manually indicate the point at which the stimulus disappeared, for example by pointing to a position on the computer screen using the mouse cursor (e.g. Hubbard, 1995). The distinction between the two is that the former entails a response based on visual information, whereas the latter requires that this information be encoded into spatial information for the purpose of making a corresponding motor response. A greater displacement effect has been found when a motor response is required rather than a visual response (Ashida,

2004), with the latter exploiting dorsal visual pathways and the former exploiting ventral visual pathways (Brouwer, Franz, & Thornton, 2004).

*Forward memory displacements reflect the anticipation of object motion*

The effects of RI and response mode highlight the possible functional role that memory displacement plays in anticipating object motion. The time course of the displacement effect, as reflected in its relationship with RI length, suggests that the memory displacement occurs in real time (Freyd & Johnson, 1987). This combined with the enhanced effect when a motor response is required has lead several authors to suggests that forward memory displacements serve to compensate for the sensory lag between perception and action by anticipating where the object will be in the immediate future when an action is performed on it (Freyd, 1992; Hubbard, 2005, 2006; Kerzel, 2005). This sensory lag entails two components. Firstly, visual information takes around 100 ms to be processed, meaning that by the time a percept is made of an object, its position has already changed, and any action will be directed to the incorrect point in space. Secondly, the objects position will have changed during the time the action takes to reach the object. Therefore, by extrapolating along the observed path of motion, the object is represented in the position it will occupy by the time an action reaches it, not the position when the action is initiated.

Several studies have investigated if representational momentum indeed reflects the capacity to anticipate an objects motion in the immediate future by linking RM effects with that of motion extrapolation effects. As with RM, participants are presented with a stimulus in motion. The difference is that the test pattern was either the same, before or after *the next most likely position in the sequence* rather than the final position itself. Participants were required to judge if the test pattern was the same as the position one would expect given the previously observed motion. There is a robust finding of a backwards

displacement, in that participant's judgments are biased to choosing a test pattern that is slightly before the actual next position as being correct. Munger and Minchew (2002) found that this backwards displacement is smaller when the axis of rotation is aligned with the observer's line of sight (rather than, for example, around a component of the object itself) and that such rotation axes also elicit a larger forward displacement in RM tasks. Also, as the speed of rotation increases, then the extent of the forward and backward displacements in the RM and extrapolation tasks respectively also increases, suggesting that estimations of both the actual final position and the next most likely position are more accurate at slower velocities. Such motion extrapolation necessitates the ability to mentally rotate an object and again, this is quicker for axes of rotation and speeds that facilitate motion extrapolation and also elicit the largest RM effects (Munger, Solberg, & Horrocks, 1999). Finke and Shyi (1988) used linear translations of dot patterns and found that as the implied velocity of the motion increased so too did both the forward displacement in the RM task and the backward displacement in the extrapolation task. Furthermore, by estimating the rate at which the motion was extrapolated (i.e. deg/sec), they found that this correlated with the extent of the RM effect. That is, for a given velocity, the extent of the RM effect is proportional to the speed with which the motion is extrapolated along its implied trajectory. These studies highlight the association between RM effects and motion extrapolation effects, and suggest that motion prediction and RM are governed by the same cognitive processes. Further support for the role of motion prediction in the RM effect comes from studies showing that so long as the motion can be reliably predicted to continue along its observed trajectory, RM can be elicited. No memory displacement is observed when the object's motion is unpredictable or is not expected to continue after the stopping point is reached (Getzmann & Lewald, 2009; Makin, Stewart, & Poliakoff, 2009; Verfaillie & Dydewalle, 1991).

Several authors have proposed that such a process entails higher level cognitive mechanisms. For Freyd (1992) this necessitates the formation of a cognitive

representation of the temporal as well as the spatial aspects of an object's motion.

Hubbard (2005, 2006) proposed that this takes the form of a second order isomorphism by which the kinematics and dynamics of the object's motion are represented as a functional analogue. This produces a default displacement based, not upon objective physical principles, but on the observer's subjective interpretation of those principles. However, he extends this to accommodate a second level of processing by which the context of the object's motion and the observer's own expectancies are also incorporated into the anticipation. However, the notion that anticipatory memory displacements are the result of higher level cognitive processes has been disputed. For example, Kerzel (2005, 2006) argues that anticipatory memory displacements are due to a purely perceptual process caused by the visual tracking of the objects motion. When monitoring an object in motion, the path of eye movements follows the path of the object's motion (smooth pursuit). When the object abruptly disappears, as in studies of displacement, there is a lag between offset of the stimulus and cessation of the eye movements. Therefore, the eyes overshoot the true stopping point further along the observed trajectory and it is the point in space to which they are looking that participants recall the object to have vanished. Crucially, the size of this lag is 250 ms, the same amount of time found to elicit the maximal amount of displacement. Such oculomotor overshoot is even more pronounced for objects with apparent motion, as the saccadic jump to the next expected location is greater than for smooth motion. In support of this, Kerzel (2000) found that no displacement is evident when participants are instructed to fixate at the same spot during presentation of the moving stimulus in order to remove the effects of visual tracking.

Furthermore, other effects found for anticipatory memory displacements can similarly be accounted for by low level perceptual biases. The effect of implied gravity can be explained by a bias to remembering objects as being nearer the fovea than they were (Kerzel, 2002). In addition, the presence of other objects attracts attention away from the moving target and disrupts the visual tracking, explaining the decreased displacement

when observed to collide with or move along another object. It must be noted though, that Kerzel is not completely disputing that these results reflect anticipatory functions, just the mechanisms by which they are achieved. However, this explanation does not account for the reduction in displacement observed for objects whose paths of motion and velocities are unpredictable, as the oculomotor overshoot would be equivalent despite differences in motion type. In addition, displacement has been reported for objects rotating in depth, whose spatial position remains in the fovea at all times and for which no visual tracking is necessary. Furthermore, as Hubbard (2006) pointed out, this explanation does not account for the memory displacements observed for static objects with implied motion, again as no visual tracking is necessary, nor does it explain the effect of top-down expectations on the displacement effect. Additionally, Maus and Nijhawan (2006) found that displacement occurred for objects which gradually faded in luminance, demonstrating that the effect persists in the absence of abrupt stimulus offsets that would cause oculomotor overshoot.

### *Summary and hypothesis*

When observing an object in motion, the observer is able to extrapolate beyond the object's current position further along the implied trajectory, and anticipate its motion in the immediate future. The manipulations outlined above suggest the observer uses cues to infer the dynamics underpinning the motion and a representation of these are integrated with the representation of the kinematics of the motion. In the case of non-biological stimuli, these inferences are informed by visual cues conveying information regarding the physical dynamics underlying the motion. However, the motion of biological stimuli (agents) is additionally caused by psychological aspects such as their goals, motivations and intentions. This information is similarly conveyed visually through social cues such as gaze direction. As RM for non-biological stimuli is modulated by inferences as to the physical dynamics underpinning the motion, it is plausible that RM for biological motion is

sensitive to cues regarding the intentional dynamics motivating the action. The aim of the first experiment is therefore to investigate if the displacement of motion for biological stimuli is influenced by the gaze direction of the agent as they are moving.

Specifically, it is hypothesised that judgments of how far an action has proceeded will be overestimated when gaze is directed at the goal of an action and underestimated when gaze is directed in the opposite direction. For this a head was chosen that rotated in depth towards the observer. This was appropriate for several reasons. Firstly, it provides a clear platform from which to present variation in social cues conveyed by the face. Secondly, these manipulations can be made without altering the nature of the motion. Thirdly, as the stimulus maintains the same screen position throughout, the observer does not have to visually track the objects motion to maintain it in the fovea, either with saccades or smooth pursuit. Therefore any displacement observed cannot be attributed to the effects of oculomotor overshoot identified by Kerzel as a possible explanation of displacement for objects changing screen position.

However, the effect may also be the result of several low level factors, including the visual appearance of the pupil shifting within the sclera, which does not entail any processing of the social significance of the gaze cue. For this reason, a non-biological control stimulus was used to investigate this alternative explanation. It possessed features that imitated the visual appearance of the eyes of the biological stimulus in the different gaze direction conditions, yet did not invoke the appearance of actually being eyes. These variations did not convey information regarding either the physical forces underpinning the motion nor the goal of the motion (as the object itself was incapable of intentionality). It is therefore expected that the pattern of black and white contained in these visual features will not affect estimations of how far the non-biological object has rotated.

## *Experiment 1a*

### *Method*

#### *Participants*

Participants (N = 28, 27 females) had a mean age mean age of 21.5 years (SD = 9.1). All participants were students at the University of Hull, UK, and participated in exchange for course credit. All had normal or corrected to normal vision, and gave written informed consent prior to taking part.

#### *Apparatus*

All stimuli were presented on a 21 inch monitor (100 Hz refresh rate) using E-Prime software (Psychology Software Tools, Inc) from which participants sat approximately 50 cm away.

#### *Stimuli*

Stimuli were created using Poser 6 animation software (Curious Labs, Inc. & e-frontier, Inc). The general methodology used derived from that typically employed by previous studies of memory displacement. Participants first observed a moving stimulus consisting of an object in motion on a computer screen, the final position of which must be remembered.

#### *Biological stimulus*

The biological stimulus consisted of a head that rotated 60° along the vertical axis from a profile view (90° from full front view) to a semi-profile view (30° from full front view). Motion was induced by presenting 16 static frames at 4° interpolations for 40 ms each (total duration 640 ms, 93.75° per second). This was fast enough to induce an impression of smooth continuous motion. The gaze direction of the rotating head varied horizontally along three levels. In 1/3 of the trials the gaze was directed 30° in advance of the head



direction (gaze-ahead condition), in 1/3 of the trials the gaze direction was the same as the head direction (gaze-congruent condition), and in 1/3 of the trials the gaze direction was 30° lagging behind the head direction (gaze-lagging condition). Two different identities were used, one male and one female. The subtended width between the outer edges of the two test stimuli was between 16.2° and 18.4°, with the inner edge of each between 0.8° and 1.7° from the centre, and outer edge between 8.4° and 9.6° from the centre (Figure 2.1A).

### *Non-biological stimulus*

The non-biological stimulus consisted of a cylinder of comparable size, colour and texture to the biological stimulus (Figure 2.1B). The subtended angle of the stimulus height was 6.3°, and 4.3° to 3.3° for stimulus width. It was placed on a disc of the same diameter as the cylinder (but with different texture), which provided a base upon which the object rotated, analogous to that provided by the torso in the biological stimulus. Three white fins protruding from the cylinder provided additional cues to the degree of rotation in the same way as the chin and nose of the biological stimulus did. Placed in-between the three fins were two white cubes half submerged into the cylinder. Half of the surface area of the cubes was coloured black; this area was either on the left, right or centre of the cube. This pattern of colouration mimicked the pupil/sclera configuration in the three gaze conditions. The nature of rotation was identical to that of the biological stimulus. This controlled for any low-level contribution to a displacement effect by the horizontal shift of the pupil location.

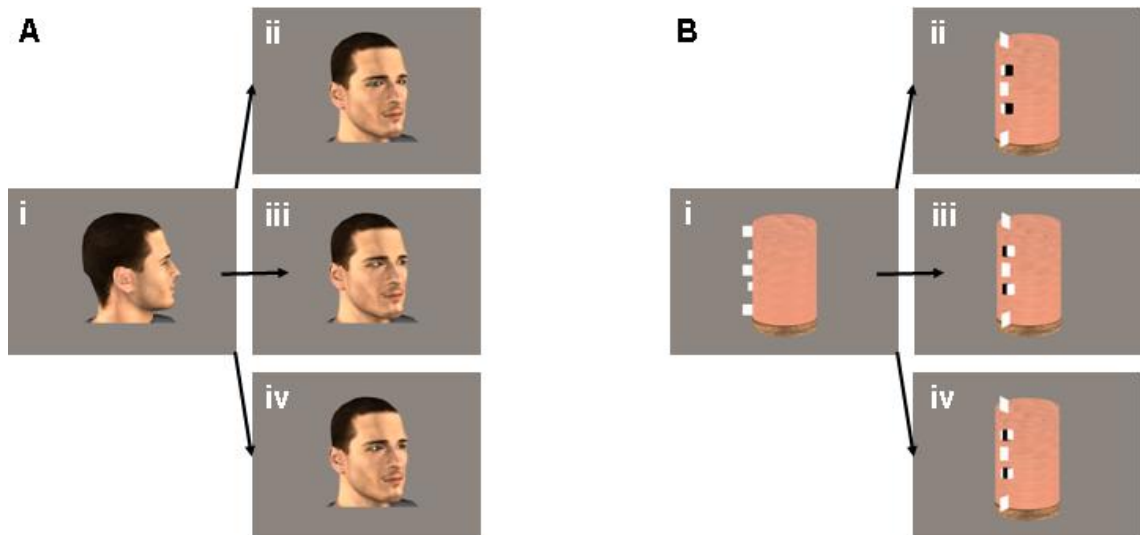


Figure 2.1. The three gaze conditions of the agentive (A) and non-agentive (B) stimuli. The starting point was a profile view ( $90^\circ$ ), facing either to the right (Ai) or left (Bi). The end-points were at  $30^\circ$  from full frontal view in the gaze-ahead (ii), gaze-lagging behind (iii) and gaze-congruent (iv) conditions.

### *Test stimulus*

To measure the remembered position of rotation, participants compared a pair of test stimuli with the end-point of the video-clip (which was always at  $30^\circ$ , left or right). Several pilot studies were conducted which aimed to evaluate the efficacy of different test stimuli and methods (see Appendix). The strongest result was obtained with a test stimulus consisting of two still images of the rotating stimulus and was adopted in the first experiment. They were shown simultaneously, side by side, each oriented at a different angle. One was oriented before the end-point (i.e. at an orientation encompassed within the rotation trajectory of the moving stimulus), the other after that point (i.e. extrapolated beyond the end-point of the moving stimulus further along the trajectory). One of the choices always deviated by  $10^\circ$  either before ('-') or after ('+') the stopping angle of the rotating stimulus, while the other choice deviated by  $10^\circ$ ,  $20^\circ$  or  $40^\circ$  in the opposite

direction. This created five test stimulus levels ( $-40^{\circ}/+10^{\circ}$ ,  $-20^{\circ}/+10^{\circ}$ ,  $-10^{\circ}/+10^{\circ}$ ,  $-10^{\circ}/+20^{\circ}$ ,  $-10^{\circ}/+40^{\circ}$ ; left/right positions on the screen were counterbalanced).

In symmetrical experimental trials, both test choices deviated  $10^{\circ}$  from the stopping angle ( $-10^{\circ}/+10^{\circ}$ , Figure 2.2A). For these trials there was no correct answer. If no memory displacement occurs, participants would be no more likely to choose the 'before' or 'after' option, yielding a 50/50 split on average. Occurrence of a memory displacement would result in a bias for one choice over the other: a bias toward choosing the 'after' choice would be indicative of overestimation and a bias toward choosing the 'before' choice of underestimation.

In the asymmetrical experimental trials, the remaining test choice was oriented  $20^{\circ}$  in the opposite direction. In these trials either the 'before' choice ( $-10^{\circ}/+20^{\circ}$ ) or the 'after' choice ( $-20^{\circ}/+10^{\circ}$ ) was correct (Figure 2.2B and C). The aim was to see if gaze direction could induce errors in the presence of a correct answer. Although a weaker effect of gaze direction is expected in asymmetrical compared to symmetrical experimental trials, an effect of gaze direction would strengthen the hypothesis should it be present.

In the final two levels, the asymmetry was increased even further by pairing the  $10^{\circ}$  choice with a  $40^{\circ}$  choice (Figure 2.2D and E). The correct answers, either 'before' ( $-10^{\circ}/+40^{\circ}$ ) or 'after' ( $-40^{\circ}/+10^{\circ}$ ), could easily be given and ceiling performance was expected. Incorrect answers here could be attributed to insufficient attention being paid to the task, so these were designated as catch trials and performance on these trials was used as a selection criterion.

The height of the test stimuli were the same as for the rotating stimuli. The two test stimuli were positioned in the centre of the screen, at equal distances at either side of fixation. The width and distance from the centre varied according to the test stimulus used. The subtended width between the outer edges of the two test stimuli was between  $16.2^{\circ}$  and  $18.4^{\circ}$ , with the inner edge of each between  $0.8^{\circ}$  and  $1.7^{\circ}$  from the centre, and outer edge between  $8.4^{\circ}$  and  $9.6^{\circ}$  from the centre. In the test stimuli, the gaze direction (or its

non-biological equivalent) was always congruent with the angle of the head (or the control object). Left/right screen positions of the 'before' and 'after' choices were counterbalanced across trials.

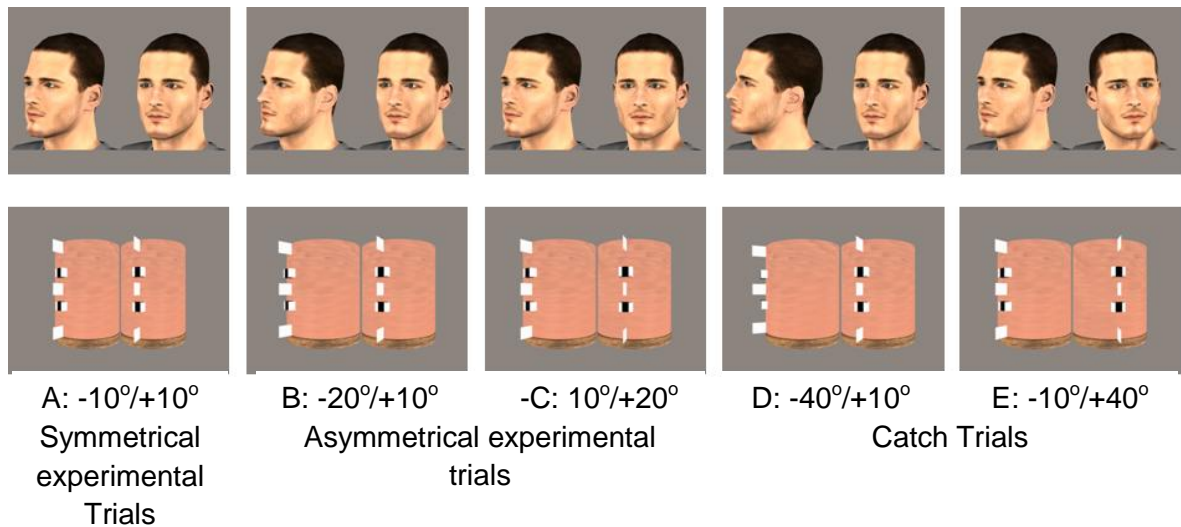


Figure 2.2. Examples of test stimuli for the biological (top) and non-biological stimuli (bottom). A: Symmetrical experimental trials where neither choice is more similar to the end-point of the moving stimulus. B-C: Asymmetrical experimental trials where the 'after' (B) and 'before' (C) response was correct. D-E: Catch trials in which the 'after' (D) and 'before' (E) response was correct.

### *Procedure*

Participants were instructed they would see a face or object rotate along the vertical axis towards them, and that this would be followed by two still faces or objects. Their task was to indicate by pressing one of two keys on the keyboard which of the two faces/objects was at an angle most similar to the final angle of the moving face/object. The 'J' and 'L' keys were used, labelled as 'left' and 'right' respectively. No mention of gaze

direction was made. It was stressed that accuracy was more important than speed of response, but that answers were to be made within a few seconds.

Participants completed 12 practice trials representative of the range of manipulations. This was followed by the experimental session which contained 2 blocks of 108 trials (216 trials in total). In one block, a retention interval of 1000 ms was placed in between the rotating stimulus and the test stimulus. In the other block, the retention interval was absent. The presentation order of the two blocks was counterbalanced across participants.

The choice of retention interval length was based on studies using a similar method of data analysis. For example, Finke and Freyd (1985) varied the retention interval between 500 ms and 2000 ms and found the magnitude of errors to peak within 500 ms and only to slowly decay thereafter. Freyd and Finke (1984) used retention intervals of 250 ms, 500 ms and 750 ms and observed displacement at each. In contrast, a study by Freyd and Johnson (1987) found the displacement effect to peak at 250-300 ms and to rapidly decline thereafter. However, this latter study used a different methodology in which the data was subjected to a quadratic regression. It was therefore expected that in this study a displacement effect would not rapidly diminish after 250-300 ms and would still be evident at a 1000 ms retention interval.

Each block contained three different types of trials: symmetrical experimental trials ( $n=36$ , 12 male, 12 female, 12 non-biological), asymmetrical experimental trials ( $n=36$ , 12 male, 12 female, 12 non-biological; for half of each group the correct answer was 'before' the end-point, i.e.  $-10^\circ/+20^\circ$ , for the other half 'after' the end-point, i.e.  $-20^\circ/+10^\circ$ ), and catch trials ( $n=36$ , 12 male, 12 female, 12 non-biological; for half of each group the correct answer was 'before' the end-point, i.e.  $-10^\circ/+40^\circ$ , for the other half 'after' the end-point, i.e.  $-40^\circ/+10^\circ$ ). The rotation started either from the left profile (anti-clockwise) or from the right profile (clockwise), with an equal number of trials for each direction.

Each trial began with a 1000 ms fixation cross at the centre of the screen. This was followed by a rotating face/object (duration 640 ms). In trials with a retention interval, the rotating stimulus was followed by a blank screen of identical colour to the background of the rotating stimulus for 1000 ms. Next, the test stimuli were displayed, and remained on screen until a response was made. In trials without a retention interval, the test stimulus was presented immediately after the rotating stimulus. The inter-trial-interval was 1000 ms. Figure 2.3 shows an example of a trial.

After completion of the experiment, the participants completed a feedback form. The purpose of this was to assess whether participants had been aware of the gaze-manipulation, to see how they experienced the control object, and to gauge what methods, if any, they used to complete the task. For example, they were asked to describe what they thought the rotating non-agentive stimulus was and why it was moving.

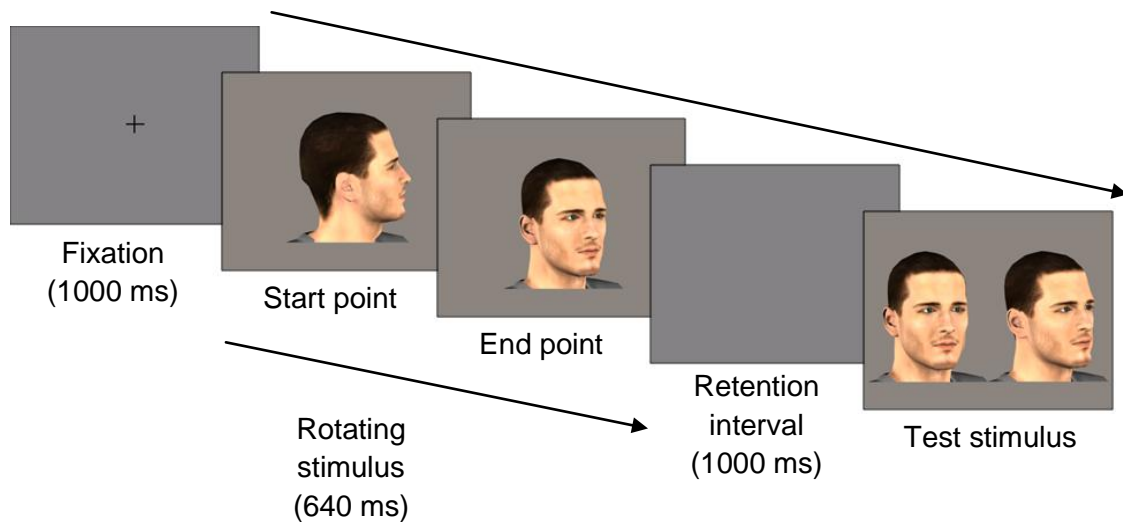


Figure 2.3. Trial procedure for experiment 1a. The trial started with a fixation cross, followed after 1000 ms by the rotating stimulus. In half the trials, this was followed by a retention interval of 1000ms duration, followed by the test stimulus. In the remaining trials,

no retention interval was present, and the test stimulus followed immediately after the rotating stimulus.

## *Results*

### *Data reduction*

The overall error rate in the catch trials was 13.9% (SD = 9.1%). The mean reaction time was 1378 ms (SD = 387). Those participants whose mean error rate exceeded 20% were excluded ( $n = 6$ , mean 27.2%, SD = 6.6%). The mean error rate of the remaining 22 participants was 10.0% (SD = 5.5%). Trials with a response time less than 250 ms and in excess of 2SD of each participant mean RT were excluded. This led to 2.4% of trials being excluded (mean = 2837 ms, SD = 896 ms), reducing the mean RT to 1308 ms (SD = 366 ms).

### *The effect of gaze on biological and non-biological motion*

Trials in which the 'before' stimulus was judged as more similar to the stopping point were coded as '0', and those in which the 'after' stimulus was chosen were coded as '1'. The resulting scores thus reflected the mean percentage of trials in which the 'after' test choice was judged as more similar to the stopping angle than the 'before' test choice. These values were entered into a 2 X 2 X 3 X 3 repeated measures ANOVA with Stimulus type (biological vs. non-biological), Retention interval (absent vs. present), Gaze direction (ahead vs. congruent vs. lagging behind) and Test stimulus ( $-20^\circ/+10^\circ$  vs.  $-10^\circ/+10^\circ$  vs.  $-10^\circ/+20^\circ$ ) entered as the main factors. Since the  $-40^\circ/+10^\circ$  and  $-10^\circ/+40^\circ$  conditions were used as a means to exclude participants, these were not included as levels in the test stimulus condition.

As expected, there was a significant main effect of Test stimulus ( $F(2, 42) = 157, p < .001, \eta_p^2 = .88$ ) with the percentage of 'after' responses decreasing as the similarity of the 'after' choice to the moving stimulus' end-point decreased. There was no main effect of

Retention interval ( $F(1, 21) = .15, p = .704, \eta_p^2 = .007$ ). There was a main effect of Stimulus type, with the non-biological stimulus eliciting significantly more ‘after’ responses than the biological stimulus ( $F(1, 21) = 19.9, p < .001, \eta_p^2 = .49$ ), and a main effect of Gaze direction ( $F(2, 42) = 13.3, p < .001, \eta_p^2 = .39$ ). There was a significant interaction between Gaze direction and Stimulus type ( $F(2, 42) = 3.84, p = .029, \eta_p^2 = .16$ ), and a significant interaction between Stimulus type and Test stimulus ( $F(2, 42) = 9.66, p < .001, \eta_p^2 = .315$ ). None of the other interactions were significant.

The crucial interaction between Gaze direction and Stimulus type was investigated further by conducting one way repeated measures ANOVAs with Gaze direction as the main effect for each stimulus type (biological and non-biological) for each test stimulus level (Table 2.1).

	Biological Stimulus			Non-biological Stimulus		
	Ahead	Congruent	Lagging	Ahead	Congruent	Lagging
<b>-40°/+10°</b>	96.4 (6.9)	95.4 (8.0)	92.9 (9.4)	97.2 (7.6)	96.0 (8.1)	97.7 (6.3)
<b>-20°/+10°</b>	79.4 (14.7)	75.3 (16.9)	66.2 (22.0)	82.2 (17.5)	80.2 (18.2)	76.7 (21.8)
<b>-10°/+10°</b>	59.0 (15.3)	57.4 (22.2)	40.8 (19.2)	70.5 (22.7)	64.6 (19.4)	58.4 (25.6)
<b>-10°/+20°</b>	39.8 (22.5)	35.6 (25.4)	23.0 (16.8)	55.3 (26.9)	48.4 (25.1)	49.5 (27.5)
<b>-10°/+40°</b>	11.4 (14.5)	9.9 (11.7)	8.7 (10.3)	28.6 (24.3)	25.3 (23.6)	14.0 (19.8)

Table 2.1. Mean percentage of ‘after’ responses for each gaze direction across each level of test stimulus for the biological and non-biological stimuli (RI collapsed). The SD of the mean percentages is shown between brackets.

#### *The biological stimulus*

For the biological stimulus, there was a significant main effect of gaze direction in each of the three test stimulus levels (Figure 2.4). In the -20°/+10° asymmetrical



experimental trials ( $F(2, 42) = 5.76, p = .006, \eta_p^2 = .22$ ), the gaze-ahead condition elicited significantly more 'after' choices than the gaze-lagging condition ( $t(21) = 3.71, p = .001, d = .72$ ). However, responses in the gaze-congruent condition did not differ significantly from responses in either the gaze-ahead ( $t(21) = 1.86, p = .08, d = .26$ ) or gaze-lagging conditions ( $t(21) = 1.42, p = .17, d = .47$ ).

In the symmetrical experimental ( $-10^\circ/+10^\circ$ ) trials, ( $F(2, 42) = 15.11, p < .001, \eta_p^2 = .42$ ), the gaze-lagging condition elicited significantly less 'after' choices than both the gaze-ahead ( $t(21) = 5.44, p < .001, d = 1.1$ ) and gaze-congruent conditions ( $t(21) = 3.92, p = .001, d = .81$ ), the responses of which did not differ from each other ( $t(21) = .93, p = .36, d = .08$ ). Because of this difference, the one sample t-tests were conducted for each gaze direction condition ( $p = .017$ ), which showed only responses in the gaze-lagging condition to differ significantly from 50% ( $t(21) = 2.9, p = .008, d = .48$ ), whereas responses in the gaze-ahead ( $t(21) = 2.27, p = .03, d = .59$ ) and gaze-congruent ( $t(21) = .95, p = .36, d = .34$ ) levels did not.

In the  $-10^\circ/+20^\circ$  asymmetrical experimental trials ( $F(2, 42) = 8.77, p = .001, \eta_p^2 = .3$ ), the mean percentage of 'after' choices was significantly greater in the gaze-ahead condition than in the gaze-congruent ( $t(21) = 2.63, p = .016, d = .18$ ) and gaze-lagging conditions ( $t(21) = 4.04, p = .001, d = .86$ ), between which responses did not differ significantly from each other ( $t(21) = 1.88, p = .08, d = .6$ ).

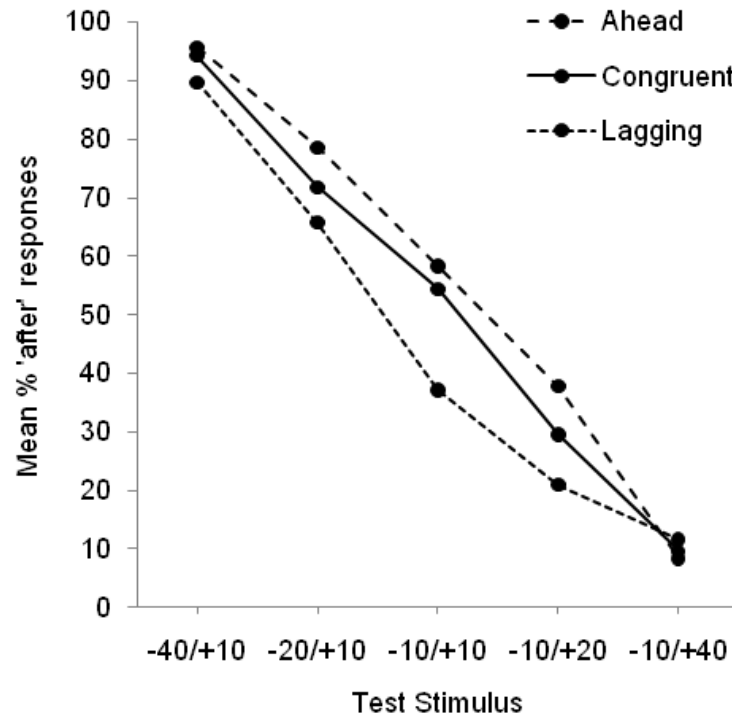


Figure 2.4. Mean percentage of 'after' responses for each gaze direction across the levels of the test stimulus for the biological stimulus (RI collapsed).

#### *The non-biological stimulus*

For the non-biological stimulus, there was no main effect of gaze direction in any of the test stimulus levels (Figure 2.5). Because of this, the gaze direction levels were collapsed in the experimental trials for the one sample t-test. This showed that the mean percentage of 'after' responses was significantly greater than the test value of 50% both with ( $t(21) = 2.66, p = .015, d = .57$ ) and without an RI ( $t(21) = 3.73, p = .001, d = .8$ ).

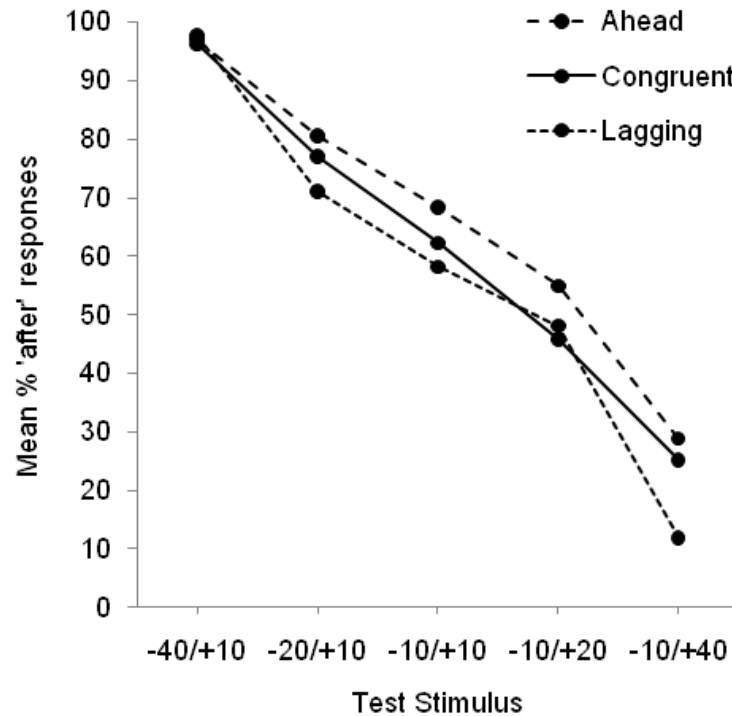


Figure 2.5. Mean percentage of 'after' responses for each gaze direction across the levels of the test stimulus for the non-biological stimulus (RI collapsed).

For the interaction between Stimulus Type and Test stimulus, one-way ANOVAs with Stimulus type as a repeated measures factor show the non-biological stimulus to elicit more 'after' responses in the  $-10^{\circ}/+10^{\circ}$  ( $F(1, 21) = 10.31, p = .004, \eta_p^2 = .33$ ) and  $-10^{\circ}/+20^{\circ}$  ( $F(1, 21) = 41.07, p < .001, \eta_p^2 = .66$ ), but not in the  $-20^{\circ}/+10^{\circ}$  ( $F(2, 21) = 3.06, p = .095, \eta_p^2 = .13$ ) trials. The different effects of gaze direction between the Stimulus types can account for this interaction. The percentage of 'after' responses for the biological stimulus was reduced in the gaze-lagging condition, whereas the non-biological stimulus elicited overestimation irrespective of 'gaze' direction. A higher overall percentage of 'after' responses would therefore be expected for the non-biological stimulus than the biological stimulus, especially where the effect of gaze for the latter was strongest.

## *Discussion*

The biological and non-biological nature of the stimuli produced different results. There was a significant overall effect of gaze direction for the biological stimulus. That is, despite the stopping angle of the head being equivocal ( $30^\circ$  from frontal view) in all conditions, estimations of how far it had rotated were influenced by the direction of its gaze. Specifically, head rotations were underestimated when gaze was looking in the opposite direction of motion, as compared to looking straight ahead or in advance of head rotation. The equivalent of the gaze manipulation in the non-biological condition had no such effect. In the non-biological condition, estimations of the degree of rotation were the same irrespective of the visual appearance of the black and white cubes designed to mimic the relative positions of the pupil and sclera in the biological condition. This is all the more remarkable as the black squares in the non-biological condition were larger and considerably more pronounced than the pupils in the biological condition. It supports the contention that the biases in estimating head rotation elicited by gaze direction can be attributed to social inferences made by the observer regarding the goals and intentions of the agent, and are not due to the low-level visual appearance of the pupil shifting within the sclera.

However, whilst the black and white cubes of the non-biological stimulus may have imitated the sclera/pupil positions of the eye, they failed to replicate other important aspects of gaze processing necessary for the inference of social significance. Firstly, the face presents a unique pattern of internal features, with the eyes occupying an important place within it (Barton et al., 2003). The vertical orientation of the white cubes in the current study failed to replicate this distinctive configuration.

Secondly, the social significance of gaze direction depends on its spatial meaning, which is used by the observer to unambiguously determine where the other person is looking. This directional information is processed reflexively, as indicated by studies in which the execution of a lateralised manual response, or the detection of a target, was

facilitated if preceded by a spatially congruent, but not by a spatially incongruent, gaze direction (Driver et al., 1999; Ricciardelli, Bonfiglioli, Iani, Rubichi, & Nicoletti, 2007). Again, the non-biological stimulus did not possess this quality and therefore the observer could not determine the ‘direction’ of the manipulations in the same way as for the biological stimulus. For these reasons, a second experiment was conducted with two new non-biological stimuli devised to address these issues.

### *Experiment 1b*

#### *Method*

##### *Participants*

Thirty-three participants (27 females), with a mean age of 20.3 years (SD = 4.4 years), took part. All other information is the same as for experiment 1a.

##### *Apparatus*

All stimuli were created and presented using the same software and hardware as in experiment 1a.

##### *Stimuli*

##### *Horizontal ‘eyes’ stimulus*

The black and white cubes of the non-biological stimulus were placed in a horizontal orientation to reflect the position of the eyes in a face. However, even the most rudimentary resemblance to a facial configuration is sufficient to evoke the perception of a face. In order to implement the design without creating the impression of a face, four additional white squares were introduced to disrupt the face-like configuration (Figure 2.6A).

### *Arrow 'eyes' stimulus*

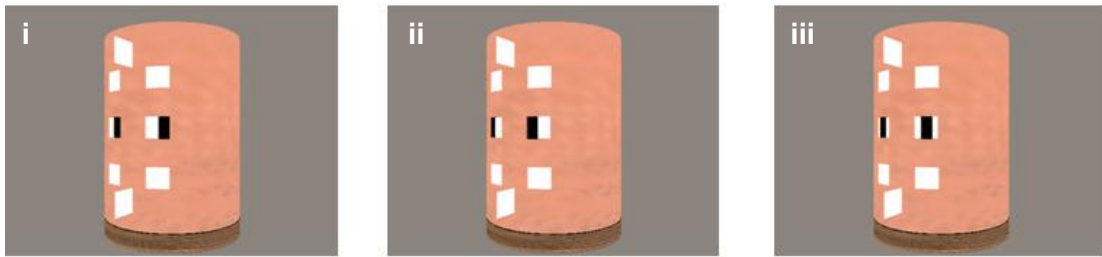
The black and white cubes of experiment 1a were replaced by two arrows. Arrows are a symbolic cue of spatial direction (Ricciardelli et al., 2007), and orient an observer's attention in a similar manner as gaze direction (Frischen, Bayliss, & Tipper, 2007). The surface was given a brick texture in order to reinforce the impression of a non-biological object (Figure 2.6B).

For both stimuli, these variable features were superimposed onto the surface of the stimulus rather than protruding from it, and the number of fins was reduced from three to two. These changes were implemented to better resemble the eyes, nose and chin of the biological stimulus in experiment 1a so as to provide a more accurate control.

### *Procedure*

There were 192 trials in total, with 96 consisting of symmetrical experimental trials (2 Stimulus Type X 2 Retention Interval X 3 Gaze Direction X 8 repetitions). The direction of motion (left/right) and screen positions of the test stimulus choices were counterbalanced across trials. The remaining trials were distributed equally amongst the other levels of Test stimulus (24 trials each). All other aspects of the stimuli, experimental design, procedure and method of analysis were identical to experiment 1a.

### A: Horizontal 'eyes'



### B: Arrows

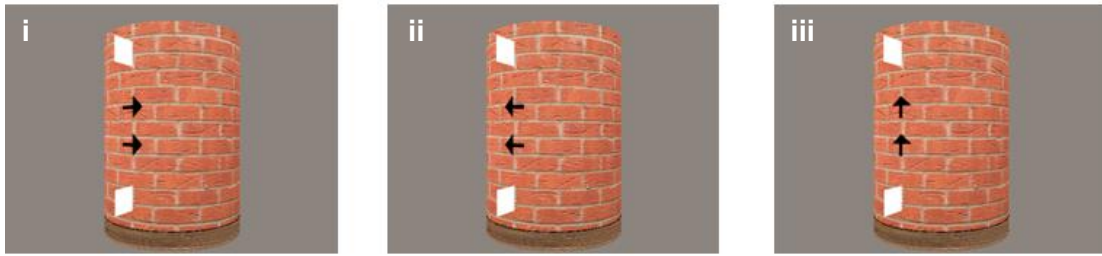


Figure 2.6. The two non-biological stimuli used in experiment 1b. (A) The white cubes are oriented horizontally. (B) The white cubes are replaced by arrows. Examples show the end-points in each 'gaze' direction condition (i) 'gaze' ahead, (ii) 'gaze' lagging and (iii) 'gaze' congruent. For the arrows stimulus, an additional congruent condition was used with the arrows pointing down.

### Results

The mean error rate was 13.6% (SD = 9.6%) and the mean RT was 1643 ms (SD = 548 ms). Participant and trial exclusion criteria were the same as in experiment 1a. Participants with a mean error rate of >20% were excluded ( $n = 7$ , mean = 29.4%, SD = 3.7%) resulting in a mean error rate of 9.3% (SD = 5.1%). Of the remaining 26 participants, 2.6% of trials were excluded (mean = 4712 ms, SD = 2163 ms) resulting in a mean RT of 1576 ms (SD = 491 ms).

A 2 X 2 X 3 X 3 repeated measures ANOVA was conducted with Stimulus type (horizontal eyes vs. arrows), Retention interval (absent vs. present), Gaze direction (ahead

vs. congruent vs. lagging behind) and Test stimulus ( $-20^\circ/+10^\circ$  vs.  $-10^\circ/+10^\circ$  vs.  $-10^\circ/+20^\circ$ ) entered as the main effects. As in Experiment 1a, the  $-40^\circ/+10^\circ$  and  $-10^\circ/+40^\circ$  (catch trials) were not included as levels in the test stimulus condition.

Apart from the expected significant main effect of test stimulus ( $F(2, 50) = 77.9, p < .001, \eta_p^2 = .76$ ), there were no other significant main effects or any significant interactions. Crucially, there was no effect of Gaze direction ( $F(2, 50) = .813, p = .449, \eta_p^2 = .032$ ) nor of Stimulus type ( $F(1, 25) = 3.44, p = .075, \eta_p^2 = .121$ ), and there was no interaction between the two ( $F(2, 50) = .937, p = .399, \eta_p^2 = .036$ ) (see Table 2.2 and Figure 2.7).

With gaze direction and stimulus type collapsed, there was a significant response bias in favour of choosing the ‘after’ responses both with ( $t(25) = 3.34, p = .003, d = .66$ ) and without an RI ( $t(25) = 2.69, p = .013, d = .53$ ).

	Horizontal ‘eyes’			Arrows		
	Ahead	Congruent	Lagging	Ahead	Congruent	Lagging
<b><math>-40^\circ/+10^\circ</math></b>	97.1 (8.1)	98.1 (6.8)	97.1 (8.1)	97.8 (8.0)	97.1 (8.1)	95.8 (10.1)
<b><math>-20^\circ/+10^\circ</math></b>	77.2 (20.6)	83.7 (18.2)	76.9 (25.5)	76.3 (23.5)	76.6 (22.9)	76.0 (25.1)
<b><math>-10^\circ/+10^\circ</math></b>	65.1 (27.0)	68.5 (23.8)	67.2 (25.1)	62.1 (23.2)	59.7 (26.5)	55.8 (25.2)
<b><math>-10^\circ/+20^\circ</math></b>	42.6 (34.5)	37.8 (29.6)	42.0 (35.2)	32.4 (28.2)	40.1 (28.8)	30.4 (28.9)
<b><math>-10^\circ/+40^\circ</math></b>	9.9 (16.3)	17.0 (20.9)	19.2 (23.1)	3.8 (9.2)	19.2 (26.7)	11.5 (18.3)

Table 2.2. Mean percentage of ‘after’ responses for each ‘gaze’ direction across each level of test stimulus for the two non-biological stimuli (RI collapsed). SD of the mean percentages is shown between brackets.



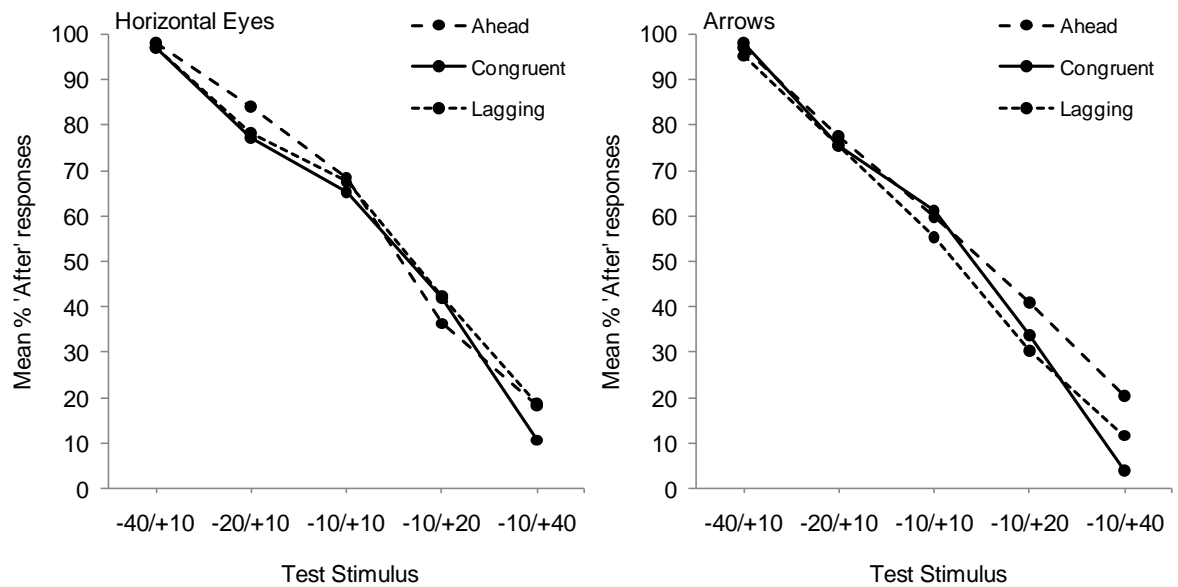


Figure 2.7. Mean percentage of 'after' responses for each 'gaze' direction across each level of test stimulus for two non-biological stimuli with horizontal 'eyes' (left) and arrows (right) (RI collapsed).

To directly compare these results to those of experiment 1a, the two non-biological stimulus types of experiment 1b were collapsed, and entered into a between-subjects ANOVA with the biological stimulus of experiment 1a as the second level. Retention interval, Test stimulus and Gaze direction were entered as repeated within-subjects factors. There was a significant main effect of Gaze direction ( $F(2, 92) = 18.2, p < .001, \eta_p^2 = .28$ ), and crucially this interacted with the between-subjects factor Stimulus type ( $F(2, 92) = 9.62, p < .001, \eta_p^2 = .17$ ). There were no other significant main effects or interactions, apart from a main effect of Test stimulus ( $F(2, 92) = 176.32, p < .001, \eta_p^2 = .79$ ).

### Discussion

The aim of experiment 1b was to incorporate two facets of gaze processing into the non-biological stimulus that were absent in experiment 1a: horizontal alignment of the eyes and the directional meaning of gaze. The results showed that estimations of object rotation

were not influenced by these visual manipulations, neither when oriented to simulate the configuration of the eyes in the biological stimulus, nor when they held an analogous spatial meaning to that of gaze direction. These results are comparable to those of the non-biological stimulus in experiment 1a and therefore further corroborated the main conclusion drawn from experiment 1a, which is that social information conveyed by gaze direction underlies the variations in estimations of head rotation, not the low level visual appearance nor the spatial meaning.

### *Overall discussion*

The aims of these experiments were, firstly, to investigate whether the processing of social cues that are indicative of an agent's intentions mediated the remembered final position of an action sequence performed by the agent. Secondly, if such effects are influenced by the absence or presence of a RI in the same way that RM for non-biological motion is. Thirdly, to verify that variations in estimations of head rotation caused by gaze direction are attributable to the social information conveyed by gaze direction regarding the agent's goals and intentions, and not due to a low level perceptual factor caused by the relative positions of the pupil and sclera, or the spatial meaning of gaze direction.

### *The social effect of gaze direction*

The results for the biological stimulus were consistent with the central hypothesis. Estimations of how far the head had rotated varied as a function of gaze direction. The non-biological stimuli were also subject to an anticipatory memory displacement. However, the extent of this displacement did not vary as a result of the equivalent 'gaze' conditions. That is, whereas judging the extent of head rotation is influenced by its gaze direction, judging the extent to which a cylinder has rotated is not affected by the appearance of black and white patterns that are comparable to the appearance of the different gaze directions, nor by the direction of arrows superimposed onto its surface that point in the

same directions. Therefore, this suggests that the influence of gaze direction on estimations of head rotation is not solely due to the differing visual appearance of the gaze direction conditions, nor to the purely spatial information they convey. This supports the hypothesis that the observed effect can be attributed to the social quality of the stimulus and its motion, and to the social information conveyed by the gaze direction.

#### *The effect of retention interval*

The variations of head rotation estimations were not influenced by the presence or absence of an RI. Furthermore, the memory displacement observed for the non-biological stimuli was similarly evident both with and without an RI. These findings contradict previous research which suggests that, as memory displacements occur in real time, an RI, no matter how brief (e.g. 13 ms), is required for distorted estimations of the extent of motion to be evident. This has been explicitly investigated for the motion anticipation of non-biological stimuli (Bertamini, 1993; Freyd & Johnson, 1987), and indirect evidence suggests a similar role for that of biological stimuli (Kourtzi & Shiffrar, 1999). This argues against the suggestion that anticipating the motion of biological and non-biological stimuli is underpinned by separate cognitive mechanisms, with an RI required for the latter and not the former.

However, a plausible explanation for this is related to the particular test method used in the current study. Previous studies used one test object, which the participant had to compare with the remembered end-point. The test stimulus in the current study consisted of two objects. This entailed looking at both choices and making a decision, which is a more time consuming process. Hence, a considerable delay between test stimulus onset and pressing the response key was always present (mean = 1415 ms, SD = 665 ms), sufficiently long for displacement to occur, which is consistent with the proposed necessity of higher level off-line mechanisms for the anticipatory memory displacement to manifest itself.

*The relative effects of gaze-ahead and gaze-lagging on anticipatory memory displacement*

As the rotation of the head itself is intentional, it was expected that displacement would also occur in the gaze-congruent condition. However, there was no significant response bias elicited in this condition, suggesting that just the motion of the head itself was not subject to an anticipatory memory displacement. This could be because stopping rotation of the head occurs near instantaneously with the intention to do so, and is therefore not subject to a temporal lag between removing the impetus to move and actual cessation of the rotation. However, this is also true of other biological action sequences such as walking, for which previous studies have reported a memory displacement effect (Graf et al., 2007; Jarraya et al., 2005). It is reasonable to assume that stopping rotation of the head is not subject to inertia to the same extent as is walking. Therefore, the lack of RM in the gaze-congruent condition may be due to the nature of the action. An alternative explanation is that the current method is not sensitive enough, and that memory displacement for a rotating head in the absence of additional goal oriented information conveyed by the eyes is too small to be evident using the current method.

It was hypothesised that when the gaze of an agentic stimulus was directed at the goal of the action (gaze-ahead condition), participants would overestimate the rotational angle of the head, and when gaze was directed opposite to the direction of the goal of the action (gaze-lagging condition) participants would underestimate the angle. It was assumed that gaze directed at the action goal reflects a larger degree of intentional motivation to reach or achieve the goal than gaze that was lagging behind head rotation. However, estimations of how far the head had rotated did not differ between the gaze-ahead and gaze-congruent conditions, but the gaze-lagging condition differed from both. Furthermore, it was the gaze-lagging condition that elicited a significant bias to choosing the 'before' response. It suggests that the main effect of gaze direction may lie predominantly with the gaze-lagging condition. Apparently participants did not infer any greater intentional information when gaze was directed in advance of head rotation. There

are at least three possible reasons for this asymmetry. Firstly, as a change in gaze direction is a faster and more energy-efficient way to direct attention than a head turn, gaze direction typically 'leads' the motion of the head and other body parts (Bertenthal & Von Hofsten, 1998). As a result, gaze-ahead is more perceptually common than gaze-lagging. Possibly, the atypical configuration of gaze and head movement in the gaze-lagging condition made it more conspicuous and was 'picked up' and processed more readily. Secondly, even though the deviations of the 'ahead' and 'lagging' gaze directions from head orientation were  $30^\circ$  either way, there was an asymmetry in the amount of sclera visible, with more sclera visible in the gaze-lagging than in the gaze-ahead condition. The ratio of dark pixels in the iris to light pixels in the sclera in the gaze-congruent condition was 1.9 for the male and 2.0 for the female (averaged across both eyes) showing that there was more iris visible than sclera. In the gaze-ahead condition the amount of sclera and iris was more equal, as the ratio was 1.1 for the male stimulus and 0.9 for the female. For the gaze-lagging condition, there was far more sclera visible than iris, both for the male (0.4) and female stimuli (0.4). Therefore, the visible difference between the 'lagging' and 'congruent' conditions was greater than that between the 'ahead' and 'congruent' conditions. The ratio of visible dark pupil with respect to white sclera is a determining factor in ascertaining gaze direction (Symons, Lee, Cedrone, & Nishimura, 2004). It must be noted, though, that the same would also apply to the equivalent 'gaze' conditions of the non-biological stimulus. The ratio of dark to light pixels for the non-biological stimulus in experiment 1a was greater in the gaze-ahead condition (1.9) than in both the gaze-congruent (0.6) and gaze-lagging conditions (0.6). The visual difference was therefore more noticeable in the gaze-ahead condition, however no effect of gaze direction was found. Therefore, should this asymmetry be a factor, it would not necessarily refute the notion of a social component to the observed effect. Lastly, the difference between gaze-ahead and gaze-congruent may have been too subtle to detect using the current method. A more sensitive measure using a set of test stimuli with smaller

differences in orientation between the two choices may have elicited an effect. However, these factors do not detract from the robust finding of a consistent difference in the estimation of the degree of head rotation between the gaze-ahead and gaze-lagging conditions.

### *Summary*

Overall, these experiments suggested that the gaze direction exerts a strong effect on estimations of how far an action has proceeded. Furthermore, the lack of variation observed for the non-biological stimuli suggest that this is due to social inferences made on the part of the observer regarding the psychological/mental state of the agent. The nature of the stimulus itself enables the observer to interpret the motion as intentional. Social cues contribute to these inferences and enhance the attribution of goal directedness to the action. This informs the observer's anticipation of how the action will unfold in the immediate future.

### Chapter 3. The effect of stimulus inversion

#### *The face inversion effect*

Presenting participants with a face that is oriented upside down (inverted) has been found to have a detrimental effect on the perception of faces. The ability to extract configural information has been proposed to be impaired when faces are inverted. That is, inversion prevents the perceptual system from processing the spatial relations between features, and relies only on information gained from the individual features themselves. Configural processing entails the combined processing of the features that constitute a face, and is distinguished from featural processing whereby the individual components of a face are processed separately. Because each face shares the same first order relations between the features (two eyes above the nose, with a mouth below), it is necessary to process the subtle spatial differences between these features in order to identify individuals, and within the same face at different points in time, in order to extract relevant social information (Ganel, 2006). Although there are differences in opinion with regards to the specific role of configural information in face perception, a common description of configural processing entails the integration of the individual components that constitute a face and that they are processed in relation to one another (Anaki & Moscovitch, 2007). The aim of this experiment was to investigate how the disruption of configural processing through stimulus inversion affects the effect of gaze direction on action anticipation.

#### *The effect of face inversion on gaze processing*

Given that the disruption of configural information caused by face inversion has been found to impair the processing of faces, several studies have investigated the effect of face inversion on the processing of gaze direction, in terms of either head orientation, the direction of gaze, or the integration of eye gaze with other facial features.

Inversion has been found not to influence the encoding of the direction to which a head is averted. Behavioural adaptation studies have shown that viewing a head averted in one direction will cause the perception of subsequently presented heads to be averted in the opposite direction. These adaptation induced after-effects are evident both when the stimuli are upright as well as inverted, suggesting that the direction in which a head is averted from the observer is encoded in the same way when inverted as when upright (Bi, Su, Chen, & Fang, 2009). However, no adaption effects are evident when the adapting and test stimuli are in upright and inverted orientations (e.g. measuring the perception of an upright head after adapting to an inverted head). This implies that, despite the common mechanisms, different neural populations are involved in encoding the direction of upright and inverted heads (Fang, Murray, & He, 2007).

In terms of the effect of face inversion on the discrimination of eye gaze direction, there is evidence that it affects some aspects of gaze discrimination but not others. Determining whether two faces had the same horizontal gaze shift is as accurate and fast when the faces were inverted than when upright (Mondloch, Geldart, Maurer, & Le Grand, 2003). Tipples (2005) found that reflexive re-orienting of one's spatial attention in response to a left or right aversion of another person's gaze is not influenced by the orientation of the face stimulus. However, it did affect the response to gaze shifts of up and down. As such effects are based on gross judgments of gaze aversion (left, right, up, down); inversion does appear to impair vertical, but not horizontal, shifts of attention. This may be attributable to the larger effect of inversion on processing vertical spatial relations than horizontal spatial relations (Goffaux & Rossion, 2007). However, inversion has been found to affect fine discriminations of horizontal gaze direction necessary for joint attention, for example when discriminating gaze deviations that differ in increments of  $0.23^\circ$  (Jenkins & Langton, 2003), or when indicating exactly to where another's gaze is fixated (Schwaninger, Lobmaier, & Fischer, 2005). Campbell et al (1990) demonstrated this dissociative effect of inversion on gaze processing by showing that inversion impaired the



detection of small deviations in gaze direction (e.g.  $5^\circ$ ) but not detecting larger deviations (e.g.  $10^\circ$  or  $20^\circ$ ).

It must also be noted that the detrimental effect of face inversion on gaze processing is evident irrespective of the orientation of the face, and also when the eyes are presented in isolation (Jenkins & Langton, 2003; Schwaninger et al., 2005). Furthermore, the faster detection times for faces with direct gaze than averted gaze evident for upright faces is absent when the eyes are inverted in either an upright or inverted face, or when the surrounding face is absent (Senju & Hasegawa, 2006). This suggests that the gaze processing impairments associated with face inversion are due to an eye inversion effect rather than a face inversion effect, and that processing the eyes entails configural encoding that is independent of the global configural encoding provided by the context of the face (Jenkins & Langton, 2003; Schwaninger et al., 2005).

The above suggests that discerning whether someone is looking to the left or right, either by the direction of their head or their eye gaze, is not affected by face inversion (Bi et al., 2009; Tipples, 2005). However, inversion does seem to have a detrimental effect on the integration of gaze direction with head orientation. The adaptation effect for head aversion observed for upright stimuli is attenuated when the gaze direction is incongruently aligned with head direction (Bi et al., 2009). This suggests that the neural populations being exploited are sensitive to the direction of someone's attention, rather than head aversion per se, and that information from both sources is being integrated. However, the modulating effect is only apparent when the faces are upright. When inverted, the direction of gaze has no effect on the after-effects caused by adaptation to an averted head. Therefore, information from the head and eyes is not being processed in relation to one another to determine social attention, in keeping with the notion that inversion disrupts the ability to integrate the features of a face into a unified configuration. This impairment in integrating gaze direction with other facial features was also demonstrated by Ganel et al (2005) who showed that inverting the face eliminated the interference effects (evident for

upright faces) caused by varying emotional expression when judging whether gaze was left, right or direct.

### *Summary and hypothesis*

Stimulus inversion affects the processing of faces more than that of non-face stimuli, and this is thought to be a consequence of an impaired ability to process the spatial relationship between individual features, and therefore to integrate them in relation to one another (configural processing). With respect to the processing of gaze direction, inversion prevents fine discrimination of where someone's gaze is fixated, and whether they are looking up or down, but it does not affect judgments of whether they are looking left or right. Furthermore, inversion does not impair processing of whether the head is averted to the left or right, but does prevent the integration of gaze direction with head orientation. The aim of experiment 2 is therefore to investigate if the integration of gaze direction with action perception is impaired when the stimuli are inverted, and if this attenuates the effect of gaze direction on action anticipation. As perception of head orientation is not affected by inversion, participants should be able to compare the remembered final angle of the rotating stimulus with the test stimuli as accurately as when upright. Similarly, as inversion does not impair judgment of whether gaze is directed to the left or right, participants will be able to perceive the gaze direction of the stimulus as well as when the stimuli is upright. However, as inversion affects configural processing of faces, and therefore the integration of facial features, participants will not be able to relate the direction of gaze with the direction in which the head is rotating. As such, the goal oriented information conveyed by gaze direction will not be attributed to the movement of the head, and estimations of head rotation will not vary as a function of gaze direction.

## *Experiment 2*

### *Method*

#### *Participants*

Participants (N = 31, 23 females), with a mean age of 27 years (SD = 10.9 years), were recruited and screened following the same criteria as used in experiment 1a and 1b.

#### *Apparatus*

All stimuli were created and presented using the same software and hardware as in experiment 1a and 1b.

#### *Stimuli*

##### *Rotating stimulus*

The stimuli in the upright condition were the same as in experiment 1a and 1b. For the inverted condition, the frames were inverted and retained the same size and position on screen as the upright stimulus (Figure 3.1).

##### *Test stimulus*

The moderate trials were not included in this experiment, leaving three levels of the test stimulus condition (experimental trials  $[-10^\circ/+10^\circ]$ , catch 'after' trials  $[-40^\circ/+10^\circ]$ , catch 'before' trials  $[-10^\circ/+40^\circ]$ ). In addition, as the previous experiments had consistently shown the retention interval to have no effect, this factor was removed and all trials were presented without the retention interval.

#### *Procedure*

The experiment was a 2 X 3 X 3 repeated measures factorial design, with 8 repetitions, totalling 144 trials. The faces were upright in 72 of these trials, and inverted in

the remaining 72. In both of the orientation conditions, the three levels of gaze direction were presented for 24 trials. The three test stimulus levels were distributed equally (8 trials each) for each of the gaze direction conditions. Participants completed two blocks of 72 trials each, with each experimental condition presented in a pseudo-random order across trials. Task instructions were the same as in the previous experiments, and no mention of the experimental manipulations were made. Participants initially completed several practice trials representative of the range of experimental manipulations (Figure 3.1).

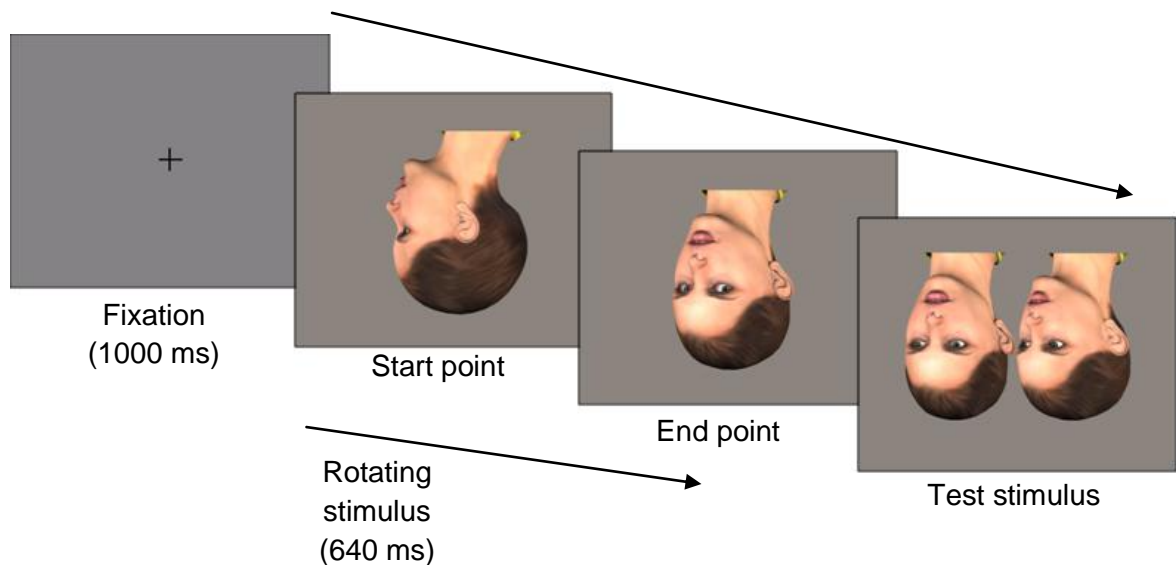


Figure 3.1. Trial procedure in the inverted condition. This example shows the female stimulus in a symmetrical experimental trial rotating from the left in the gaze-ahead condition.

### *Results*

#### *Error analysis*

Initially, the errors in the catch trials were entered into a two-way ANOVA with Orientation (upright vs. inverted) and Catch trial type (correct answer is the 'before' choice

vs. the 'after' choice) as within subjects factors. This showed that there was a main effect of catch trial type ( $F(1, 30) = 4.44, p = .044, \eta_p^2 = .129$ ), with more errors made when the correct answer was the 'before' choice (mean = 19.0%, SD = 21.7%) than when it was the 'after' choice (mean = 9.1%, SD = 12.8%). There was no main effect of orientation ( $F(1, 30) = .121, p = .73, \eta_p^2 = .004$ ) and no interaction between orientation and catch trial type ( $F(1, 30) = .207, p = .652, \eta_p^2 = .007$ ). Therefore, stimulus orientation had no effect on errors, suggesting that inversion did not impair the accuracy of head rotation judgments.

*Comparing the effect of gaze direction between the upright and inverted conditions*

The mean error rate in the catch trials was 14.1% (SD = 12.1%). Participants with a mean error rate of 20% or more were excluded. This resulted in the exclusion of nine participants (mean = 29.1%, SD = 10.3%). The resulting mean error rate of the remaining 22 participants was 7.9% (SD = 5.6%). The mean reaction time was 1882 ms (SD = 713 ms). Trials with a response time less than 250 ms or greater than 2SD above each participant's mean RT were excluded. Of the remaining participants, 3.6% of trials were excluded, resulting in a mean RT of 1693 ms (SD = 571 ms).

The data were entered into a two-way ANOVA with Orientation (upright vs. inverted) and Gaze direction (ahead vs. congruent vs. lagging) as within subjects factors. Again, as the catch trials were used to exclude participants, the analyses were conducted for the  $-10^\circ/+10^\circ$  trials only. This analysis revealed a significant main effect of Gaze direction ( $F(1, 21) = 3.93, p = .027, \eta_p^2 = .158$ ) with the gaze-ahead condition eliciting significantly more 'after' responses than the gaze-lagging condition ( $t(21) = 3.01, p = .007, d = .37$ ), but that the gaze-congruent condition did not differ from either the gaze-ahead ( $t(21) = 1.11, p = .279, d = .15$ ) or gaze-lagging conditions ( $t(21) = 1.66, p = .112, d = .19$ ). Furthermore, neither of the gaze conditions differed significantly from 50% (ahead:  $t(21) = .185, p = .855, d = .04$ ; congruent:  $t(21) = .82, p = .422, d = .17$ ; lagging:  $t(21) = 1.9, p = .071, d = .07$ ). There was no main effect of orientation ( $F(1, 21) = .728, p = .403, \eta_p^2 = .034$ ), and,

crucially, the interaction between Gaze direction and Orientation was also not significant ( $F(1, 21) = 1.07, p = .353, \eta_p^2 = .048$ ).

The non-significant interaction between Gaze direction and Orientation suggests that the effect of gaze direction on estimations of head orientation was not affected by stimulus inversion. To further investigate a possible modulatory effect of orientation, one-way ANOVAs with Gaze direction (ahead vs. congruent vs. lagging) entered as a repeated measures were conducted for the two orientation conditions separately (Table 3.1 and Figure 3.2).

These showed a significant effect of Gaze direction for the upright condition ( $F(2, 42) = 3.91, p = .028, \eta_p^2 = .16$ ) but not for the inverted condition ( $F(2, 42) = 1.02, p = .369, \eta_p^2 = .046$ ). Paired sample  $t$ -tests between the three gaze direction levels in the upright condition ( $\alpha_{Bon} = .0167$ ) showed that there was a significant difference between the gaze-ahead and gaze-lagging conditions ( $t(21) = 2.72, p = .013, d = .5$ ), but that the gaze-congruent condition did not differ from either the gaze-ahead ( $t(21) = .926, p = .365, d = .14$ ) nor the gaze-lagging condition ( $t(21) = 1.8, p = .086, d = .3$ ). One sample  $t$ -tests showed that only the gaze-lagging condition differed from the test value of 50% ( $t(21) = 2.68, p = .014, d = .08$ ), whereas the gaze-ahead ( $t(21) = .159, p = .875, d = .03$ ) and gaze-congruent conditions ( $t(21) = .712, p = .484, d = .15$ ) did not. As there was no effect of gaze direction in the inverted condition, the conditions were collapsed for the one sample  $t$ -test which showed no significant difference from 50% ( $t(21) = .723, p = .478, d = .15$ ).

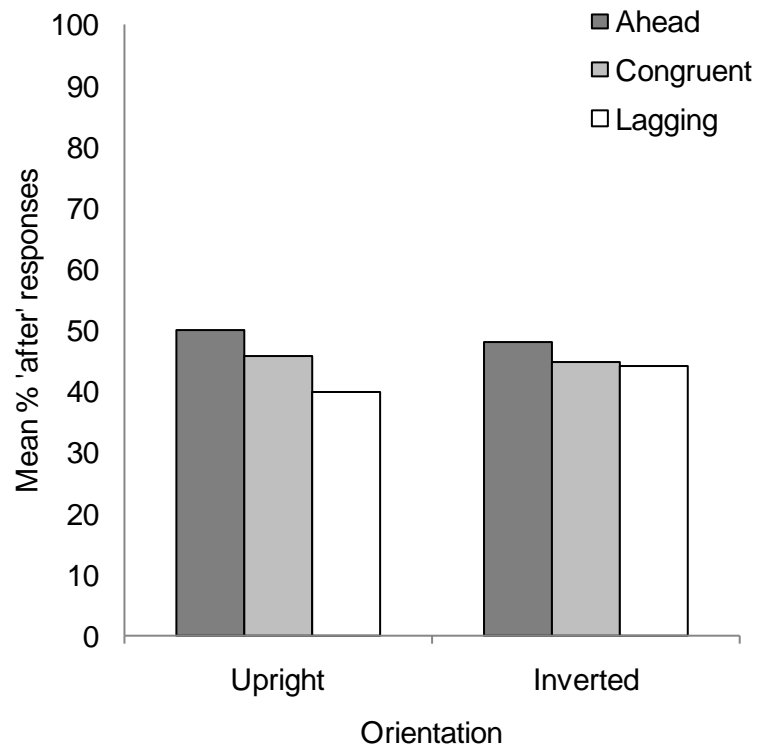


Figure 3.2. Mean percentage of 'after' responses in the experimental trials for each level of Gaze direction when stimuli were either upright or inverted.

### *Discussion*

The effect of gaze direction on estimations of head rotation observed in the previous experiments was proposed to be due to the integration of the action (head rotation) and the social cue (gaze direction) conveying the underlying intention. The aim of this study was to dissociate the processing of the action and the social cue by inverting the stimuli. As such, it was hypothesised that the ability to integrate the gaze direction of the agent with their head rotation would be impaired, and that the goal-oriented information conveyed by the eyes would not be attributed to the action.

### *The effect of gaze for upright faces*

When the stimuli were upright, there was a significant effect of gaze direction, with estimations of how far the head had rotated being greater when gaze was directed in advance of head rotation than when lagging behind head rotation. Furthermore, the gaze-lagging condition elicited a significant response bias, whereby the stopping point was judged as more similar to a head oriented  $10^\circ$  before than a head oriented  $10^\circ$  after the stopping point. This pattern of results replicated those observed in experiment 1a, emphasising the robustness of the gaze effect on action anticipation.

However, the effect was only observed between the gaze-ahead and gaze-lagging conditions, whereas the gaze-congruent condition did not differ significantly from either of the other gaze conditions. Furthermore, the overall effect size (0.16) was considerably smaller than that obtained in experiment 1a (0.42). The observed effect may have been weaker due to the fewer number of trials (symmetrical experimental trials after exclusions) upon which the analyses were conducted in this experiment (495) compared to experiment 1a (959). Nevertheless, gaze is a meaningful cue to the goal of the action only when articulated from head orientation. Therefore, the role of gaze in the anticipation of head rotation derives from its incongruence with head orientation rather than its congruence, and a difference between the two incongruent conditions is sufficient to uphold the conclusion that anticipation of how an action will proceed is mediated by the gaze direction of the actor.

### *The effect of gaze for inverted faces*

In contrast to the upright condition, there was no effect of gaze direction on estimations of head rotation when the stimuli were presented in an inverted orientation. Estimations of how far the head had rotated did not differ between the different gaze direction conditions. Extensive research has demonstrated that inversion impairs face processing, and to some extent the processing of bodies too, by disrupting the ability to



integrate and process the individual features in relation to one another. The absence of an effect of gaze direction is therefore most likely attributable to an inability to relate the direction of gaze with the rotation of the head. The disruption of configural information has previously been found to impair the processing of information conveyed by both the face and body (Loucks & Baldwin, 2009; Maurer et al., 2002; Pavlova & Sokolov, 2003). However, it must be noted that configural processing is not exclusively employed for the perception of social stimuli, but is necessary for the perception of any type of stimulus for which the observer must rely on the spatial relationships between features. The finding of an inversion effect in the current experiment does not therefore preclude the possibility that the mechanisms employed to integrate the gaze and actions of others are also necessary for the configural processing of non-social stimuli.

This lack of an effect cannot be attributed to an inability to accurately process the orientation of the head. Previous research has shown that the orientation of inverted heads is processed in the same way as that of upright heads (Bi et al., 2009). Furthermore, the error rates for the inverted condition were no different from those in the upright condition. This suggests that participants were as accurate in comparing the stopping angle of the rotating stimulus with the angles of the two test stimulus choices, irrespective of whether they were upright or inverted. Furthermore, it is also not likely due to an inability to discriminate in which direction the eyes of the rotating stimulus are looking. Although inversion of the eyes has been found to impair the fine discrimination of different gaze directions (Campbell et al., 1990; Jenkins & Langton, 2003; Schwaninger et al., 2005), and to affect judgments of whether the eyes are looking up or down (Tipples, 2005), it does not impair the processing of left/right judgments required in this study (Mondloch et al., 2003; Tipples, 2005). Therefore, participants would still perceive the different gaze direction conditions despite the inversion. However, the eye region was displaced vertically between the two orientation conditions. In the upright condition, the horizontal midline of the eye region was  $0.8^\circ$  of visual angle above the horizontal midline of the screen, in the inverted

orientation it was the same distance below it. In principle, this may have predicated a differential allocation of attention toward the eye region, but since the differences were small, this is unlikely.

It must be noted, though, that the differential effect of gaze direction as a function of head orientation was apparent only when the two conditions were analysed separately, whereas there was no significant interaction between gaze direction and stimulus orientation. The simple main effect analyses test if the effect of gaze direction is different from zero. However, the omnibus F-test investigates if the effect of gaze direction is different between the two orientation conditions. Therefore, the effect of gaze direction did not differ significantly between the two orientation conditions, yet did differ significantly from zero when in the upright orientation but did not differ significantly from zero when in the inverted orientation. Although this presents a logical contradiction, the different analyses test different hypotheses (difference from zero vs. difference between conditions), and so this contradictory result may be a consequence of the weak effect of gaze direction observed in the upright condition. As such, it must be emphasised that the conclusions drawn from these results remain tentative.

#### **Chapter 4. The influence of emotional expression on the effect of gaze direction when anticipating the actions of others**

Gaze direction is often not observed in isolation but in concert with other social cues. The information conveyed by these other cues can both enhance and refine the information obtained from the eyes. Of these, emotional facial expression shares an intricate relationship with gaze direction, both being manipulated by changes in facial features, and conveying similar motivational information. The aim of this chapter is investigate if the effect of gaze direction on action anticipation is influenced by the emotional expression of the agent.

##### *The interaction between gaze direction and emotional expression*

Several studies have shown that the processing of gaze and expression interacts, with the perception of and behavioural response to one cue affected by the quality of the other. For instance, emotional expression can affect the perception and response to gaze direction. The time taken to discriminate gaze direction is prolonged when the expression of the face varies (Ganel et al., 2005; Graham & LaBar, 2007), whilst an averted gaze is more likely to be perceived as looking at the observer if the expression is angry or happy than when neutral or fearful (Lobmaier et al., 2006). Conversely, emotional expression has implications for the social significance of a specific gaze direction. As such, a great deal of research has sought to establish if joint attention abilities are affected by the expression of the gazer. The reflexive tendency to orient one's own spatial attention to where another person is looking has been found to be enhanced when they are expressing fear (De Jong, van Engeland, & Kemner, 2008; Tipples, 2006). However, several studies have not found such an enhancement (Hietanen & Leppanen, 2003), whilst other have found it only in a sample who are high in trait anxiety (Mathews, Fox, Yiend, & Calder, 2003) or when the task requires an affective evaluation of the target (Pecchinenda, Pes, Ferlazzo, &

Zoccolotti, 2008). Disgust (Pecchinenda et al., 2008) and happy faces (Hori et al., 2005) have also been observed to potentiate joint attention (although Hietanen & Leppanen, 2003 found this not to be the case), whilst no effect has been observed in response to angry faces (Bonifacci, Ricciardelli, Lugli, & Pellicano, 2008; Hietanen & Leppanen, 2003). There is also evidence that the joint attention abilities in the first year of life are enhanced by happy expression (Striano & Stahl, 2005), although De Groote et al (2007) found no effect of expression and Flom and Pick (2005) found joint attention to be more likely in response to neutral expressions than happy or sad.

The effect of expression on the processing of gaze is mirrored by an effect of gaze on the perception and response to emotional expressions. Just as variations in expression impair the discrimination of gaze, so too does varying the gaze direction slow discrimination times of emotional expressions (Ganel et al., 2005; Graham & LaBar, 2007). Angry faces are detected faster and perceived with greater intensity when the expresser's social attention is directed toward the observer rather than away, whilst an averted gaze enhances the detection and perception of fearful faces (Adams & Kleck, 2005; Hess, Adams, & Kleck, 2007; Sander, Grandjean, Kaiser, Wehrle, & Scherer, 2007), although Bindemann et al (2008) contest that this effect is task and stimulus specific. Furthermore, the on-screen duration of an angry face is perceived as longer if the gaze is mutual rather than averted (Doi & Shinohara, 2009).

The integrative nature of expression and gaze influences the processing of other social behaviours. For example, the positive evaluation afforded to objects that other people look at is enhanced if they are expressing happiness but reduced if they are expressing disgust (Bayliss et al., 2006). This also extends to the evaluations of the person themselves. Someone whose gaze direction consistently predicts the location of a target is perceived as more trustworthy if they are smiling than if they are angry (Bayliss, Griffiths, & Tipper, 2009). Furthermore, as early as the second year of life, infants will anticipate that an adult will grasp an object if they are looking at it whilst smiling (Phillips,

Wellman, & Spelke, 2002), and infants themselves are more likely to approach an object in response to this (Repacholi, 1998). The interdependency between the processing of gaze direction and expression is reflected in a modulation of neural activity. Measurements of ERPs indicate that cortical activity is modulated by both gaze and expression, but that the time course of this occurs relatively late, at around 270 ms (Klucharev & Sams, 2004). Such an effect is evident in the first year of life, with a greater response for angry and happy expressions with a direct gaze than an averted gaze (Striano, Reid, & Hoehl, 2006), but no modulation to fearful faces by gaze direction (Hoehl & Striano, 2008). Furthermore, ERP responses to objects are greater if they have been looked at by an adult with a fearful expression than if with a neutral expression (Hoehl, Wiese, & Striano, 2008).

Neuroimaging studies have revealed cortical areas that are responsive to both gaze direction and emotional expression, and that the activity of these areas is modulated by specific combinations of the two. Activity in the STS has been observed in response to emotional expressions (Critchley et al., 2000; Narumoto, Okada, Sadato, Fukui, & Yonekura, 2001), in keeping with its role in processing dynamic facial information (Haxby et al., 2000), although it shows no ability to discriminate between expressions (Phillips et al., 1998). Nevertheless, there is greater activity in the STS in response to fear expressions with an averted gaze than with a direct gaze (Hadjikhani, Hoge, Snyder, & de Gelder, 2008), and a PET study by Wicker et al (2003) revealed that judging if someone was happy or angry elicited greater activity in the anterior STG when their gaze was direct than when averted. The amygdala is another area implicated in processing both gaze and expression, and exhibits activity in response to several different emotional expressions, most notably fear, sadness, anger and disgust (Blair, Morris, Frith, Perrett, & Dolan, 1999; Phillips et al., 1998; Whalen et al., 2001), but not happy expressions (Adolphs, 1999; Morris et al., 1998). The activity of the amygdala has been found to be greater for angry expressions that are looking at the observer (Sato, Yoshikawa, Kochiyama, & Matsumura, 2004), and for fear expressions that are directed away (Hadjikhani et al., 2008). However,

Adams et al (2003) found the opposite, with greater amygdala activity for fearful faces with a direct gaze and for angry faces with an averted gaze. Although Hadjikhani et al (2008) point to task and stimulus differences that could account for these apparently discrepant findings, Adams et al (2003) attributed them to the ambiguity inherent when gaze and expression contradicted each other, necessitating an increased involvement of the amygdala in accordance with its role in assessing the emotional significance of environmental stimuli (Blair, 2003).

However, this modulation of activity cannot be conclusively attributed to the same neuronal populations. Engell and Haxby (2007) showed that gaze and expression elicited spatially discrete patches of activity in the STS, with an area of partial overlap. Similarly separate coding of gaze and expression has been observed in cell populations in the amygdala of macaque monkeys (Hoffman, Gothard, Schmid, & Logothetis, 2007). This suggests the presence of distinct cell populations encoding either expression or gaze in both areas, although the existence of cells encoding both in the area of overlap cannot be refuted.

### *Models of the interaction between gaze and expression*

The Shared Signal Hypothesis has been proposed as a functional account of the interaction between gaze direction and emotional expression (Adams et al., 2006; Adams & Franklin, 2009; Adams & Kleck, 2005). Processing (in terms of discrimination times, perceived intensity) of either gaze direction or emotional expression is enhanced when the other cue conveys the same social information. For example, direct gaze and expressions of anger or happiness are characteristic of a disposition to approach a stimulus, whereas averted gaze and expressions of fear, sadness or disgust are characteristic of a disposition to avoid a stimulus.

The shared signal hypothesis does not posit a solution to the problem created when cues contradict each other and induce ambiguity. However, another model, called the Fuzzy Logical Model of Perception (FLMP) proposes that in the event of an agent's social cues conveying ambiguous social information, judgments of their behavioural intention will be based on the least ambiguous cue (Ellison & Massaro, 1997). This is because social cues are integrated by a multiplicative process acting on continuous rather than discrete information. The information conveyed by social cues is rarely categorical but is often vague, ambiguous or imprecise. In order to draw definite conclusions from this complex information, the FLMP assumes that each social cue is evaluated independently and assigned a 'truth' value representing the probability that it belongs to a particular category prototype that is stored in long term memory, such as a particular emotional expression. These probabilities are then multiplied to give an overall probability to which the integration of the components fits any number of alternatives. These alternatives are then assessed to select the most likely fit to a stored prototype, which is then converted into a response. This results in reducing the uncertainty at each successive stage. Because the integration is multiplicative, the contribution of one cue to the overall probability depends on the contribution of the other cue. This contrasts with additive models, whereby the contribution of one cue remains the same irrespective of the value of the other. Both the SSH and the FLMP predict the same when both cues convey the same information, that of an enhanced ability to process either cue or the overall intention. However, as the truth value of one cue is reduced, and therefore becomes more ambiguous, the FLMP predicts that the contribution of the other cue to the integrated probability increases.

Ellison and Massaro (1997) found support for the FLMP when integrating facial features in classifying emotional expressions. Participants were presented with a face whose brow varied along five levels between up and down, and whose mouth varied along five levels between up and down. Participants had to indicate if the face was expressing happiness or anger. The frequency of happy responses was maximal when both brow and

mouth were upturned and the frequency of angry responses was maximal when both brow and mouth were downturned. As the brow turned downwards, the frequency of happy responses was unaffected so long as the mouth was turned upwards. Therefore, increasing the ambiguity of the expression by making the brow more neutral increased the reliance on the mouth as a cue to the expression of the stimulus. Similarly, Massaro and Egan (1996) found support for the integration of emotional information from the face and voice. When both face and voice were angry, the proportion of angry responses was close to 1. Changing the voice to either neutral or happy, and thus increasing the ambiguity of the overall stimulus did not affect judgments. Therefore, observers relied more heavily on the emotional information conveyed by one cue (the face) as the match of the other cue to the angry prototype decreased. This was not simply due to an exclusive processing of facial information, as the ability to identify anger from the voice alone was also high.

In terms of gaze direction and emotional expression, several studies have highlighted a role for gaze direction in resolving ambiguity caused by emotional expression. For instance, gaze can help identify the referent of another person's emotional expression (Hanna & Brennan, 2007; Repacholi, 1998), and can be used as a cue to someone's disposition when their facial expression is neutral (Adams & Kleck, 2005), or when the expression is rendered ambiguous via morphing procedures (Graham & LaBar, 2007). The use of gaze to disambiguate behaviour is evident early in development. When the intentions underlying an observed action are unclear, 9 month olds will attend more to the actor's gaze than when the intentions are easily discernable (Phillips et al., 1992).

### *Summary and Hypothesis*

Attributing the goals and motivations of others is based on an array of social cues, of which gaze direction is just one. An individual's emotional expression affords the observer with additional information with which to infer someone's intentions and anticipate the



actions they are most likely to make in the immediate future. The conjoint role of gaze direction and emotional expression in such inferences is emphasised by the comparable processing characteristics and developmental emergence in the abilities to process them, as well as the shared cortical regions implicated in doing so. Furthermore, the conjunction of gaze and expression can enhance these attributions when the information conveyed by both cues is congruent. However, when the information conveyed by one cue is ambiguous, the FLMP predicts that the contribution of the remaining cue to such attributions will increase.

The aim of this experiment was to investigate the role of gaze direction on the anticipation of other's actions in situations when the emotional expression of the agent conveyed either an ambiguous or unambiguous motivation. This was achieved by combining a rotation toward the observer with an emotional expression conveying either a motivation to approach (happy, angry) or to avoid (fear, disgust). When the rotation of the head is toward the observer with an expression of approach, the meaning of both the action and the expression are congruent and the goal of the action is unambiguously to move toward. However, when the head rotates toward the observer with an expression of avoidance, the meaning of the action is ambiguous as the direction of movement and the motivation expressed are incongruent with one another. This contention is supported by a study by Adams, Ambady, Macrae and Kleck (2006), who presented fearful and angry faces that subsequently either increased or decreased in size, making them appear to move toward or away from the observer, respectively. Participants had to detect the motion as quickly as possible. It was found that the angry faces primed motion toward the observer (shorter RTs), while fearful faces did not. This suggests that observers associated and expected a face with an approach expression to move toward them, but did not for a face expressing an avoidance emotion. It is therefore expected that for approach expression, there would be no need to scrutinize gaze direction to clarify information, and it should not influence estimations of the degree of head rotation. For

avoidance expressions, the observer should involuntarily prioritise the processing of the agent's gaze direction to try and resolve the ambiguity. If this were the case, then the anticipations that the observer makes regarding the agent's actions will be influenced by their gaze direction.

### *Experiment 3*

#### *Method*

##### *Participants*

Participants (N = 30, 26 females) had a mean age of 23.2 years (SD = 8.2) and were recruited and screened using the same procedures as described in the previous experiments.

##### *Apparatus*

Stimuli were created and presented to participants using the same hardware and software as in previous experiments.

##### *Stimuli*

No non-agentive stimulus was presented, with only the agentive stimulus (one male, one female) presented.

##### *Rotating stimulus*

The movement of the rotating stimulus was the same as in previous experiments. The rotation began from either the left or right profile. Gaze direction varied along three levels as in previous experiments (gaze-ahead, gaze-congruent, gaze-lagging). In addition, the face expressed one of four facial expressions throughout the rotation (anger,

happy, fear and disgust). The first two reflect an approach-oriented motivation, the last two an avoidance-oriented motivation (see Figure 4.1).

### *Test stimulus*

There were five levels of test stimulus, as the asymmetrical experimental trials of experiment 1a were reinstated. These depicted the stimulus of the rotating display with a congruent gaze and neutral expression at varying orientations from the end-point of the rotation. The size and positions of the stimuli on screen were the same as in previous experiments. No retention interval was presented in between the rotating and test stimuli in any of the trials.



Figure 4.1. The emotional expressions conveyed by the rotating stimulus. The stopping point of the rotating stimuli conveyed an approach (A) or an avoidance motivation (B). The approach motivation was represented by Angry (i) and Happy (ii) expression, and the avoidance motivation was represented by Fear (iii) and Disgust (iv) expressions.

### *Procedure*

The trial procedure and experimental set up was the same as in previous experiments. Participants completed 192 trials (Figure 1) over three blocks (10 minutes each). The gaze and motivation conditions (2 X 3 levels) contained 96 symmetrical experimental trials (16 repetitions), 48 asymmetric experimental trials (8 repetitions) and

48 catch trials (8 repetitions). The correct answer in the asymmetric experimental trials and catch trials was 'before' in half the trials and 'after' in the other half. The sex of the stimulus (male, female), direction of rotation (from the left or right) and position of the 'before' and 'after' choices (left, right) were counterbalanced across trials. Written and verbal instructions were given, in which no reference was made to the gaze and expression manipulations, nor were participants told that the test choices were oriented either side of the final angle. It was emphasised that accuracy was more important than speed, but that responses were to be made within 3 seconds.

## *Results*

### *Data reduction*

The mean error rate in the catch trials was 14.9% ( $SD = 11.7\%$ ) and the mean RT was 1837 ms ( $SD = 484$  ms). Nine participants were excluded due to high error rates ( $>20\%$ ), with a mean percentage of errors of 29.2% ( $SD = 7.7\%$ ) leaving 21 participants in the analysis (mean errors 8.73%,  $SD = 6.61\%$ ). Next 4.7% of trials were removed due to RTs being less than 250 ms, or greater than 2SD of each participant's mean (mean = 3908 ms,  $SD = 1034$  ms) resulting in a mean RT of 1662 ms ( $SD = 365$  ms).

Responses to the binary choice of either the 'before' or 'after' test head were coded as '0' (before) or '1' (after), providing a score for each participant of the mean percentage of 'after' responses (overestimation). These percentage scores were entered in a 2 X 3 X 3 ANOVA with Motivation (Approach vs. Avoid), Gaze direction (Ahead vs. Congruent vs. Lagging) and Test-stimulus ( $-20^\circ/+10^\circ$  vs.  $-10^\circ/+10^\circ$  vs.  $-10^\circ/+20^\circ$ ) as within-subjects factors (see Table 4.1 and Figure 4.2). As participant exclusion created ceiling performance in the catch trials, these were not included as levels in the Test-stimulus condition.

	Approach			Avoidance		
	Ahead	Congruent	Lagging	Ahead	Congruent	Lagging
<b>-40°/+10°</b>	96.4 (9.0)	93.7 (11.8)	97.6 (7.5)	96.4 (12.0)	97.6 (10.9)	95.2 (12.8)
<b>-20°/+10°</b>	76.2 (21.1)	78.6 (19.8)	81.0 (23.6)	74.2 (23.6)	72.2 (23.6)	66.7 (28.5)
<b>-10°/+10°</b>	56.2 (18.2)	52.0 (23.0)	50.5 (19.9)	65.0 (16.6)	52.6 (17.1)	46.8 (19.7)
<b>-10°/+20°</b>	36.5 (33.0)	20.2 (19.8)	28.6 (27.3)	34.5 (32.9)	34.1 (25.8)	23.4 (27.5)
<b>-10°/+40°</b>	10.7 (18.7)	11.9 (19.5)	13.1 (24.5)	13.9 (15.9)	11.9 (18.7)	11.5 (19.1)

Table 4.1. Mean proportion of ‘after’ responses elicited by the different gaze direction conditions in the five test stimulus levels when the stimulus expressed either an approach or avoidance emotion.

There was a significant main effect of Test-stimulus ( $F(2, 40) = 76, p < .001, \eta_p^2 = .792$ ), reflecting the decreasing percentage of ‘after’ responses as the ‘after’ choice became increasingly different from the end-point (all comparisons  $p < .001$ ). There was no significant main effect of Motivation ( $F(1, 20) = .562, p = .462, \eta_p^2 = .027$ ). There was a significant main effect of Gaze direction ( $F(2, 40) = 6.27, p = .004, \eta_p^2 = .239$ ), with the gaze-ahead condition eliciting significantly more ‘after’ responses than the gaze-lagging condition ( $t(20) = 3.22, p = .004, d = .45$ ). The gaze-congruent condition did not differ significantly from either the gaze-ahead ( $t(20) = 2.22, p = .038, d = .375$ ) or gaze-lagging conditions ( $t(20) = 1.22, p = .238, d = .152$ ). There was a significant interaction between Test-stimulus and Motivation ( $F(2,40) = 3.28, p = .048, \eta_p^2 = .141$ ) and, importantly, a significant interaction between Motivation and Gaze direction ( $F(2, 40) = 4.03, p = .025, \eta_p^2 = .168$ ). The interaction between Test-stimulus and Gaze direction was not significant ( $F(4, 80) = .97, p = .429, \eta_p^2 = .046$ ) nor was there a significant three-way interaction ( $F(4, 80) = 1.33, p = .267, \eta_p^2 = .062$ ).

### *Modulation of the effect of gaze direction by motivation*

The crucial interaction between gaze direction and motivation was significant. Since the symmetrical condition ( $-10^\circ/+10^\circ$ ) was most sensitive to a possible interaction effect, while the asymmetrical conditions ( $-20^\circ/+10^\circ$  and  $-10^\circ/+20^\circ$ ), in which a correct answer was present, were far less sensitive, the symmetrical trials were analysed separately in a two-way ANOVA with Gaze and Motivation as factors.

The 3 X 2 ANOVA on the symmetrical trials revealed a significant main effect of Gaze direction ( $F(2, 40) = 8.18, p = .001, \eta_p^2 = .29$ ), with the percentage of 'after' responses being significantly higher in the gaze-ahead condition than the gaze-congruent ( $t(20) = 3.5, p = .002, d = .5$ ) and gaze-lagging conditions ( $t(20) = 3.83, p = .001, d = .68$ ), which did not differ from each other ( $t(20) = 1.05, p = .31, d = .2$ ). Furthermore, the proportion of 'after' responses was significantly greater than 50% in the gaze-ahead condition ( $t(20) = 2.96, p = .008, d = .65$ ), but did not differ from 50% in either the gaze-congruent ( $t(20) = .582, p = .567, d = .13$ ) or gaze-lagging conditions ( $t(20) = .328, p = .746, d = .07$ ). There was no main effect of Motivation ( $F(1, 20) = 1.19, p = .288, \eta_p^2 = .056$ ) but there was a significant interaction between Motivation and Gaze direction ( $F(2, 40) = 3.85, p = .03, \eta_p^2 = .161$ ).

### *The effect of gaze for the avoidance expressions*

One way ANOVAs were performed to further investigate the interaction between gaze direction and motivation in the symmetrical and asymmetrical experimental trials. In the symmetrical trials, when the agent displayed an avoidance expression, there was a significant main effect of Gaze direction ( $F(2, 40) = 14.3, p < .001, \eta_p^2 = .417$ ). The gaze-ahead condition elicited significantly more 'after' responses than gaze-congruent ( $t(20) = 4.21, p < .001, d = .74$ ) and gaze-lagging conditions ( $t(20) = 4.79, p < .001, d = 1$ ), which did not differ from each other ( $t(20) = 1.59, p = .128, d = .31$ ). Responses were significantly biased in favour of the 'after' choice in the gaze-ahead condition ( $t(20) = 4.14, p = .001, d$

= .9, tested with respect to 50% level), but there were no significant response biases in the gaze-congruent ( $t(20) = .696, p = .494, d = .15$ ) or gaze-lagging conditions ( $t(20) = .736, p = .47, d = .16$ ).

To investigate if the effect of gaze direction for the avoidance condition was present for both of the expressions (fear and disgust) or if it was driven by a large effect in one expression but not the other, the effect of gaze was entered into a within-subjects ANOVA along with Expression (fear vs. disgust). As expected there was a significant main effect of gaze direction ( $F(2, 40) = 14.4, p < .001, \eta_p^2 = .418$ ) but no main effect of Expression ( $F(1, 20) = .353, p = .559, \eta_p^2 = .017$ ), nor an interaction between Expression and Gaze direction ( $F(2, 40) = .139, p = .871, \eta_p^2 = .007$ ). Therefore the effect of gaze did not differ significantly between the fear and disgust expression conditions (Figure 4.3).

#### *The effect of gaze for the approach expressions*

When the agent displayed an approach expression in the symmetrical trials, there was no main effect of Gaze direction ( $F(2, 40) = 1.04, p = .363, \eta_p^2 = .049$ ). Because of this, the gaze direction conditions were collapsed to test for the presence of a response bias with respect to 50% level. The responses did not differ significantly from 50% ( $t(20) = .763, p = .454, d = .17$ ). Again, a two-way ANOVA was conducted with Gaze direction and Expression (angry vs. happy) as within-subjects factors. There was no effect of Gaze direction ( $F(2, 40) = 1.07, p = .352, \eta_p^2 = .051$ ), but there was a main effect of Expression, with the percentage of 'after' responses significantly greater in the happy condition than in the angry condition ( $F(1, 20) = 6.48, p = .019, \eta_p^2 = .245$ ). However, there was no significant response bias with respect to the 50% level for either the angry ( $t(20) = .135, p = .894, d = .03$ ) or happy conditions ( $t(20) = 1.575, p = .131, d = .34$ ). There was no interaction between Gaze direction and Expression ( $F(2, 40) = .246, p = .783, \eta_p^2 = .012$ ).

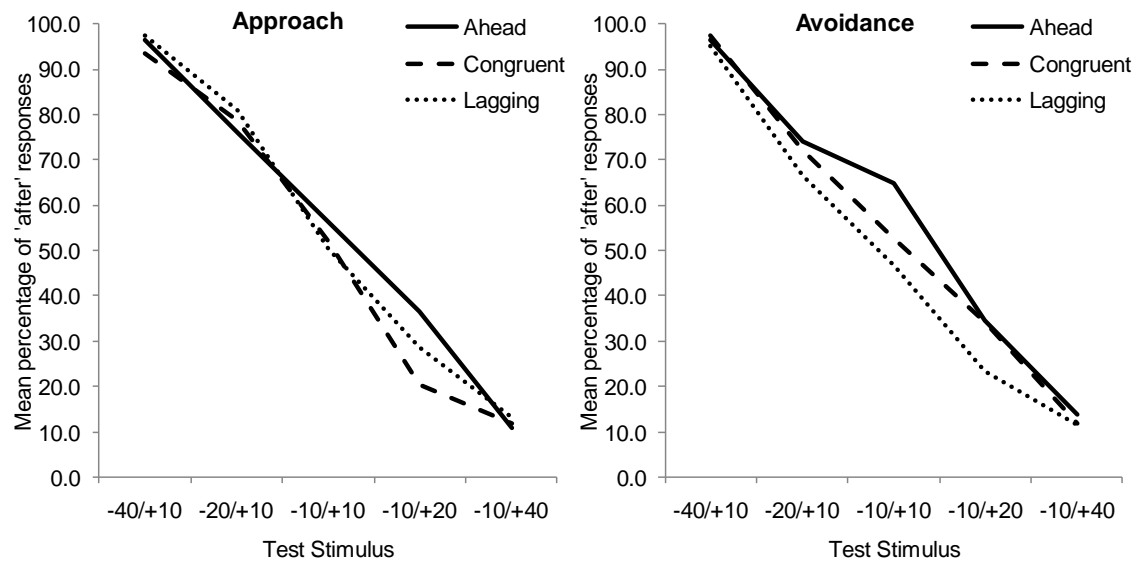


Figure 4.2. The mean percentage of 'after' responses elicited by each gaze direction for each test stimulus type when the expression of the agent was of either approach or avoidance.



Figure 4.3. The mean proportion of 'after' responses elicited by each gaze direction condition for the individual emotional expressions in the symmetrical experimental ( $-10^{\circ}/+10^{\circ}$ ) trials.



In the asymmetrical experimental trials where the ‘after’ choice was correct, there was no main effect of Gaze direction ( $F(2, 40) = .115, p = .892, \eta_p^2 = .006$ ), Motivation ( $F(1, 20) = 3.91, p = .062, \eta_p^2 = .163$ ), nor an interaction between them ( $F(2,40) = 1.03, p = .367, \eta_p^2 = .049$ ). Similarly, when the ‘before’ choice was correct, there were no main effects of Gaze direction ( $F(2,40) = 1.72, p = .193, \eta_p^2 = .079$ ) or Motivation ( $F(1, 20) = .635, p = .435, \eta_p^2 = .031$ ) or an interaction ( $F(2, 40) = 2.59, p = .088, \eta_p^2 = .115$ ).

#### *Interaction between Motivation and Test-stimulus*

There was an interaction between Test-stimulus and Motivation. However, one way AVOVAs with Motivation as a within subjects factor did not reveal a significant main effect in the symmetrical trials ( $F(1, 20) = 1.02, p = .324, \eta_p^2 = .049$ ), nor in either the asymmetrical trial conditions when the ‘after’ ( $F(1, 20) = 3.79, p = .066, \eta_p^2 = .159$ ) or ‘before’ choice was correct ( $F(1, 20) = .4, p = .534, \eta_p^2 = .02$ ).

#### *Discussion*

The aim of this experiment was to investigate if the emotional expression of the agent affects the role of gaze direction in anticipating the actions of others. Specifically, as gaze direction can be utilised as a means to resolve ambiguity created by emotional expressions, estimations of how far the head had rotated would be differentially modulated by gaze direction depending on the uncertainty generated by the expression. Expressions that conveyed a motivation to either approach or avoid were used as a means to manipulate such ambiguity. An action that approached the observer with an avoidance expression (fear, disgust) constituted an ambiguous stimulus. Determining which course of action the agent will make therefore necessitates a reliance on gaze direction, which would modulate estimations of how far the action proceeded. Conversely, an approaching action coupled with an approach expression (happy, anger) is unambiguous, therefore gaze

direction would not afford any greater specificity regarding the goals of the agent, and no modulation of action anticipation would be observed as a function of gaze direction.

The observed results confirm the hypothesis. When the expression of the stimulus conveyed an avoidance motivation there was a significant effect of gaze direction. When the gaze of the agent was directed ahead of the direction of rotation, participants were significantly biased to judging the test head oriented  $10^\circ$  after the stopping angle as being more similar to the head at the end of the video clip than the test head oriented  $10^\circ$  before it. Furthermore, the proportion of these responses was significantly greater than when gaze was congruent with head orientation, or looking in the opposite direction to that of head rotation, neither of which elicited a significant response bias. This pattern of results was equally strong for both the fear and disgust expressions individually. Importantly, such variation as a function of gaze direction was not observed when the stimulus expressed approach emotions of angry or happiness. No response biases (with respect to the 50% level) were observed and there were no differences between the three gaze direction conditions.

However, estimations of how far the head had rotated were influenced by the expression. The happy condition elicited a greater proportion of 'after' responses than the angry condition. This suggests that the observer anticipated that the action was more likely to continue in that direction if the agent expressed happiness than if expressing anger, irrespective of the direction of gaze. This supports the contention that the combined approach cues of the action and the expression (or at least happy expressions) conveyed sufficient information with which to reliably attribute the motivations of the agent without necessitating the use of gaze. However, the lack of a response bias for either expression precludes any firm conclusions.

### *The integration of gaze and expression*

The results largely replicate those of experiments 1a and 2 and support the contention that the anticipation of biological action sequences assimilates social information conveyed by dynamic facial cues in order to incorporate inferences as to the agent's goals and motivations. However, this experiment extends these findings by showing that such an effect is context specific. That is, rather than being mandatory, the use of gaze as a means to anticipate behaviour is selectively deployed based on the context provided by other social cues, especially when the intentions conveyed by such cues are vague. This is consistent with several lines of research showing that, firstly, the direction of another person's visual attention is used to resolve ambiguities caused by emotional expression, and that secondly, the interaction between social cues causes the meaning of one to depend on the meaning of the other.

As for the nature of this integration, the results reflect the predictions of the FLMP in which the perception of social cues is a non-holistic and non-additive feature-based process. Furthermore, the processing of such cues proceeds independently, and in parallel with one another, prior to integration. This is consistent with studies indicating that gaze direction and expression are indeed processed separately and are integrated at a relatively late stage (Graham & LaBar, 2007; Klucharev & Sams, 2004). Some models of emotion recognition have incorporated the fuzzy nature of emotions (Fiorentini & Viviani, 2009; Russell, 1997). This experiment extends the reach of the FLMP to encompass not only the integration of social cues for the purposes of perceptual categorisation of emotion (Ellison & Massaro, 1997; Massaro & Egan, 1996), but also the attribution of goals and intentions to the actions of others. The facial expression of approach combined with the face rotating toward the observer already exhibited a high degree of correspondence with the goal-prototype of approach, which was attributed to the agent. The gaze cue was not needed to reach this decision, i.e. there was no need to prioritise gaze processing. However, in case of avoidance expressions, there were equivalent degrees of

correspondence with the goal-prototypes of both approach (the action) and avoidance (the expression), which meant the behavioural intention remained unclear. Consequently, processing of the gaze cue was prioritised to try and clarify the intention.

#### *Comparison with previous experiments*

The effect of gaze observed in the experiments 1a and 2 can also be understood within this framework. The stimuli employed possessed a neutral expression throughout the presentation duration. In light of the lack of motivational information conveyed by the neutral facial expression, gaze direction became the most informative cue regarding the goal/intention of the action. Consequently, judgments of head rotation were influenced by gaze direction. The significant difference between the two conditions in which gaze was incongruently aligned with head orientation (both overall and just in the avoidance condition) is consistent with previous experiments; however the precise pattern of results is less reliable. The estimations in the gaze-ahead condition were significantly higher than in the gaze-congruent condition, and from 50%, suggesting that the effect of gaze was due to an overestimation of the degree of head rotation in the gaze-ahead condition. This pattern of results differs from experiment 1a in which the effect of gaze was due to underestimation of the degree of rotation when gaze was directed in the opposite direction to that of head rotation.

#### *Critical evaluation of possible alternative explanations*

In principle several alternative explanations can be offered to account for the observed results. Firstly, fear expressions require greater attention to the eye region (Bindemann et al., 2008; Smith et al., 2005) which may have facilitated an effect of gaze compared to happy expressions, for which attention is biased to the mouth region (Smith et al., 2005). However, determining anger expressions also relies on the eye region (Adolphs et al., 2005), for which no effect of gaze was found, suggesting selective

allocation of attention to the eyes cannot account for the observed results. Secondly, the fear condition may have elicited a gaze effect as the distinctive widening of the eyes characteristic of fear expressions increases the conspicuousness of the gaze signal (Tipples, 2005), in contrast to happy expressions in which the eyes are narrowed (Mehu, Little, & Dunbar, 2007). However, this does not account for the effect obtained for the disgust expression, which is similarly characterised by a squinting of the eyes. Furthermore, whilst not explicitly controlled for, inspection of the maximum on screen size of the eye showed only marginal variation between expressions (between  $0.006^\circ$  and  $0.01^\circ$  in height, and between  $0.026^\circ$  and  $0.03^\circ$  in width). Nevertheless, whilst in combination these factors may have played a role, none of them alone can account fully for the findings.

### *Conclusion*

Overall, the results of this experiment are consistent with those of the previous experiments. Anticipations of how an action will proceed in the immediate future are influenced by social cues. This emphasises the reliability of the effect and supports the hypothesis that information regarding the goals and intentions of the actor are incorporated into the representation of the action itself, and facilitate predictions of their behaviour. The novel contribution of this experiment is that the influence of social cues is not obligatory. Whilst information conveyed by gaze may be processed in the same way, it is not always exploited for the purpose of action anticipation. The determining factor identified in this study is that of the specificity of information conveyed by other social cues, namely emotional expression. The necessity of using gaze direction is heightened when the combination of the action and the facial expression is either uninformative regarding the motivations of the actor (such as when possessing a neutral expression) or is ambiguous (as when expressing fear or disgust), whereas gaze direction seems redundant as a cue

when clear motivational information is conveyed (such as an expression of happy or anger).

## **Chapter 5. The effect of intentional attribution from gaze and expression on reflexive joint attention abilities and the influence of individual differences.**

The experiments so far have investigated the contribution of social cues in anticipating how another person's behaviour will unfold in the immediate future. That is, the role that gaze direction and emotional expression play in predicting the end-point of the action currently being observed. This form of social cognition has been referred to as motor empathy, and is distinguished from other components of social cognition such as the ability to represent another's emotional state (emotional empathy) or their intentions, beliefs, and knowledge (cognitive empathy) (Blair, 2005). These latter forms of empathy enable an observer to anticipate the behaviour of others over longer periods of time, for example in future social interactions. The aim of this study was to assess the role of social cues in these other forms of empathy by investigating if specific combinations of gaze direction and emotional expression behaviour are used to infer the prosocial or antisocial disposition of another individual. Moreover, if this information is retained over a larger time period to influence anticipations of their behaviour in a future social interaction, specifically the speed with which they follow another person's gaze direction.

### *Attributing intentions from social cues*

Emotional expressions are one means by which an observer can gauge the altruistic or deceptive intentions of others. Specifically, the expressions of happiness and anger convey a prosocial and antisocial disposition respectively, and have been found to influence decision making in cooperative exchanges in economic games of trust and fairness (Allen & Courchesne, 2001; Schmidt & Cohn, 2001; van Dijk, van Kleef, Steinel, & van Beest, 2008). Smiling elicits attributions of generosity and cooperation (Mehu, Little et al., 2007; Scharlemann, Eckel, Kacelnik, & Wilson, 2001), and those who do so are afforded greater degrees of trust and fairer allocations of resources in games requiring

reciprocated cooperation in order to increase mutual pay-offs (Brown & Moore, 2002; Mehu, Grammer, & Dunbar, 2007; Scharlemann et al., 2001). Conversely, those likely to defect on such exchanges can be denoted by facial expressions of fear or anger (Vanneste, Verplaetse, Van Hiel, & Braeckman, 2007). The faces of those depicted at the moment of defecting on another's cooperation are processed implicitly and automatically, as evidenced in the automatic orienting of attention to such faces (Vanneste et al., 2007), and observers are better able to recall and discriminate the identity of such defectors than those who reciprocated another's cooperation (Brown & Moore, 2002; Verplaetse, Vanneste, & Braeckman, 2007; Yamagishi, Tanida, Mashima, Shimoma, & Kanazawa, 2003). These effects are obtained despite the irrelevance of the stimulus differences to the demands of the task, but require that such stimuli are obtained in situations of real financial stakes and not from simulated interactions. As such, these cues are used in a variable and context dependant nature. Moreover, they are processed and acted upon swiftly and accurately by a sophisticated perceptual system that can discriminate real from simulated cues. The necessity of doing so could mean the difference between benefiting from a reciprocal exchange, and incurring a cost by having one's own cooperative actions defected on (Mehu, Grammer et al., 2007).

#### *Spatial orienting of attention in response to gaze direction*

Managing costs and benefits in social interactions by inferring the prosocial or antisocial intentions of others extends beyond situations of resource distribution. Reacting appropriately to the gaze behaviour of others is similarly advantageous (Emery, 2000), and orienting attention to where another is looking (joint attention) facilitates locating and learning about potentially threatening or beneficial stimuli and language acquisition (Charman et al., 2000; Hadjikhani et al., 2008). The importance of this is reflected in the reflexive and automatic orienting of one's spatial attention in the direction that another



person is looking (Frischen et al., 2007). Cueing of attention by gaze direction is distinguished from other cues in that it has ecological relevance that other symbolic cues lack. A peripheral target is preceded by a centrally presented gaze that is either averted to the location that the target will appear at (valid cue) or averted to a location that it will not appear at (invalid cue). Even though the gaze cue is non-predictive of target location, target processing is facilitated, in terms of detection or localization, when the gaze cue is valid than if invalid.

The time course of the gaze cueing effect can be measured by varying the delay between onset of the cue and onset of the target (Stimulus Onset Asynchrony, SOA). The minimum SOA at which a gaze cueing effect is reliably observed is 100 ms, and there is evidence that it may occur before this (Hietanen & Leppanen, 2003). It is also evident at SOAs as long as 1005 ms (Friesen & Kingstone, 2003; Ristic et al., 2005) with inconsistent reports of an effect at 1200 ms (Frischen & Tipper, 2004; Tipples, 2008). The rapid onset of such an effect is characteristic of the automatic stimulus driven orienting of attention in response to exogenous cues, but its length is characteristic of the top-down mechanisms of voluntary orienting of attention in response to endogenous cues, suggesting gaze cueing to be subject to both obligatory and voluntary processes at different time courses (Friesen, Ristic, & Kingstone, 2004). An initial involuntary reflex to follow another's gaze emerges early, but diminishes as a slower voluntary control of attention orienting emerges later (Friesen et al., 2004).

#### *Spatial predictability of the gaze cue*

Evidence for the automatic nature of the gaze cueing effect comes from studies that explicitly manipulate the spatial predictability of the gaze cue with respect to target location. Participants are expected to exhibit a greater gaze cueing effect when the probability that the target will appear at the gazed at location is predictive (> 50%), and

should not follow the gaze cue when cue target congruency is counter-predictive ( $< 50\%$ ). The magnitude of the gaze cueing effect should therefore reflect the likelihood of the target appearing at the gazed at location and be either potentiated or attenuated. However, these studies suggest that cueing of spatial attention is not mediated by varying the spatial contingencies between gaze direction and target location. Explicitly informing participants that the cue-target congruency rate will be 80% does not increase the speed with which targets at the cued location are processed (Driver et al., 1999; Friesen et al., 2004; Ristic et al., 2005; Tipples, 2008). Similarly, cueing of attention in the direction of gaze direction persists when the likelihood of the target appearing in that location is only 20% (Downing, Dodds, & Bray, 2004; Kuhn & Kingstone, 2009). Only after SOAs in excess of 600 ms do processing times of the target reflect the likelihood that the gaze cue was directed in that location (Friesen et al., 2004; Kuhn & Kingstone, 2009; Tipples, 2008). This suggests that immediately after observing an averted gaze, participants cannot help but orient attention in that direction, and only after 600 ms can voluntary processes act on explicit knowledge to control orienting of attention (Friesen et al., 2004; Tipples, 2008).

Bayliss and Tipper (2006) sought to investigate if the spatial predictability of specific identities could be implicitly learnt during the course of the cueing experiment. They presented four identities, two of which were non-predictive (50% congruency), one who was predictive (80% congruency) and one who was counter-predictive (20% congruency). Participants were not explicitly aware of the varying gaze target contingencies of the four identities. It was anticipated that an equivocal cueing effect would be evident at the start, with the magnitude of the gaze cueing effect varying between the identities by the end (predictive  $>$  non-predictive  $>$  counter-predictive). However, this was not found. Although there was a gaze cueing effect overall, the predictive and counter-predictive identities did not elicit an effect that was different from that of the non-predictive identities. However, subsequent attributions of trustworthiness were greater for the predictive identity, and recall for the face of the counter-predictive identity was greater than for the predictive

identity, reflecting the memory bias exhibited for the face of those defecting in social exchanges (Yamagishi et al., 2003).

*The effect of individual differences in empathising, systemising and autistic traits on the gaze cueing effect*

Despite its relevance in social interactions, the extent to which attention is oriented in response to the gaze direction of others shows considerable individual variation, with some individuals showing no gaze-cueing effect at all (Frischen et al., 2007). The nature of this variation is associated with individual differences in the ability to empathise, which enables social information to be processed in order to understand and interpret the behaviour of others in terms of intentionality. Baron-Cohen et al (2004) devised the empathising quotient (EQ) to assess an individual's propensity to empathise. An individual's empathising skills shows an inverse relationship with their ability to systemise (Carroll & Yung, 2006; Wheelwright et al., 2006), which enables the rules and lawful principles governing the behaviour of systems to be deduced. Wheelwright et al (2006) devised an equivalent self-assessment measure for systemising called the systemising quotient (SQ-R). An extreme asymmetry between empathising and systemising is characteristic of those with disorders along the autistic spectrum, who show abnormal deficits in empathising, but greatly enhanced systemising abilities. As autism represents an extreme phenotype of traits that are present in the normal population, those who exhibit more of these traits, as measured by the Autistic-Spectrum Quotient (AQ; Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001), show a significant but smaller gaze cueing effect than those who exhibit few of these traits (Bayliss, di Pellegrino, & Tipper, 2005; Bayliss & Tipper, 2005). However, studies investigating the presence of a gaze cueing effect in those with high functioning autism have found mixed results. Some studies have demonstrated an absence of spatial orienting in response to a non-predictive gaze cue

(Johnson et al., 2005; Ristic et al., 2005), whilst others have found that gaze cueing effect remains intact in such populations (Chawarska, Klin, & Volkmar, 2003; Kemner, Schuller, & van Engeland, 2006; Kylliainen & Hietanen, 2004; Senju, Tojo, Dairoku, & Hasegawa, 2004; Swettenham, Condie, Campbell, Milne, & Coleman, 2003; Vlamings, Stauder, van Son, & Mottron, 2005).

Several authors have proposed that those with autism are capable of computing and following another's direction of gaze, but do so in a way that is qualitatively different from that of non-autistic people (Nation & Penny, 2008). Driver et al (1999) refer to this as mechanistic versus mentalistic processing, while Ristic et al (2005) call it the feature correspondence versus social reading hypotheses (see also Jellema & Perrett (2005) for a description of this distinction applied to biological motion in general). In essence, gaze processing in typically developing individuals is accompanied by a psychological component that appreciates the perceptual experience, goals and intentions of the gazer. It is this comprehension of the social meaning that distinguishes it from other, non-social, types of cue. However, for autistic individuals, gaze is devoid of any social meaning and can be based solely on the association between the low level visual appearance of the pupil shifting within the sclera and the target location. This is supported by De Jong et al (2008) who found that, even though those with ASD exhibited a gaze cueing effect, it was based on local featural information from high spatial frequencies, whereas those without ASD used global information from low spatial frequencies. Furthermore, whilst the gaze cueing effect for the typically developing control group was modulated by the emotional expression of the stimulus, it was not for the ASD group. Further studies have suggested that gaze direction cues the attention of autistic individuals in a manner comparable to that of other non-social cues, such as arrows. In TD individuals, gaze cues to the observer's right side elicit a greater cueing effect than those to their left side, yet no such laterality effects are observed in response to arrows cues. In contrast, those with ASD show no laterality effects in response to either gaze or arrows (Vlamings et al., 2005). Furthermore,

the response times of TD individuals is slower to gaze cues than to arrow cues, but the response times in ASD individuals is equivalent for both social and non-social cues (Chawarska et al., 2003; Vlamings et al., 2005).

Two studies have assessed the effect of spatial predictability on the gaze cueing effect of those with high autistic traits. Bayliss and Tipper (2006) found that no effect of spatial predictability was observed for those who scored either high or low on the AQ. However, these participants were taken from the general population and therefore did not have abnormally high levels of autistic traits. Ristic et al (2005) tested those with high functioning autism and found that, whilst they showed no gaze cueing effect in response to a non-predictive gaze cue, they did orient attention in response to a predictive gaze cue. Furthermore, this was evident at SOAs typically thought to be indicative of automatic mechanisms that are not modulated by spatial predictability in non-autistic individuals. This makes sense in light of their proficiency in processing systematic regularities, as they would be more sensitive to the probabilistic nature of gaze cues, and therefore to its spatial predictability.

### *Hypotheses*

The aim of this study was to investigate if emotional expression and gaze direction contribute to an observers attributions of whether the individual has a prosocial or antisocial disposition, and if these inferences affect subsequent cueing of spatial attention in response to their gaze direction. Specifically, the gaze cueing effect in response to a prosocial identity should be greater than in response to an antisocial identity. Furthermore, this difference should be greater for those who are more sensitive to social information (high empathisers, low in autistic traits) than those who are less sensitive to social information (low empathisers, high in autistic traits). Conversely, those who exhibit a greater sensitivity to systematic regularities (high systemisers, high in autistic traits) will

show a greater gaze cueing effect in response to identities whose gaze is spatially predictive of target location.

Participants will initially complete a learning phase consisting of repeated exposure to three identities. Through a combination of changes in gaze direction and emotional expression, participants will learn that one identity has a prosocial disposition toward the observer, the second has an antisocial disposition toward the observer, and the gaze direction of the third is spatially predictive of target location. The three identities will then be used in a subsequent gaze cueing study with a non-predictive gaze cue (the test phase). The use of a separate learning phase was deemed necessary for two reasons. Firstly, Bayliss and Tipper (2006) did not find implicit learning of spatial contingencies during the course of a gaze cueing experiment. An effect of learning may be maximised if it occurs before hand. Secondly, emotional expressions have been previously utilised in gaze cueing studies, but in order to imply the gazer's emotional reaction to the target, not to the observer (Hori et al., 2005; Tipples, 2006). The stimuli therefore had a neutral expression in the gaze cueing paradigm.

#### *Experiment 4*

##### *Method*

##### *Participants*

Participants (N = 95, 48 females, mean age = 20.7 years, SD = 1.9 years) were all students at the University of Hull, UK, and gave written informed consent prior to taking part. All had normal or corrected-to-normal vision.

##### *Apparatus*

All stimuli were presented using e-Prime software (Psychology Software Tools, Inc) on a 21 inch monitor (100 Hz refresh rate) from which participants sat approximately 50

cm. All stimuli were created using Poser 7 animation software (Curious Labs, Inc & e frontier, Inc). Prior to completing the experimental phase participants were administered online versions of the AQ (Baron-Cohen et al., 2001), EQ (Baron-Cohen & Wheelwright, 2004) and SQ-R (Wheelwright et al., 2006). Each took 10 minutes to complete and was scored automatically.

### *Stimulus*

#### *Learning phase*

The learning phase consisted of repeated exposure to video clips of three different identities. The gaze direction of the agents varied with a smooth and continuous motion within a  $30^\circ$  range during the course of the video clip. Gaze was either initially fixated at the observer ( $0^\circ$ ) at the start of the clip and was horizontally averted  $30^\circ$  by the end, or began at a  $30^\circ$  aversion from mutual gaze and was looking at the observer ( $0^\circ$ ) at the end of the clip. The stimulus was oriented facing the observer throughout and depicted from the top of the shoulders upwards. The subtended angle of the stimulus's width varied depending on the character used but ranged from between  $11.8^\circ$  to  $19.7^\circ$ , whilst the height of all the characters was  $18.1^\circ$ . For all three identities, a red square was positioned to the left or right of the stimulus along the horizontal midline. The red square was of a height and width of  $2.1^\circ$ , the inner edge of which was positioned  $6.9^\circ$  from the centre of the screen and between  $1.3^\circ$  and  $0.9^\circ$  from the edge of the face stimulus (depending on the character). Three learning conditions were created by making the gaze aversion either socially or spatially meaningful (detailed below, see Table 5.1 and Figure 5.1). Each of the different conditions was assigned to a specific identity, which were counterbalanced across participants and presented in a random order during the learning phase. A total of four identities were used (2 males and 2 females), however each participant was only exposed to three of them which was also counterbalanced across participants.

### *Predictive identity*

In this condition, the direction of gaze movement was spatially congruent with the position of the target. The gaze movement towards or away from the observer occurred on the same side of the screen as the position of the red square. The spatial relationship of the gaze behaviour with the target position was therefore predictive. The aim was that the participant would associate the gaze behaviour of this identity with the correct location of the target. The expression of this identity was neutral throughout.

### *Positive identity*

For this condition, the direction of gaze was not spatially contingent on the position of the target. That is, the gaze movement was to the same side of the screen as the targets position as often as it was to the opposite side. However, the change in gaze direction was accompanied by a change in emotional expression, thus making it socially contingent to the observer. A gaze movement away from the observer accompanied a change from happy to angry, and a gaze movement toward the observer accompanied a change from angry to happy. Because of this, a positive social disposition to the observer was implied, as the happy expression was directed at the observer and the angry expression was directed away.

### *Negative identity*

Like the socially positive condition, the relationship between the gaze behaviour and target location was spatially non-predictive and meaningless. However, the relationship with the change in expression was reversed, such that a gaze movement away from the observer coincided with an expression change from angry to happy, and a gaze movement toward the observer coincided with an expression change from happy to angry. This therefore implied a negative social disposition to the observer, as the angry expression was directed at the observer, and the happy expression was directed away.



	Gaze Movement	Expression	Gaze – Target Congruency
<b>Identity 1: Predictive</b>	Direct – Away	Neutral	100%
	Away - Direct	Neutral	100%
<b>Identity 2: Positive</b>	Direct – Away	Happy – Angry	50%
	Away - Direct	Angry - Happy	50%
<b>Identity 3: Negative</b>	Direct – Away	Angry – Happy	50%
	Away - Direct	Happy – Angry	50%

Table 5.1. The gaze behaviour in relation to the emotional expression and target position for the three identities.

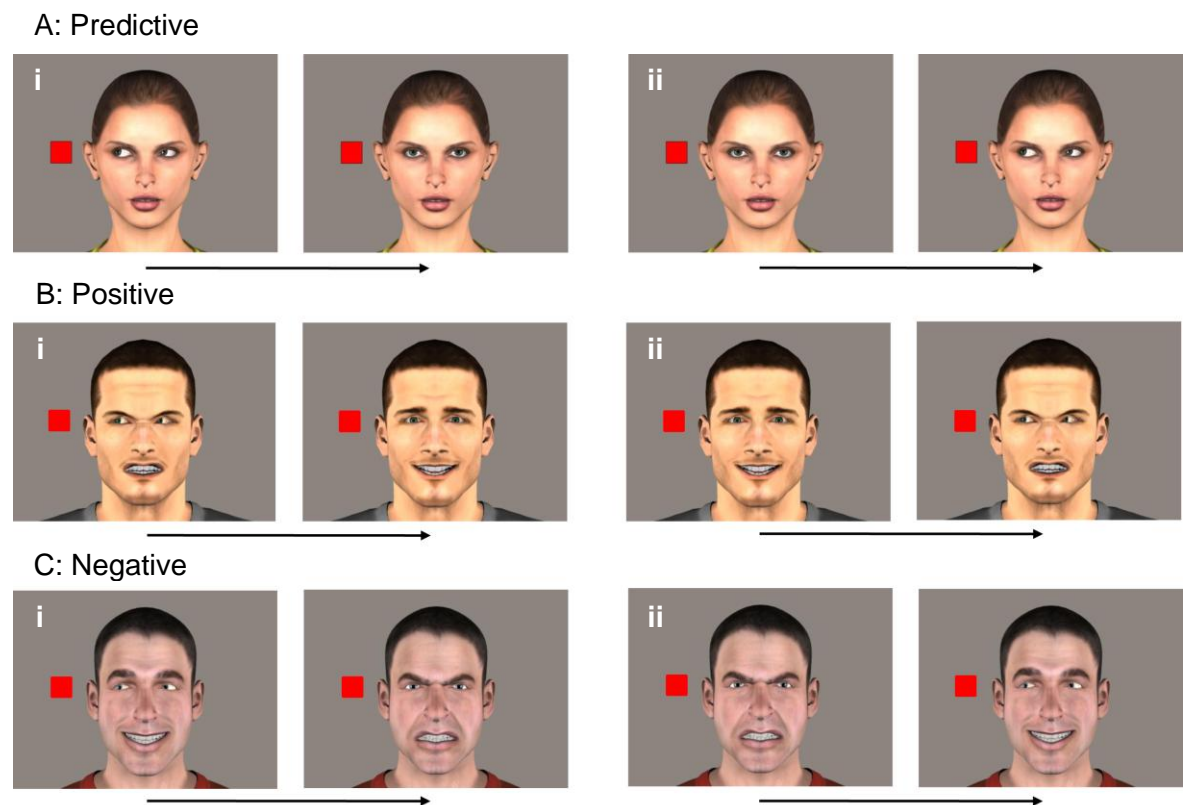


Figure 5.1. Stimuli in the learning phase for the Predictive (A), Positive (B) and Negative (C) identities. For all identities the gaze changed from averted to direct (i) or from direct to averted (ii). For the predictive identity, the expression was neutral throughout but the gaze

direction was always congruent with target location. For the positive and negative identities the expression changed from happy to angry or from angry to happy. For the positive identity, the happy expression was always directed toward the observer whereas the angry expression always directed away from the observer. For the negative identity, the angry expression was always directed at the observer whereas the happy expression was always directed away from the observer. The target appeared at the gazed at location in half the trials (shown) and on the opposite side in the remaining half.

### *Testing phase*

The test phase consisted of a reflexive social orienting paradigm involving the three identities previously observed in the learning phase. A centrally presented face with gaze averted towards either the left or right of the screen preceded the appearance of a peripheral target along the horizontal midline either in a location congruent with the direction of gaze (valid) or on the opposite side of the screen (invalid). The orientation of the face and shoulders and its size on screen was the same as in the learning phase. The expression of each face was neutral and the extent of gaze aversion was 30° from a mutual gaze (0°). The target was a red square, the size and appearance of which was the same as that of the target in the learning phase, both on screen and in relation to the face stimulus.

### *Procedure*

#### *Learning phase*

Participants were required to watch each video clip and press the spacebar when the eyes stopped moving. This task ensured that the stimuli were attended to throughout. Participants observed 96 trials (32 each of the positive, negative and predictive identities). The movement of gaze direction was on the left in half of the trials, and on the right in the remaining half (distributed evenly across the conditions). Each trial began with a blank

screen of 1500ms duration (which also served as the ITI) after which the video clip was presented. This consisted of 20 static frames presented in quick succession, with the first frame on screen for 750ms and all subsequent frames for 50ms (1.7 seconds total duration), with the final frame on screen until a response was made or 3 seconds had elapsed. There were 24 additional trials in which the gaze did not move (8 for each identity). These were catch trials in which the participant was not required to make a response, and were used to assess performance. The social or spatial contingency of the identity was maintained in these catch trials. The static gaze of the socially meaningful identities remained fixated at the observer and was combined with either an expression change from either angry to happy (positive) or happy to angry (negative). For the spatially predictive identity, the gaze remained averted to the same side as the target position. The total 120 trials were split into two blocks of 60 lasting approximately 10 minutes.

### *Testing phase*

Participants observed 144 trials in total (48 each for socially positive, 48 for socially negative and 48 for spatially predictive) lasting approximately 10 minutes (Figure 5.2). Each trial of the test phase began with a fixation cross (500 ms) followed by the gaze cue consisting of a face with gaze averted to the left or right. The duration of the gaze cue before onset of the target was either 300 ms or 800 ms. The target appeared on 96 of the trials, 48 on the side of the screen congruent with the direction of gaze, 48 on the incongruent side, thus ensuring that the gaze cue was non-predictive of the target's location. Participants were required to make a speeded response by pressing the spacebar as soon as they saw the target. The design was a 3 (Identity) X 2 (SOA) X 2 (Validity) design with each iteration represented by 8 trials. On the remaining 48 trials (16 per identity) the target did not appear and participants were not required to make a response.

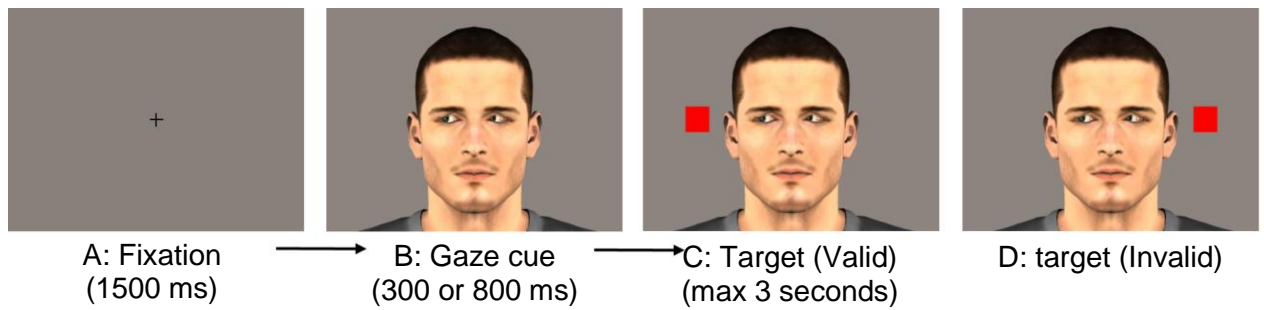


Figure 5.2. Trial procedure for the gaze cueing paradigm used in the test phase. A fixation cross (A) was followed by the presentation of a face with gaze averted to the left or right (B). After either 300 or 800 ms a red target appeared either at the gazed at location (C: Valid) or on the opposite side of the screen (D: Invalid).

## Results

### *Questionnaire data and group allocation*

The results of the questionnaires are summarised in Table 5.2. Bivariate correlation analysis (Spearman's rho, two-tailed,  $N = 95$ ) showed that the scores on the AQ were negatively correlated with EQ scores ( $\rho = -.288$ ,  $p = .005$ ) and were positively correlated with SQ scores ( $\rho = .384$ ,  $p < .001$ ). The relationship between EQ and SQ-R scores was negative but not significant ( $\rho = -.095$ ,  $p = .359$ ).

There were two methods of group allocation used. The first was based on AQ scores (Figure 5.3 left panel). Participants scoring equal to or less than the median AQ score of 15 were allocated to the low AQ group ( $n = 47$ , mean = 11.6, SD = 2.6) and those scoring higher than 15 were allocated to the high AQ group ( $n = 48$ , mean = 19.2, SD = 2.6). The AQ groups differed significantly on scores on the AQ ( $t(94) = -14.2$ ,  $p < .001$ ), EQ ( $t(94) = 2.16$ ,  $p = .033$ ) and SQ-R ( $t(94) = -3.44$ ,  $p = .001$ ). The second method of group allocation was determined by the asymmetry between EQ and SQ scores (following the method of (Goldenfeld, Baron-Cohen, & Wheelwright, 2005; Wheelwright et al., 2006). Scores were

first normalised by subtracting the mean score from the participant's score and dividing the result by the maximum possible score obtainable (EQ = 80, SQ-R = 150). Figure 5.3 (right panel) shows these normalised scores plotted against each other. The difference between these new scores (normalised SQ-R – normalised EQ) were divided by 2 producing a new value D. Where D had a negative value, the participant's score was asymmetric in favour of empathising, whilst a positive value denoted an asymmetry biased toward systemising. There was a significant positive correlation between D values and AQ scores (*Spearman's rho* = .458,  $p < .001$ ,  $N = 95$ , two-tailed), suggesting that as a participant's asymmetry became increasingly biased towards systemising, then the number of autistic traits they exhibited also increased, in keeping with the positive relationship between AQ scores and SQ-R scores and the negative relationship between AQ scores and EQ scores. Previous studies have defined the balanced group as those participants scoring a D value of less than 0.1 and higher than -0.1, with those scoring -0.1 or less defined as empathisers, and those scoring 0.1 or more defined as systemisers. However, when applied to the current sample, this resulted in highly uneven group sizes (systemisers = 23, balanced = 54, empathisers = 19). Therefore, a different method was favoured in which those participants whose D value was -0.05 or less were allocated to the empathising group ( $n = 31$ ), those with a D value of 0.05 or more to the systemising group ( $n = 31$ ), and those in between -0.05 and 0.05 to the balanced group ( $n = 33$ ). The AQ, EQ and SQ data for all groups are summarised in Table 5.2.

	AQ Group			EQ/SQ-R Asymmetry Group		
	All (N = 95)	Low (n = 47)	High (n = 48)	E > S (n = 31)	B (n = 33)	S > E (n = 31)
<b>AQ</b>	15.5 (4.6)	11.6 (2.6)	19.2 (2.6)	13.3 (3.8)	15.0 (4.5)	18.3 (4.1)
<b>EQ</b>	43.2 (11.4)	45.7 (11.0)	40.7 (11.1)	54.3 (6.0)	41.4 (8.1)	33.5 (8.7)
<b>SQ-R</b>	50.3 (20.5)	43.3 (14.0)	57.0 (23.6)	36.9 (12.0)	47.9 (15.3)	66.6 (22.5)

Table 5.2. Mean (SD) scores on the AQ, EQ and SQ-R for all participants, and separately for the low and high AQ groups and for the Empathising, Balanced and Systemising groups.

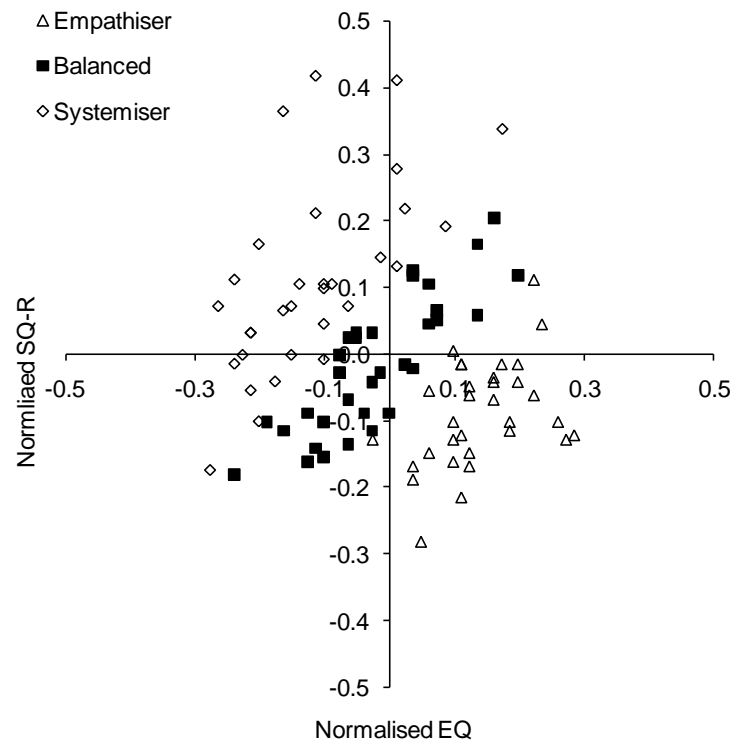


Figure 5.3. The distribution of the three Empathising - Systemising asymmetry groups when normalised EQ scores are plotted against normalised SQ-R scores. X-axis: Normalised EQ scores, Y-axis: Normalised SQ-R scores.

### *Data reduction*

Error rates in the learning phase (mean = 3.1%, SD = 11.3%) and test phase (mean = 0.6%, SD = 0.9%) were averaged (mean = 1.8%, SD = 5.6%). Participants with an average error rate in excess of 5% were excluded ( $n = 5$ , mean = 17.1%, SD = 18.5), leaving 90 participants (mean = 1.0%, SD = 2.2%, Low AQ = 46, High AQ = 44,  $E > S = 31$ ,  $B = 30$ ,  $S > E = 29$ ). The mean RT in the test phase was 342 ms (SD = 41 ms). Catch trials and incorrect trials were excluded, as were trials where responses were made less than 100 ms or above 2SD of each participant's mean RT ( $n = 4.4\%$ , mean = 567 ms, SD = 148 ms), resulting in a new mean RT of 332 ms (SD = 38 ms).

### *Spatial orienting in response to gaze direction*

To verify the presence of a cueing effect, the data were initially subject to a 2 X 2 ANOVA with Validity and SOA entered as within-subjects factors. This showed that there was no significant effect of SOA ( $F(1, 89) = .498$ ,  $p = .482$ ,  $\eta_p^2 = .006$ ). Response times were significantly faster in valid trials than invalid trials ( $F(1, 89) = 16.5$ ,  $p < .001$ ,  $\eta_p^2 = .156$ ). There was a significant interaction between SOA and Validity ( $F(1, 89) = 6.31$ ,  $p = .014$ ,  $\eta_p^2 = .066$ ), due to the valid trials eliciting significantly faster response times than the invalid trials at an SOA of 300 ms ( $t(89) = 4.62$ ,  $p < .001$ ,  $d = .2$ ) but not at an SOA of 800 ms ( $t(89) = 1.473$ ,  $p = .144$ ,  $d = .05$ ) (Figure 5.4).

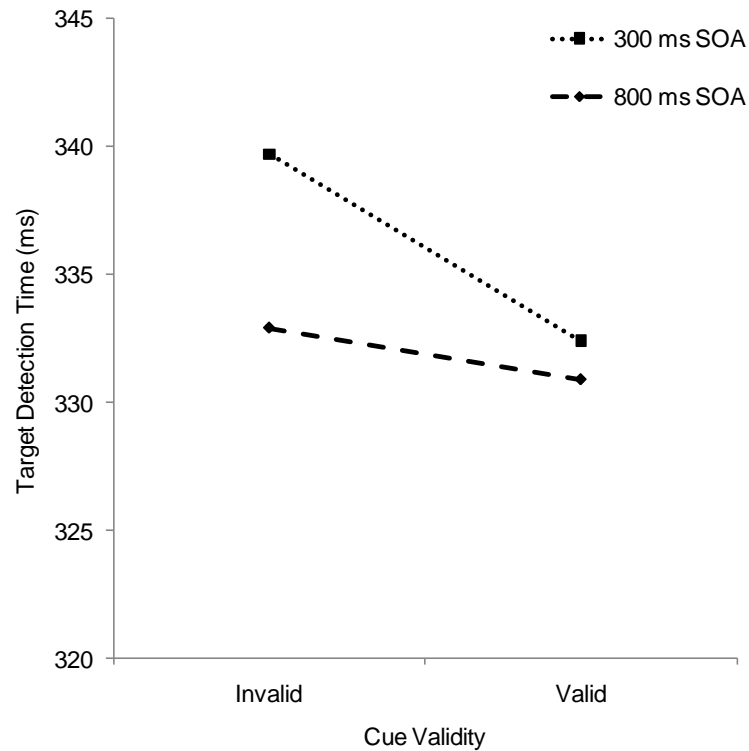


Figure 5.4. Mean target detection times when the gaze cue correctly predicted (valid) and incorrectly predicted (invalid) target location for the 300 ms and 800 ms conditions separately. The effect of gaze cueing can be measured by subtracting target detection times in the valid trials from those in the invalid trials (300 ms SOA: mean = 7.2 ms, SD = 14.9 ms; 800 ms SOA: mean = 2.0 ms, SD = 12.9 ms).

#### *The effect of AQ group and stimulus identity on the cueing effect at 300 ms SOA*

As the focus of this study was to investigate if the extent of the gaze cueing effect differed between identities, the response times in the valid trials were subtracted from those in the invalid trials. This provided a measure of the magnitude of the cueing effect. This was entered into a two-way ANOVA with identity (positive vs. negative vs. predictive) as a within subjects factor and AQ Group (low vs. high) as a between subjects factor. There was no significant main effect of identity ( $F(2, 176) = .43, p = .65, \eta_p^2 = .005$ ) and no



significant main effect of AQ Group ( $F(1, 88) = 1.59, p = .21, \eta_p^2 = .018$ ). There was a significant interaction between identity and AQ Group ( $F(2, 176) = 3.3, p = .038, \eta_p^2 = .036$ ) (Figure 5.5).

Paired sample t-tests ( $\alpha_{Bon} = .0167$ ) showed that for the low AQ group, the cueing effect in response to the negative identity was significantly less than that in response to the positive identity ( $t(45) = 2.76, p = .008, d = .5$ ). The cueing effect elicited by the predictive identity did not differ from that elicited by either the positive ( $t(45) = .18, p = .858, d = .04$ ) or negative identities ( $t(45) = 1.84, p = .073, d = .41$ ). For the high AQ group the cueing effect did not differ between any of the identities (positive vs. negative:  $t(43) = .951, p = .347, d = .2$ ; positive vs. predictive:  $t(43) = .486, p = .629, d = .1$ ; negative vs. predictive:  $t(43) = 1.21, p = .231, d = .3$ ).

*The effect of AQ group and stimulus identity on the cueing effect at 800 ms SOA*

There was no significant effect of identity ( $F(2, 176) = .061, p = .94, \eta_p^2 = .001$ ) nor was there a significant effect of AQ group ( $F(1, 88) = .196, p = .659, \eta_p^2 = .002$ ). There was a significant interaction between identity and AQ group ( $F(2, 176) = 3.611, p = .029, \eta_p^2 = .039$ ) (Figure 5.5).

Paired sample t-tests showed that for the low AQ group there was no differences in the gaze cueing effect between the different identities (positive vs. negative:  $t(45) = .743, p = .461, d = .2$ ; positive vs. predictive:  $t(45) = 1.07, p = .289, d = .2$ ; negative vs. predictive:  $t(45) = 1.81, p = .078, d = .4$ ). For the high AQ group the gaze cueing effect in response to the positive identity did not differ from either the negative ( $t(43) = 1.23, p = .227, d = .3$ ) or predictive identities ( $t(43) = .728, p = .471, d = .2$ ). The difference between the negative and predictive identities was significant at  $p = .05$  but did not survive the bonferroni adjustment ( $t(43) = 2.12, p = .04, d = .4$ ).

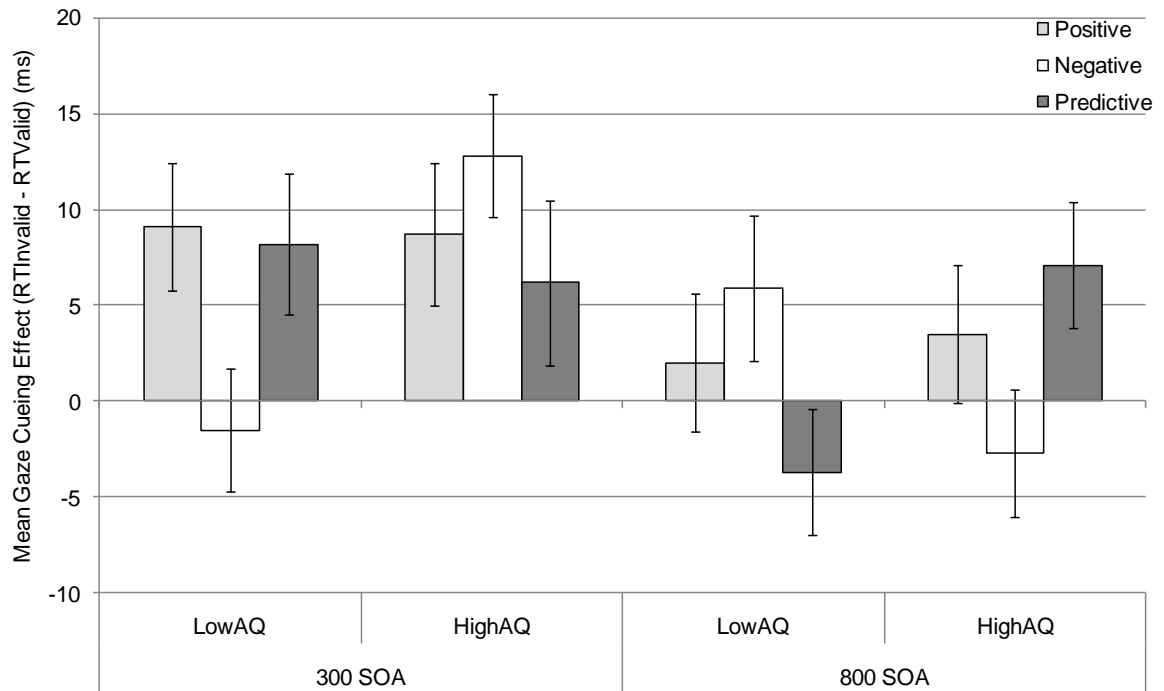


Figure 5.5. Mean gaze cueing effect elicited by each of the stimulus identities for the low AQ and High AQ groups when the SOA was either 300 or 800 ms. Error bars represent +/- 1 standard error of the mean.

#### *The effect of empathising/systemising asymmetry and identity*

The same analysis was conducted after participants were grouped according to their D value (see Figure 5.6), which is a measure of the degree of asymmetry they exhibit in terms of empathising and systemising (E > S vs. Balanced vs. S > E). At 300 ms SOA, there was no significant main effects of identity ( $F(2, 174) = .436, p = .65, \eta_p^2 = .005$ ) or of D group ( $F(2, 87) = 1.27, p = .285, \eta_p^2 = .028$ ), nor was there a significant interaction ( $F(4, 174) = .459, p = .766, \eta_p^2 = .01$ ). At 800 ms SOA, there were similarly no significant main effects of identity ( $F(2, 174) = .45, p = .956, \eta_p^2 = .001$ ) or of D group ( $F(2, 87) = .127, p = .881, \eta_p^2 = .003$ ). However, there was a significant interaction ( $F(4, 174) = 3.56, p =$

.008,  $\eta_p^2 = .076$ ). One way ANOVAs with identity as a within subjects factor were conducted for each identity group.

There was no main effect of identity for either the Empathising group ( $F(2,60) = 1.37$ ,  $p = .262$ ,  $\eta_p^2 = .044$ ) or Balanced group ( $F(2,58) = 1.88$ ,  $p = .162$ ,  $\eta_p^2 = .061$ ). There was a significant main effect of identity for the Systemising group ( $F(2,56) = 4.68$ ,  $p = .013$ ,  $\eta_p^2 = .143$ ). Paired sample t-tests showed that the gaze cueing effect in response to the negative identity did not differ from that in response to the positive ( $t(28) = 1.31$ ,  $p = .2$ ,  $d = .3$ ) or predictive identities ( $t(28) = 1.81$ ,  $p = .081$ ,  $d = .5$ ). The gaze cueing effect elicited by the Predictive identity was significantly greater than that elicited by the positive identity ( $t(28) = 2.97$ ,  $p = .006$ ,  $d = .8$ ).

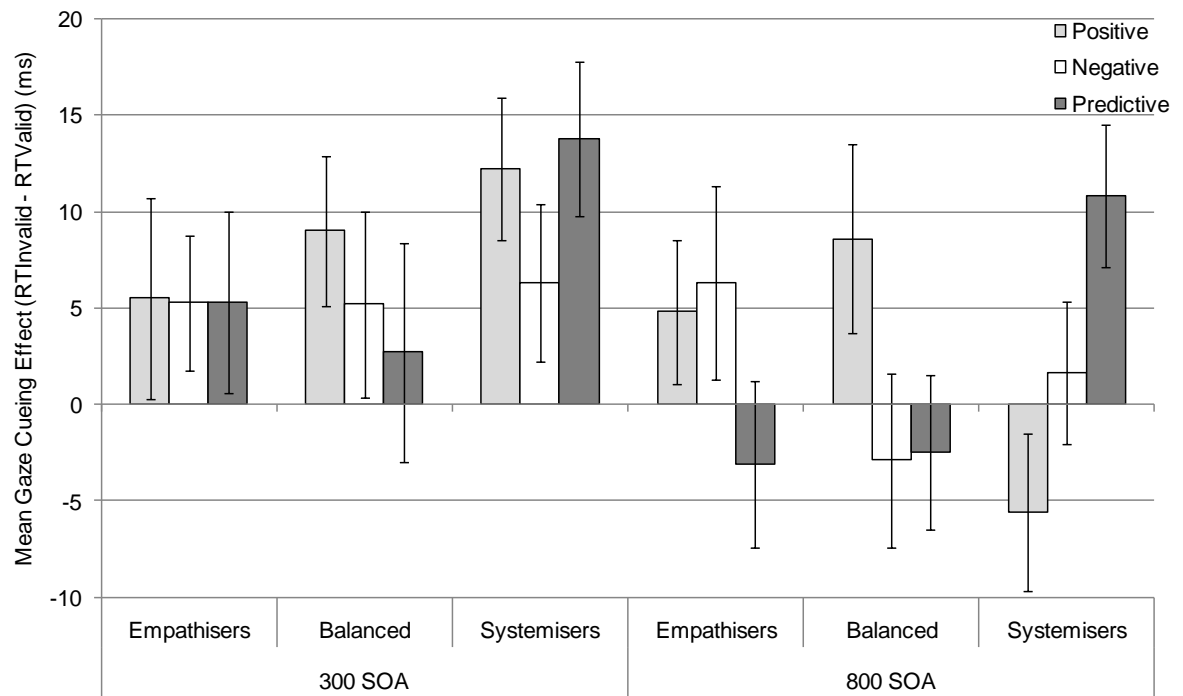


Figure 5.6. Mean gaze cueing effects for the three empathising/systemising asymmetry groups in response to the three stimulus identities with an SOA of either 300 or 800ms. Error bars represent +/- 1 standard error of the mean.

### *Correlation analysis*

The effect of individual differences in autistic traits and empathising/systemising asymmetries was further explored by conducting a correlation analysis (Spearman's Rho, two-tailed) between the magnitude of the cueing effect in response to the three identities and a participant's AQ score and D value (Figure 5.7).

With an SOA of 300 ms ( $N = 90$ ), AQ scores were positively correlated with the cueing effect in response to the negative identity ( $\rho = .305$ ,  $p = .003$ ), but not the positive ( $\rho = -.005$ ,  $p = .962$ ) or predictive identities ( $\rho = .053$ ,  $p = .616$ ). D values showed no significant relationship with the cueing effect for either the positive ( $\rho = .085$ ,  $p = .423$ ), negative ( $\rho = -.031$ ,  $p = .769$ ) or predictive identities ( $\rho = .077$ ,  $p = .47$ ).

With an SOA of 800 ms, ( $N = 90$ ), there was a significant positive correlation between AQ and the cueing effect elicited by the predictive identity ( $\rho = -.275$ ,  $p = .009$ ) but not with the positive ( $\rho = -.085$ ,  $p = .071$ ) or negative identity ( $\rho = -.160$ ,  $p = .131$ ). Furthermore, D values also positively correlated with the cueing effect for the predictive identity ( $\rho = .239$ ,  $p = .024$ ) but not the positive ( $\rho = -.202$ ,  $p = .056$ ) nor negative identities ( $\rho = -.131$ ,  $p = .219$ ).

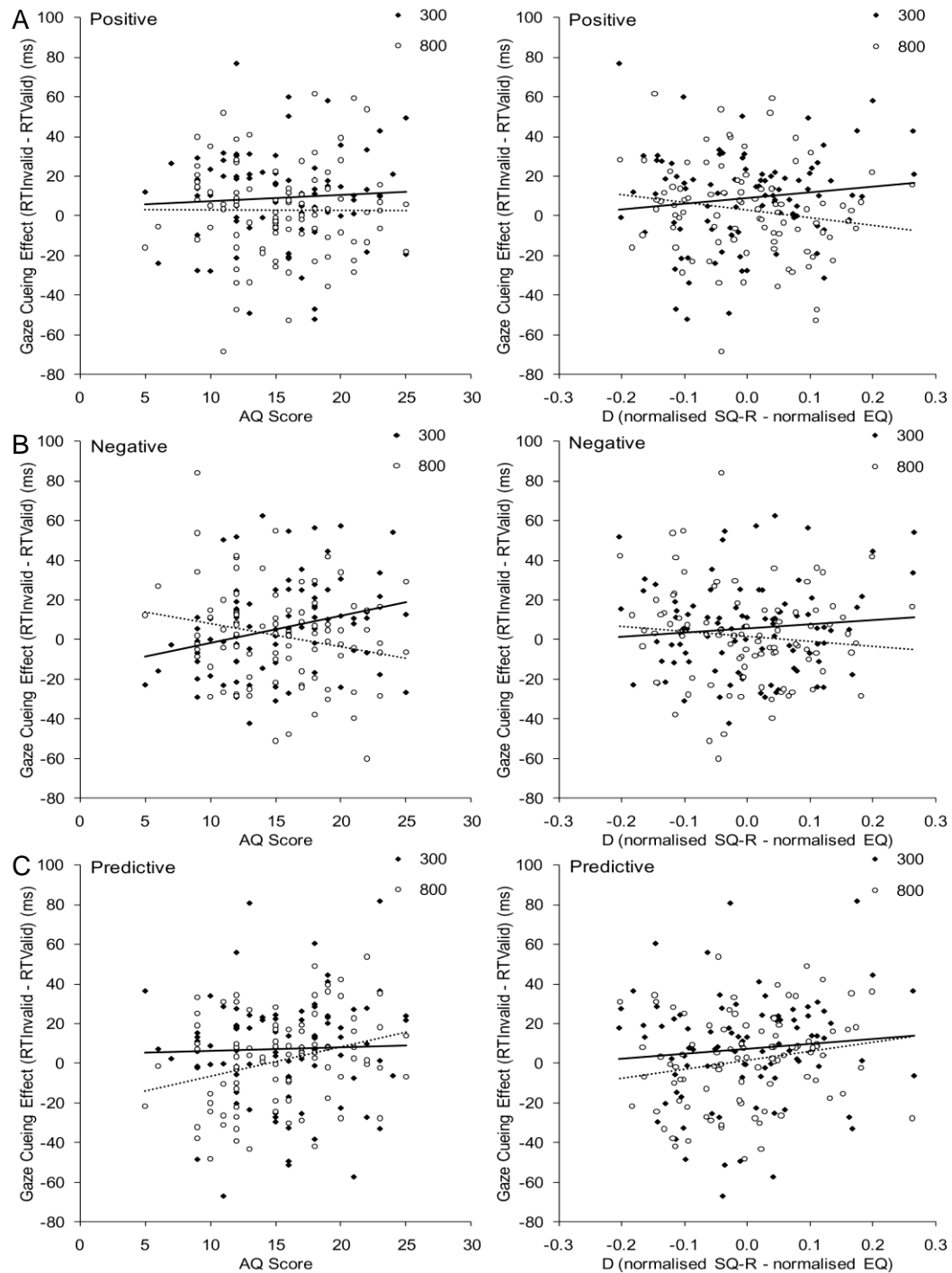


Figure 5.7. The relationship between gaze cueing and individual differences in empathising, systemising and autistic traits. The size of the cueing effect (invalidRT – validRT) is plotted against AQ score (left column) and D value (right column) for the Positive (A), Negative (B) and Predictive (C) identities with an SOA of 300 (filled circle, solid line) and 800 ms (empty circle, dashed line).

### *Discussion*

The aim of this study was to dissociate two styles of gaze processing that are related to individual differences. The size of the gaze cueing effect in response to a specific identity should depend on whether the observer anticipates their behaviour to be prosocial, antisocial or predictive. These attributions were manipulated by varying either social or spatial contingencies for different identities in an initial learning phase. These identities were then used in a subsequent gaze cueing experiment, in which participants were required to detect a peripheral target after observing a non-predictive gaze cue averted in either a congruent or incongruent direction. It was expected that reflexive cueing in response to the gaze direction of the three identities would vary according to what the observer had learnt during the learning phase. Specifically, it was expected that the gaze cueing effect for those who score highly on empathising measures and low on autistic traits would be affected by attributions derived from emotional expressions. In contrast, the gaze cueing effect in those who exhibit greater systemising skills and autistic traits would be more affected by the spatial predictability of the gaze cue.

Firstly a discussion of the data related to individual differences in empathising, systemising and autistic traits. The relationships between the scores support previous studies. Baron-Cohen's (2002) empathising-systemising model proposes that autism is characterised by a concurrent impairment in empathising skills and an enhanced ability to systemise, and that this inverse relationship is evident in the normal population (Carroll & Yung, 2006; Wheelwright et al., 2006). Accordingly, scores on the AQ were significantly correlated with scores on the EQ and SQ-R, with those exhibiting more autistic traits showing greater systemising abilities and fewer empathising abilities. However, although empathising and systemising did show a negative correlation, this was not significant. The direction of the relationship is consistent with previous research. Its non-significance may depend on sample size. Those finding a significant correlation used samples of 1761 (Wheelwright et al., 2006) and 278 (Baron-Cohen & Wheelwright, 2004) participants,

exceeding that of the current study (95), and of Carroll and Kin Yung (2006) whose non-significant finding was from a sample of 20.

Furthermore, in none of the analyses was there a differential effect of empathising/systemising asymmetry or autistic traits on the gaze cueing effect. However, it must be kept in mind that all participants were taken from the general population and would therefore not have abnormal deficits in empathising or excessive autistic traits. An individual's degree of asymmetry in empathising and systemising was relative to the rest of the sample, and not derived from an absolute diagnostic criterion. Baron-Cohen et al (2001) has proposed that an AQ score in excess of 32 is indicative of clinical levels of autistic traits. However no participant in this study exceeded this score. Abnormal deficits in empathising may therefore be required if an effect of individual differences on the differential cueing effect is apparent.

#### *The gaze cueing effect*

Overall there was a significant gaze cueing effect, with target detection times faster if the preceding gaze cue was averted in a direction congruent with the target than if averted in an incongruent direction. This agrees with previous research and confirms that the current stimuli and method were successful at eliciting such an effect. However, the interaction with SOA showed that the gaze cueing effect was significant only when the delay between gaze cue onset and target onset was short (300 ms) and not when it was long (800 ms). Previous studies have found the gaze cueing effect to be evident at both short and long SOAs, even though they may be the result of either automatic or voluntary processes, respectively. Furthermore, the significant effect observed with an SOA of 300 ms was only small (7.3 ms) which is in contrast to the larger effects found in other studies (typically 10 - 20 ms). This suggests that the current method may not have been optimal in eliciting a gaze cueing effect. Conversely, the smaller effects observed here may have

been due to the modulations observed in response to the experimental manipulations. These are discussed below.

Also, there was no main effect of SOA. Previous studies of gaze cueing have frequently found that RTs are significantly shorter at longer SOAs than shorter SOAs. This reflects a foreperiod effect whereby the onset of the gaze cue prepares the observer for the onset of the target. In the current experiment, the RT in the 800 ms SOA condition (mean = 331.9 ms, SD = 39.6 ms) was indeed less than that in the 300 ms SOA condition (mean = 336 ms, SD = 39.8 ms), but this was not significant ( $F(1, 89) = .498, p = .482, \eta_p^2 = .006$ ). As the foreperiod effect is such a robust finding in studies of spatial attention cueing, it is therefore unknown as to why the difference in RTs between the two SOA conditions was not significant, and is a weakness of the results.

#### *The effect of stimulus identity on the gaze cueing effect*

With an SOA of 300 ms, the gaze cueing effect of the low AQ group in response to the negative identity was significantly smaller than in response to the positive identity, and was marginally smaller than in response to the predictive identity. Furthermore, the gaze cueing effect elicited by the negative identity correlated significantly with AQ scores. The cueing effect in response to the predictive and positive identities did not correlate with AQ scores and were not significantly different from one another. Even though AQ scores were positively correlated with SQ-R scores and negatively correlated with EQ scores, there was no effect of identity on the gaze cueing effect for either of the empathising/systemising asymmetry groups, nor did the gaze cueing effects correlate with measures of empathising/systemising asymmetry. These differences suggest an effect of attributing the intentions of the individual in a previous social interaction (a learning phase) from social cues that denote prosocial or antisocial intentions (happy or angry expression). Furthermore, that this effect is affected by individual differences in autistic traits and asymmetries in empathising and systemising. Those with a better ability to 'pick up' the



meaning of social contingencies implicitly learned that one identity held a negative disposition towards them, and consequently showed a smaller gaze cueing effect. Those with more autistic traits did not pick up on such cues, and the cueing effect was the same as for the other identities.

However, it is not possible to determine from the difference between the positive and negative identities at 300 ms SOA in the low AQ group whether or not the positive identity elicited an enhancement of the gaze cueing effect or if the negative identity elicited an attenuation of the gaze cueing effect. The fact that the negative identity was marginally different to the predictive identity, and that the positive and predictive identities did not differ suggests that the effect of learning was due to a reduction of the gaze cueing effect for the negative identity. This is further supported by the finding that AQ scores only correlated with the gaze cueing effect for the negative identity. Nevertheless, if the gaze cueing effect for the negative identity was reduced in the low AQ group, then it was expected that the gaze cueing effect to the positive identity would be enhanced. This may be indicative of a biased sensitivity to detecting potential antisocial intentions in others rather than prosocial intentions. Memory recall for identities implied to be untrustworthy is better than for those implied to be trustworthy, both when such attributions are based on spatial predictability of gaze direction or from emotional expression (Bayliss & Tipper, 2006; Yamagishi et al., 2003). Therefore the effect obtained for the negative but not for the positive identity may reflect a greater tendency to avoid individuals who may incur a cost in social interactions than to promote engagement with those whose interactions may be beneficial.

With an SOA of 800 ms, the cueing effect elicited by the positive and negative identities did not differ in either of the AQ groups or empathising/systemising asymmetry groups, and did not correlate with any of the measures of autistic traits or empathising/systemising asymmetry. However, the gaze cueing effect for the predictive identity was marginally larger than for the negative identity for the high AQ group (although

this did not meet the significance threshold) and correlated with AQ score. In the systemising group the predictive identity elicited a cueing effect that was significantly greater than for the positive identity, and the size of the cueing effect for the predictive identity correlated with the magnitude of this asymmetry. Those with a greater ability to process systematic regularities were better able to detect the spatial congruency between the target location and the gaze direction of the predictive identity. This supports the notion that higher AQ individuals would learn the probabilistic patterns of a spatially predictive gaze cue. They therefore showed a greater cueing effect in response to the predictive identity. However, this contradicts the bias highlighted above, that the gaze cueing effect is more affected by negative rather than positive intentions. A comparison with a spatially counter-predictive identity would enable the investigation of whether such a bias also exists for spatial predictability.

As with the findings at 300 ms SOA, it is not possible to establish whether the effect observed for the systemising group at 800 ms SOA was due to an enhancement of gaze cueing for the predictive identity or a reduction of gaze cueing for the positive identity. Again though, as the gaze cueing effect for the predictive identity differed marginally from that of the negative identity and also correlated with the degree of empathising/systemising asymmetry, it suggests that those who are more sensitive to spatial regularities showed an enhancement of the gaze cueing effect in response to the spatially predictive identity. However, future studies would have to compare the gaze cueing effects to a baseline in order to establish if the observed effects were due to enhancement or reduction. This could be achieved by including a novel identity in the test phase with which to compare the gaze cueing effect to that of the other identities, or to use the three identities in a gaze cueing study prior to the learning phase and then compare this to the gaze cueing effects in response to the identities after the learning phase to establish the effects of learning.

A possible alternative explanation for the enhanced gaze cueing effect observed at 800 ms SOA in the systemising group for the predictive identity could be attributable to the

“unique pattern of attention function and dysfunction” (Allen & Courchesne, 2001, p105) that characterises the broader autistic phenotype. That is, those with autism possess a narrow attentional focus that manifests in several areas of attentional functioning. Of relevance to the current study, they exhibit an impaired ability to disengage attention and an enhanced selective attention ability (although this may be impaired under specific circumstances). It can only be assumed that as the systemising group exhibit a greater degree of autistic like traits that they also possess, albeit to a lesser degree, the same attentional strengths and weakness as those with autism. A narrow attentional focus would result in a slower ability to disengage attention from the face stimulus toward the target and also a better ability to ignore the gaze cue and detect the target. In invalid trials, a slower disengagement of attention would mean they had not oriented attention to the invalid spatial location by the time the target appeared on the opposite side of the screen. This would result in a faster target detection time than low systemisers whose attention would have been oriented by the gaze cue to the incorrect spatial location. Enhanced selective attention abilities would mean they were better able to ignore the gaze cue and detect the target when it appeared. This would also result in a decreased RT in invalid trials for the systemising group compared to the other groups whose attention would have been oriented in the direction of the gaze cue. However, there was no effect of group for RTs in invalid trials for the predictive identity at 800 ms SOA ( $F(2,89) = 2.15, p = .123, \eta_p^2 = .047$ ). In valid trials, an inability to disengage attention would have slowed the orienting of attention away from the face once the target appeared whilst the other groups would have had no such impairment. An enhanced selective attention ability would have enabled them to ignore the gaze cue (which they knew to be non-predictive) which would have impaired target detection times compared to the other groups who followed the gaze cue. In either case, the RTs for systemising group should be slower in valid trials than the other groups. Indeed there was a significant effect of group for RTs in the valid trials ( $F(2,89) = 4.87, p = .01, \eta_p^2 = .101$ ). However, this was due to the systemising group having a quicker RT than

the empathising group ( $t(58) = 3.79, p = .000, d = 1$ ) whereas the balanced group did not differ from either the empathising ( $t(59) = 1.59, p = .118, d = .4$ ) or systemising groups ( $t(57) = 1.27, p = .207, d = .4$ ). As the systemising group was quicker to detect the target than the empathising group on valid trials, this implies that the gaze cue of the predictive identity facilitated target detection in the systemising group, and that the greater cueing effect observed in this group was not due to a general inability to disengage attention from the face or enhanced selective attention abilities. This conclusion is further supported by correlating the size of the cueing effect elicited by the predictive identity at 800 ms SOA with scores on two subscales of the AQ designed to measure different facets of an individual's attentional focus. Spearman's rho correlations ( $n = 89$ ) revealed no significant relationship between the cueing effect in this condition and either the ability to switch attention ( $r = .114, p = .3$ ) or an individual's attention to detail ( $r = .045, p = .682$ ). Despite these non significant relationships, future studies of the effect of autistic like traits on gaze cueing should specify the nature of the relationship with the specific sub-scales of the AQ to ensure that any observed effect can be attributed to social deficits rather than differences in generalised attentional abilities.

The task in the learning phase did not necessitate explicit processing of such contingencies and the participants were unaware that they would encounter these identities again in the test phase. Therefore the participants had no motivation to learn the social or spatial contingencies, and indeed debriefing of participants afterwards revealed they had not noticed that each identity had an idiosyncratic pattern of gaze and expression behaviour. This suggests that these attributions were automatic and implicit. That is, participants were unaware of the effect that the motion of the social cues had on their inferences made to the agent. These involuntary attributions then became evident in the response to the gaze direction of the identity in the cueing paradigm. The experimental manipulations of gaze direction and identity were again incidental to completion of the

task. Nevertheless, the influence they had on response times suggests an automatic influence of identity on reflexive gaze cueing.

*Two different styles of gaze processing?*

The group differences in gaze cueing in response to the predictive identity agree with the results of Ristic et al (2005) who found that those with high functioning autism showed a gaze cueing effect if the gaze-target congruency was 80% predictive but not when non-predictive (50%) (although many other gaze cueing studies show intact gaze orienting in when gaze is non-predictive e.g. Chawarska et al., 2003; Kemner et al., 2006; Kylliainen & Hietanen, 2004; Senju et al., 2004; Swettenham et al., 2003; Vlamings et al., 2005). The current study shows that such sensitivity is carried over to future social interactions to influence cueing in response to a non-predictive cue, in much the same way that the gaze direction of familiar people can be remembered, and influences cueing, three minutes after initial exposure (Frischen & Tipper, 2006). The influence of either spatial predictability or social disposition supports the proposed distinction between those on different ends of the autistic spectrum in gaze processing style (Driver et al., 1999; Nation & Penny, 2008; Ristic et al., 2005). Those with higher autistic traits and systemising skills, and lower empathising skills, are thought to afford gaze with less social salience and process the gaze cue in a manner comparable to that of other non-social cues such as arrows. As such, they were more likely to alter their gaze following behaviour in light of the non-social manipulation (spatial predictability) rather than the social manipulation. Those with fewer autistic traits and better empathising skills comprehend gaze in social terms of the attentional state of the gazer. They therefore altered their gaze following behaviour in light of the social disposition of the gazer (the interaction between gaze and expression).

A novel contribution of this study is that the different influence of social or spatial manipulations was also evident in the different time courses at which the effects emerged. Effects of social manipulations were only apparent with an SOA of 300 ms, whilst the

effects of spatial manipulations were evident with an SOA of 800 ms. Previous studies have shown that cueing effects that emerge within around 600 ms are the result of rapid reflexive and automatic processes whereas those after 600 ms are largely voluntary. An effect of spatial predictability has not been previously found at SOAs less than 600 ms and the current results support this. This suggests that the automatic gaze cueing is not modulated by prior knowledge of the spatial predictability of the gaze cue. However, this makes the modulation observed at 300 ms by the social manipulations interesting, in that the automatic gaze cueing effect can be modulated by information regarding the gazer's intentions. Such information regarding the gazer's past interactions with oneself may therefore be afforded with greater importance and be incorporated into the reflexive reactions to the social behaviour of others. In contrast, the non-social information regarding the gazer's past interactions with the target only affect voluntary responses to their behaviour.

#### *The integration of identity information with gaze information*

The modulation of the gaze cueing effect in the test phase in response to stimulus identity necessitated integration of identity and gaze direction information. In the neurocognitive model proposed by Haxby and Hoffman (2000), dynamic properties of faces, such as gaze and expression, are processed separately from that of invariant facial features, such as identity. However, previous gaze cueing studies in both humans and monkeys attest to the integration of identity with gaze processing to modulate the gaze cueing effect in light of the familiarity or social status of the gazer (Deaner, Shepherd, & Platt, 2007; Frischen & Tipper, 2006). It makes sense for identity and gaze to be integrated somewhere down the line, as the meaning of gaze direction can be affected by the person whose gaze it is. This is supported by studies showing that STS activity (traditionally thought to process dynamic facial attributes) is sensitive to identity, and that the FFA (traditionally implicated in identity processing) is sensitive to gaze direction (George,

Driver, & Dolan, 2001). Therefore the separate role of the STS and FFA are relative rather than categorical, with both areas involved in processing gaze and identity, but with the former occurring more in the STS and the latter more in the FFA (Calder & Young, 2005).

### *Conclusion*

Gaze direction and emotional expression contribute to an observer's inferences as to the intentions of that individual and can be carried over into future social interactions. An observer subsequently adapts their response to the other person's social behaviour in light of these attributions, in this case the establishment of joint attention in response to their averted gaze. The social relationship between the gazer and observer as well as the spatial relationship between the gazer and the target contribute to the speed with which they will subsequently follow that individual's gaze direction. However, adapting one's response in light of the individual's gaze and expression is more likely in those who are more sensitive and better able to process social information (those with few autistic traits and systemising abilities but higher empathising abilities). Furthermore, such modulation takes effect in the rapid and reflexive response to other's behaviour. Conversely, those who are less sensitive to social information but more sensitive to systematic regularities and detecting lawful patterns (high AQ and systemising skills but low empathising skills), show a greater sensitivity to the spatial predictability of the individual's gaze direction, and this was evident in the later emerging response traditionally assumed to be more under voluntary control.

This highlights a difference in gaze processing style between those who process gaze in terms of the psychological state of the gazer, and those who process merely the visual properties of gaze in a manner comparable to that of non-social cues (e.g. arrows). The former is characteristic of those sensitive to social information, and as such their orienting response to gaze direction incorporated information regarding the social intentions of the identity. The latter is characteristic of those who afford gaze with less

social salience, but who are more sensitive to gaze as a probabilistic cue to target location, and whose orienting response to gaze direction was sensitive to the spatial predictability of the identity.



## Chapter 6. General Discussion

An implicit understanding of others' behaviour is possible simply from observing their actions. This understanding is facilitated by the processing and integration of social cues which convey the behavioural intentions and possibly the mental/emotional state of the actor. The aim of this thesis was to investigate the role of the integration of social cues with action perception in ascribing goals and intentions to the behaviour of others, and how it may contribute to an anticipation of how they will act in the immediate future.

Experiments 1 to 3 (Chapters 2 to 4) investigated how gaze cues influence action anticipation in the immediate future (motor empathy). Previous research has established that the end-point of an action is encoded during observation of the action itself and that, when using either priming or RM methods, this becomes evident as either a facilitated processing of postures that occur after the end of the action, or as a displacement in memory for the final position of the movement (Freyd & Miller, 1992; Graf et al., 2007; Jarraya et al., 2005; Thornton & Hayes, 2004; Verfaillie & Daems, 2002).

Experiment 1 (Chapter 2) sought to establish a social cue related anticipation of movement (for short SCRAM), whereby the anticipated end-point is modulated by the gaze direction of the actor during the action. Indeed, estimations of how far a head had rotated were affected by the gaze direction. The stopping point of a rotating head was underestimated when its gaze direction was lagging behind head rotation. Control conditions established that this was not due to the visual appearance of the location of the pupil within the sclera, nor to the role that gaze plays in specifying spatially directional information. It therefore required a higher level interpretation of gaze direction, leading to the inference of the behavioural intention (or mental state) of the actor. That is, a representation of the goals and intentions of the agent was assimilated into the representation of the action itself. Furthermore, this was an automatic process as processing of gaze direction was not necessary for performing the task. It must be noted

though that the control stimuli were comparable only in size and colouration but were not perceptually similar. Ideally, further experiments would include a control stimulus that was more akin to the biological stimulus to fully control for these variables.

Experiment 2 (Chapter 3) replicated this finding but introduced a further condition in which the stimulus was spatially inverted in order to disrupt the integration of the action and the gaze direction. As predicted, gaze direction had no effect on estimations of head rotation when the stimulus was inverted, confirming the necessity of a conjoint representation of social cues and action perception in the SCRAM effect. However, this conclusion is speculative as a differential effect of gaze direction between the orientation conditions was only evident in separate ANOVAs and not in an interaction analysis.

Experiment 3 (Chapter 4) demonstrated that the SCRAM effect is context dependant. Gaze was not used when the facial expression of the actor was of an approach motivation (happy or angry expression). However, it was when an avoidance motivation was expressed (disgust or fear expression). These results show that the use of gaze direction to determine the likely end-point of an action is strongest when other cues related to the goals of the agent are ambiguous.

Experiment 4 (Chapter 5) extended this principle by demonstrating that gaze can be integrated with expression to implicitly learn the social relevance of another's emotional expression. Moreover, it showed that such information is retained and employed in order to modify one's own responses to those individuals in an unrelated social interaction. However, this effect very much relied on the individual's ability to empathise and process social information. Those who showed few autistic traits and who were better able to empathise were less likely to engage in joint attention with an identity whose gaze and expression behaviour had previously conveyed an antisocial disposition to the observer. In contrast, those who showed more autistic traits and who were better able to systemise were more likely to engage in joint attention with an identity whose gaze behaviour had previously correctly predicted the location of a target.

*The nature of the SCRAM effect*

In principle, there are weak and strong versions of the hypothesis that the perception of head rotation is affected by social cues. The weak version states that, because gaze is likely to be articulated from head orientation when making a goal directed action, an effect of gaze direction on estimations of head rotation would be most evident when they are incongruently aligned. In support of this, a reliable and robust difference between the gaze-ahead and gaze-lagging conditions was found in all three experiments, as well as in several of the pilot studies. That is, estimations of how far the head had rotated were consistently greater when gaze was directed in advance of head rotation than when lagging behind head rotation. This supports the contention made by several authors that a static picture of an incongruently aligned head and gaze implies motion and conveys increased social saliency as a result (Conty et al., 2006; Hietanen, 1999; Vuilleumier et al., 2005). However, as yet, this proposal has never been explicitly tested. The current results provide initial encouraging evidence that incongruent head and gaze orientation conveys dynamic information from which an observer can infer motion cues.

However, even though a static posture of an incongruent gaze and head orientation may imply motion, it does not specify the future direction of motion. Participants may infer that the head will either rotate towards the target to align it with gaze direction, or that the gaze will be redirected to align it with head direction. In the current experiments, the immediate perceptual history was provided by the rotating head and so inferences as to the future direction of motion were unambiguous. This is relevant because whether participants under or overestimated the degree of head rotation would be suggestive of the how gaze was used to anticipate motion when incongruently aligned with head orientation. This can be considered the strong version of the hypothesis, whereby the gaze-ahead and lagging conditions differed not only from each other but also from the 50% mark indicative of a response bias, and from the gaze-congruent condition in which no additional goal-

oriented information was conveyed by gaze direction. However, this pattern of results was not consistent across the experiments. In experiment 1a (see also pilot 4 in the appendix), the gaze-lagging condition was found to be significantly different from the gaze-congruent condition and elicited a significant response bias, whereas this was not so for the gaze-ahead condition. This suggests that participants under-estimated the degree of head rotation in the gaze-lagging condition. Conversely, in experiment 3 (see also pilot 2 in the appendix) it was the gaze-ahead condition that elicited a significant response bias and which differed from the gaze-congruent condition, while the gaze-lagging condition did not differ from gaze-congruent. Despite these inconsistencies, the pattern of results consistently showed a trend for the gaze-ahead condition to be always above 50% and the gaze-lagging condition always below 50%, with the gaze-congruent condition always in between them. Furthermore, if one condition differed from the gaze-congruent condition then it differed from 50% as well. Nevertheless, the exact nature of the SCRAM effect cannot be confidently asserted: does the gaze-ahead condition lead to overestimation or does gaze-lagging lead to under estimation?

#### *Comparison with previous studies of RM*

The finding of a memory displacement for the final position of an action sequence compliments previous research into the anticipation of biological motion. However, in each of the current experiments the rotation of the head itself was insufficient to cause a displacement effect. When the face was neutrally expressive with a congruent gaze, and therefore conveying no (additional) intentional information other than that attributed to the biological motion itself, no response bias was observed (the mean percentage of 'after' responses did not differ from 50%). This may either be due to the fact that the methodology used was perhaps not sensitive enough to detect the displacement, or to the fact that the type of action used was not influenced by momentum in the same way that

the type of actions used in previous studies are (e.g. walking, see discussion of experiment 1). Further experiments are necessary to establish why the action itself was not subject to a memory displacement effect (see below). Despite several previous studies incorporating gaze direction into studies of action anticipation (Adams et al., 2006; Freyd & Miller, 1992; Jellema et al., 2009; Nummenmaa et al., 2009; Thornton & Hayes, 2004), the experiments reported here are the first to demonstrate that social cues mediate the remembered final position of a biological action sequence.

This dovetails nicely with the extensive body of literature describing similar memory displacements for non-biological motion. The need to infer causality, understand motions and generate predictions is not confined to the social domain. Anticipating the motion of non-biological objects is mediated by inferences of the physical dynamics causing and constraining the motion (momentum, gravity, friction). Just as in the SCRAM effect, cues of the dynamics underpinning the motion are assimilated with the observation of the motion itself. These representations are of a similarly high level as they involve concepts that cannot directly be observed, but are inferred from cues that are apparent during the movement.

These parallels beg the question of whether the two processes are underpinned by the same or different cognitive mechanism(s). Hubbard (2006) proposed that the displacement of non-biological motion is the result of a two factor process. Firstly, the kinematics and dynamics of the object's motion are represented as a functional analogue by means of a second order isomorphism (Shepard & Chipman, 1970). This produces a default displacement based, not upon objective physical principles, but on the observer's subjective interpretation of those principles. Secondly, this displacement can be modulated by the context in which the motion is embedded, such as the type of object and the presence of stimuli, which modulate the displacement. The displacement of biological motion as a function of social cues observed here concords with this model and could be the product of a similar isomorphism. The action itself is subject to a displacement

(although not observed in the current studies), but when contextualised in terms of goal-directedness by the gaze direction, this displacement is modulated.

However, the dynamics being inferred are fundamentally different. Non-biological objects are inherently inanimate and incapable of intentionality, whereas in the case of biological objects, which are animate and possess intentionality, motion is self-propelled and motivated by the goals and objectives of the actor. This dichotomy maps onto Baron-Cohen's (2006) distinction between empathising and systemising. Empathising is a process employed for the attribution of intentions to agents for understanding, predicting and reacting appropriately to the behaviour of others. In contrast, systemising assimilates the physical dynamics of movement to comprehend the behaviour of non-biological objects. However, it is not suggested if, how, or when these systems diverge (Currie & Ravenscroft, 1997; Gopnik, 2003; Leslie, 1994). In principle, the understanding and prediction of biological and non-biological motion could be underpinned by the same cognitive capacities. For example, the MT/MST network, which is implicated in processing motion, is also sensitive to extrapolating motion cues from static pictures of both non-biological objects (Senior et al., 2000) and biological objects (Kourtzi & Kanwisher, 2000; Lorteije et al., 2006; 2007).

However, other areas are involved in processing biological motion and social cue processing which are not sensitive to the movement of non-biological stimuli, suggesting that the two domains could exploit different dedicated cognitive substrates. The neural substrates for the anticipation of biological motion can be speculated about with more confidence than that for non-biological motion. A likely network of regions necessary for the kind of social computations performed in the current task is formed by the Superior Temporal Sulcus (STS), in conjunction with areas in the medial temporal lobe (amygdala) and the mirror neuron areas. The STS is sensitive to biological action sequences, and is able to extrapolate beyond what is immediately observable to encode actions based on the most likely end-point. This is evident in cell populations which continue firing when the

action becomes occluded from view (Baker et al., 2001; Saxe et al., 2004) and others that respond to static pictures of implied motion (Jellema & Perrett, 2003a). The STS is specifically implicated in representing the direction of attention of others, based on a range of bodily cues, such as gaze direction, head orientation with respect to trunk, and whole body orientation (Perrett et al., 1989). The cell responses to these cues tend to be governed by a hierarchical principle, such that gaze direction can overrule head orientation, which in turn can overrule bodily orientation, in determining other's direction of attention (Perrett, Hietanen, Oram, & Benson, 1992). Furthermore, STS cell populations show the ability to integrate action perception and gaze direction to selectively code the goal-directedness of specific actions (Jellema et al., 2000; Perrett et al., 1985), in keeping with its general role in comprehending the social meaning of other people's behaviour (Redcay, 2008). Through its connections with the emotional processing areas of the amygdala, which in turn also responds selectively to another's direction of gaze (Calder, 2007), observed actions are afforded an emotional salience that enhances their subjective relevance. This information could be used to predict the outcomes of actions and infer intentions by feeding it to neurons in the intraparietal lobule and area F5 of the premotor cortex that fire when performing goal-directed actions. These areas form the mirror neuron system, where observing an action activates areas involved with its execution (Rizzolatti & Craighero, 2004). This system has been proposed to enable an observer to embody and 'simulate' the actions of others, as if one were preparing to perform the action themselves, providing a conduit by which their goals and intentions can be accessed (Gallese, 2006).

Deducing whether the processes enabling anticipation of biological and non-biological motion are completely independent is not possible from the data reported here. The results of experiment 2 are suggestive of independence, as no effect of gaze direction was found when the stimuli were inverted. As inversion has been found to disproportionately impair the processing of social stimuli (such as faces and bodies, e.g. Diamond & Carey, 1986) more than non-social stimuli (such as houses and dot patterns,

e.g. Husk et al., 2007; Tanaka & Farah, 1991) it could be said that this manipulation revealed a mechanism involved exclusively in the perception of social stimuli. However, no non-biological stimulus was used in this study. Furthermore, no variation was observed for the upright non-biological stimulus in experiment 1. Presumably, inverting the non-biological stimulus would also elicit no variation and it would therefore not be possible to conclude that inversion affects only the biological stimulus.

The dissociation between empathising and systemising in social cue processing was further elucidated in experiment 4. Those individuals who are better at empathising were more prone to infer the emotional disposition or intentions of an agent by learning the associations between gaze direction and emotional expression and the meaning it conveys than those who were less empathetic. This is not to say that those who are less sensitive to social information were not capable of learning gaze direction contingencies. They were more likely to base their inference on the statistical reliability with which gaze was congruent with target location, in keeping with their greater sensitivity to systematic regularities. This suggests that both cognitive systems can be deployed for the processing of social cues, but that they lead to different interpretations of the agents goals and intentions, and thus differing anticipations of their behaviour. That is, empathising enables a psychological interpretation of social cues and actions in terms of their social meaning, and provides access to the mental state of the agents. Systemising, on the other hand, leads to a mechanistic representation of social behaviour caused by a more literal description of immediately observable visual information.

#### *The role of social cue processing in Theory of Mind*

Representing the mental/emotional states of others is the hallmark of ToM, and includes the comprehension of the other person's beliefs and knowledge, and to understand that they may differ from one's own and from reality (second order



intentionality). The ability to predict behaviour and respond appropriately based on this information is arguably one of the most significant social functions that it enables. ToM relies in part on the accurate processing and interpretation of social cues, therefore integrating them with action perception may contribute to full scale ToM. That said, there is every possibility that the use of social cues in order to predict behaviour is evident before the age at which full scale ToM develops. Infants are sensitive to social cues and biological motion soon after birth (Farroni et al., 2002; Simion et al., 2008). Moreover, children are able to generate expectancies regarding the reaching behaviour of others based on gaze and expression by the second year of life (Phillips et al., 2002), well before the emergence of a fully formed ToM (approximately 4 years). Tomasello and Rokoczy (2003) propose that the ability to interpret others' behaviour in terms of more basic, but no less psychological, concepts such as goal-directedness, desire and emotions emerges early in life. Furthermore, that this is the foundation upon which more sophisticated social cognition is built. The tasks described in the current experiments may therefore represent the functioning of more rudimentary socio-cognitive abilities.

A similar stance can be taken on the evolution of ToM. ToM is considered to be an adaptive cognitive mechanism that permits the processing of vast amounts of dynamic social information (Dunbar, 1992, 1995, 1998). This is necessary in order for us to inhabit the complex social networks that characterize human sociality, for which there have been strong selection pressures (Brune & Brune-Cohrs, 2006). However, many other primate species live in groups as a response to the same selection pressures, and have evolved sophisticated social skills as a result. Their societies differ from those of humans, though, in that they are less spatially and temporally distributed, and the regularity with which individual group members are encountered is more frequent. Social information does not therefore need integrating over space and time and is processed in a more expedient manner (Barrett, Henzi, & Dunbar, 2003). Again, this is based on perceptual information that is immediately available, including social cues and action perception. Moreover, there

is evidence that some primate species use gaze direction to predict which object a conspecific is most likely to interact with (Call & Tomasello, 1998; Santos & Hauser, 1999; Scerif et al., 2004) in the same way that human children do. It would therefore be expected that non-human primates would also be able to integrate social cues and action perception in order to perform the tasks described in these experiments. However, whether this would indicate that they have a concept of even the most basic psychological states of others remains open to debate. Call (2001) argues that they are capable of representing schemas of intention and deducing the goals and intentions underpinning the behaviour of others (1.5 level intentionality). However, many researchers are critical of assuming that identical behaviours across species are affirmative of identical cognitive processes causing them (Barrett, Henzi, & Rendall, 2007; Heyes, 1998; Povinelli, Bering, & Giambrone, 2000). They point to low level processes of learned associations between behavioural and contextual cues and contingencies that explain the social behaviour of non-human primates equally well. In the current experiments, forming an association between observable social cues and the trajectory of an action would enable a probabilistic judgment of how an action is most likely to continue without invoking a representation of goals and intentions. It therefore remains contestable as to whether or not similar behaviours in non-human primates can be attributed to comparable social processes. Nevertheless, despite these divergent views, there is a consensus that such abilities represent a homologous ability that serves as a crucial evolutionary precursor to the evolution of ToM in humans.

#### *Future research*

The results reported here are promising, yet there are several unanswered questions, which should propagate future research. As noted previously, there are individual differences in the general population in the ability to process social information

and in the ability to empathise. The effect of gaze direction on action anticipation should therefore correlate with an individual's propensity to empathise with others. If such a relationship were found, this would add weight to the contention that the SCRAM effect is due to social inferences. What's more, this ability to empathise is proposed to show an inverse relationship with the ability to systemise. Those whose cognitive style is asymmetric in favour of systemising are expected to show an enhanced ability to anticipate the motion of non-biological objects based on physical dynamics. Thus, future research could exploit this double dissociation to see if displacement of biological and non-biological motion is correlated with placement on the systemising-empathising spectrum. This is most likely to be evident in those occupying positions higher up on the autistic spectrum, who are characterised by an extreme cognitive bias in favour of systemising.

Unlike previous research, the current experiments did not find a memory displacement for the action itself, irrespective of the direction of gaze. This may be because the amount of displacement may have been too small for the current method to have detected. A more sensitive measure may pick up on such displacement. An alternative test stimulus could be to present single test heads that differ from the final position in  $1^\circ$  increments, and ask participants whether it is at the same or a different angle as the stopping point. This would pick up smaller amounts of memory displacement. Moreover, the amount of memory displacement in the gaze-congruent condition could then be compared to the memory displacement when gaze is incongruent with head orientation. Measuring the difference in estimation errors between the gaze-congruent and gaze lagging/ahead condition would provide an estimate of the extent to which gaze direction contributes to the memory displacement and thus to action anticipation. The role of gaze direction could further be elucidated by varying the degree to which gaze direction is averted from head orientation and measuring the extent of the memory shift. That is, does the memory displacement increase monotonically with increases in gaze aversion, or is it affected merely by a categorical description of gaze direction (e.g. left or right)?

The inference of motion is possible from just static structural information regarding the relative positions of body parts (implied motion). There is evidence that this also applies to the articulation of gaze and head orientation (see above). It is therefore plausible that the effect of gaze direction on estimations of head rotation would be possible from implied motion. After observing a static image of a head with an incongruent gaze direction, subsequent estimations of the head angle should show a comparable influence of gaze direction as reported in the current experiments. This would also be compatible with what is known about the neural substrates of action perception in being sensitive to the degree of articulation depicted in static body postures.

It would also seem pertinent to measure the gaze behaviour of the participant as well. Kerzel (2005, 2006) has proposed that memory displacements for objects translating across a screen are the result of ocular-motor overshoot. The observer tracks the moving object with their gaze (smooth pursuit) but such eye movements continue after the object has disappeared, causing the final position of the object to be misremembered. No such smooth pursuit is necessary for the head rotation used in the current study. In fact, this may have caused the lack of displacement for gaze-congruent condition, although previous research has established a RM effect for objects rotating in depth (Munger & Minchew, 2002; Munger, Solberg, Horrocks et al., 1999). Nevertheless, gaze aversion does cause an automatic shift of attention in a congruent direction (Driver et al., 1999). Therefore, the observed displacements caused by gaze direction may result from participants orienting their attention in the same direction. For example, in the gaze-ahead condition, the observer's attention may similarly have been averted ahead of head rotation, causing the final angle to be distorted in a congruent direction. This does not refute the notion that the observed effects are due to action anticipation, but reveals a mechanism which may contribute to it. Furthermore, monitoring of participant eye movements would confirm the role that gaze direction plays when the expression is either ambiguous or unambiguous (Chapter 4). That is, as gaze direction is afforded a greater degree of

relevance when the expression is of avoidance, it would be expected that participants would monitor the eye region more closely than when the expression was of approach. For these reasons, it would be advantageous to monitor the gaze behaviour of the participant during the task.

The observed effect rests on the ability to integrate gaze and action in order to infer the goal of the agent and anticipate their actions. However, the attributions made to the rotating stimulus must be carried over to the test stimulus in order for an effect to be evident. The use of a congruent gaze in the test stimulus may therefore have impaired the full extent of the effect. If the observer infers the agent's goal from the gaze direction during presentation of the rotating stimulus, then observing them with a congruent gaze in the test stimulus may create the impression that the agent no longer has that goal, and may have reduced the magnitude of the memory displacement caused by gaze direction. Averting the gaze of the test stimulus so that it is congruent with that of the rotating stimulus may therefore potentiate the effect. But, as note before, it may also itself cause an RM effect due to the implied motion.

A related point would be the effect of changing the stimulus identity between the rotating stimulus and the test stimulus. If the inferences made were truly psychological in nature, then they would also be identity specific. That is, the attributions made regarding the goals of the rotating stimulus would not be transferable to the test stimulus if its identity was different. On the other hand, the observation of a SCRAM effect across different identities would suggest that maybe it is due to less sophisticated processes that do not encompass the full social context in which they are presented.

### *Conclusion*

Social stimuli occupy a prominent position in everyday life and this is reflected in the sophisticated cognitive mechanisms that are employed in processing such information.

Moreover, successful navigation of the social world relies on predicting other people's behaviour. The ability to go beyond what is immediately observable in order to infer the future behaviour of others is therefore a burgeoning field of research. The studies reported here make a valuable contribution to this rapidly developing field by showing a robust and reliable effect in which the information conveyed by gaze and expression is assimilated into the representation of the action itself, and contributes to the observer's inferences as to how the action is most likely to continue. In this way, predicting how others will behave encompasses not only an analysis of the kinematics of their actions but also the intentional dynamics that underpin the movement.

## **Appendix: Pilot studies**

Four pilot studies were conducted which aimed to establish the presence of an effect of gaze direction on estimations of how far a head had rotated, whilst also evaluating the efficacy of different stimuli and methods that would best elicit a displacement effect.

### *Pilot study 1*

#### *Method*

##### *Participants*

Participants (N = 12) were all students at the University of Hull, UK, and participated in exchange for course credit. All had normal or corrected to normal vision, and gave written informed consent prior to taking part.

##### *Apparatus*

All stimuli were presented on a 21 inch monitor (100 Hz refresh rate) using E-Prime software (Psychology Software Tools, Inc) from which participants sat approximately 50 cm away.

##### *Stimuli*

The stimuli were created from the Human ID Effort at the University of South Florida (2002), a database of 3D face images obtained from laser-scanned models (access courtesy of Dr. Hong Liu, University of Hull). One identity was selected and its gaze direction was manipulated using Corel graphics suite.

##### *Rotating stimulus*

The rotating stimulus consisted of a head that rotated 60° along the vertical axis from a profile view (90° from full front view) to a semi-profile view (30° from full front view).

Motion was induced by presenting 16 static frames at  $4^\circ$  interpolations for 40 ms each (total duration 640 ms,  $93.75^\circ$  per second). This was fast enough to induce an impression of smooth continuous motion. The gaze direction of the rotating head varied horizontally along three levels: (1) In advance of head rotation in the direction of motion (gaze-ahead); (2) looking straight ahead throughout the rotation (gaze-congruent); (3) lagging behind head rotation in the opposite direction of motion (gaze-lagging). The subtended angle of the stimulus's height was  $16^\circ$ , and its width varied between  $10.1^\circ$  at the start of the rotation to  $11.1^\circ$  at the end. The head rotated from the left profile in all trials (Figure 7.1).

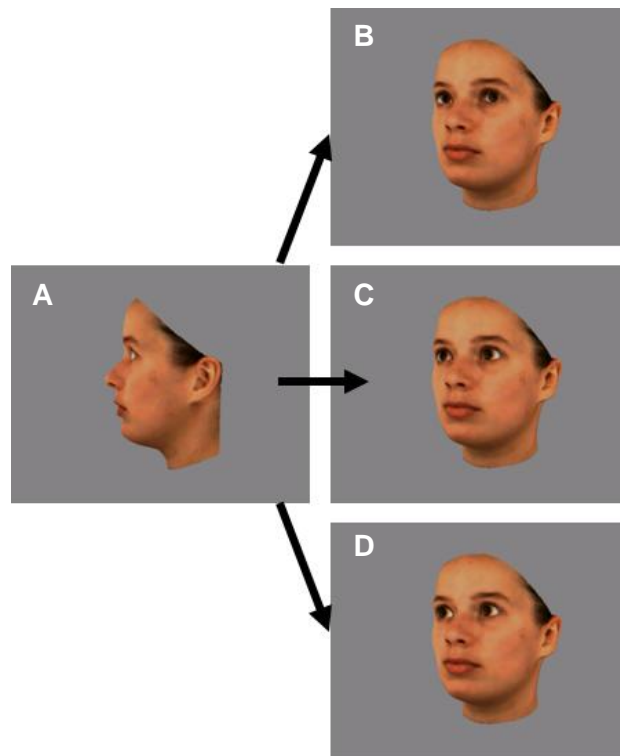


Figure 7.1. The rotating stimulus. The head rotated from a profile view (A) to a  $30^\circ$  orientation from full front view. The gaze direction was either in advance of head orientation (B: gaze-ahead), looking straight ahead (C: gaze-congruent), or lagging behind head rotation (D: gaze-lagging).



*Test stimulus*

The test stimulus consisted of a static image of the head, the angle of which varied along three levels in relation to the stopping point of the rotating stimulus: (1)  $20^\circ$  before it; (2)  $0^\circ$  identical to it; (3)  $20^\circ$  after it (Figure 7.2). Participants were required to judge whether the stopping point of the rotating stimulus was before or after the test stimulus. In levels 1 and 3 of the test stimulus condition, the correct answer was 'before' and 'after' respectively. These trials served as catch trials, with poor performance assumed to indicate insufficient attention to the task demands and were used as a participant selection criterion. In level 2, there was no correct answer as the test stimulus and the stopping point of the rotating stimulus were the same. It was hypothesised that memory displacement would be revealed by a consistent response bias, with a predominance of 'after' responses indicative of overestimation, and a predominance of 'before' responses indicative of underestimation. These were designated as experimental trials. Where responses were, on average, evenly distributed between 'before' and 'after', this was assumed to be an accurate estimation of head rotation. The test stimulus was either presented in the right or left half of the screen, with the inner edge at a subtended angle of  $3.5^\circ$  from the centre of the screen. This, along with the retention interval, served to disrupt any visual persistence of the rotating stimulus from facilitating similarity judgments with the test stimulus.

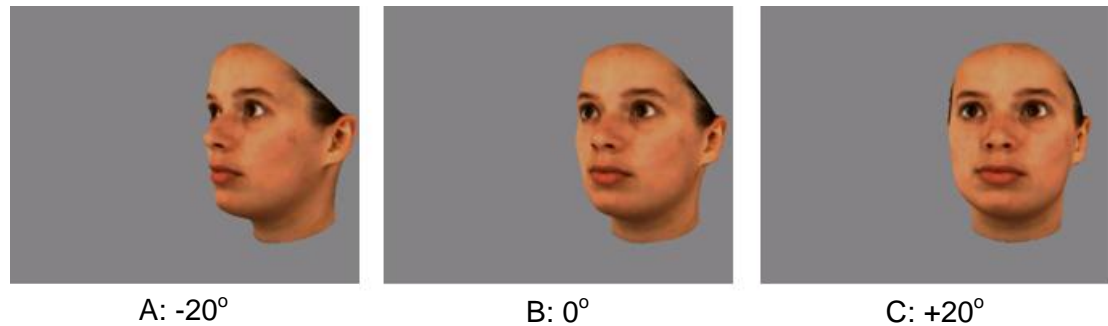


Figure 7.2. Examples of the test stimuli used in pilot 1. The orientation of the test stimulus was positioned along the motion trajectory of the rotating stimulus either (A)  $20^\circ$  before it ( $50^\circ$  from full front view), (B) at the same angle as the stopping point ( $30^\circ$  from full front view), or (C)  $20^\circ$  after the stopping point ( $10^\circ$  from full front view). Positions were presented at the left (shown) and right of the screen.

### *Procedure*

Participants were instructed they would see a face rotate along the vertical axis towards them, and that this would be followed by a static picture of the same face. Their task was to indicate if the stopping point of the rotating stimulus was oriented at an angle before or after the static face. No reference was made to the gaze direction of the stimulus. It was stressed that reaction times were not important, but that answers should be made within 3 seconds. Participants completed several practice trials representative of the range of experimental manipulations before commencing the experiment.

Each trial (Figure 7.3) began with a fixation cross at the centre of the screen (1500 ms). This was followed by the rotating stimulus after which a blank screen was presented for 1000 ms (retention interval), and then the test stimulus, which remained on screen until a response was made. Responses were made by pressing one of two keys on the keyboard ('z' = before, 'm' = after, labeled accordingly). The experiment was a 3 X 3 factorial design with Gaze direction and Test stimulus as the main factors. Each iteration

was repeated 10 times, leading to a total of 90 trials taking approximately 8 minutes to complete.

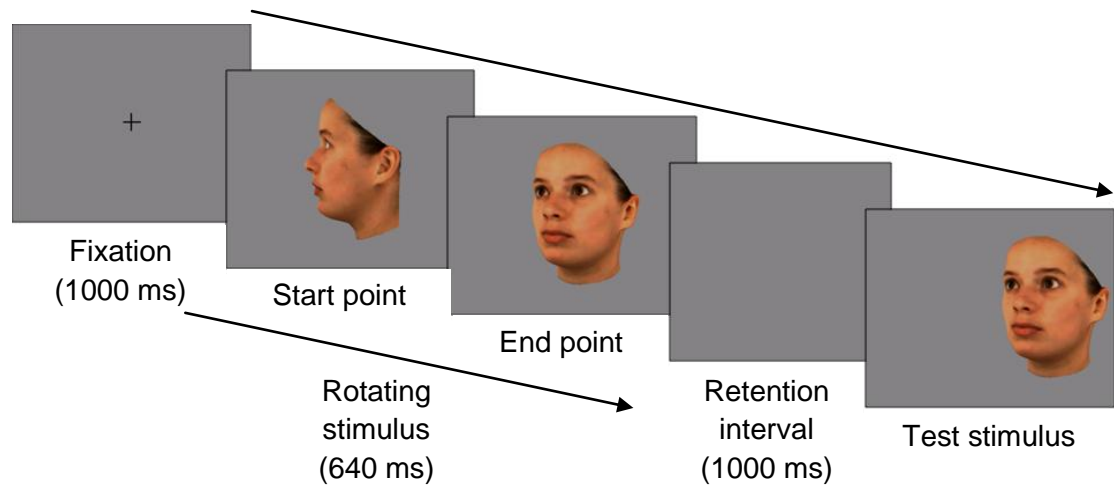


Figure 7.3. Trial sequence for pilot study 1. A fixation of 1500 ms was followed by the rotating stimulus (640 ms). After a retention interval of 1000 ms, the test stimulus was presented which remained on screen until a response was made.

### Results

The mean error rate was 10.0% (SD = 10.5%). The mean reaction time was 1607 ms (SD = 404 ms). Participants were excluded from the analysis if their mean error rate exceeded 20%. This led to the removal of one participant (error rate of 36.7%). The subsequent mean error rate was 7.6% (SD = 6.6%). Trials were excluded based on reaction time. Responses made less than 250 ms or in excess of 2SD above each participants mean reaction time were excluded from the analysis resulting in a new mean reaction time of 1491 ms (SD = 372 ms).

	Ahead	Congruent	Lagging
<b>-20°</b>	95.1 (7.6)	92.7 (12.7)	90.3 (9.1)
<b>0°</b>	59.4 (18.1)	51.6 (17.8)	44.8 (20.2)
<b>+20°</b>	6.9 (10.7)	4.7 (7.4)	9.5 (12.8)

Table 7.1. Mean percentage of 'after' responses (SD) for each gaze direction for each level of test stimulus.

Responses were coded as either 1 for 'after' or 0 for 'before', which were averaged and expressed as the mean percentage of 'after' responses. These were entered into a two-way repeated measures ANOVA with Gaze direction and Test stimulus as the main factors. As expected there was a significant main effect of Test stimulus ( $F(2, 20) = 171.59, p < .001, \eta_p^2 = .95$ ). However, there was no main effect of Gaze direction ( $F(2, 20) = 2.69, p = .092, \eta_p^2 = .21$ ) nor was there an interaction between Gaze direction and Test stimulus ( $F(4, 40) = 2.5, p = .058, \eta_p^2 = .2$ ). One sample t-tests conducted on the experimental trials showed that neither the gaze-ahead ( $t(10) = 1.73, p = .11$ ), gaze-congruent ( $t(10) = .31, p = .77$ ), nor the gaze-lagging ( $t(10) = .85, p = .42$ ) differed from the test value of 50 indicative of no response bias. No response bias was evident when the gaze direction conditions were collapsed ( $t(10) = .489, p = .635$ ).

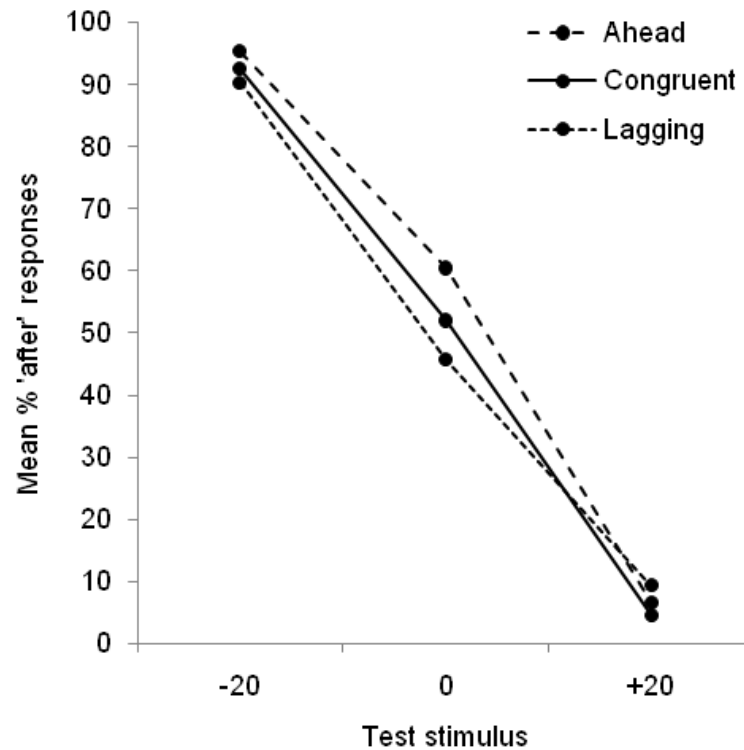


Figure 7.4. Mean Percentage of 'after' responses for each gaze direction across each test stimulus level.

### Discussion

The results showed no significant difference in estimations of head rotation between the gaze directions. Participants were no more likely to judge the stopping point of the rotating head as before or after a head at an identical angle if its gaze direction was either in advance of head rotation or in the opposite direction. Furthermore, the non-significant difference of each gaze direction from 50% suggested there were no biases to over or underestimate the degree of rotation. That is, the frequency that participants judged the stopping point to be before or after the test stimulus was on average equal. This lack of response bias remained when the gaze direction conditions were collapsed, suggesting that the motion of the head was not subject to a RM effect.

However, the means for the respective gaze directions were in the predicted direction (gaze-ahead > gaze-congruent > gaze-lagging). In addition, the ANOVA elicited  $p$  values that were close to significance and moderate effect sizes for both the overall effect of Gaze direction and the interaction with Test stimulus. A second pilot study was therefore conducted with a different test stimulus.

### *Pilot Study 2*

#### *Method*

##### *Participants*

Participants' (N = 21) details are the same as for pilot study 1.

##### *Apparatus*

Hardware and software for the creation and display of stimuli were the same as for pilot study 1.

##### *Stimuli*

The rotating stimuli were the same as in pilot study 1.

##### *Test stimulus*

The test stimulus in pilot study 2 was modified from a single stimulus to a two-alternative forced-choice paradigm consisting of two static heads side by side. Each test choice was at a different angle of orientation. Participants were required to choose which was at an angle most similar to the final angle of the rotating stimulus. One of the choices was oriented before (-) the stopping point (at an angle contained within the previously observed motion trajectory) and the remaining choice was after (+) the stopping point (oriented at an angle extrapolated along the path of motion beyond the stopping point).

The difference in angular orientation between each test choice and the stopping point was equivalent in all trials. However, between trials the difference was varied along four levels (Figure 7.5): (1)  $20^\circ$ ; (2)  $15^\circ$ ; (3)  $10^\circ$ ; (4)  $5^\circ$ . As such, there was no correct answer, as the orientation of neither the 'before' or 'after' choice was more similar to that of the stopping point of the rotating stimulus. It was expected that the absence of a correct answer would elicit a response bias that would reveal a memory displacement, and that the effect would be greater as the ambiguity of the answer increased (that is, there would be a more equal distribution of 'before' and 'after' choices where the difference between the choices was at its greatest, and a more biased distribution where the differences between the test choices was closest). A bias to selecting the 'after' choice as more similar than the 'before' choice would be indicative of overestimation, and was hypothesised to occur when gaze direction was in advance of head orientation. A reversed bias would be indicative of underestimation and was expected when gaze was looking in the opposite direction. The absence of a response bias would be indicative of an accurate estimation of head rotation.

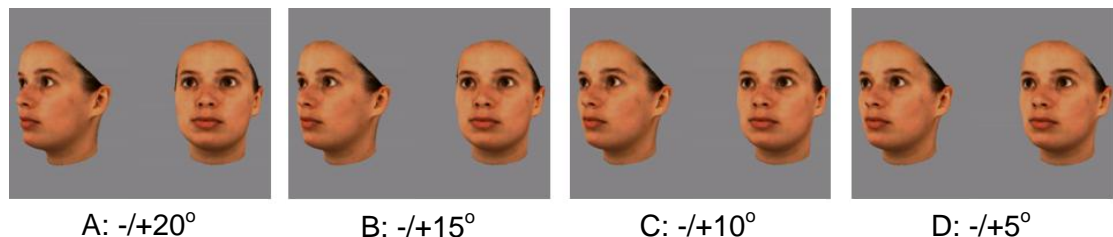


Figure 7.5. Examples of test stimuli in pilot study 2. The deviation of each test choice from the stopping point of the rotating stimulus varied along four levels, from (A)  $20^\circ$ , to (B)  $15^\circ$ , (C)  $10^\circ$  and (D)  $5^\circ$ .

### *Procedure*

Participants were instructed that their task was to indicate which of the two static faces was at an angle most similar to the final angle of the rotating face. The trial procedure was the same as for pilot study 1. There were 120 trials in total with each level

of gaze direction and test stimulus (3 X 4) presented 10 times. The left/right screen positions of the test stimulus choices were counterbalanced across trials. Participants chose either the head on the left or right of the screen as being at an angle more similar to the end-point of the rotating stimulus ('1' = left, '0' = right, labelled accordingly). The experiment lasted approximately 10 min. All other procedural information is the same as for pilot study 1.

### Results

The mean reaction time was 1437 ms (SD = 522 ms). Trial exclusions based on reaction time used the same criterion as pilot study 1 and resulted in 4.37% of trials being excluded, resulting in a mean reaction time of 1339 ms (SD = 523 ms). Responses were coded and analysed in the same way as for pilot study 1.

	Ahead	Congruent	Lagging
<b>-/+20°</b>	65.3 (26.0)	46.5 (31.0)	47.1 (30.2)
<b>-/+15°</b>	64.0 (16.2)	46.6 (24.6)	46.0 (30.7)
<b>-/+10°</b>	64.8 (19.2)	55.4 (24.8)	47.6 (27.0)
<b>-/+5°</b>	54.6 (25.3)	49.0 (26.1)	39.6 (26.6)

Table 7.2. Mean percentage of 'after' responses (SD) for each gaze direction for each level of test stimulus.

A two-way repeated measures ANOVA with Gaze direction and Test stimulus entered as the main factors (Table 7.2, Figure 7.6) revealed no main effect of Test stimulus ( $F(3, 60) = 2.53, p = .066, \eta_p^2 = .11$ ). The magnitude of difference between the test choices and the stopping point of the rotating stimulus had no effect on judgments as to which of the choices was more similar. However, there was a significant effect of Gaze direction ( $F(2, 40) = 10.2, p < .001, \eta_p^2 = .34$ ). Paired sample *t*-tests between the three



gaze conditions (Bonferroni  $p = .017$ ) showed that the mean percentage of 'after' responses was significantly greater in the gaze-ahead condition than in either the gaze-congruent ( $t(20) = 2.98, p = .007$ ) or gaze-slower conditions ( $t(20) = 3.55, p = .002$ ), which did not differ from each other ( $t(20) = 1.75, p = .096$ ). One sample t-test with a test value of 50 show only the gaze-ahead condition to differ significantly from 50% ( $t(20) = 3.03, p = .007$ ) with no response bias evident for the gaze-congruent ( $t(20) = .117, p = .91$ ) and gaze-lagging conditions ( $t(20) = .826, p = .419$ ). However, the effect of Gaze direction was not affected by the difference between the test choices and the stopping point, as there was no interaction between Gaze direction and Test stimulus ( $F(6, 120) = 1.4, p = .22, \eta_p^2 = .065$ ).

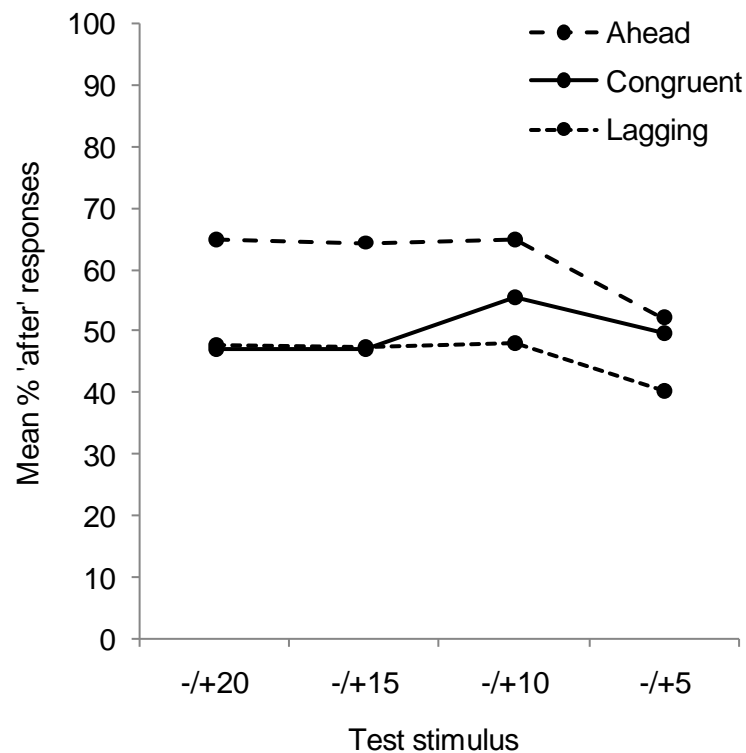


Figure 7.6. Mean Percentage of 'after' responses for each gaze direction across each test stimulus level.

## *Discussion*

The results show that memory displacement of an action sequence was modulated by gaze direction. Judgments as to how far a head had rotated were overestimated when gaze was looking in advance of head rotation, compared to when looking straight ahead or in the opposite direction, and to the 50% criterion of no response bias. This is consistent with the hypothesis that anticipating the future movements of an agent is enhanced when gaze direction conveys the goal of the action. Furthermore, this result proved robust across all of the test stimulus levels. At first sight, it may appear that the amount of memory displacement elicited when gaze was directed in advance of head rotation encompasses the full range of test stimulus deviations (i.e. up to 20°). However, this seems implausible and cannot be verified with the current methodology. A memory displacement of just 1° would make the 'after' test choice appear more similar to the stopping point than the before choice, irrespective of the distance between the choices. For example, if participants overestimated the degree of rotation by just 1°, then technically the test choice that was 20° after the stopping angle would be perceived as more similar than the test choice that was 20° before the stopping angle, and would lead to a greater proportion of 'after' responses. However, it could not be concluded that the participant overestimated the degree of rotation by the full 20°. The test stimulus was therefore further modified in a third pilot study to include conditions where the deviation of the test choices from the stopping point was asymmetrical. That is, one of the test choices was closer to the stopping point than the other. Errors in the presence of a correct answer would suggest the extent of memory displacement, such that selecting the farthest choice would imply that the amount of memory displacement is within the range between the stopping point and the test choice. Furthermore, error rates provide a criterion by which to assess participant reliability in task performance. This criterion was absent from pilot study 2 and was a shortfall of the design. The inclusion of test stimuli with asymmetric deviations from the stopping point of the rotating stimulus reintroduced a means of participant selection, as

well as enabling an estimation of the extent of memory displacement elicited by variation in gaze direction.

### *Pilot Study 3*

#### *Method*

##### *Participants*

Participant's (N = 9) details are the same as for pilot studies 1 and 2.

##### *Apparatus*

Hardware and software for the creation and display of stimuli were the same as for pilot studies 1 and 2.

##### *Stimuli*

The stimulus source and the rotating stimuli were the same as for pilot studies 1 and 2.

##### *Test stimulus*

The test stimulus retained the two-forced choice design of pilot study 2. However, they were positioned closer together on screen, such that the inner edges lay at the centre of the screen and the outer edges subtended at an angular width of  $11.5^\circ$ . As the test choices were now in the same field of view, the need to make saccades between the two test choices was removed. This was expected to reduce the amount of memory degradation for the stopping point by decreasing the amount of time between offset of the rotating stimulus and a response being made. One of the test choices was oriented at  $10^\circ$  either before or after the stopping point of the rotating stimulus, with the remaining choice oriented  $10^\circ$ ,  $20^\circ$  or  $30^\circ$  in the opposite direction. This yielded five levels of test stimulus:

(1)  $-30^{\circ}/+10^{\circ}$ ; (2)  $-20^{\circ}/+10^{\circ}$ ; (3)  $-10^{\circ}/+10^{\circ}$ ; (4)  $-10^{\circ}/+20^{\circ}$ ; (5)  $-10^{\circ}/+30^{\circ}$  (Figure 7.7). Again, participants were required to choose which test choice was at an angle most similar to the final angle of the rotating stimulus by pressing one of two keys on the keyboard ('1' = left, '0' = right, labelled accordingly). As in pilot studies 1 and 2, it was expected that an effect of memory displacement would be most evident where each test choice was equivalently similar to the stopping point, and there was no correct answer ( $-10^{\circ}/+10^{\circ}$ ). As such, these were termed the symmetrical experimental trials. In the remaining trials, there was a correct answer. In those levels where the test choices were at their most asymmetrical ( $-30^{\circ}/+10^{\circ}$ ,  $-10^{\circ}/+30^{\circ}$ ), it was assumed the correct answer was sufficiently unambiguous to elicit very few errors. Therefore, these trials were used as catch trials with which to assess participant performance. In the remaining trials where the correct answer was less ambiguous, it was expected that more errors would be made. These were called asymmetrical experimental trials. The pattern of errors may reveal biases caused by the gaze direction of the rotating stimulus, such that the gaze-lagging condition may elicit errors where the 'after' test choice is correct ( $-20^{\circ}/+10^{\circ}$ ) and the gaze-ahead condition may elicit errors where the 'before' answer is correct ( $-10^{\circ}/+20^{\circ}$ ).

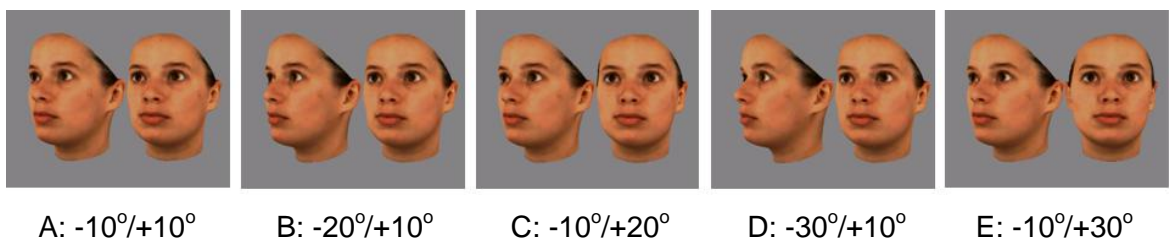


Figure 7.7. Examples of test stimuli in Pilot 3. A: Symmetrical experimental trials where neither answer was more similar to the end-point of the rotating stimulus. B & C: Asymmetric experimental trials where the 'after' (B) and 'before' (C) test choices were more similar. D & E: Catch trials where the 'after' (D) and 'before' (E) test choices were more similar.

### *Procedure*

There were 108 trials in total, 36 trials for the symmetrical experimental condition, 36 trials for asymmetrical experimental condition, and 36 trials for the catch condition, with the three gaze direction levels being represented by 12 trials each. The position of the test choices were counterbalanced across the trials. For the asymmetrical experimental trials and catch trials, the number of trials was distributed evenly between those where the ‘after’ test choice was correct and those where the ‘before’ test choice was correct. Participant instructions and trial procedure were the same as for pilot study 2. The experiment lasted approximately 9 minutes.

### *Results*

The mean error rate was 8.6% (SD = 8.5%). No participants were removed due to poor performance (mean error rate of >20%). The mean reaction time was 1217 ms (SD = 270 ms). Responses made less than 250ms or in excess of 2SD above each participants mean reaction times were removed resulting in 4.1% of trials being excluded, and a subsequent mean reaction time of 1162 ms (SD = 245 ms). The data were coded and analysed as in pilot studies 1 and 2.

	<b>Ahead</b>	<b>Congruent</b>	<b>Lagging</b>
<b>-30°/+10°</b>	92.6 (12.1)	94.1 (12.2)	90.7 (12.1)
<b>-20°/+10°</b>	78.5 (22.2)	79.6 (21.7)	74.4 (21.5)
<b>-10°/+10°</b>	56.4 (21.0)	49.2 (22.3)	54.0 (21.0)
<b>-10°/+20°</b>	27.8 (16.5)	23.3 (19.1)	19.3 (17.5)
<b>-10°/+30°</b>	11.9 (13.4)	5.6 (8.3)	10.4 (14.1)

Table 7.3. Mean percentage of ‘after’ responses for each gaze direction across each level of test stimulus.

A two way repeated measures ANOVA with Gaze direction and Test stimulus entered as the main factors showed the expected main effect of Test stimulus ( $F(4, 32) = 82.67, p < .001, \eta_p^2 = .91$ ), but no main effect of Gaze direction ( $F(2, 16) = .63, p = .55, \eta_p^2 = .07$ ), nor an interaction between Gaze direction and Test stimulus ( $F(8, 64) = .38, p = .93, \eta_p^2 = .05$ ). One sample t-tests with a test value of 50 revealed there to be no response biases in the symmetrical experimental trials that would indicate a memory displacement in either the gaze-ahead ( $t(8) = .91, p = .39$ ), gaze-congruent ( $t(8) = .113, p = .91$ ) or gaze-lagging conditions ( $t(8) = .57, p = .58$ ). These levels were collapsed to investigate the presence of an overall displacement effect, but this too was not significant ( $t(8) = .51, p = .63$ ).

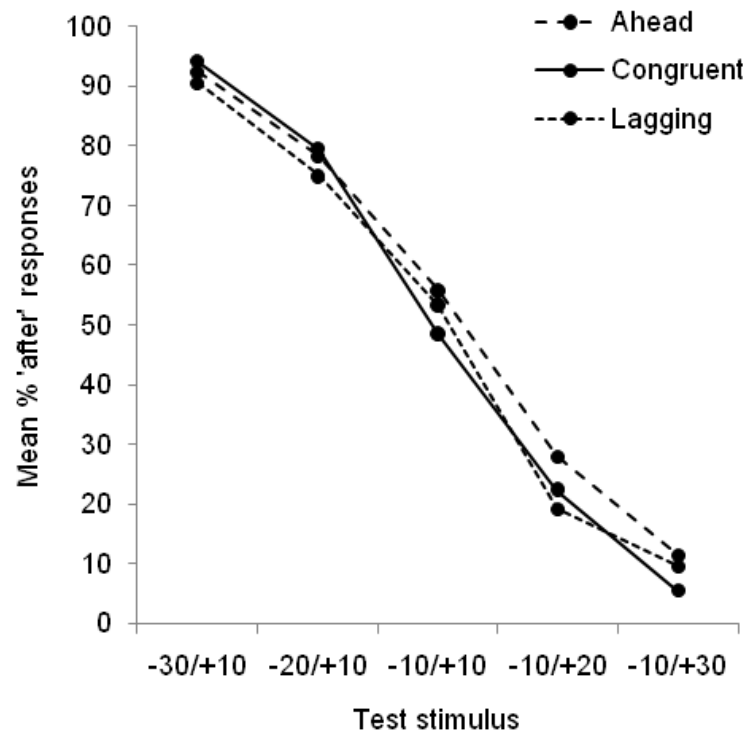


Figure 7.8. Mean percentage of 'after' responses for each gaze direction across each level of test stimulus.

## *Discussion*

The manipulations of gaze direction in pilot study 3 failed to elicit any variation in how far participants estimated the head to have rotated. These results do not support the hypothesis, and stand in contrast to the findings of the previous pilot studies, in particular to those of pilot study 2 in which an identical experimental condition ( $-10^{\circ}/+10^{\circ}$ ) elicited a strong effect of gaze direction. However, the number of trials contributing to the respective analyses were not equivalent, with pilot study 2 drawing from 630 trials and the experimental trials of pilot study 3 only consisting of 324 trials. The non-significant result in the current study may therefore be due to a lack of power. It must also be noted that reaction times did not decrease appreciably by placing the two test choices closer together on the screen, and this is supported by a non-significant difference in reaction times between the experimental trials of pilot study 3 and the equivalent trials of pilot study 2 (one-way independent measures ANOVA  $F(1, 28) = .29, p = .594, \eta_p^2 = .01$ ).

A fourth pilot study was therefore conducted in which the methodology of pilot study 3 was replicated with a larger sample. An additional factor of retention interval was also included, whereby all trials were presented both with and without the blank screen of 1000 ms in between offset of the rotating stimulus and onset of the test stimulus. Previous research has shown that the magnitude of RM increases with the length of retention interval up to 250 ms, after which the effect levels off. In Pilot study 4, it was expected that any re-occurrence of RM, and its modulation due to changes in the gaze direction of the rotating stimulus, would be absent when the RI was zero.

## *Pilot Study 4*

### *Method*

### *Participants*

Participant's (N = 15) details are the same as for previous pilot studies.

### *Apparatus*

Hardware and software for the creation and display of stimuli were the same as for previous pilot studies.

### *Stimuli*

The stimuli in pilot study 4 were created using different software (Poser 6 animation software, Curious Labs, Inc. & e frontier, Inc) than for previous pilot studies. This provided more accurate and realistic stimuli than used in pilot studies 1 to 3 in several ways. Firstly, the stimuli were more naturalistically human, whereas the previous stimuli suffered from flaws in the rendering of the features. Secondly, the stimuli were more comprehensive, in that it was possible to now present the back of the head and also other body parts such as the neck and shoulders, which was not possible in previous pilot studies. Thirdly, it was now possible to present two different characters, one male and one female, to afford the experiment with more variation. Finally, and most importantly, the software enabled highly accurate manipulations of the rotation of the head and the variations in gaze direction, such that each could now be quantified and specified to within  $1^\circ$ . The eyes in the gaze-ahead and gaze-lagging conditions were now oriented at  $30^\circ$  from the orientation of the head, with the gaze-congruent condition showing no deviation from head orientation ( $0^\circ$ ). These parameters provided for a more conspicuous variation in gaze direction than in the previous pilot studies.

### *Rotating stimulus*

The nature of rotation was the same as for the previous pilot studies (Figure 7.9). In addition, the rotating head was placed within the context of the body by making the top part of the shoulders visible. These remained fixed at a  $45^\circ$  angle away to the observers left throughout the rotation. The subtended angle of the stimulus' width was between  $11.5^\circ$



and  $9.2^\circ$  for the male, and between  $10.3^\circ$  and  $9.2^\circ$  for the female stimulus. The height of both was  $14.8^\circ$ .

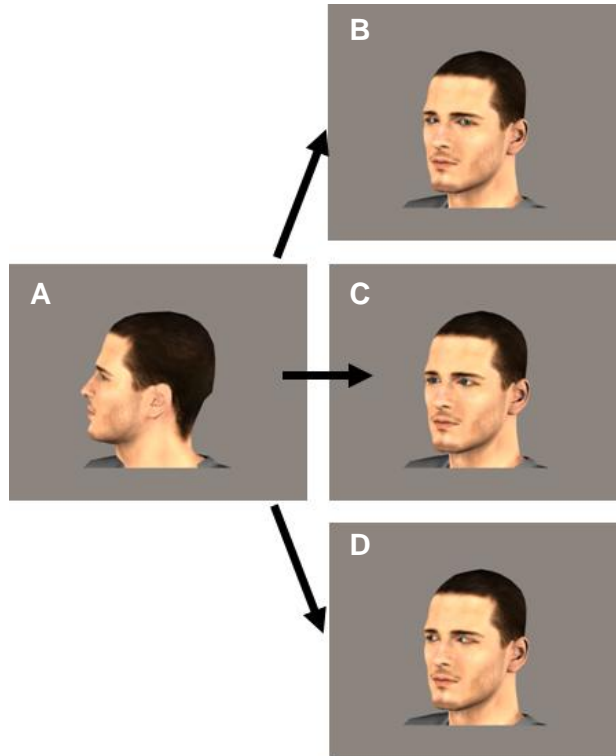


Figure 7.9. The rotating stimulus of pilot study 4 using stimuli created in Poser 6. As in the previous pilot studies, the head rotated  $60^\circ$  from a full left profile view (A), and the gaze direction was either in advance of head orientation (B: gaze-ahead), looking straight ahead (C: gaze-congruent), or lagging behind head rotation (D: gaze-lagging).

### *Test stimulus*

The nature of the task performed by the participant, and the levels of test stimulus orientation were the same as for pilot study 3 (Figure 7.10). The subtended angle of the width of the test stimulus between the outer edges was  $22.3^\circ$  for the male stimulus and  $19^\circ$  for the female stimulus.

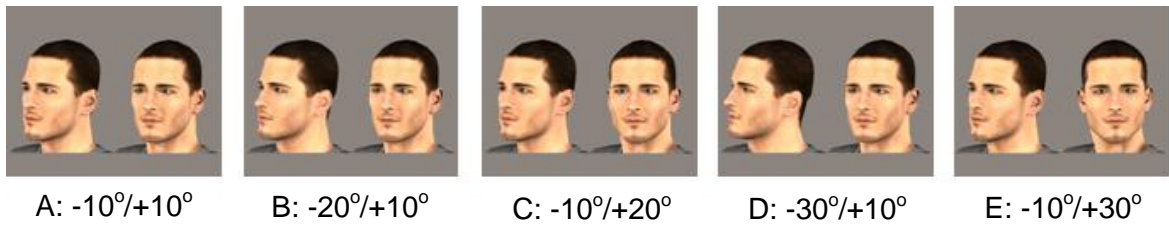


Figure 7.10. Examples of test stimuli in pilot study 4. A: Symmetrical experimental trials where neither answer was more similar to the end-point of the rotating stimulus. B & C: Asymmetrical experimental trials where the 'after' (B) and 'before' (C) test choices were more similar. D & E: Catch trials where the 'after' (D) and 'before' (E) test choices were more similar.

### *Procedure*

Participant instructions were the same as for pilot studies 2 and 3, except that responses were made by pressing the 'J' and 'L' buttons for 'left' and 'right' respectively (labelled accordingly). Participants completed a total of 120 trials, lasting approximately 10 minutes. The combinations of gaze direction and test stimulus (3 X 5) were presented four times for each of the male and female stimuli. These were conducted in two blocks of 60 trials, one with a retention interval (1000 ms) in between the rotating stimulus and test stimulus, and one without. The order of these blocks was counterbalanced across participants.

### *Results*

The mean error rate was 16.9% (SD = 14.0%) and the mean reaction times was 1171 ms (SD = 273 ms). Those participants with a mean error rate exceeding 20% were excluded ( $n = 5$ , mean error rate = 33.3%, SD = 9.1%) reducing the error rate to 8.8% (SD = 6.8). Trials with a response time less than 250ms or in excess of 2SD above each

participant mean were removed from the analysis, leading to 4.8% of trials being excluded, resulting in a mean reaction time of 1127 ms (258 ms).

	Retention Interval Absent			Retention Interval Present		
	Ahead	Congruent	Lagging	Ahead	Congruent	Lagging
<b>-30°/+10°</b>	87.5 (24.3)	86.7 (18.5)	81.7 (21.1)	83.3 (18.8)	95.0 (10.5)	90.8 (21.7)
<b>-20°/+10°</b>	80.0 (23.0)	70.0 (19.7)	65.0 (26.9)	72.5 (23.3)	65.0 (31.6)	57.5 (39.2)
<b>-10°/+10°</b>	69.2 (31.7)	48.3 (34.2)	32.5 (30.0)	62.5 (24.3)	49.2 (29.3)	12.5 (21.2)
<b>-10°/+20°</b>	30.8 (32.9)	41.7 (34.7)	33.3 (33.3)	25.0 (21.9)	18.3 (26.9)	15.8 (18.2)
<b>-10°/+30°</b>	7.5 (16.9)	0.0 (0.0)	2.5 (7.9)	10.0 (12.9)	2.5 (7.9)	7.5 (12.1)

Table 7.4. Mean percentage of ‘after’ responses for each gaze direction across each level of test stimulus both with and without retention interval.

The ‘before’ and ‘after’ responses were coded in the same way as in pilot study 3 and entered into a three-way repeated measures ANOVA with RI, Gaze direction and Test stimulus as the main effects (2 X 3 X 5). There was no significant main effect of RI ( $F(1, 9) = 1.4, p = .27, \eta_p^2 = .14$ ), nor did this interact with either Gaze direction ( $F(2, 18) = .19, p = .83, \eta_p^2 = .02$ ) or Test stimulus ( $F(4, 36) = 2.33, p = .08, \eta_p^2 = .21$ ). There was the expected effect of Test stimulus ( $F(3, 36) = 81.4, p < .001, \eta_p^2 = .9$ ), a significant main effect of Gaze direction ( $F(2, 18) = 7.2, p = .005, \eta_p^2 = .45$ ), and significant interaction between the two ( $F(8, 72) = 4.9, p < .001, \eta_p^2 = .35$ ). With RI collapsed due to its lack of influence on the results, one-way repeated measures ANOVAs were conducted with gaze direction as the main effect for each of the symmetrical and asymmetrical experimental trial conditions of test stimulus (see Table 7.4 and Figure 7.11, an effect was not sought in the catch trials as performance in these trials was used as a means to exclude participants). This showed a significant effect of gaze direction in the symmetrical experimental trials ( $F(2, 18) = 15.24, p < .001, \eta_p^2 = .629$ ), which paired sample t-tests showed to be due to the gaze-lagging

condition being significantly different from both the gaze-ahead ( $t(9) = 6, p < .001$ ) and gaze-congruent conditions ( $t(9) = 3.24, p = .01$ ), which did not differ from each other ( $t(9) = 2.1, p = .06$ ). Furthermore, one-sample t-test showed that, whilst the gaze-congruent condition did not differ significantly from the test value of 50 ( $t(9) = .23, p = .83$ ), the mean percentage of 'after' responses in the gaze-lagging condition was significantly less than 50% ( $t(9) = 3.84, p = .004$ ), whereas those for the gaze-ahead condition approached significance but did not survive the Bonferroni correction ( $t(9) = 2.48, p = .035$ ). There was no significant effect of gaze direction in either the 'after' ( $F(2, 18) = 1.79, p = .2, \eta_p^2 = .17$ ) or 'before' asymmetric experimental trials ( $F(2, 18) = .27, p = .76, \eta_p^2 = .03$ ).

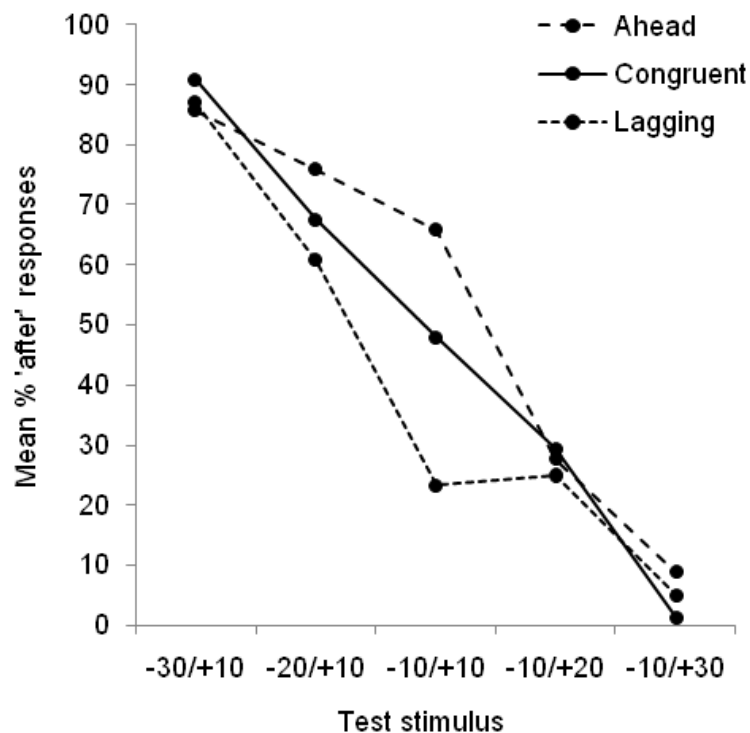


Figure 7.11. Mean percentage of 'after' responses for each gaze condition across each level of test stimulus (RI collapsed).

### *Discussion*

The results of pilot study 4 are the most emphatic of all of the pilot studies. The effect of gaze direction was not only highly significant, in contrast to the results of pilots studies 1 and 3, but also obtained an effect size (.629) considerably larger than that of pilot study 2 (.34). On first glance, this seems to have fulfilled the aim of rectifying the null effect of pilot study 3 by increasing the sample size. However, after participant exclusions had been made, the data analysed consisted of only one more participant than in pilot study 3, resulting in even fewer experimental trials being analysed (240). The augmented effect may be attributed to the nature of the stimuli, which afforded an enhanced conspicuousness of the gaze manipulations and a greater ease with which the different directions could be discriminated. This would have made the gaze cues more discernable, facilitating the inference of the action goals, resulting in a greater memory displacement.

However, the expected effect of RI in determining the presence of an effect of gaze direction was not found. Previous research has established that memory displacement requires an optimum time lapse of 250 ms within which the representational continuation of the object's motion occurs. However, the memory displacement attributed to variation in gaze direction in pilot study 4 occurred both in the absence and presence of a RI. In the experimental trials, the effect of gaze was highly significant and of comparable size in the RI absent condition ( $F(2,18) = 6.78, p = .006, \eta_p^2 = .43$ ) and in the RI present condition ( $F(2,18) = 14.13, p < .001, \eta_p^2 = .61$ ). Therefore, unlike memory displacement for non-biological stimuli, memory displacement caused by intentional attribution to biological stimuli may not be affected by the absence or presence of an RI. This suggests the possibility that the two processes are governed by different cognitive mechanisms. This hypothesis is investigated further in experiment 1.

### *Overall discussion*

This series of pilot studies show that estimations of how far a head has rotated are affected by the gaze direction of the agent. This supports the hypothesis that anticipation of biological motion is subject to social cues conveying the goal of the action. Observers attribute the action with goal-directedness, which subsequently affects their anticipation of how the action will proceed in the immediate future. As the strongest result was obtained in pilot study 4, the stimulus array and test stimulus method employed will form the basis for the subsequent experiments.

There are several outstanding questions that arise from the results of these pilot studies that further experiments will have to address. Firstly, the effect of RI requires further investigation on the grounds already outlined above. Secondly, the results of the pilots were inconclusive as to which condition(s) produced the effect (gaze-ahead and/or gaze-lagging). In all but one of the pilot studies, the weak version of the hypothesis was supported (gaze-ahead > gaze-lagging). However, in Pilot study 2, the gaze-ahead condition was overestimated compared to the 50% mark and compared to the other gaze direction conditions (i.e. ahead > 50% = congruent = lagging). Conversely, in pilot study 4, the effect lay in an underestimation of the gaze-lagging condition, which differed significantly from 50% and the other gaze direction conditions (i.e. ahead = congruent = 50% > lagging).

Thirdly, error rates were high in the catch trials, even though they were designed to be easy (so as to be able to exclude participants not paying proper attention). As they stand now, the catch trials may remain too difficult even for those completing the task with due attentiveness, resulting in the unnecessary exclusion of participants. The threshold by which participants are excluded will be reduced in subsequent experiments by making the catch trials easier to complete.

Finally, and most importantly, the assertion that the effect of gaze direction on estimations of head rotation are the result of higher level attributions of intentionality remained untested. The effect may also be the result of several low-level factors, including the visual appearance of the pupil shifting within the sclera, or the encoding of a spatial relationship between the gaze direction and head rotation that does not entail any processing of the social significance of the gaze cue. Experiment 1 will introduce several control conditions with which to investigate these alternative explanations.

## References

- Adams, R. B., Ambady, N., Macrae, C. N., & Kleck, R. E. (2006). Emotional expressions forecast approach-avoidance behavior. *Motivation and Emotion*, 30,(2) 179-188.
- Adams, R. B., & Franklin, R. G. (2009). Influence of emotional expression on the processing of gaze direction. *Motivation and Emotion*, 33,(2) 106-112.
- Adams, R. B., Gordon, H. L., Baird, A. A., Ambady, N., & Kleck, R. E. (2003). Effects of gaze on amygdala sensitivity to anger and fear faces. *Science*, 300,(5625) 1536-1536.
- Adams, R. B., & Kleck, R. E. (2005). Effects of direct and averted gaze on the perception of facially communicated emotion. *Emotion*, 5,(1) 3-11.
- Adolphs, R. (1999). Social cognition and the human brain. *Trends in Cognitive Sciences*, 3,(12) 469-479.
- Adolphs, R., Gosselin, F., Buchanan, T. W., Tranel, D., Schyns, P., & Damasio, A. R. (2005). A mechanism for impaired fear recognition after amygdala damage. *Nature*, 433,(7021) 68-72.
- Aguado, L., Garcia-Gutierrez, A., & Serrano-Pedraza, I. (2009). Symmetrical interaction of sex and expression in face classification tasks. *Attention Perception & Psychophysics*, 71,(1) 9-25.
- Akiyama, T., Kato, M., Muramatsu, T., Saito, F., Nakachi, R., & Kashima, H. (2006). A deficit in discriminating gaze direction in a case with right superior temporal gyrus lesion. *Neuropsychologia*, 44,(2) 161-170.
- Allen, G., & Courchesne, E. (2001). Attention function and dysfunction in autism. *Frontiers in Bioscience*, 6, D105-D119.
- Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: Role of the STS region. *Trends in Cognitive Sciences*, 4,(7) 267-278.



- Amorim, M. A. (2003). "What is my avatar seeing?": The coordination of "out-of-body" and "embodied" perspectives for scene recognition across views. *Visual Cognition*, 10,(2) 157-199.
- Anaki, D., & Moscovitch, M. (2007). When a face is (or is not) more than the sum of its features: Configural and analytic processes in facial temporal integration. *Visual Cognition*, 15,(6) 741-763.
- Anderson, J. R., Kuroshima, H., Kuwahata, H., & Fujita, K. (2004). Do squirrel monkeys (*Saimiri sciureus*) and capuchin monkeys (*Cebus apella*) predict that looking leads to touching? *Animal Cognition*, 7,(3) 185-192.
- Anderson, N. D., & Wilson, H. R. (2005). The nature of synthetic face adaptation. *Vision Research*, 45,(14) 1815-1828.
- Ando, S. (2002). Luminance-induced shift in the apparent direction of gaze. *Perception*, 31,(6) 657-674.
- Ando, S. (2004). Perception of gaze direction based on luminance ratio. *Perception*, 33,(10) 1173-1184.
- Apperly, I. A. (2008). Beyond Simulation-Theory and Theory-Theory: Why social cognitive neuroscience should use its own concepts to study "theory of mind". *Cognition*, 107,(1) 266-283.
- Ashida, H. (2004). Action-specific extrapolation of target motion in human visual system. *Neuropsychologia*, 42,(11) 1515-1524.
- Astafiev, S. V., Stanley, C. M., Shulman, G. L., & Corbetta, M. (2004). Extrastriate body area in human occipital cortex responds to the performance of motor actions. *Nature Neuroscience*, 7,(5) 542-548.
- Bach, P., Knoblich, G., Gunter, T. C., Friederici, A. D., & Prinz, W. (2005). Action comprehension: Deriving spatial and functional relations. *Journal of Experimental Psychology-Human Perception and Performance*, 31,(3) 465-479.

- Baker, C. I., Keysers, C., Jellema, T., Wicker, B., & Perrett, D. I. (2001). Neuronal representation of disappearing and hidden objects in temporal cortex of the macaque. *Experimental Brain Research*, 140,(3) 375-381.
- Baldwin, D. A., & Baird, J. A. (2001). Discerning intentions in dynamic human action. *Trends in Cognitive Sciences*, 5,(4) 171-178.
- Baldwin, D. A., Baird, J. A., Saylor, M. M., & Clark, M. A. (2001). Infants parse dynamic action. *Child Development*, 72,(3) 708-717.
- Baron-Cohen, S. (1995). *Mindblindness: An essay on autism and Theory of Mind*. Cambridge, Mass MIT Press.
- Baron-Cohen, S. (2002). The extreme male brain theory of autism. *Trends in Cognitive Sciences*, 6,(6) 248-254.
- Baron-Cohen, S. (2005). The Empathizing System: A revision of the 1994 model of the Mindreading System. In Ellis, B. & Bjorklund, D. (Eds.), *Origins of the Social Mind: Evolutionary Psychology and Child Development*. New York: Guilford Press.
- Baron-Cohen, S. (2006). Two new theories of autism: hyper-systemising and assortative mating. *Archives of Disease in Childhood*, 91,(1) 2-5.
- Baron-Cohen, S., Campbell, R., Karmiloff-Smith, A., Grant, J., & Walker, J. (1995). Are children with autism blind to the mentalistic significance of the eyes. *British Journal of Developmental Psychology*, 13,(4) 379-398.
- Baron-Cohen, S., O'Riordan, M., Stone, V., Jones, R., & Plaisted, K. (1999). Recognition of faux pas by normally developing children and children with Asperger syndrome or high-functioning autism. *Journal of Autism and Developmental Disorders*, 29,(5) 407-418.
- Baron-Cohen, S., Ring, H., Moriarty, J., Shmitz, P., Costa, D., & Ell, P. (1994). Recognition of mental state terms: A clinical study of autism, and a functional neuroimaging study of normal adults. *British Journal of Psychiatry*, 165,(5) 640-649.

- Baron-Cohen, S., & Wheelwright, S. (2004). The empathy quotient: An investigation of adults with Asperger syndrome or high functioning autism, and normal sex differences. *Journal of Autism and Developmental Disorders*, 34,(2) 163-175.
- Baron-Cohen, S., Wheelwright, S., Skinner, R., Martin, J., & Clubley, E. (2001). The Autism-Spectrum Quotient (AQ): Evidence from Asperger syndrome/high-functioning autism, males and females, scientists and mathematicians. *Journal of Autism and Developmental Disorders*, 31,(1) 5-17.
- Barrett, L., Henzi, P., & Dunbar, R. (2003). Primate cognition: from 'what now?' to 'what if?'. *Trends in Cognitive Sciences*, 7,(11) 494-497.
- Barrett, L., Henzi, P., & Rendall, D. (2007). Social brains, simple minds: does social complexity really require cognitive complexity? *Philosophical Transactions of the Royal Society B-Biological Sciences*, 362,(1480) 561-575.
- Barton, J. J. S. (2001). Discrimination of spatial relations and features in faces: Effects of inversion and viewing duration. *British Journal of Psychology*, 92,(3) 527-549.
- Barton, J. J. S., Radcliffe, N., Cherkasova, M. V., Edelman, J., & Intriligator, J. M. (2006). Information processing during face recognition: The effects of familiarity, inversion, and morphing on scanning fixations. *Perception*, 35,(8) 1089-1105.
- Barton, J. J. S., Zhao, J. H., & Keenan, J. P. (2003). Perception of global facial geometry in the inversion effect and prosopagnosia. *Neuropsychologia*, 41,(12) 1703-1711.
- Batki, A., Baron-Cohen, S., Wheelwright, S., Connellan, J., & Ahluwalia, J. (2000). Is there an innate gaze module? Evidence from human neonates. *Infant Behavior & Development*, 23,(2) 223-229.
- Baudouin, J. Y., & Humphreys, G. W. (2006). Configural information in gender categorisation. *Perception*, 35,(4) 531-540.
- Bauml, K. H., Schnelzer, M., & Zimmer, A. (1997). The influence of inversion on the judgment of facial and non-facial attributes. *Acta Psychologica*, 96,(1-2) 27-42.

- Bayliss, A. P., di Pellegrino, G., & Tipper, S. P. (2005). Sex differences in eye gaze and symbolic cueing of attention. *Quarterly Journal of Experimental Psychology Section a-Human Experimental Psychology*, 58,(4) 631-650.
- Bayliss, A. P., Griffiths, D., & Tipper, S. P. (2009). Predictive gaze cues affect face evaluations: The effect of facial emotion. *European Journal of Cognitive Psychology*, 21,(7) 1072-1084.
- 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. *Psychonomic Bulletin & Review*, 13,(6) 1061-1066.
- Bayliss, A. P., & Tipper, S. P. (2005). Gaze and arrow cueing of attention reveals individual differences along the autism spectrum as a function of target context. *British Journal of Psychology*, 96,(1) 95-114.
- Bayliss, A. P., & Tipper, S. P. (2006). Predictive gaze cues and personality judgments: Should eye trust you? *Psychological Science*, 17,(6) 514-520.
- Becchio, C., Bertone, C., & Castiello, U. (2008). How the gaze of others influences object processing. *Trends in Cognitive Sciences*, 12,(7) 254-258.
- Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, 8,(6) 551-565.
- Bertamini, M. (1993). Memory for position and dynamic representations. *Memory & Cognition*, 21,(4) 449-457.
- Bertenthal, B., & Von Hofsten, C. (1998). Eye, head and trunk control: The foundation for manual development. *Neuroscience and Biobehavioral Reviews*, 22,(4) 515-520.
- Bi, T. Y., Su, J. Z., Chen, J., & Fang, F. (2009). The role of gaze direction in face viewpoint aftereffect. *Vision Research*, 49,(18) 2322-2327.

- Biguer, B., Jeannerod, M., & Prablanc, C. (1982). The coordination of eye, head, and arm movements during reaching at a single visual target. *Experimental Brain Research*, 46,(2) 301-304.
- Bindemann, M., Burton, A. M., & Langton, S. R. H. (2008). How do eye gaze and facial expression interact? *Visual Cognition*, 16,(6) 708-733.
- Bindemann, M., Scheepers, C., & Burton, A. M. (2009). Viewpoint and center of gravity affect eye movements to human faces. *Journal of Vision*, 9,(2) 1-16.
- Binkofski, F., & Buccino, G. (2006). The role of ventral premotor cortex in action execution and action understanding. *Journal of Physiology-Paris*, 99,(4-6) 396-405.
- Blair, R. J. R. (2003). Facial expressions, their communicatory functions and neuro-cognitive substrates. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, 358,(1431) 561-572.
- Blair, R. J. R. (2005). Responding to the emotions of others: Dissociating forms of empathy through the study of typical and psychiatric populations. *Consciousness and Cognition*, 14,(4) 698-718.
- Blair, R. J. R., Morris, J. S., Frith, C. D., Perrett, D. I., & Dolan, R. J. (1999). Dissociable neural responses to facial expressions of sadness and anger. *Brain*, 122,(5) 883-893.
- Blakemore, S. J., & Decety, J. (2001). From the perception of action to the understanding of intention. *Nature Reviews Neuroscience*, 2,(8) 561-567.
- Blakemore, S. J., & Frith, C. (2005). The role of motor contagion in the prediction of action. *Neuropsychologia*, 43,(2) 260-267.
- Bock, S. W., Dicke, P., & Thier, P. (2008). How precise is gaze following in humans? *Vision Research*, 48,(7) 946-957.
- Bonifacci, P., Ricciardelli, P., Lugli, L., & Pellicano, A. (2008). Emotional attention: Effects of emotion and gaze direction on overt orienting of visual attention. *Cognitive Processing*, 9,(2) 127-135.

- Brass, M., & Heyes, C. (2005). Imitation: Is cognitive neuroscience solving the correspondence problem? *Trends in Cognitive Sciences*, 9,(10) 489-495.
- Brouwer, A. M., Franz, V. H., & Thornton, I. M. (2004). Representational momentum in perception and grasping: Translating versus transforming objects. *Journal of Vision*, 4,(7) 575-584.
- Brown, W. M., & Moore, C. (2002). Smile asymmetries and reputation as reliable indicators of likelihood to cooperate: An evolutionary analysis. In Shohov, S. P. (Ed.), *Advances in psychology research* (Vol. 11, pp. 19-36). Hauppauge, New York: Nova Science Publishers.
- Brune, M., & Brune-Cohrs, U. (2006). Theory of mind: Evolution, ontogeny, brain mechanisms and psychopathology. *Neuroscience and Biobehavioral Reviews*, 30,(4) 437-455.
- Buccino, G., Lui, F., Canessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., Porro, C. A., & Rizzolatti, G. (2004). Neural circuits involved in the recognition of actions performed by nonconspecifics: An fMRI study. *Journal of Cognitive Neuroscience*, 16,(1) 114-126.
- Buchan, J. N., Pare, M., & Munhall, K. G. (2007). Spatial statistics of gaze fixations during dynamic face processing. *Social Neuroscience*, 2,(1) 1-13.
- Burrows, A. M. (2008). The facial expression musculature in primates and its evolutionary significance. *BioEssays*, 30,(3) 212-225.
- Caldara, R., Seghier, M. L., Rossion, B., Lazeyras, F., Michel, C., & Hauert, C. A. (2006). The fusiform face area is tuned for curvilinear patterns with more high-contrasted elements in the upper part. *Neuroimage*, 31,(1) 313-319.
- Calder, A. J. (2007). Face cells: Separate processing of expression and gaze in the amygdala. *Current Biology*, 17,(10) R371-R372.

- Calder, A. J., Beaver, J. D., Winston, J. S., Dolan, R. J., Jenkins, R., Eger, E., & Henson, R. N. A. (2007). Separate coding of different gaze directions in the superior temporal sulcus and inferior parietal lobule. *Current Biology*, 17,(1) 20-25.
- Calder, A. J., & Jansen, J. (2005). Configural coding of facial expressions: The impact of inversion and photographic negative. *Visual Cognition*, 12,(3) 495-518.
- Calder, A. J., Jenkins, R., Cassel, A., & Clifford, C. W. G. (2008). Visual representation of eye gaze is coded by a nonopponent multichannel system. *Journal of Experimental Psychology-General*, 137,(2) 244-261.
- Calder, A. J., Lawrence, A. D., Keane, J., Scott, S. K., Owen, A. M., Christoffels, I., & Young, A. W. (2002). Reading the mind from eye gaze. *Neuropsychologia*, 40,(8) 1129-1138.
- Calder, A. J., & Young, A. W. (2005). Understanding the recognition of facial identity and facial expression. *Nature Reviews Neuroscience*, 6,(8) 641-651.
- Call, J. (2001). Chimpanzee social cognition. *Trends in Cognitive Sciences*, 5,(9) 388-393.
- Call, J., & Tomasello, M. (1998). Distinguishing intentional from accidental actions in orangutans (*Pongo pygmaeus*), chimpanzees (*Pan troglodytes*), and human children (*Homo sapiens*). *Journal of Comparative Psychology*, 112,(2) 192-206.
- Calvo-Merino, B., Grezes, J., Glaser, D. E., Passingham, R. E., & Haggard, P. (2006). Seeing or doing? Influence of visual and motor familiarity in action observation. *Current Biology*, 16,(19) 1905-1910.
- Campbell, R., Heywood, C. A., Cowey, A., Regard, M., & Landis, T. (1990). Sensitivity to eye gaze in prosopagnosic patients and monkeys with superior temporal sulcus ablation. *Neuropsychologia*, 28,(11) 1123-1142.
- Carroll, J. M., & Yung, C. K. (2006). Sex and discipline differences in empathising, systemising and autistic symptomatology: Evidence from a student population. *Journal of Autism and Developmental Disorders*, 36,(7) 949-957.

- Castiello, U. (2003). Understanding other people's actions: Intention and attention. *Journal of Experimental Psychology-Human Perception and Performance*, 29,(2) 416-430.
- Cerf, M., Harel, J., Einhaeuser, W., & Kock, C. (2007). Predicting human gaze using low-level saliency combined with face detection. *Advances in Neural Information Processing Systems (NIPS)*, 20, 241-248.
- Charman, T., Baron-Cohen, S., Swettenham, J., Baird, G., Cox, A., & Drew, A. (2000). Testing joint attention, imitation, and play as infancy precursors to language and theory of mind. *Cognitive Development*, 15,(4) 481-498.
- Chawarska, K., Klin, A., & Volkmar, F. (2003). Automatic attention cueing through eye movement in 2-year-old children with autism. *Child Development*, 74,(4) 1108-1122.
- Chen, C. C., Kao, K. L. C., & Tyler, C. W. (2007). Face configuration processing in the human brain: The role of symmetry. *Cerebral Cortex*, 17,(6) 1423-1432.
- Chen, M., & Bargh, J. A. (1999). Consequences of automatic evaluation: Immediate behavioral predispositions to approach or avoid the stimulus. *Personality and Social Psychology Bulletin*, 25,(2) 215-224.
- Cohen, J. D., & Tong, F. (2001). Neuroscience - The face of controversy. *Science*, 293,(5539) 2405-2407.
- Conty, L., Tijus, C., Hugueville, L., Coelho, E., & George, N. (2006). Searching for asymmetries in the detection of gaze contact versus averted gaze under different head views: a behavioural study. *Spatial Vision*, 19,(6) 529-545.
- Coricelli, G. (2005). Two-levels of mental states attribution: From automaticity to voluntariness. [Article]. *Neuropsychologia*, 43,(2) 294-300.
- Cretenet, J., & Dru, V. (2008). A neurobehavioral investigation into judgmental processes: Effect of bilateral motor behaviors. *Brain and Cognition*, 68,(1) 81-91.
- Critchley, H., Daly, E., Phillips, M., Brammer, M., Bullmore, E., Williams, S., Van Amelsvoort, T., Robertson, D., David, A., & Murphy, D. (2000). Explicit and implicit



- neural mechanisms for processing of social information from facial expressions: A functional magnetic resonance imaging study. *Human Brain Mapping*, 9,(2) 93-105.
- Csibra, G. (2003). Teleological and referential understanding of action in infancy. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 358,(1431) 447-458.
- Csibra, G. (2005). Mirror neurons and action observation. Is simulation involved? *Interdisciplines*. Retrieved from <http://www.interdisciplines.org/mirror/papers/4>
- Currie, G., & Ravenscroft, I. (1997). Mental simulation and motor imagery. *Philosophy of Science*, 64,(1) 161-180.
- Davidson, R. J., Saron, C. D., Senulis, J. A., Ekman, P., & Friesen, W. V. (1990). Approach withdrawal and cerebral asymmetry: Emotional expression and brain physiology. 1. *Journal of Personality and Social Psychology*, 58,(2) 330-341.
- Davies, T. N., & Hoffman, D. D. (2002). Attention to faces: A change-blindness study. *Perception*, 31,(9) 1123-1146.
- de Gelder, B., & Rouw, R. (2001). Beyond localisation: A dynamical dual route account of face recognition. *Acta Psychologica*, 107,(1-3) 183-207.
- De Groote, I., Roeyers, H., & Striano, T. (2007). Gaze following as a function of affective expression in 3, 6- and 9-month-old infants. *Infant Behavior & Development*, 30,(3) 492-498.
- de Haan, M., Pascalis, O., & Johnson, M. H. (2002). Specialization of neural mechanisms underlying face recognition in human infants. *Journal of Cognitive Neuroscience*, 14,(2) 199-209.
- De Jong, M. C., van Engeland, H., & Kemner, C. (2008). Attentional effects of gaze shifts are influenced by emotion and spatial frequency, but not in autism. *Journal of the American Academy of Child and Adolescent Psychiatry*, 47,(4) 443-454.
- Deaner, R. O., Shepherd, S. V., & Platt, M. L. (2007). Familiarity accentuates gaze cuing in women but not men. *Biology Letters*, 3,(1) 64-67.

- Desimone, R., Albright, T. D., Gross, C. G., & Bruce, C. (1984). Stimulus-selective properties of inferior temporal neurons in the macaque. *Journal of Neuroscience*, 4,(8) 2051-2062.
- Diamond, R., & Carey, S. (1986). Why faces are and are not special: An effect of expertise. *Journal of Experimental Psychology-General*, 115,(2) 107-117.
- Dinstein, I., Thomas, C., Behrmann, M., & Heeger, D. J. (2008). A mirror up to nature. *Current Biology*, 18,(1) R13-R18.
- Doi, H., & Shinohara, K. (2009). The perceived duration of emotional face is influenced by the gaze direction. *Neuroscience Letters*, 457,(2) 97-100.
- Downing, P. E., Bray, D., Rogers, J., & Childs, C. (2004). Bodies capture attention when nothing is expected. *Cognition*, 93,(1) B27-B38.
- Downing, P. E., Chan, A. W. Y., Peelen, M. V., Dodds, C. M., & Kanwisher, N. (2006). Domain specificity in visual cortex. *Cerebral Cortex*, 16,(10) 1453-1461.
- Downing, P. E., Dodds, C. M., & Bray, D. (2004). Why does the gaze of others direct visual attention? *Visual Cognition*, 11,(1) 71-79.
- Downing, P. E., Jiang, Y. H., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science*, 293,(5539) 2470-2473.
- Downing, P. E., Peelen, M. V., Wiggett, A. J., & Tew, B. D. (2006). The role of the extrastriate body area in action perception. *Social Neuroscience*, 1,(1) 52-62.
- Downing, P. E., Wiggett, A. J., & Peelen, M. V. (2007). Functional magnetic resonance imaging investigation of overlapping lateral occipitotemporal activations using multi-voxel pattern analysis. *Journal of Neuroscience*, 27,(1) 226-233.
- 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.
- Duchaine, B., Jenkins, R., Germine, L., & Calder, A. J. (2009). Normal gaze discrimination and adaptation in seven prosopagnosics. *Neuropsychologia*, 47,(10) 2029-2036.

- Dunbar, R. I. M. (1992). Neocortex size as a constraint on group-size in primates. *Journal of Human Evolution*, 22,(6) 469-493.
- Dunbar, R. I. M. (1995). Neocortex size and group-size in primates: A test of the hypothesis. *Journal of Human Evolution*, 28,(3) 287-296.
- Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology*, 6,(5) 178-190.
- Dwyer, D. M., Mundy, M. E., Vladeanu, M., & Honey, R. C. (2009). Perceptual learning and acquired face familiarity: Evidence from inversion, use of internal features, and generalization between viewpoints. *Visual Cognition*, 17,(3) 334-355.
- Ekman, P. (1997). Should we call it expression or communication? *Innovations in social science research*, 10,(4) 333-344.
- Ekman, P. (1999). Basic emotions. In Dalgleish, T. & Power, M. (Eds.), *Handbook of Cognition and Emotion*. Sussex U.K.: John Wiley & Sons, Ltd.
- Ellison, J. W., & Massaro, D. W. (1997). Featural evaluation, integration, and judgment of facial affect. *Journal of Experimental Psychology-Human Perception and Performance*, 23,(1) 213-226.
- Emery, N. J. (2000). The eyes have it: The neuroethology, function and evolution of social gaze. *Neuroscience and Biobehavioral Reviews*, 24,(6) 581-604.
- Engell, A. D., & Haxby, J. V. (2007). Facial expression and gaze-direction in human superior temporal sulcus. *Neuropsychologia*, 45,(14) 3234-3241.
- Falck-Ytter, T., Gredeback, G., & von Hofsten, C. (2006). Infants predict other people's action goals. *Nature Neuroscience*, 9,(7) 878-879.
- Fang, F., Murray, S. O., & He, S. (2007). Duration-dependent fMRI adaptation and distributed viewer-centered face representation in human visual cortex. *Cerebral Cortex*, 17,(6) 1402-1411.

- Farroni, T., Csibra, G., Simion, G., & Johnson, M. H. (2002). Eye contact detection in humans from birth. *Proceedings of the National Academy of Sciences of the United States of America*, 99,(14) 9602-9605.
- Ferrari, P. F., Kohler, E., Fogassi, L., & Gallese, V. (2000). The ability to follow eye gaze and its emergence during development in macaque monkeys. *Proceedings of the National Academy of Sciences of the United States of America*, 97,(25) 13997-14002.
- Ferrari, P. F., Rozzi, S., & Fogassi, L. (2005). Mirror neurons responding to observation of actions made with tools in monkey ventral premotor cortex. *Journal of Cognitive Neuroscience*, 17,(2) 212-226.
- Finke, R. A., Freyd, J., & Shyl, G. C. W. (1985). Memory distortions induced by implied velocity and acceleration. *Bulletin of the Psychonomic Society*, 23,(4) 276-276.
- Finke, R. A., & Freyd, J. J. (1985). Transformations of visual memory induced by implied motions of pattern elements. *Journal of Experimental Psychology-Learning Memory and Cognition*, 11,(4) 780-794.
- Finke, R. A., Freyd, J. J., & Shyi, G. C. W. (1986). Implied velocity and acceleration induce transformations of visual memory. *Journal of Experimental Psychology-General*, 115,(2) 175-188.
- Finke, R. A., & Shyi, G. C. W. (1988). Mental extrapolation and representational momentum for complex implied motions. *Journal of Experimental Psychology-Learning Memory and Cognition*, 14,(1) 112-120.
- Fiorentini, C., & Viviani, P. (2009). Perceiving facial expressions. *Visual Cognition*, 17,(3) 373-411.
- Flanagan, J. R., & Johansson, R. S. (2003). Action plans used in action observation. *Nature*, 424,(6950) 769-771.
- Flavell, J. H. (1999). Cognitive development: Children's knowledge about the mind. *Annual Review of Psychology*, 50, 21-45.

- Flavell, J. H. (2004). Theory-of-mind development: Retrospect and prospect. *Merrill-Palmer Quarterly-Journal of Developmental Psychology*, 50,(3) 274-290.
- Fletcher, P. C., Happe, F., Frith, U., Baker, S. C., Dolan, R. J., Frackowiak, R. S. J., & Frith, C. D. (1995). Other minds in the brain: A functional imaging study of Theory of Mind in story comprehension. *Cognition*, 57,(2) 109-128.
- Flom, R., & Pick, A. D. (2005). Experimenter affective expression and gaze following in 7-month-olds. *Infancy*, 7,(2) 207-218.
- Fogassi, L., Ferrari, P. F., Gesierich, B., Rozzi, S., Chersi, F., & Rizzolatti, G. (2005). Parietal lobe: From action organization to intention understanding. *Science*, 308,(5722) 662-667.
- Fox, E. (2005). The role of visual processes in modulating social interactions. *Visual Cognition*, 12,(1) 1-11.
- Freedman, E. G. (2008). Coordination of the eyes and head during visual orienting. *Experimental Brain Research*, 190,(4) 369-387.
- Freyd, J. J. (1983). The mental representation of movement when static stimuli are viewed. *Perception & Psychophysics*, 33,(6) 575-581.
- Freyd, J. J. (1992). Dynamic representations guiding adaptive behavior. In Macar, F., Pouthas, V. & Friedman, W. J. (Eds.), *Time, Action and Cognition: Towards Bridging the Gap* (pp. 309-323). Dordrecht: Kluwer Academic Publishers.
- Freyd, J. J., & Finke, R. A. (1984). Representational momentum. *Journal of Experimental Psychology-Learning Memory and Cognition*, 10,(1) 126-132.
- Freyd, J. J., & Finke, R. A. (1985). A velocity effect for representational momentum. *Bulletin of the Psychonomic Society*, 23,(6) 443-446.
- Freyd, J. J., & Johnson, J. Q. (1987). Probing the time course of representational momentum. *Journal of Experimental Psychology-Learning Memory and Cognition*, 13,(2) 259-268.

- Freyd, J. J., Kelly, M. H., & Dekay, M. L. (1990). Representational momentum in memory for pitch. *Journal of Experimental Psychology-Learning Memory and Cognition*, 16,(6) 1107-1117.
- Freyd, J. J., & Miller, G. F. (1992). Creature motion. *Bulletin of the Psychonomic Society*, 30,(6) 470-470.
- Freyd, J. J., Pantzer, T. M., & Cheng, J. L. (1988). Representing statics as forces in equilibrium. *Journal of Experimental Psychology-General*, 117,(4) 395-407.
- Friesen, C. K., & Kingstone, A. (2003). Covert and overt orienting to gaze direction cues and the effects of fixation offset. *Neuroreport*, 14,(3) 489-493.
- Friesen, C. K., Ristic, J., & Kingstone, A. (2004). Attentional effects of counterpredictive gaze and arrow cues. *Journal of Experimental Psychology-Human Perception and Performance*, 30,(2) 319-329.
- Frischen, A., Bayliss, A. P., & Tipper, S. P. (2007). Gaze cueing of attention: Visual attention, social cognition, and individual differences. *Psychological Bulletin*, 133,(4) 694-724.
- Frischen, A., Loach, D., & Tipper, S. P. (2009). Seeing the world through another person's eyes: Simulating selective attention via action observation. *Cognition*, 111,(2) 212-218.
- Frischen, A., & Tipper, S. P. (2004). Orienting attention via observed gaze shift evokes longer term inhibitory effects: Implications for social interactions, attention, and memory. *Journal of Experimental Psychology-General*, 133,(4) 516-533.
- Frischen, A., & Tipper, S. P. (2006). Long-term gaze cueing effects: Evidence for retrieval of prior states of attention from memory. *Visual Cognition*, 14,(3) 351-364.
- Frith, U., & Frith, C. D. (2003). Development and neurophysiology of mentalizing. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 358,(1431) 459-473.

- Gallagher, H. L., & Frith, C. D. (2003). Functional imaging of 'theory of mind'. *Trends in Cognitive Sciences*, 7,(2) 77-83.
- Gallagher, H. L., Jack, A. I., Roepstorff, A., & Frith, C. D. (2002). Imaging the intentional stance in a competitive game. *Neuroimage*, 16,(3) 814-821.
- Gallese, V. (2006). Intentional attunement: A neurophysiological perspective on social cognition and its disruption in autism. *Brain Research*, 1079, 15-24.
- Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, 119,(2) 593-609.
- Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Sciences*, 2,(12) 493-501.
- Ganel, T. (2006). The objects of face perception. *Neuron*, 50,(1) 7-10.
- Ganel, T., Goshen-Gottstein, Y., & Goodale, M. A. (2005). Interactions between the processing of gaze direction and facial expression. *Vision Research*, 45,(9) 1191-1200.
- Gauthier, I., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). Expertise for cars and birds recruits brain areas involved in face recognition. *Nature Neuroscience*, 3,(2) 191-197.
- Gauthier, I., & Tarr, M. J. (1997). Becoming a "greeble" expert: Exploring mechanisms for face recognition. *Vision Research*, 37,(12) 1673-1682.
- Gauthier, I., Tarr, M. J., Anderson, A. W., Skudlarski, P., & Gore, J. C. (1999). Activation of the middle fusiform 'face area' increases with expertise in recognizing novel objects. *Nature Neuroscience*, 2,(6) 568-573.
- Ge, L. Z., Wang, Z., McCleery, J. P., & Lee, K. (2006). Activation of face expertise and the inversion effect. *Psychological Science*, 17,(1) 12-16.
- George, N., & Conty, L. (2008). Facing the gaze of others. *Neurophysiologie Clinique-Clinical Neurophysiology*, 38,(3) 197-207.

- George, N., Dolan, R. J., Fink, G. R., Baylis, G. C., Russell, C., & Driver, J. (1999). Contrast polarity and face recognition in the human fusiform gyrus. *Nature Neuroscience*, 2,(6) 574-580.
- George, N., Driver, J., & Dolan, R. J. (2001). Seen gaze-direction modulates fusiform activity and its coupling with other brain areas during face processing. *Neuroimage*, 13,(6) 1102-1112.
- Getzmann, S., & Lewald, J. (2009). Constancy of target velocity as a critical factor in the emergence of auditory and visual representational momentum. *Experimental Brain Research*, 193,(3) 437-443.
- Giese, M. A., & Poggio, T. (2003). Neural mechanisms for the recognition of biological movements. *Nature Reviews Neuroscience*, 4,(3) 179-192.
- Gliga, T., & Csibra, G. (2007). Seeing the face through the eyes: A developmental perspective on face expertise. *Progress in Brain Research: From Action to Cognition*, 164, 323-339.
- Goffaux, V., & Rossion, B. (2007). Face inversion disproportionately impairs the perception of vertical but not horizontal relations between features. *Journal of Experimental Psychology-Human Perception and Performance*, 33,(4) 995-1002.
- Goffaux, V., Rossion, B., Sorger, B., Schiltz, C., & Goebel, R. (2009). Face inversion disrupts the perception of vertical relations between features in the right human occipito-temporal cortex. *Journal of Neuropsychology*, 3,(1) 45-67.
- Goldenfeld, N., Baron-Cohen, S., & Wheelwright, S. (2005). Empathizing and systemizing in males, females and autism. *Clinical Neuropsychiatry*, 2,(6) 338-345.
- Gopnik, A. (2003). The theory theory as an alternative to the innateness hypothesis. In Antony, L. & Hornstein, N. (Eds.), *Chomsky and his critics* (pp. 238-254). Oxford: Blackwells.
- Gorbet, D. J., & Sergio, L. E. (2009). The behavioural consequences of dissociating the spatial directions of eye and arm movements. *Brain Research*, 1284, 77-88.



- Goren, D., & Wilson, H. R. (2006). Quantifying facial expression recognition across viewing conditions. *Vision Research*, 46,(8-9) 1253-1262.
- Graf, M., Reitzner, B., Corves, C., Casile, A., Giese, M., & Prinz, W. (2007). Predicting point-light actions in real-time. *Neuroimage*, 36,(Supplement 2) T22-T32.
- Grafton, S. T., Arbib, M. A., Fadiga, L., & Rizzolatti, G. (1996). Localization of grasp representations in humans by positron emission tomography. 2. Observation compared with imagination. *Experimental Brain Research*, 112,(1) 103-111.
- Graham, R., & LaBar, K. S. (2007). Garner interference reveals dependencies between emotional expression and gaze in face perception. *Emotion*, 7,(2) 296-313.
- Gray, J. A. (1994). Three fundamental emotion systems. In Ekman, P. & Davidson, R. J. (Eds.), *The nature of emotion: Fundamental questions* (pp. 243-247). New York: Oxford University Press.
- Grezes, J., Armony, J. L., Rowe, J., & Passingham, R. E. (2003). Activations related to "mirror" and "canonical" neurones in the human brain: An fMRI study. *Neuroimage*, 18,(4) 928-937.
- Griffiths, P. E. (2003). Basic emotions, complex emotions, machiavellian emotions. In Hatzimoysis, A. (Ed.), *Philosophy and the Emotions*. Cambridge: Cambridge University Press.
- Grill-Spector, K., Knouf, N., & Kanwisher, N. (2004). The fusiform face area subserves face perception, not generic within-category identification. *Nature Neuroscience*, 7,(5) 555-562.
- Guo, K., Mahmoodi, S., Robertson, R. G., & Young, M. P. (2006). Longer fixation duration while viewing face images. *Experimental Brain Research*, 171,(1) 91-98.
- Guo, K., Robertson, R. G., Mahmoodi, S., Tadmor, Y., & Young, M. P. (2003). How do monkeys view faces? A study of eye movements. *Experimental Brain Research*, 150,(3) 363-374.

- Hadjikhani, N., Hoge, R., Snyder, J., & de Gelder, B. (2008). Pointing with the eyes: The role of gaze in communicating danger. *Brain and Cognition*, 68,(1) 1-8.
- Hager, J. C., & Ekman, P. (1983). The inner and outer meanings of facial expressions. In Cacioppo, J. T. & Petty, R. E. (Eds.), *Social Psychophysiology: A sourcebook*. New York: The Guilford Press.
- Hanna, J. E., & Brennan, S. E. (2007). Speakers' eye gaze disambiguates referring expressions early during face-to-face conversation. *Journal of Memory and Language*, 57,(4) 596-615.
- Hare, B., Call, J., & Tomasello, M. (2001). Do chimpanzees know what conspecifics know? *Animal Behaviour*, 61,(1) 139-151.
- Hare, B., & Tomasello, M. (2004). Chimpanzees are more skilful in competitive than in cooperative cognitive tasks. *Animal Behaviour*, 68,(3) 571-581.
- Haselton, M. G., & Buss, D. M. (2000). Error management theory: A new perspective on biases in cross-sex mind reading. *Journal of Personality and Social Psychology*, 78,(1) 81-91.
- Haselton, M. G., & Nettle, D. (2006). The paranoid optimist: An integrative evolutionary model of cognitive biases. *Personality and Social Psychology Review*, 10,(1) 47-66.
- Hassin, R. R., Aarts, H., & Ferguson, M. J. (2005). Automatic goal inferences. *Journal of Experimental Social Psychology*, 41,(2) 129-140.
- Hassin, R. R., Bargh, J. A., & Uleman, J. S. (2002). Spontaneous causal inferences. *Journal of Experimental Social Psychology*, 38,(5) 515-522.
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, 4,(6) 223-233.
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2002). Human neural systems for face recognition and social communication. *Biological Psychiatry*, 51,(1) 59-67.

- Hayes, A. E., Paul, M. A., Beuger, B., & Tipper, S. P. (2008). Self produced and observed actions influence emotion: The roles of action fluency and eye gaze. *Psychological Research-Psychologische Forschung*, 72,(4) 461-472.
- Hernandez, N., Metzger, A., Magne, R., Bonnet-Brilhaut, F., Roux, S., Barthelemy, C., & Martineau, J. (2009). Exploration of core features of a human face by healthy and autistic adults analyzed by visual scanning. *Neuropsychologia*, 47,(4) 1004-1012.
- Hershler, O., & Hochstein, S. (2005). At first sight: A high-level pop out effect for faces. *Vision Research*, 45,(13) 1707-1724.
- Hess, U., Adams, R. B., & Kleck, R. E. (2007). Looking at you or looking elsewhere: The influence of head orientation on the signal value of emotional facial expressions. *Motivation and Emotion*, 31,(2) 137-144.
- Heyes, C. M. (1998). Theory of mind in nonhuman primates. *Behavioral and Brain Sciences*, 21,(1) 101-114.
- Hietanen, J. K. (1999). Does your gaze direction and head orientation shift my visual attention? *Neuroreport*, 10,(16) 3443-3447.
- Hietanen, J. K., & Leppanen, J. M. (2003). Does facial expression affect attention orienting by gaze direction cues? *Journal of Experimental Psychology-Human Perception and Performance*, 29,(6) 1228-1243.
- Hietanen, J. K., Leppanen, J. M., Peltola, M. J., Linna-Aho, K., & Ruuhiala, H. J. (2008). Seeing direct and averted gaze activates the approach-avoidance motivational brain systems. *Neuropsychologia*, 46,(9) 2423-2430.
- Hoehl, S., & Striano, T. (2008). Neural processing of eye gaze and threat-related emotional facial expressions in infancy. *Child Development*, 79,(6) 1752-1760.
- Hoehl, S., Wiese, L., & Striano, T. (2008). Young infants' neural processing of objects is affected by eye gaze direction and emotional expression. *PLoS One*, 3,(6) e2389.

- Hoffman, E. A., & Haxby, J. V. (2000). Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nature Neuroscience*, 3,(1) 80-84.
- Hoffman, K. L., Gothard, K. M., Schmid, M. C., & Logothetis, N. K. (2007). Facial-expression and gaze-selective responses in the monkey amygdala. *Current Biology*, 17,(9) 766-772.
- Hollands, M. A., Patla, A. E., & Vickers, J. N. (2002). "Look where you're going!": Gaze behaviour associated with maintaining and changing the direction of locomotion. *Experimental Brain Research*, 143,(2) 221-230.
- Hood, B. M., Macrae, C. N., Cole-Davies, V., & Dias, M. (2003). Eye remember you: The effects of gaze direction on face recognition in children and adults. *Developmental Science*, 6,(1) 67-71.
- Hori, E., Tazumi, T., Umeno, K., Kamachi, M., Kobayashi, T., Ono, T., & Nishijo, H. (2005). Effects of facial expression on shared attention mechanisms. *Physiology & Behavior*, 84,(3) 397-405.
- Hubbard, T. L. (1995). Cognitive representation of motion: Evidence for friction and gravity analogs. *Journal of Experimental Psychology-Learning Memory and Cognition*, 21,(1) 241-254.
- Hubbard, T. L. (1997). Target size and displacement along the axis of implied gravitational attraction: Effects of implied weight and evidence of representational gravity. *Journal of Experimental Psychology-Learning Memory and Cognition*, 23,(6) 1484-1493.
- Hubbard, T. L. (1998). Some effects of representational friction, target size, and memory averaging on memory for vertically moving targets. *Canadian Journal of Experimental Psychology-Revue Canadienne De Psychologie Experimentale*, 52,(1) 44-49.

- Hubbard, T. L. (2005). Representational momentum and related displacements in spatial memory: A review of the findings. *Psychonomic Bulletin & Review*, 12,(5) 822-851.
- Hubbard, T. L. (2006). Bridging the gap: Possible roles and contributions of representational momentum. *Psicologica*, 27,(1) 1-34.
- Hubbard, T. L., Blessum, J. A., & Ruppel, S. E. (2001). Representational momentum and Michotte's (1946/1963) "launching effect" paradigm. *Journal of Experimental Psychology-Learning Memory and Cognition*, 27,(1) 294-301.
- Hubbard, T. L., & Favretto, A. (2003). Naive impetus and Michotte's "tool effect": Evidence from representational momentum. *Psychological Research-Psychologische Forschung*, 67,(2) 134-152.
- Hubbard, T. L., & Ruppel, S. E. (2002). A possible role of naive impetus in Michotte's "launching effect": Evidence from representational momentum. *Visual Cognition*, 9,(1-2) 153-176.
- Husk, J. S., Bennett, P. J., & Sekuler, A. B. (2007). Inverting houses and textures: Investigating the characteristics of learned inversion effects. *Vision Research*, 47,(27) 3350-3359.
- Hynes, C. A., Baird, A. A., & Grafton, S. T. (2006). Differential role of the orbital frontal lobe in emotional versus cognitive perspective-taking. *Neuropsychologia*, 44,(3) 374-383.
- Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J. C., & Rizzolatti, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *Plos Biology*, 3,(3) 529-535.
- Jacob, P., & Jeannerod, M. (2005). The motor theory of social cognition: A critique. *Trends in Cognitive Sciences*, 9,(1) 21-25.
- Jarraya, M., Amorim, M. A., & Bardy, B. G. (2005). Optical flow and viewpoint change modulate the perception and memorization of complex motion. *Perception & Psychophysics*, 67,(6) 951-961.

- Jeannerod, M. (2001). Neural simulation of action: A unifying mechanism for motor cognition. *Neuroimage*, 14,(1) S103-S109.
- Jellema, T., Baker, C. I., Wicker, B., & Perrett, D. I. (2000). Neural representation for the perception of the intentionality of actions. *Brain and Cognition*, 44,(2) 280-302.
- Jellema, T., Lorteije, J., van Rijn, S., van t' Wout, M., de Haan, E., van Engeland, H., & Kemner, C. (2009). Involuntary Interpretation of Social Cues is Compromised in Autism Spectrum Disorders. *Autism Research*, 2,(4) 192-204.
- Jellema, T., & Perrett, D. (2005). Neural basis for the perception of goal directed actions. In Easton, A. & Emery, N. (Eds.), *The cognitive neuroscience of social behaviour*. UK: Psychology Press.
- Jellema, T., & Perrett, D. (2007). Neural pathways of social cognition. In Dunbar, R. I. M. & Barrett, L. (Eds.), *The Oxford handbook of evolutionary psychology*. Oxford/New York: Oxford University Press.
- Jellema, T., & Perrett, D. I. (2003a). Cells in monkey STS responsive to articulated body motions and consequent static posture: A case of implied motion? *Neuropsychologia*, 41,(13) 1728-1737.
- Jellema, T., & Perrett, D. I. (2003b). Perceptual history influences neural responses to face and body postures. *Journal of Cognitive Neuroscience*, 15,(7) 961-971.
- Jellema, T., & Perrett, D. I. (2006). Neural representations of perceived bodily actions using a categorical frame of reference. *Neuropsychologia*, 44,(9) 1535-1546.
- Jenkins, J., & Langton, S. R. H. (2003). Configural processing in the perception of eye-gaze direction. *Perception*, 32,(10) 1181-1188.
- Johnson, M. H. (2005). Subcortical face processing. *Nature Reviews Neuroscience*, 6,(10) 766-774.
- Johnson, M. H., Griffin, R., Csibra, G., Halit, H., Farroni, T., De Haan, M., Tucker, L. A., Baron-Cohen, S., & Richards, J. (2005). The emergence of the social brain

- network: Evidence from typical and atypical development. *Development and Psychopathology*, 17,(3) 599-619.
- Johnson, M. H., Grossmann, T., & Farroni, T. (2008). The social cognitive neuroscience of infancy: Illuminating the early development of social brain functions. *Advances in Child Development and Behavior*, 36, 331-372.
- Johnson, S. (2000). The recognition of mentalistic agents in infancy. *Trends in Cognitive Sciences*, 4,(1) 22-28.
- Johnson, S., Slaughter, V., & Carey, S. (1998). Whose gaze will infants follow? The elicitation of gaze following in 12-month-olds. *Developmental Science*, 1,(2) 233-238.
- Johnson, S. C. (2003). Detecting agents. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 358,(1431) 549-559.
- Joseph, J. E., Gathers, A. D., Liu, X., Corbly, C. R., Whitaker, S. K., & Bhatt, R. S. (2006). Neural developmental changes in processing inverted faces. *Cognitive Affective & Behavioral Neuroscience*, 6,(3) 223-235.
- Kadosh, K. C., & Johnson, M. H. (2007). Developing a cortex specialized for face perception. *Trends in Cognitive Sciences*, 11,(9) 367-369.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, 17,(11) 4302-4311.
- 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,(4) 779-783.
- Kelly, M. H., & Freyd, J. J. (1987). Explorations of representational momentum. *Cognitive Psychology*, 19,(3) 369-401.

- Kemner, C., Schuller, A. M., & van Engeland, H. (2006). Electrocortical reflections of face and gaze processing in children with pervasive developmental disorder. *Journal of Child Psychology and Psychiatry*, 47,(10) 1063-1072.
- Kerzel, D. (2000). Eye movements and visible persistence explain the mislocalization of the final position of a moving target. *Vision Research*, 40,(27) 3703-3715.
- Kerzel, D. (2002). The locus of "memory displacement" is at least partially perceptual: Effects of velocity, expectation, friction, memory averaging, and weight. *Perception & Psychophysics*, 64,(4) 680-692.
- Kerzel, D. (2005). Representational momentum beyond internalized physics: Embodied mechanisms of anticipation cause errors in visual short-term memory. *Current Directions in Psychological Science*, 14,(4) 180-184.
- Kerzel, D. (2006). Why eye movements and perceptual factors have to be controlled in studies on "representational momentum". *Psychonomic Bulletin & Review*, 13,(1) 166-173.
- Keysers, C., & Gazzola, V. (2006). Towards a unifying neural theory of social cognition. *Progress in Brain Research: Understanding Emotions*, 156, 379-401.
- Keysers, C., & Gazzola, V. (2007). Integrating simulation and theory of mind: From self to social cognition. *Trends in Cognitive Sciences*, 11,(5) 194-196.
- Kleiner, K. A., & Banks, M. S. (1987). Stimulus energy does not account for 2-month-olds face preferences. *Journal of Experimental Psychology-Human Perception and Performance*, 13,(4) 594-600.
- Kloth, N., & Schweinberger, S. R. (2008). The temporal decay of eye gaze adaptation effects. *Journal of Vision*, 8,(11) 1-11.
- Klucharev, V., & Sams, M. (2004). Interaction of gaze direction and facial expressions processing: ERP study. *Neuroreport*, 15,(4) 621-625.
- Kluttz, N. L., Mayes, B. R., West, R. W., & Kerby, D. S. (2009). The effect of head turn on the perception of gaze. *Vision Research*, 49,(15) 1979-1993.



- Kourtzi, Z., & Kanwisher, N. (2000). Activation in human MT/MST by static images with implied motion. *Journal of Cognitive Neuroscience*, 12,(1) 48-55.
- Kourtzi, Z., & Shiffrar, M. (1999). Dynamic representations of human body movement. *Perception*, 28,(1) 49-62.
- Kuhn, G., & Kingstone, A. (2009). Look away! Eyes and arrows engage oculomotor responses automatically. *Attention Perception & Psychophysics*, 71,(2) 314-327.
- Kuzmanovic, B., Georgescu, A. L., Eickhoff, S. B., Shah, N. J., Bente, G., Fink, G. R., & Vogeley, K. (2009). Duration matters: Dissociating neural correlates of detection and evaluation of social gaze. *Neuroimage*, 46,(4) 1154-1163.
- Kylliainen, A., & Hietanen, J. K. (2004). Attention orienting by another's gaze direction in children with autism. *Journal of Child Psychology and Psychiatry*, 45,(3) 435-444.
- Lambrey, S., Amorim, M. A., Samson, S., Noulhiane, M., Hasboun, D., Dupont, S., Baulac, M., & Berthoz, A. (2008). Distinct visual perspective-taking strategies involve the left and right medial temporal lobe structures differently. *Brain*, 131,(2) 523-534.
- Land, M., Mennie, N., & Rusted, J. (1999). The roles of vision and eye movements in the control of activities of daily living. *Perception*, 28,(11) 1311-1328.
- Land, M. F., & Furneaux, S. (1997). The knowledge base of the oculomotor system. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, 352,(1358) 1231-1239.
- Lang, P. J., & Davis, M. (2006). Emotion, motivation and the brain: Reflex foundations in animal and human research. *Progress in Brain Research: Understanding Emotions*, 156, 3-29.
- Langleben, D. D., Schroeder, L., Maldjian, J. A., Gur, R. C., McDonald, S., Ragland, J. D., O'Brien, C. P., & Childress, A. R. (2002). Brain activity during simulated deception: An event-related functional magnetic resonance study. *Neuroimage*, 15,(3) 727-732.

- Large, M. E., Cavina-Pratesi, C., Vilis, T., & Culharn, J. C. (2008). The neural correlates of change detection in the face perception network. *Neuropsychologia*, 46,(8) 2169-2176.
- Leder, H., & Bruce, V. (2000). When inverted faces are recognized: The role of configural information in face recognition. *Quarterly Journal of Experimental Psychology Section a-Human Experimental Psychology*, 53,(2) 513-536.
- Leder, H., Candrian, G., Huber, O., & Bruce, V. (2001). Configural features in the context of upright and inverted faces. *Perception*, 30,(1) 73-83.
- Leder, H., & Carbon, C. C. (2006). Face-specific configural processing of relational information. *British Journal of Psychology*, 97,(1) 19-29.
- Lee, K., Eskritt, M., Symons, L. A., & Muir, D. (1998). Children's use of triadic eye gaze information for "mind reading". *Developmental Psychology*, 34,(3) 525-539.
- Leopold, D. A., O'Toole, A. J., Vetter, T., & Blanz, V. (2001). Prototype-referenced shape encoding revealed by high-level after effects. *Nature Neuroscience*, 4,(1) 89-94.
- Leopold, D. A., Rhodes, G., Muller, K. M., & Jeffery, L. (2005). The dynamics of visual adaptation to faces. *Proceedings of the Royal Society B-Biological Sciences*, 272,(1566) 897-904.
- Leslie, A. M. (1994). ToMM, ToBy, and Agency: Core architecture and domain specificity. In Hirschfeld, L. & Gelman, S. (Eds.), *Mapping the mind: Domain specificity in cognition and culture* (pp. 119–148). New York: Cambridge University Press.
- Leube, D. T., Yoon, H. W., Rapp, A., Erb, M., Grodd, W., Bartels, M., & Kircher, T. T. J. (2003). Brain regions sensitive to the face inversion effect: A functional magnetic resonance imaging study in humans. *Neuroscience Letters*, 342,(3) 143-146.
- Lieberman, M. D. (2003). Reflective and reflexive judgment processes: A social cognitive neuroscience approach. In Forgas, J. P., Williams, K. R. & von Hippel, W. (Eds.), *Social Judgments: Implicit and Explicit Processes* (pp. 46-67). New York: Cambridge University Press.

- Liu, C. H., & Chaudhuri, A. (2003). What determines whether faces are special? *Visual Cognition*, 10,(4) 385-408.
- Lobmaier, J. S., Fischer, M. H., & Schwaninger, A. (2006). Objects capture perceived gaze direction. *Experimental Psychology*, 53,(2) 117-122.
- Loffler, G., Yourganov, G., Wilkinson, F., & Wilson, H. R. (2005). fMRI evidence for the neural representation of faces. *Nature Neuroscience*, 8,(10) 1386-1390.
- Lorteije, J. A. M., Kenemans, J. L., Jellema, T., van der Lubbe, R. H. J., de Heer, F., & van Wezel, R. J. A. (2006). Delayed response to animate implied motion in human motion processing areas. *Journal of Cognitive Neuroscience*, 18,(2) 158-168.
- Lorteije, J. A. M., Kenemans, J. L., Jellema, T., van der Lubbe, R. H. J., Lommers, M. W., & van Wezel, R. J. A. (2007). Adaptation to real motion reveals direction-selective interactions between real and implied motion processing. *Journal of Cognitive Neuroscience*, 19,(8) 1231-1240.
- Loucks, J., & Baldwin, D. (2009). Sources of information for discriminating dynamic human actions. *Cognition*, 111,(1) 84-97.
- Luo, Y., & Baillargeon, R. (2005). Can a self-propelled box have a goal? Psychological reasoning in 5-month-old infants. *Psychological Science*, 16,(8) 601-608.
- Luo, Y., & Baillargeon, R. (2007). Do 12.5-month-old infants consider what objects others can see when interpreting their actions? *Cognition*, 105,(3) 489-512.
- Luo, Y. Y., & Johnson, S. C. (2009). Recognizing the role of perception in action at 6 months. *Developmental Science*, 12,(1) 142-149.
- Macrae, C. N., Hood, B. M., Milne, A. B., Rowe, A. C., & Mason, M. F. (2002). Are you looking at me? Eye gaze and person perception. *Psychological Science*, 13,(5) 460-464.
- Makin, A. D. J., Stewart, A. J., & Poliakoff, E. (2009). Typical object velocity influences motion extrapolation. *Experimental Brain Research*, 193,(1) 137-142.

- Massaro, D. W., & Egan, P. B. (1996). Perceiving affect from the voice and the face. *Psychonomic Bulletin & Review*, 3,(2) 215-221.
- Materna, S., Dicke, P. W., & Thier, P. (2008). Dissociable roles of the superior temporal sulcus and the intraparietal sulcus in joint attention: A functional magnetic resonance Imaging study. *Journal of Cognitive Neuroscience*, 20,(1) 108-119.
- Mathews, A., Fox, E., Yiend, J., & Calder, A. (2003). The face of fear: Effects of eye gaze and emotion on visual attention. *Visual Cognition*, 10,(7) 823-835.
- Maurer, D., Grand, R. L., & Mondloch, C. J. (2002). The many face of configural processing. *Trends in Cognitive Sciences*, 6,(6) 255-260.
- Maus, G. W., & Nijhawan, R. (2006). Forward displacements of fading objects in motion: The role of transient signals in perceiving position. *Vision Research*, 46,(26) 4375-4381.
- Mazard, A., Schiltz, C., & Rossion, B. (2006). Recovery from adaptation to facial identity is larger for upright than inverted faces in the human occipito-temporal cortex. *Neuropsychologia*, 44,(6) 912-922.
- McCabe, K., Houser, D., Ryan, L., Smith, V., & Trouard, T. (2001). A functional imaging study of cooperation in two-person reciprocal exchange. *Proceedings of the National Academy of Sciences of the United States of America*, 98,(20) 11832-11835.
- McCleery, J. P., Zhang, L. Y., Ge, L. Z., Wang, Z., Christiansen, E. M., Lee, K., & Cottrell, G. W. (2008). The roles of visual expertise and visual input in the face inversion effect: Behavioral and neurocomputational evidence. *Vision Research*, 48,(5) 703-715.
- Mehu, M., Grammer, K., & Dunbar, R. I. M. (2007). Smiles when sharing. *Evolution and Human Behavior*, 28,(6) 415-422.

- Mehu, M., Little, A. C., & Dunbar, R. I. M. (2007). Duchenne smiles and the perception of generosity and sociability in faces. *Journal of Evolutionary Psychology*, 5,(1-4) 133-146.
- Melis, A. P., Call, J., & Tomasello, M. (2006). Chimpanzees (*Pan troglodytes*) conceal visual and auditory information from others. *Journal of Comparative Psychology*, 120,(2) 154-162.
- Meltzoff, A. N. (2005). Imitation and other minds: The "Like Me" hypothesis. In Hurley, S. & Chater, N. (Eds.), *Perspectives on imitation: From cognitive neuroscience to social science* (pp. 55-77). Cambridge: MIT Press.
- Meltzoff, A. N. (2007a). The 'like me' framework for recognizing and becoming an intentional agent. *Acta Psychologica*, 124,(1) 26-43.
- Meltzoff, A. N. (2007b). 'Like me': A foundation for social cognition. *Developmental Science*, 10,(1) 126-134.
- Metzger, M. M. (2001). Which transformations of stimuli are the most disruptive to facial recognition? *Perceptual and Motor Skills*, 92,(2) 517-526.
- Miall, R. C. (2003). Connecting mirror neurons and forward models. *NeuroReport*, 14,(17) 2135-2137.
- Michelon, P., & Zacks, J. M. (2006). Two kinds of visual perspective taking. *Perception & Psychophysics*, 68,(2) 327-337.
- Mitchell, J. P. (2005). The false dichotomy between simulation and theory-theory: The argument's error. *Trends in Cognitive Sciences*, 9,(8) 363-364.
- Mondloch, C. J., Geldart, S., Maurer, D., & Le Grand, R. (2003). Developmental changes in face processing skills. *Journal of Experimental Child Psychology*, 86,(1) 67-84.
- Morewedge, C. K., Preston, J., & Wegner, D. M. (2007). Timescale bias in the attribution of mind. *Journal of Personality and Social Psychology*, 93,(1) 1-11.

- Morris, J. P., Pelphrey, K. A., & McCarthy, G. (2006). Occipitotemporal activation evoked by the perception of human bodies is modulated by the presence or absence of the face. *Neuropsychologia*, 44,(10) 1919-1927.
- Morris, J. S., Friston, K. J., Buchel, C., Frith, C. D., Young, A. W., Calder, A. J., & Dolan, R. J. (1998). A neuromodulatory role for the human amygdala in processing emotional facial expressions. *Brain*, 121,(1) 47-57.
- Morton, J., & Johnson, M. H. (1991). Conspic and Conlern: A 2-process theory of infant face recognition. *Psychological Review*, 98,(2) 164-181.
- Mosconi, M. W., Mack, P. B., McCarthy, G., & Pelphrey, K. A. (2005). Taking an "intentional stance" on eye-gaze shifts: A functional neuroimaging study of social perception in children. *Neuroimage*, 27,(1) 247-252.
- Munger, M. P., & Minchew, J. H. (2002). Parallels between remembering and predicting an object's location. *Visual Cognition*, 9,(1-2) 177-194.
- Munger, M. P., Solberg, J. L., & Horrocks, K. K. (1999). The relationship between mental rotation and representational momentum. *Journal of Experimental Psychology-Learning Memory and Cognition*, 25,(6) 1557-1568.
- Munger, M. P., Solberg, J. L., Horrocks, K. K., & Preston, A. S. (1999). Representational momentum for rotations in depth: Effects of shading and axis. *Journal of Experimental Psychology-Learning Memory and Cognition*, 25,(1) 157-171.
- Nachson, I., & Shechory, M. (2002). Effect of inversion on the recognition of external and internal facial features. *Acta Psychologica*, 109,(3) 227-238.
- Nagai, M., Kazai, K., & Yagi, A. (2002). Larger forward memory displacement in the direction of gravity. *Visual Cognition*, 9,(1-2) 28-40.
- Narumoto, J., Okada, T., Sadato, N., Fukui, K., & Yonekura, Y. (2001). Attention to emotion modulates fMRI activity in human right superior temporal sulcus. *Cognitive Brain Research*, 12,(2) 225-231.

- Nation, K., & Penny, S. (2008). Sensitivity to eye gaze in autism: Is it normal? Is it automatic? Is it social? *Development and Psychopathology*, 20,(1) 79-97.
- Nelson, C. A. (2001). The development and neural bases of face recognition. *Infant and Child Development*, 10,(1-2) 3-18.
- Neri, P., Morrone, M. C., & Burr, D. C. (1998). Seeing biological motion. *Nature*, 395,(6705) 894-896.
- Nesse, R. M. (1990). Evolutionary explanations of emotions. *Human Nature*, 1,(3) 261-289.
- Neuhoff, J. G. (1998). Perceptual bias for rising tones. *Nature*, 395,(6698) 123-124.
- Neuhoff, J. G. (2001). An adaptive bias in the perception of looming auditory motion. *Ecological Psychology*, 13,(2) 87-110.
- New, J., Cosmides, L., & Tooby, J. (2007). Category-specific attention for animals reflects ancestral priorities, not expertise. *Proceedings of the National Academy of Sciences of the United States of America*, 104,(42) 16598-16603.
- Nummenmaa, L., Hyönä, J., & Hietanen, J. K. (2009). I'll walk this way: Eyes reveal the direction of locomotion and make passersby look and go the other way. *Psychological Science*, 20,(12) 1454-1458.
- O'Toole, A. J., Roark, D. A., & Abdi, H. (2002). Recognizing moving faces: A psychological and neural synthesis. *Trends in Cognitive Sciences*, 6,(6) 261-266.
- Oommen, B. S., Smith, R. M., & Stahl, J. S. (2004). The influence of future gaze orientation upon eye-head coupling during saccades. *Experimental Brain Research*, 155,(1) 9-18.
- Oosterhof, N. N., & Todorov, A. (2008). The functional basis of face evaluation. *Proceedings of the National Academy of Sciences of the United States of America*, 105,(32) 11087-11092.

- Oram, M. W., & Perrett, D. I. (1996). Integration of form and motion in the anterior superior temporal polysensory area (STPa) of the macaque monkey. *Journal of Neurophysiology*, 76,(1) 109-129.
- Pascalis, O., & Kelly, D. J. (2009). The origins of face processing in humans: Phylogeny and ontogeny. *Perspectives on Psychological Science*, 4,(2) 200-209.
- Passarotti, A. M., Smith, J., DeLano, M., & Huang, J. (2007). Developmental differences in the neural bases of the face inversion effect show progressive tuning of face-selective regions to the upright orientation. *Neuroimage*, 34,(4) 1708-1722.
- Pavlova, M., & Sokolov, A. (2003). Prior knowledge about display inversion in biological motion perception. *Perception*, 32,(8) 937-946.
- Pecchinenda, A., Pes, M., Ferlazzo, F., & Zoccolotti, P. (2008). The combined effect of gaze direction and facial expression on cueing spatial attention. *Emotion*, 8,(5) 628-634.
- Peelen, M. V., & Downing, P. E. (2005). Selectivity for the human body in the fusiform gyrus. *Journal of Neurophysiology*, 93,(1) 603-608.
- Peelen, M. V., & Downing, P. E. (2007). The neural basis of visual body perception. *Nature Reviews Neuroscience*, 8,(8) 636-648.
- Peigneux, P., Salmon, E., van der Linden, M., Garraux, G., Aerts, J., Delfiore, G., Degueldre, C., Luxen, A., Orban, G., & Franck, G. (2000). The role of lateral occipitotemporal junction and area MT/V5 in the visual analysis of upper-limb postures. *Neuroimage*, 11,(6) 644-655.
- Pelphrey, K. A., Morris, J. P., Michelich, C. R., Allison, T., & McCarthy, G. (2005). Functional anatomy of biological motion perception in posterior temporal cortex: An fMRI study of eye, mouth and hand movements. *Cerebral Cortex*, 15,(12) 1866-1876.



- Pelphrey, K. A., Sasson, N. J., Reznick, J. S., Paul, G., Goldman, B. D., & Piven, J. (2002). Visual scanning of faces in autism. *Journal of Autism and Developmental Disorders*, 32,(4) 249-261.
- Pelphrey, K. A., Singerman, J. D., Allison, T., & McCarthy, G. (2003). Brain activation evoked by perception of gaze shifts: The influence of context. *Neuropsychologia*, 41,(2) 156-170.
- Pelphrey, K. A., Viola, R. J., & McCarthy, G. (2004). When strangers pass: Processing of mutual and averted social gaze in the superior temporal sulcus. *Psychological Science*, 15,(9) 598-603.
- Perrett, D. I., Harries, M. H., Bevan, R., Thomas, S., Benson, P. J., Mistlin, A. J., Chitty, A. J., Hietanen, J. K., & Ortega, J. E. (1989). Frameworks of analysis for the neural representation of animate objects and actions. *Journal of Experimental Biology*, 146,(1) 87-113.
- Perrett, D. I., Hietanen, J. K., Oram, M. W., & Benson, P. J. (1992). Organization and functions of cells responsive to faces in the temporal cortex. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, 335,(1273) 23-30.
- Perrett, D. I., Rolls, E. T., & Cavan, W. (1982). Visual neurones responsive to faces in the monkey temporal cortex. *Experimental Brain Research*, 47,(3) 329-342.
- Perrett, D. I., Smith, P. A. J., Potter, D. D., Mistlin, A. J., Head, A. S., Milner, A. D., & Jeeves, M. A. (1985). Visual cells in the temporal cortex sensitive to face view and gaze direction. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 223,(1232) 293-317.
- Perrett, D. I., Xiao, D., Jellema, T., Barraclough, N., & Oram, M. W. (2006). Social perception from static and dynamic visual information. *Perception*, 35,(ECP Abstract Supplement) 120-120.

- Phillips, A. T., Wellman, H. M., & Spelke, E. S. (2002). Infants' ability, to connect gaze and emotional expression to intentional action. *Cognition*, 85,(1) 53-78.
- Phillips, M. L., Young, A. W., Scott, S. K., Calder, A. J., Andrew, C., Giampietro, V., Williams, S. C. R., Bullmore, E. T., Brammer, M., & Gray, J. A. (1998). Neural responses to facial and vocal expressions of fear and disgust. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 265,(1408) 1809-1817.
- Phillips, W., Baron-Cohen, S., & Rutter, M. (1992). The role of eye contact in goal detection: Evidence from normal infants and children with autism or mental handicap. *Development and Psychopathology*, 4,(3) 375-383.
- Pierno, A. C., Becchio, C., Tubaldi, F., Turella, L., & Castiello, U. (2008). Motor ontology in representing gaze-object relations. *Neuroscience Letters*, 430,(3) 246-251.
- Pierno, A. C., Becchio, C., Wall, M. B., Smith, A. T., Turella, L., & Castiello, U. (2006). When gaze turns into grasp. *Journal of Cognitive Neuroscience*, 18,(12) 2130-2137.
- Pinsk, M. A., DeSimone, K., Moore, T., Gross, C. G., & Kastner, S. (2005). Representations of faces and body parts in macaque temporal cortex: A functional MRI study. *Proceedings of the National Academy of Sciences of the United States of America*, 102,(19) 6996-7001.
- Pitcher, D., Walsh, V., Yovel, G., & Duchaine, B. (2007). TMS evidence for the involvement of the right occipital face area in early face processing. *Current Biology*, 17,(18) 1568-1573.
- Potter, T., & Corneille, O. (2008). Locating attractiveness in the face space: Faces are more attractive when closer to their group prototype. *Psychonomic Bulletin & Review*, 15,(3) 615-622.
- Povinelli, D. J., Bering, J. M., & Giambrone, S. (2000). Toward a science of other minds: Escaping the argument by analogy. *Cognitive Science*, 24,(3) 509-541.

- Preston, S. D., & de Waal, F. B. M. (2002). Empathy: Its ultimate and proximate bases. *Behavioral and Brain Sciences*, 25,(1) 1-20.
- Puce, A., & Perrett, D. (2003). Electrophysiology and brain imaging of biological motion. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, 358,(1431) 435-445.
- Rakison, D. H., & Poulin-Dubois, D. (2001). Developmental origin of the animate-inanimate distinction. *Psychological Bulletin*, 127,(2) 209-228.
- Ramnani, N., & Miall, R. C. (2004). A system in the human brain for predicting the actions of others. *Nature Neuroscience*, 7,(1) 85-90.
- Redcay, E. (2008). The superior temporal sulcus performs a common function for social and speech perception: Implications for the emergence of autism. *Neuroscience and Biobehavioral Reviews*, 32,(1) 123-142.
- Reed, C. L., Stone, V. E., Bozova, S., & Tanaka, J. (2003). The body-inversion effect. *Psychological Science*, 14,(4) 302-308.
- Reed, C. L., Stone, V. E., Grubb, J. D., & McGoldrick, J. E. (2006). Turning configural processing upside down: Part and whole body postures. *Journal of Experimental Psychology-Human Perception and Performance*, 32,(1) 73-87.
- Repacholi, B. M. (1998). Infants' use of attentional cues to identify the referent of another person's emotional expression. *Developmental Psychology*, 34,(5) 1017-1025.
- Rhodes, G., Brake, S., & Atkinson, A. P. (1993). Whats lost in inverted faces. *Cognition*, 47,(1) 25-57.
- Rhodes, G., & Jeffery, L. (2006). Adaptive norm-based coding of facial identity. *Vision Research*, 46,(18) 2977-2987.
- Ricciardelli, P., Baylis, G., & Driver, J. (2000). The positive and negative of human expertise in gaze perception. *Cognition*, 77,(1) B1-B14.
- Ricciardelli, P., Bonfiglioli, C., Iani, C., Rubichi, S., & Nicoletti, R. (2007). Spatial coding and central patterns: Is there something special about the eyes? *Canadian Journal*

*of Experimental Psychology-Revue Canadienne De Psychologie Experimentale*, 61,(2) 79-90.

Ricciardelli, P., & Driver, J. (2008). Effects of head orientation on gaze perception: How positive congruency effects can be reversed. *Quarterly Journal of Experimental Psychology*, 61,(3) 491-504.

Riesenhuber, M., Jarudi, I., Gilad, S., & Sinha, P. (2004). Face processing in humans is compatible with a simple shape-based model of vision. *Proceedings of the Royal Society B-Biological Sciences*, 271,(Suppl 6) S448-S450.

Ristic, J., Mottron, L., Friesen, C. K., Iarocci, G., Burack, J. A., & Kingstone, A. (2005). Eyes are special but not for everyone: The case of autism. *Cognitive Brain Research*, 24,(3) 715-718.

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27, 169-192.

Rizzolatti, G., Fadiga, L., Fogassi, L., & Gallese, V. (1999). Resonance behaviors and mirror neurons. *Archives Italiennes De Biologie*, 137,(2-3) 85-100.

Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*, 3,(2) 131-141.

Rochat, M. J., Serra, E., Fadiga, L., & Gallese, V. (2008). The evolution of social cognition: Goal familiarity shapes monkeys' action understanding. *Current Biology*, 18,(3) 227-232.

Rogers, T. T., Hocking, J., Mechelli, A., Patterson, K., & Price, C. (2005). Fusiform activation to animals is driven by the process, not the stimulus. *Journal of Cognitive Neuroscience*, 17,(3) 434-445.

Rosenblum, L. D., Yakel, D. A., & Green, K. P. (2000). Face and mouth inversion effects on visual and audiovisual speech perception. *Journal of Experimental Psychology-Human Perception and Performance*, 26,(2) 806-819.

- Rossion, B., Schiltz, C., & Crommelinck, M. (2003). The functionally defined right occipital and fusiform "face areas" discriminate novel from visually familiar faces. *Neuroimage*, 19,(3) 877-883.
- Rotman, G., Troje, N. F., Johansson, R. S., & Flanagan, J. R. (2006). Eye movements when observing predictable and unpredictable actions. *Journal of Neurophysiology*, 96,(3) 1358-1369.
- Rotshtein, P., Henson, R. N. A., Treves, A., Driver, J., & Dolan, R. J. (2005). Morphing Marilyn into Maggie dissociates physical and identity face representations in the brain. *Nature Neuroscience*, 8,(1) 107-113.
- Rowe, A. D., Bullock, P. R., Polkey, C. E., & Morris, R. G. (2001). 'Theory of mind' impairments and their relationship to executive functioning following frontal lobe excisions. *Brain*, 124,(3) 600-616.
- Ruby, P., & Decety, J. (2003). What you believe versus what you think they believe: A neuroimaging study of conceptual perspective-taking. *European Journal of Neuroscience*, 17,(11) 2475-2480.
- Russell, J. A. (1997). How shall an emotion be called? In Plutchik, R. & Conte, H. R. (Eds.), *Circumplex Models of Personality and Emotions* (pp. 205-220). Washington D.C.: American Psychological Association.
- Sander, D., Grandjean, D., Kaiser, S., Wehrle, T., & Scherer, K. R. (2007). Interaction effects of perceived gaze direction and dynamic facial expression: Evidence for appraisal theories of emotion. *European Journal of Cognitive Psychology*, 19,(3) 470-480.
- Sangrigoli, S., & de Schonen, S. (2004). Effect of visual experience on face processing: A developmental study of inversion and non-native effects. *Developmental Science*, 7,(1) 74-87.
- Santos, I. M., & Young, A. W. (2008). Effects of inversion and negation on social inferences from faces. *Perception*, 37,(7) 1061-1078.

- Santos, L., & Hauser, M. D. (1999). How monkeys see the eyes: Cotton-top tamarins reaction to changes in visual attention and action. *Animal Cognition*, 2,(3) 131-139.
- Sato, W., Yoshikawa, S., Kochiyama, T., & Matsumura, M. (2004). The amygdala processes the emotional significance of facial expressions: An fMRI investigation using the interaction between expression and face direction. *Neuroimage*, 22,(2) 1006-1013.
- Satpute, A. B., & Lieberman, M. D. (2006). Integrating automatic and controlled processes into neurocognitive models of social cognition. *Brain Research*, 1079, 86-97.
- Saxe, R. (2006). Uniquely human social cognition. *Current Opinion in Neurobiology*, 16,(2) 235-239.
- Saxe, R., Xiao, D. K., Kovacs, G., Perrett, D. I., & Kanwisher, N. (2004). A region of right posterior superior temporal sulcus responds to observed intentional actions. *Neuropsychologia*, 42,(11) 1435-1446.
- Scerif, G., Gomez, J. C., & Byrne, R. W. (2004). What do Diana monkeys know about the focus of attention of a conspecific? *Animal Behaviour*, 68,(6) 1239-1247.
- Scharlemann, J. P. W., Eckel, C. C., Kacelnik, A., & Wilson, R. K. (2001). The value of a smile: Game theory with a human face. *Journal of Economic Psychology*, 22,(5) 617-640.
- Schmidt, K. L., & Cohn, J. F. (2001). Human facial expressions as adaptations: Evolutionary questions in facial expression research. *Yearbook of Physical Anthropology*, 44, 3-24.
- Scholl, B. J., & Leslie, A. M. (1999). Modularity, development and 'theory of mind'. *Mind & Language*, 14,(1) 131-153.
- Schwaninger, A., Lobmaier, J. S., & Fischer, M. H. (2005). The inversion effect on gaze perception reflects processing of component information. *Experimental Brain Research*, 167,(1) 49-55.

- Schwarzlose, R. F., Baker, C. I., & Kanwisher, N. (2005). Separate face and body selectivity on the fusiform gyrus. *Journal of Neuroscience*, 25,(47) 11055-11059.
- Searcy, J. H., & Bartlett, J. C. (1996). Inversion and processing of component and spatial-relational information in faces. *Journal of Experimental Psychology-Human Perception and Performance*, 22,(4) 904-915.
- Sekuler, A. B., Gaspar, C. M., Gold, J. M., & Bennett, P. J. (2004). Inversion leads to quantitative, not qualitative, changes in face processing. *Current Biology*, 14,(5) 391-396.
- Senior, C., Barnes, J., Giampietroc, V., Simmons, A., Bullmore, E. T., Brammer, M., & David, A. S. (2000). The functional neuroanatomy of implicit-motion perception or 'representational momentum'. *Current Biology*, 10,(1) 16-22.
- Senju, A., & Hasegawa, T. (2005). Direct gaze captures visuospatial attention. *Visual Cognition*, 12,(1) 127-144.
- Senju, A., & Hasegawa, T. (2006). Do the upright eyes have it? *Psychonomic Bulletin & Review*, 13,(2) 223-228.
- Senju, A., & Johnson, M. H. (2009). The eye contact effect: Mechanisms and development. *Trends in Cognitive Sciences*, 13,(3) 127-134.
- Senju, A., Kikuchi, Y., Hasegawa, T., Tojo, Y., & Osanai, H. (2008). Is anyone looking at me? Direct gaze detection in children with and without autism. *Brain and Cognition*, 67,(2) 127-139.
- Senju, A., Tojo, Y., Dairoku, H., & Hasegawa, T. (2004). Reflexive orienting in response to eye gaze and an arrow in children with and without autism. *Journal of Child Psychology and Psychiatry*, 45,(3) 445-458.
- Seyama, J., & Nagayama, R. S. (2006). Eye direction aftereffect. *Psychological Research-Psychologische Forschung*, 70,(1) 59-67.
- Shepard, R. N., & Chipman, S. (1970). Second-Order Isomorphism of Internal Representations - Shapes of States. *Cognitive Psychology*, 1,(1) 1-17.

- Simion, F., Cassia, V. M., Turati, C., & Valenza, E. (2001). The origins of face perception: Specific versus non-specific mechanisms. *Infant and Child Development*, 10,(1-2) 59-65.
- Simion, F., Regolin, L., & Bulf, H. (2008). A predisposition for biological motion in the newborn baby. *Proceedings of the National Academy of Sciences of the United States of America*, 105,(2) 809-813.
- Sinha, P. (2000). Last but not least: Here's looking at you, kid. *Perception*, 29,(8) 1005-1008.
- Smith, M. L., Cottrell, G. W., Gosselin, F., & Schyns, P. G. (2005). Transmitting and decoding facial expressions. *Psychological Science*, 16,(3) 184-189.
- Spiridon, M., & Kanwisher, N. (2002). How distributed is visual category information in human occipito-temporal cortex? An fMRI study. *Neuron*, 35,(6) 1157-1165.
- Stone, V. E., Baron-Cohen, S., & Knight, R. T. (1998). Frontal lobe contributions to theory of mind. *Journal of Cognitive Neuroscience*, 10,(5) 640-656.
- Striano, T., Reid, V. M., & Hoehl, S. (2006). Neural mechanisms of joint attention in infancy. *European Journal of Neuroscience*, 23,(10) 2819-2823.
- Striano, T., & Stahl, D. (2005). Sensitivity to triadic attention in early infancy. *Developmental Science*, 8,(4) 333-343.
- Stuss, D. T., Gallup, G. G., & Alexander, M. P. (2001). The frontal lobes are necessary for 'theory of mind'. *Brain*, 124,(2) 279-286.
- Swettenham, J., Condie, S., Campbell, R., Milne, E., & Coleman, M. (2003). Does the perception of moving eyes trigger reflexive visual orienting in autism? *Philosophical Transactions of the Royal Society B-Biological Sciences*, 358,(1430) 325-334.
- Symons, L. A., Lee, K., Cedrone, C. C., & Nishimura, M. (2004). What are you looking at? Acuity for triadic eye gaze. *Journal of General Psychology*, 131,(4) 451-469.



- Tanaka, J. W., & Farah, M. J. (1991). 2nd-order relational properties and the inversion effect: Testing a theory of face perception. *Perception & Psychophysics*, 50,(4) 367-372.
- Tanaka, J. W., & Sengco, J. A. (1997). Features and their configuration in face recognition. *Memory & Cognition*, 25,(5) 583-592.
- Taylor, J. C., Wiggett, A. J., & Downing, P. E. (2007). Functional MRI analysis of body and body part representations in the extrastriate and fusiform body areas. *Journal of Neurophysiology*, 98,(3) 1626-1633.
- Teunisse, J. P., & de Gelder, B. (2003). Face processing in adolescents with autistic disorder: The inversion and composite effects. *Brain and Cognition*, 52,(3) 285-294.
- Theeuwes, J., & Van der Stigchel, S. (2006). Faces capture attention: Evidence from inhibition of return. *Visual Cognition*, 13,(6) 657-665.
- Thornton, I. M., & Hayes, A. E. (2004). Anticipating action in complex scenes. *Visual Cognition*, 11,(2-3) 341-370.
- Thornton, I. M., & Vuong, Q. C. (2004). Incidental processing of biological motion. *Current Biology*, 14,(12) 1084-1089.
- Tipples, J. (2005). Orienting to eye gaze and face processing. *Journal of Experimental Psychology-Human Perception and Performance*, 31,(5) 843-856.
- Tipples, J. (2006). Fear and fearfulness potentiate automatic orienting to eye gaze. *Cognition & Emotion*, 20,(2) 309-320.
- Tipples, J. (2008). Orienting to counterpredictive gaze and arrow cues. *Perception & Psychophysics*, 70,(1) 77-87.
- Todorov, A., Baron, S. G., & Oosterhof, N. N. (2008). Evaluating face trustworthiness: A model based approach. *Social Cognitive and Affective Neuroscience*, 3,(2) 119-127.

- Todorovic, D. (2006). Geometrical basis of perception of gaze direction. *Vision Research*, 46,(21) 3549-3562.
- Todorovic, D. (2009). The effect of face eccentricity on the perception of gaze direction. *Perception*, 38,(1) 109-132.
- Tomasello, M., Call, J., & Hare, B. (1998). Five primate species follow the visual gaze of conspecifics. *Animal Behaviour*, 55,(4) 1063-1069.
- Tomasello, M., & Rakoczy, H. (2003). What makes human cognition unique? From individual to shared to collective intentionality. *Mind & Language*, 18,(2) 121-147.
- Tong, F., Nakayama, K., Moscovitch, M., Weinrib, O., & Kanwisher, N. (2000). Response properties of the human fusiform face area. *Cognitive Neuropsychology*, 17,(1-3) 257-279.
- Turati, C. (2004). Why faces are not special to newborns: An alternative account of the face preference. *Current Directions in Psychological Science*, 13,(1) 5-8.
- Uddin, L. Q., Iacoboni, M., Lange, C., & Keenan, J. P. (2007). The self and social cognition: The role of cortical midline structures and mirror neurons. [Review]. *Trends in Cognitive Sciences*, 11,(4) 153-157.
- Umiltà, M. A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C., & Rizzolatti, G. (2001). I know what you are doing: A neurophysiological study. *Neuron*, 31,(1) 155-165.
- Urgesi, C., Candidi, M., Ionta, S., & Aglioti, S. M. (2007). Representation of body identity and body actions in extrastriate body area and ventral premotor cortex. *Nature Neuroscience*, 10,(1) 30-31.
- van Dijk, E., van Kleef, G. A., Steinel, W., & van Beest, I. (2008). A social functional approach to emotions in bargaining: When communicating anger pays and when it backfires. *Journal of Personality and Social Psychology*, 94,(4) 600-614.

- Vanneste, S., Verplaetse, J., Van Hiel, A., & Braeckman, J. (2007). Attention bias toward noncooperative people: A dot probe classification study in cheating detection. *Evolution and Human Behavior*, 28,(4) 272-276.
- Verfaillie, K., & Daems, A. (2002). Representing and anticipating human actions in vision. *Visual Cognition*, 9,(1-2) 217-232.
- Verfaillie, K., & Dydewalle, G. (1991). Representational momentum and event course anticipation in the perception of implied periodical motions. *Journal of Experimental Psychology-Learning Memory and Cognition*, 17,(2) 302-313.
- Verplaetse, J., Vanneste, S., & Braeckman, J. (2007). You can judge a book by its cover: The sequel. A kernel of truth in predictive cheating detection. *Evolution and Human Behavior*, 28,(4) 260-271.
- Vlamings, P. H. J. M., Stauder, J. E. A., van Son, I. A. M., & Motttron, L. (2005). Atypical visual orienting to gaze- and arrow-cues in adults with high functioning autism. *Journal of Autism and Developmental Disorders*, 35,(3) 267-277.
- Vogeley, K., Bussfeld, P., Newen, A., Herrmann, S., Happe, F., Falkai, P., Maier, W., Shah, N. J., Fink, G. R., & Zilles, K. (2001). Mind reading: Neural mechanisms of theory of mind and self-perspective. *Neuroimage*, 14,(1) 170-181.
- Vuilleumier, P., George, N., Lister, V., Armony, J., & Driver, J. (2005). Effects of perceived mutual gaze and gender on face processing and recognition memory. *Visual Cognition*, 12,(1) 85-101.
- Waller, B. M., Cray, J. J., & Burrows, A. M. (2008). Selection for universal facial emotion. *Emotion*, 8,(3) 435-439.
- Wallis, G., Siebeck, U. E., Swann, K., Blanz, V., & Bulthoff, H. H. (2008). The prototype effect revisited: Evidence for an abstract feature model of face recognition. *Journal of Vision*, 8,(3) 1-15.

- Whalen, P. J., Shin, L. M., McInerney, S. C., Fisher, H., Wright, C. I., & Rauch, S. L. (2001). A functional MRI study of human amygdala responses to facial expressions of fear vs. anger. *Emotion, 1*,(1) 70-83.
- Wheelwright, S., Baron-Cohen, S., Goldenfeld, N., Delaney, J., Fine, D., Smith, R., Weil, L., & Wakabayashi, A. (2006). Predicting autism spectrum quotient (AQ) from the systemizing quotient-revised (SQ-R) and empathy quotient (EQ). *Brain Research, 1079*,(1) 47-56.
- Wicker, B., Perrett, D. I., Baron-Cohen, S., & Decety, J. (2003). Being the target of another's emotion: A PET study. *Neuropsychologia, 41*,(2) 139-146.
- Wilkie, R. M., Wann, J. P., & Allison, R. S. (2008). Active gaze, visual look-ahead, and locomotor control. *Journal of Experimental Psychology-Human Perception and Performance, 34*,(5) 1150-1164.
- Wilson, H. R., Loffler, G., & Wilkinson, F. (2002). Synthetic faces, face cubes, and the geometry of face space. *Vision Research, 42*,(27) 2909-2923.
- Wilson, M., & Knoblich, G. (2005). The case for motor involvement in perceiving conspecifics. *Psychological Bulletin, 131*,(3) 460-473.
- Wolpert, D. M., Doya, K., & Kawato, M. (2003). A unifying computational framework for motor control and social interaction. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences, 358*,(1431) 593-602.
- Yamagishi, T., Tanida, S., Mashima, R., Shimoma, E., & Kanazawa, S. (2003). You can judge a book by its cover: Evidence that cheaters may look different from cooperators. *Evolution and Human Behavior, 24*,(4) 290-301.
- Yazbek, A., & D'Entremont, B. (2006). A longitudinal investigation of the still-face effect at 6 months and joint attention at 12 months. *British Journal of Developmental Psychology, 24*,(3) 589-601.
- Yovel, G., & Kanwisher, N. (2004). Face perception: Domain specific, not process specific. *Neuron, 44*,(5) 889-898.

- Yovel, G., & Kanwisher, N. (2005). The neural basis of the behavioral face-inversion effect. *Current Biology*, 15,(24) 2256-2262.
- Yovel, G., & Kanwisher, N. (2008). The representations of spacing and part-based information are associated for upright faces but dissociated for objects: Evidence from individual differences. *Psychonomic Bulletin & Review*, 15,(5) 933-939.