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Visual Perception of Social Directional Cues that Facilitate Joint Attention

Sarah Maeve Cooney, M.Sc.

13204547

This thesis is submitted to University College Dublin in fulfilment of the requirements for the degree of Doctor of Philosophy

School of Psychology

January 2017
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Abstract

The ability to discriminate the direction of another person's attention is an important skill in social interaction. Accurate discernment of where someone else is attending permits joint attention, an ability that emerges early in human development and is integral to the development of language and on some accounts theory of mind. Joint attention is a collaborative attentional state that involves shared attention upon an object or location in the environment. Before any shift in the observers attention takes place, they must first perceive where the other person attending in space. The direction of another person’s eye gaze, head orientation, body orientation, and hand pointing are social directional that aid perceptual discrimination of the direction of another person’s attention. Converging evidence supports high-level visual representation of some of these cues. Despite the important role that pointing plays in the development of social cognition, visual perception of pointing has received little attention in research. The aims of this thesis were to examine visual perception of these social directional cues and the relationship between the primary cues that elicit joint attention. These aims were achieved by examining how adults discern the direction of these cues and in turn reorient their attention towards the locus of another’s attention. Chapter 1 reviews the literature on the perception of social attention. Chapter 2 investigates hierarchical integration of left and right body and head orientations. Chapter 3 examines visual representation of hand pointing direction. In Chapter 4 modulation of spatial orienting of attention by social directional cue type and gender of viewer is examined. Chapter 5 examines observers’ ability to discern the direction of pointing at an object in space. The implications for understanding social perception are considered in Chapter 6.
Statement of original authorship

This thesis is my own work and no portion of the work referred to in this thesis has been submitted in support of an application for another degree or qualification at this or any other institute.

Sarah Maeve Cooney 23rd January 2017
Collaborations

The research activity for the thesis was undertaken primarily by the candidate Sarah Maeve Cooney. Experimental design, set up, data analysis and peer reviewed paper write up were conducted in collaboration with the candidates’ supervisor Dr Nuala Brady. Co-authors on each of the papers; Holly Dignam, Alanna O’Shea, Katie Ryan and Ailbhe McKinney assisted with data collection.
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I thoroughly enjoyed working and assisting in the supervision of a number of masters and undergraduate students who also aided the data collection process. Many thanks to Holly Dignam, Alanna O’Shea, and Kate Ryan without their contributions the route to completing the thesis would have been far more arduous. I would particularly like to extend my gratitude to Ailbhe McKinney who generously gave her time, her faultless vision and her gestural precision to act as ‘the pointer’ for a series of very time consuming, but thoroughly enjoyable experiments, thank you Ailbhe for your patience, commitment and energy.

My partner Benny deserves commendation for his part in meticulously cutting 100 pieces of wood to spec for an experimental apparatus. Thank you to my wonderful parents Maeve and Paddy Cooney for their continual guidance, inspiration, and love.

Finally, I extend my appreciation to the Irish Research Council for funding the work with a postgraduate scholarship.
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Chapter 1

Literature Review

1.1 The Social Visual Brain

As a social species, human beings are remarkably reliant on others for survival. To this end, we have acquired, developed, and sustained complex verbal and non-verbal communication systems that help us to establish and maintain social interactions. These communication systems, in particular the non-verbal, are reliant on fast and efficient perception of and attention towards the faces and bodies of others. Seamless analysis of the social non-verbal information conveyed by other people is primarily under the purview of the visual modality. The theoretical framework of this thesis rests at the intersection between visual perception and social cognition.

Vision permits recognition of objects (Logothetis & Sheinberg, 1996), the distal control of movement (Goodale, 1983), and to track the position of moving objects (Kosslyn, 1987). Visual perception involves extracting information from the environment and processing it in a way that facilitates knowledge acquisition (Palmer, 1999). From this, visual perception is a cognitive activity (Marr, 1982; Palmer, 1999; Ullman, 1984). Visual perception occurs at four main stages beyond the initial retinal image - image based, surface based, object based and category based (Marr, 1982; Palmer, 1999). Each stage denotes the type of information that it represents. Representation refers to the creation of types of representations of the
external environment and is ‘a state of the visual system that stands for an environmental property, object or event: it is a model of what it represents’ (Palmer, 1999, p 77). The most influential framework proposed to account for visual perception describes the visual system as operating a computational process i.e. computing outcomes from inputs (Marr, 1982; Ulman 1984). On this account, the visual system represents information that is then processed by changing one representation into the next, thus permitting the efficient analysis of information from one stage to the next (Palmer, 1999). While the boundaries between the different types of representations are not always easy to draw, in general, high-level visual representation involves recognition and categorization of objects (e.g. scenes, faces and bodies), with associated neural activation in the inferior temporal cortex (e.g. Downing & Peelen, 2016; Epstein & Kanwisher, 1998; Kanwisher & Yovel, 2006; Li, VanRullen, Koch, & Perona, 2000). Whereas, mid and low level vision occurs at earlier stages of processing where retinal information, image based information, and surface based information are processed (e.g. Carandini et al., 2005; Nakayama & Shimojo, 1995; Wandell, 1995).

The visual system has evolved exquisite sensitivity to social cues with the majority of our cortical resources dedicated to visual processing over all other sensory information. From this, vision plays an integral role in moderating social exchange, as visual analysis of simple to complex aspects of the environment shapes social interactions. The relationship between vision and social perception and cognition is reciprocal, such that aspects of
the organization and operation of the visual system are influenced by how we
guide our behaviour towards other people.

Social perception is formed by an analysis of the attentional and emotional
states of others, which in turn informs our understanding of their motivations,
intentions, desires and beliefs (Allison, Puce, & McCarthy, 2000). People
convey their tacit dispositions through a variety of visual cues, including
modifications in postural configuration that tell us where and at what they are
attending. People generally look at what they are interested in, what they
want or need, and what they want their communicative partner to know
(Langton, Watt, & Bruce, 2000). We orient our sensory receptors including
eyes, head, torso, and hands towards locations of interest. From this, the
primary visual cues that drive social perception, via transmission of socially
germane information regarding the locus of another individual’s attention, are
the direction of eye gaze, head orientation, body orientation, and hand
pointing. This chapter describes the perceptual processes that facilitate the
extraction of social directional information from the bodies of others and how
these fit within extant models of social perception and social cognition.

This thesis addresses the important question of how the visual system
processes information from socially salient directional cues and how these
cues serve to direct attention. The main research questions of this thesis are
as follows. First, in the case of head orientation and body orientation, how is
the directional information given by both of these cues coded by the visual
system? That is, do cells that code for head orientation also code for body
orientation and vice versa? Second, is hand pointing direction represented at
a high level in vision? Third, how effective are eye gaze direction, head, and body orientation in shifting the attention of the observer, and do men and women differ in their sensitivity to such cues? In addition, this thesis addresses an unresolved question regarding the perception of hand pointing - how accurate are people at estimating the focus of a pointing gesture?

This literature review draws on a number of key sources who have considered the evolution of cortical structures with respect to pressures of living in social groups (Adolphs, 2001, 2002, 2003; Allison et al., 2000; Brothers, 1990; Nakayama, 2011; Nummenmaa & Calder, 2009) and who have approached the study of joint attention and other aspects of social cognition from comparative and developmental perspectives (Baron-Cohen, 1995b; Cappuccio & Shepherd, 2013; Liszkowski & Tomasello, 2014; Mundy & Newell, 2013; Tomasello & Carpenter, 2007).

1.2 Social Cognition and the Social Brain

Social cognition is the capacity to construct representations of the relations between self and other and to use those representations flexibly to help coordinate social interaction. Perception serves cognition, such that perceptual sensitivity to social cues enables cognition to guide both automatic and planned behaviour at multiple levels of organization (Adolphs, 2001, 2003).

The social brain hypothesis posits that the social dimension of perceptual and cognitive abilities evolved out of the necessity to collaborate with others due to the increasing proximity between agents and the scale of extended communities (Brothers, 1990). The idea was originally proposed to explain...
VISUAL PERCEPTION OF SOCIAL DIRECTIONAL CUES

why primates, in particular humans, have comparatively larger brains than other mammals. A number of authors have suggested that this discrepancy is a result of the complexity of primate social systems compared to those of other species (Brothers, 1990; Dunbar, 1998). Dunbar (1998) describes a strong positive correlation between the average size of the neocortex and the average group size of different primate species. Dunbar excluded the visual cortex from the analysis due to the relatively stable size of the primary visual cortex across primates. According to the social brain hypothesis, the evolution of the brain is intimately linked with the evolution of complex social signalling, signalling to which the primate is predisposed by a reliance on vision (Dunbar, 1998). This broad socio-evolutionary perspective of social cognition has also been applied to the visual system such that the study of social vision is now an established interdisciplinary field where research efforts are motivated to uncover social tuning in the visual system (Nakayama, 2011). One of the tenets of social vision is that the social features of our environment, specifically other people, have directly influenced the evolution of our visual system. Indeed, most studies of social cognition to date have employed visual stimuli to examine the perception of social signals (Adolphs, 2003). This approach has gleaned a wealth of diverse findings that provide support for covariance between specific social features of stimuli and cortical function (Barraclough & Perrett, 2011; Nummenmaa & Calder, 2009; Peelen & Downing, 2007; Yovel & Kanwisher, 2004).
1.3 Sensitivity to Social Cues

1.3.1 Joint attention

The developmental trajectory of human sensitivity to social cues illustrates the intimate link between perception of these cues and the emergence of joint attention. Before social cognition there is joint processing of information about the attention of self and others (Mundy & Newell, 2013, p.269). Joint attention was originally adopted to describe the observation that infants follow the direction of other peoples’ eye gaze in advance of language comprehension and production (Scaife & Bruner, 1975). This seminal finding demonstrated that shared attention develops before language. Joint attention is a type of coordinated attention that is now understood to underscore the human capacity for learning, language and many aspects of social cognition (Mundy & Newell, 2013). Without the capacity for following, initiating and maintaining joint attention our ability to learn from others is limited, as is our capacity to establish social reciprocity (Baron-Cohen, 1991).

Joint attention involves shared attention upon an object or location in the environment, reciprocal attention between co-attenders, and concurrent iterative awareness of the others attention (Baron-Cohen, 1991; Cappuccio & Shepherd, 2013). Once the social signaller recognizes that their communicative partner has noticed the locus of their attention, joint attention is established and maintained by the co-attender’s engagement in a collaborative attentional state (Cappuccio & Shepherd, 2013). The developmental literature makes the distinction between following and initiating joint attention (Corkum & Moore, 1998; Mundy & Newell, 2013; Tomasello & Carpenter, 2007). Following the attentional bids of another is
accomplished when an individual follows the direction of another’s eye gaze, hand gestures, body and head orientation to a specific location in space.

1.3.2 Specialization for social objects

There is evidence from both behavioural and brain imaging studies that processing of socially relevant objects (faces and bodies) is distinct from processing of other objects. Specifically, because of their high self-similarity (all faces having two eyes, a nose and a mouth arranged in a specific configuration, and all bodies possessing a central trunk with two arms, legs and head) cortical mechanisms involved in recognition of individuals are tuned to the spatial configuration of these stimuli, e.g., the precise arrangement of the features in a face. With regards face perception there are a number of phenomena that attest to this sensitivity to configuration. For example, the ‘face inversion effect’ links holistic processing to the upright orientation of a face and shows that both recognition (Yin, 1969) and sensitivity to distortions of facial shape (Thompson, 1980) are hindered when faces are turned up-side-down. Similarly, a ‘body inversion effect’ occurs when presented with an image of a body turned upside down on the vertical axis participants tend to take longer to process the stimulus, specifically to recognize the identity of the stimulus (Brandman & Yovel, 2010; Reed, Stone, Bozova, & Tanaka, 2003). An inversion effect for a specific object category provides evidence that this class of object is represented in a canonical view. From this, the stimulus is a treated as a ‘special’ class of stimulus that may be processed preferentially in the visual system over other groups or classes of object.
This thesis is primarily concerned with perception of the social cues that facilitate joint attention. The human brain contains areas that are selective for recognizing the form of these cues, particularly faces and bodies. Specialisation for social objects is most evident in face and body perception. In particular, there is mounting evidence from behavioural, neuroimaging, and complementary lesion studies that confirms selective representation of the most socially salient objects, faces (Haxby et al., 1999; McKone, Kanwisher, & Duchaine, 2007; Yovel & Kanwisher, 2004, 2005) and bodies (Peelen & Downing, 2007; van Koningsbruggen, Peelen, & Downing, 2013). The human face and body provide a wealth of information pertaining to both categorical information (gender and age) as well as qualified information about the affective states and identity of others (de Gelder, 2006; de Gelder, de Borst, & Watson, 2015). This information is cued through both the appearance of others and their interaction with the environment. Efficient discrimination of the configuration of someone’s face and body helps us to interpret their intentions and actions. Indeed face and body perception are central features of the architecture of social interaction.

A distributed face network exists with different regions functioning to process different properties of face perception. The fusiform face area (FFA) (Kanwisher, McDermott, & Chun, 1997) in the lateral fusiform gyrus and the occipital face area (OFA) (Haxby, Hoffman, & Gobbini, 2000) in the ventral occipital lobe, and, recently neurons in the amygdala (Mormann et al., 2015) are implicated in the perception of faces, in particular the recognition of identity and biographical face related information, whereas the complex
process of distinguishing emotion from facial expressions has been shown to involve a more distributed network (see Adolphs, 2002 for review).

Subsequent research has looked at the representation of the rest of the human body. Presentation of images of the human body activates specific neural regions in the occipitotemporal cortex (OTC). Studies employing functional magnetic resonance imaging (fMRI) have identified two distinct body selective areas; the extrastriate body area (EBA) located in the posterior inferior temporal sulcus and the fusiform body area (FBA) located in the lateral posterior fusiform gyrus (Downing, Jiang, Shuman, & Kanwisher, 2001; Peelen & Downing, 2005; Taylor, Wiggett, & Downing, 2007). When compared with non-body object categories the EBA and FBA were found to selectively respond to images of the human body and are functionally dissociated from the occipital face area (OFA) and the fusiform face area (FFA) (Peelen & Downing, 2005). Taylor et al. (2007) found that EBA and FBA play different roles in the visual analysis of bodies, such that the EBA is biased towards representation of body parts, whereas FBA does not respond selectively to small body parts and is functionally biased towards larger portions of the human body.

More recently, studies have found evidence to support selective representation of the human hand in regions beyond the boundaries of face and body areas (Orlov, Makin, & Zohary, 2010). Orlov et al. (2010) describe a body part map that is topographically organized, with clusters of voxels that respond to specific body parts located beside each other. Orlov et al. (2010) report larger representation of the upper limbs relative to other body parts in
A study that looked at the representation of hands and non-hand body parts found a hand preferring region in the left lateral occipital sulcus, LOS, that partially overlaps with EBA (Bracci, Ietswaart, Peelen, & Cavina-Pratesi, 2010). Behaviourally, it has been shown that hands attract attention over other objects (Morrissey & Rutherford, 2013). Morrissey and Rutherford (2013) presented pairs of photographs of a variety of objects including hands, bodies and feet, hand tools, ovens, toasters and other animals such as dogs. Next, a target appeared in one of the two locations where the images had been. Participants were faster to respond to targets on the same side that a hand, body or foot stimulus had appeared compared to other animate (dogs, starfish) and inanimate objects (oven, toaster, tool).

Body recognition regions are suggested to be primarily concerned with the analysis of the human form via visual input rather than to the changing configurations of posture found in biological motion (Kontaris, Wiggett, & Downing, 2009). Selective tuning in EBA for particular viewpoints of the body has been reported (Taylor, Wiggett, & Downing, 2010). In addition, modest modulation of EBA was reported for allocentric over egocentric images of bodies and body parts (Saxe, Jamal, & Powell, 2006). Indeed, differential sensitivity to allocentric and egocentric presentation of hand stimuli has been reported when subjects were required to judge the handedness of the stimuli (Brady, Maguinness, & Choisdealbha, 2011).

These face and body selective visual regions constitute one feature of a larger distribution of neural regions attuned to process social signals. The STS is a region of the brain that serves a host of socio perceptual functions.
and seems to be specifically involved in processing changing social signals, e.g., head and body movement, shifts in eye gaze, mouth movements and hand movements (Hein & Knight, 2008; Pelphrey, Viola, & McCarthy, 2004). This region has links to the putative ‘human mirror system’ (Jackson, Meltzoff, & Decety, 2006) and to the intra parietal sulcus a region involved in spatial attention (Materna, Dicke, & Thier, 2008a). Crucially, the findings indicate that this region seems to be specifically concerned with changes in social signals, something that is critical for social attention (Carlin & Calder, 2013; Carlin, Calder, Kriegeskorte, Nili, & Rowe, 2011; Carlin, Rowe, Kriegeskorte, Thompson, & Calder, 2012; Materna, Dicke, & Thier, 2008b).

To summarize, there is extensive evidence that these decidedly social objects, bodies and faces, are represented in high-level vision, with some preliminary indication of selective representation of the hand that is distinct from recognition of the human face or body.

1.3.3 Specialization for the direction of social signals

How is visual processing of body and face cues related to social attention and social coordination? We are not just sensitive to the form of these cues but also to their orientation. Neurophysiological accounts of social perception generally contain some description of the behaviour of single cells that help clarify human psychophysical, psychological and neuroimaging data (Barraclough & Perrett, 2011). Perrett and colleagues employed single cell recording techniques, and report that of cells tuned to faces and head orientation in the superior temporal sulcus (STS) region of the macaque temporal lobe, a proportion of these cells fire maximally in response to the
direction that the eyes are oriented, direct facing or averted (Perrett et al., 1985). When the eyes in the stimulus are positioned looking upward, a distinct population of cells fire, similarly a separate pool of cells fire maximally to eye gaze that is oriented downward (Perrett, Hietanen, Oram, & Benson, 1992).

Using ablation techniques, Heywood and Cowey (1992) removed specific regions of macaque STS and report that while the primates were no longer able to discriminate the angle of regard in pictures of faces, there was no impairment in facial identity discrimination tasks. This study provided preliminary evidence that the STS may be preferentially engaged by the orientation of specific facial features, in this case eye gaze direction (Heywood & Cowey, 1992). Later, a number of fMRI studies provided evidence that the posterior STS in humans plays an integral role in gaze perception (Allison et al., 2000; Hoffman & Haxby, 2000). Specifically, this region appears to be involved in representing the goal oriented aspect of gaze rather than the direction of regard, as the posterior portion of STS was shown to be modulated by shifts of eye gaze away from an object (Pelphrey, Singerman, Allison, & McCarthy, 2003; Pelphrey, Viola, & McCarthy, 2004). More recently, the anterior portion of the STS in humans has been identified as containing populations of cells that code leftward and rightward eye gaze direction (Calder et al., 2007; Carlin et al., 2011). Combined with the observation of neonates preference for the eye region of faces (Batki, Baron-Cohen, Wheelwright, Connellan, & Ahluwalia, 2000), and evidence of reflexive attention to the direction of eye gaze in infants under 6 months (Farroni et al., 2000; Hood, Willen, & Driver, 1998), the neuroimaging, single
cell and lesion studies findings are in accord with a specialized neural mechanism devoted to detecting the presence of eyes and the direction of eye gaze (Baron-Cohen, 1995a; Batki et al., 2000).

1.3.4 Eye direction detector

The eye direction detector (EDD) is a core mechanism in a ‘mind reading’ system proposed by Baron-Cohen (1995a, 1995b) in which the combined output of four mechanisms produces the ability to attribute mental states to other agents. The three other components are the Intentionality Detector (ID), a Shared Attention Mechanism (SAM), and a Theory of Mind Mechanism (ToMM). The ID receives multisensory inputs concerning biological motion, information that according to Baron-Cohen’s account is the primary step to detecting agency in another organism as it uses perceptual information to ascertain volitional states. The EDD relies exclusively on visual input and its function is threefold; first, it detects the presence of an eye gaze stimulus. Second, it discerns the direction of regard of another organism. Third, the EDD ascribes agency to the eyes of the organism. Here, the act of looking in of itself determines agency, this is established either via eye contact between the agents or with an object in the environment (Baron-Cohen, 1995b, p. 39).

Baron-Cohen (1995a) proposed that the EDD is linked to the SAM, whose main function is to recognize that attention is being shared with another individual. Shared attention here is conceptualized as a step above joint attention as it involves more complex interplay of awareness of an agents epistemic states (Emery, 2000; Tomasello & Carpenter, 2007). The SAM
utilizes the information gleaned from the EDD, for example, knowing where in space someone’s eye gaze is directed, and then compares this information with the observer’s current perceptual state. If the two are aligned, visual attention is shared. According to Baron-Cohen’s model, once SAM is triggered then an individual has the capacity to infer the requisite range of mental states onto the observable behaviour of another person (ToMM). The direction of eye gaze on this model is of great import as the eyes rather than other social cues are the primary indicators of social engagement, reciprocity, and connectedness.

1.3.5 *Head and body orientation*

While eye gaze is often conceptualized as the privileged medium to convey and receive social information (Emery, 2000; Langton et al., 2000; Nummenmaa & Calder, 2009), it is not the only cue that is used to discern where and at what someone is attending. The orientation of the head and the turning direction of the body provide reliable sources of directional information. Even infants under 6 months of age have been observed to orient to the direction of an adult’s head turn (D’Entremont, Hains, & Muir, 1997). Single cell studies also provided evidence that different classes of cell code different head orientations in the monkey homologue of human STS (Perrett et al., 1985, 1992). Of cells that selectively respond to face and head stimuli, presentation of front facing views and profile views of the head resulted in differential firing of separate pools of cells (Perrett et al., 1985). Similarly, some pools of cells responded more to upward orientations of the head, while others responded more to downward views (Perrett et al., 1992).
There is also evidence from monkey studies of body-selective cells tuned to specific body orientations; left, direct and right facing bodies (Wachsmuth, Oram & Perrett, 1994). In addition, Perrett et al. (1992) examined responses to different quadrupedal and bi-pedal body positions and found separate pools of cells firing maximally in response to different body positions. Later, a study found that cells that code faces also respond to headless bodies, with optimal responses for bodies with heads. These cells showed considerable tuning to body orientation and size (Ashbridge, Perrett, Oram, & Jellema, 2000).

1.4 Integration of Social Directional Cues

1.4.1 Direction of attention detector

In order to facilitate social interaction via joint attention, the visual system must represent the orientation of head and body cues at some stage of processing, as this is crucial to understanding what the posture means. From the electrophysiological studies conducted by Perrett et al. (1985, 1992) cells that were selective for head directions were also selective for eye gaze direction and body orientation. Many of these cells’ response profiles were predicted by congruent cue orientations of eye, head and body orientation, for example, upward eye gaze and upward head orientation. Importantly, the response profile of cells that fired in response to more than one cue oriented in the same direction were organized hierarchically, with preferential firing for eye gaze over head orientation or body orientation.

To account for situations where cues are incongruently oriented, Perrett and Emery (1994) proposed a ‘direction of attention detector’ (DAD) (see
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Figure 1.1) that is hierarchically organized such that the aggregate output from cells that code for gaze, head and body posture is hierarchically organized with information from eye gaze placed at the top of the hierarchy. On this model, information coded about the direction of eye gaze would always, via inhibitory connections, override incongruent information about head orientation. Both eye and head direction information would inhibit information about incongruous body posture, as the configuration of the torso is conceptualized as the least efficient cue to the direction of attention (Perrett & Emery, 1994).

To date there is limited evidence from behavioural studies with human participants that directly supports Perrett and Emery (1994) model of social attention perception cells. Moreover, in contrast to the hierarchical model, head orientation and body orientation have both been shown to influence the perceived direction of eye gaze (Langton, 2000; Moors, Germey, Pomianowska, & Verfaillie, 2015; Moors, Verfaillie, Daems, Pomianowska, & Germey, 2016; Pomianowska, Germey, Verfaillie, & Newell, 2011; Seyama & Nagayama, 2005).
Figure 1.1 The direction of attention detector (DAD). Schematic of the hierarchical structure of Perret and Emery (1994) social attention mechanism. Eye gaze supersedes all incompatible information from cues further down the hierarchy.
1.4.2 Perception of eye gaze

**Acuity for eye gaze.** The primary visual cues used to determine the direction of gaze are the contrast between the white of the sclera and the dark of the iris and the pupil, as well as the geometrical information present in head orientation (Olk, Symons, & Kingstone, 2008; Todorović, 2006). The morphology of the primate eye is unique as it contains a white sclera surrounding a darker iris and pupil (Kobayashi & Kohshima, 2001). The high contrast in the human eye makes it relatively easy to discern where someone is looking. Indeed, accuracy in perceiving the direction of eye gaze is disrupted when the contrast of the sclera and pupil changes from positive (iris darker than white sclera) to negative polarity (the sclera darker than the iris) (Ando, 2004).

Classic studies of perceptual acuity for eye gaze direction employed naturalistic paradigms and found that acuity for the perception of eye gaze direction is remarkably high, with exceptional visual acuity for detecting even the smallest change in eye gaze direction (Bock, Dicke, & Thier, 2008; Symons, Lee, Cedrone, & Nishimura, 2004). Based on classic work by Gibson and Pick (1963), Symons et al. (2004) used a live looker to examine the threshold for detecting where someone is looking in three-dimensional space. The authors make an important distinction between dyadic gaze, which primarily functions to engage eye contact in face-to-face interaction and triadic gaze, which involves computing the direction of regard at an object or place in the environment. Both involve estimation of the asymmetry
in iris scleral contrast, but triadic gaze requires the observer to compute further geometrical information by triangulating convergence of line of sight from both eyes at an object. Acuity was defined as the amount of shift in degrees of visual angle at the objects gazed at relative to a central target. Symons et al. (2004) showed that the thresholds for detecting shifts in eye gaze are exceptionally low. Resolution for acuity was ~30 seconds arc, 1.3 degrees of visual angle at a distance of 1 metre.

The power of iris scleral contrast to drive the precision of eye gaze detection is evidenced most clearly in a large body of research that has shown robust reflexive orienting of attention to the direction of eye gaze (see Birmingham & Kingstone, 2009; Frischen, Bayliss, & Tipper, 2007 for reviews). That is, participants reflexively orient their attention to a target that a central eye gaze cue is looking at, even when the direction of the gaze cue does not accurately predict the location of the target (Friesen & Kingstone, 1998; Driver et al., 1999). Researchers have reported eye gaze cueing using a host of stimuli, including photographs of people, computer generated avatars and simple line drawings of a black filled in circle surrounded by a larger white circle. When researchers reversed the iris scleral contrast polarity, the attentional effects were abolished. This clearly demonstrates how orienting to gaze can be suppressed by altering the cues that facilitate eye gaze perception (Ricciardelli, Betta, Pruner, & Turatto, 2009).

Eye gaze and head orientation. A number of different behavioural techniques are used to examine how social directional cues, specifically those from eye gaze and head orientation, are integrated (see Table 1.1).
First, extending on the seminal works of Gibson & Pick (1963) and Cline (1967), which were the first studies to demonstrate our remarkable perceptual sensitivity to discern that someone is looking directly at us, using traditional psychophysics, a number of researchers have measured how our perception of eye gaze direction changes when combined with information from head orientation (Kluttz, Mayes, West, & Kerby, 2009; Moors et al., 2016; Todorović, 2006). A second, and very different way to measure cue integration, is to measure how target detection or discrimination at a peripheral location changes when cued by a centrally positioned social signal. This involves an adaptation of the Posner (1980) attention cueing paradigm, and has been used to measure the strength of social signals as attentional cues (Belopolsky, Olivers, & Theeuwes, 2008; Birmingham & Kingstone, 2009; Daum & Gredeback, 2011; Driver et al., 1999; Friesen & Kingstone, 1998; Friesen, Moore, & Kingstone, 2005; Frischen et al., 2007; Hietanen, 2002; Ristic, Friesen, & Kingstone, 2002). And finally, attentional interference has also been employed, adapted from the Stroop (1935) paradigm, to measure how selective attention is modulated by automatic processing of to-be-ignored social signal (Langton & Bruce, 2000; Langton, 2000; Langton, O'Malley, & Bruce, 1996).
### Table 1.1

**Summary of Key Methods and Findings in the Perception of Social Attention**

<table>
<thead>
<tr>
<th>Directional cue type</th>
<th>Experimental Method</th>
<th>Key Finding</th>
<th>Key References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eye gaze</td>
<td>Visual acuity</td>
<td>Humans can detect very small changes in the direction of eye gaze.</td>
<td>(Bock et al., 2008; Cline, 1967; Gibson &amp; Pick, 1963; Symons et al., 2004)</td>
</tr>
<tr>
<td></td>
<td>Threshold estimation</td>
<td>Reflexive orienting of attention to the direction of eye gaze.</td>
<td>(Birmingham &amp; Kingstone, 2009; Driver et al., 1999; Friesen &amp; Kingstone, 1998;;Hayward &amp; Ristic, 2015)</td>
</tr>
<tr>
<td></td>
<td>Attention cueing</td>
<td>Separable coding of left and right eye gaze direction.</td>
<td>(Calder et al., 2008; Jenkins et al., 2006; Kloth &amp; Schweinberger, 2010)</td>
</tr>
<tr>
<td></td>
<td>Posner</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Head</td>
<td>Visual acuity</td>
<td>High acuity for detecting change in head orientation</td>
<td>(Wilson et al., 2000)</td>
</tr>
<tr>
<td></td>
<td>Threshold estimation</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Visual representation</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Visual adaptation</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Body</td>
<td>Visual representation</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Visual adaptation</td>
<td>Separable coding of left and right body orientations.</td>
<td>(Lawson et al., 2009)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pointing</td>
<td>Attention cueing</td>
<td>Reflexive orienting of attention to hand pointing direction.</td>
<td>(Ariga &amp; Watanabe, 2009; Belopolsky et al., 2008; Fischer &amp; Szymkowiak, 2004; Langton &amp; Bruce, 2000)</td>
</tr>
<tr>
<td></td>
<td>Posner</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Note.* This table refers to cues examined in isolation from the rest of the body. *Italics* denote name of method employed.
Psychophysics. A considerable body of research has shown how head orientation influences the perception of eye gaze direction (Anstis, Mayhew, & Morley, 1969; Cline, 1967.; Kluttz et al., 2009; Langton, 2000; Laube, Kamphuis, Dicke, & Thier, 2011; Moors et al., 2016; Pomianowska et al., 2011; Todorović, 2006). Some biases have been reported, particularly either an attractive or repulsive effect whereby the perception of gaze shifts in the opposite direction to the direction in which the head is averted or the perception of eye gaze is pulled towards the direction of head orientation (Anstis et al., 1969; Gibson & Pick, 1963; Todorović, 2006; Maruyama & Endo, 1983; Cline 1967). One explanation for this effect considers the amount of visible sclera available due to head rotation when eye gaze position remains constant. When the head is averted this produces the perception that the pupil of the eye rotates in the direction opposite to the direction in which the head is averted (Anstis et al., 1969). A very recent study clarified some inconsistencies in the interpretation of the classic work by Gibson and Pick (1963) and Cline (1967) by replicating the studies and concluded that the majority of evidence demonstrates that the bias is predominantly repulsive (Moors et al., 2016).

Attentional Cueing. Similarly, head orientation modulates attentional allocation in response to centrally presented gaze cues. Hietanen (1999) independently manipulated eye gaze direction and head orientation in an adaptation of the Posner (1980) spatial cueing paradigm. A typical experimental procedure involves presenting a central social cue, for example eye gaze direction, oriented to the left or right, e.g., Driver et al. (1999). The participant responds to a target that appears either at the same location to
which the cue was directed (valid cue) or at the opposite (invalidly cued) location. Faster reaction times for validly cued targets provide evidence for a shift of attention to the location that the cue was oriented.

In keeping with the gaze cueing effect, when Hietanen (1999) used a face as the central cue with head directed towards the viewer and gaze averted to the left or right, participants were faster to detect targets at the gazed-at location. This is a classic eye gaze cueing effect demonstrated by many researchers (Driver et al., 1999; Friesen & Kingstone, 1998; see Frischen et al., 2007 for review) and is evidence that eye gaze direction automatically triggers a shift in the viewer’s attention. Whereas, when Hietanen (1999) shifted the head position laterally to coincide with the direction of gaze there were no subsequent cueing effect towards targets that were ‘looked at’ by the eye gaze cue. Hietanen (1999) explains this counterintuitive finding by suggesting that congruently oriented head and eye gaze are less powerful signals of the direction of another individual’s attention than incongruently oriented head and gaze. This, he notes, is because in both cases when a person’s head and gaze are oriented to the left or right the cues are not related to the viewer, such that the directional salience of these cues has less social value than when at least one of the cues is oriented towards the observer. Further, when Hietanen (1999) turned the head stimuli to the right or left with eyes gazing back to the participant this did not speed up response times when head turning predicted target location. Here, participants responded faster to targets that appeared on the opposite side to the direction the head was turned. In a similar manner to the repulsive effect, participants’ oriented their attention in the direction opposite to the head cue.
Together these findings suggest, first, that people discriminate the direction of social cues with reference to the perspective of the person they are looking at. When observing another person, averted eyes (relative to their head orientation) are strong cues to a shift in that person’s attention and they draw our attention in the same direction. Secondly, these results suggest that cues are combined hierarchically such that eye gaze is referenced to head orientation.

**Interference paradigms.** Some research that employed attention interference paradigms has provided evidence of a bidirectional interference effect whereby information from eye gaze did not completely inhibit information from head orientation nor *vice versa*. Here, participants had to judge the direction of attention of the stimulus towards a target. Subjects were required to attend to the eye gaze and ignore head orientation or vice versa, to either congruently or incongruently presented head and eye gaze stimuli. For example, Langton (2000) asked participants to judge the direction of attention of a social stimulus towards a target. They were required to either attend to eye gaze and ignore head orientation, or to attend to head orientation and ignore the direction of eye gaze. The authors presented the stimuli in two conditions, a congruent condition in which head orientation and eye gaze were in the same direction, and an incongruent condition in which head orientation and eye gaze were in different directions. In contrast to Hietanen (1999), reaction times to discern the direction of gaze slowed when incongruous head orientation to eye gaze was presented, but responses were not completely inhibited as suggested by Perrett and Emerys (1994) model (Langton 2000; Laube, Kamphuis, Dicke & Thier,
Langton (2000) found that judgments of eye direction were faster when the eye gaze and head orientation were congruent than when they were incongruently oriented. Further support was provided by Laube et al., (2011) who employed a combined psychophysical and fMRI design. The behavioural results of this experiment showed that to-be-ignored head orientation interfered with judgments of eye gaze direction. Both directional cues, eye gaze direction and head orientation, similar to Langton et al. (2000) influenced each other in a bidirectional manner.

1.4.2 Integration of head and body information

The orientation of the body has also been shown to play a part in determining the direction of eye gaze (Hietanen, 2002; Pomianowska et al., 2011; Seyama & Nagayama, 2005)(see Table 1.2). Using the same adaptation of the Posner (1980) spatial cueing paradigm, Hietanen (2002) also manipulated body orientation to examine the relative strength of this cue in deploying spatial attention. In this study, eye gaze was always compatible with head orientation. Hietanen (2002) then manipulated head orientation with respect to body orientation. Participants were required to detect a target to either the left or right of the screen. Again, the central cue did not predict the target location. When the head and body (upper torso) were oriented in incompatible directions, (head rotated left, body front facing) participants were faster at detecting targets to the left, whereas when head and body were positioned in the same direction this did not facilitate spatial cueing. Reflexive orienting was only observed when the head/gaze orientation and torso orientation were incongruently oriented (Hietanen, 2002).
In a study that required participants to judge the direction in which an avatar’s eyes were oriented with respect to the viewer, Seyama & Nagayama (2005) found that RTs were faster when head and eye gaze were oriented in the same direction than when the head and eyes were incongruently oriented. By contrast, when the eyes and torso were oriented in different directions the participants’ attention judgments concerning whether the stimulus was looking at the participant or not were faster than when the eyes and body were oriented in the same direction. Seyama and Nagayama (2005) propose that the differing response to eye-head and eye-torso combinations reveal two separate perceptual processes that work to influence the judgment of eye direction.

The Hietanen (2002) and Seyama and Nagayama (2005) studies both used just the torso and arms to depict body orientation. More recently, using a Simon task Pomianowska et al. (2012) examined automatic processing of body orientation on the deployment of spatial attention by including the rest of the human body as a directional cue, including arms, legs and torso. Rather than a target detection task or an overt spatial discrimination task, they used a Simon task to induce a spatial compatibility effect. That is, participants were required to make judgments about the facial expression of a stimulus by pressing one of two keys located to the left and right of the viewer’s midline. The head and eye gaze faced forward and only the orientation of the body changed. A Simon effect refers to the tendency for participants to respond faster and more accurately to stimuli on the same side as the response button even if the spatial location of the stimulus is task irrelevant. Here, in contrast to Seyama and Nagayama, but in line with
Hietanen (2002), they report a Simon effect only for incongruent head and body orientations. That is, they report a reverse compatibility effect such that participants were faster to respond to the correct emotional expression of the face when the body of the stimulus was oriented in the opposite direction to the required response location.

### 1.5 Models of Social Cue Integration

Two accounts, Hietanen (1999, 2002) and Langton (2000, 2011), have been proposed to describe the underlying mechanism responsible for the integration of directional information from eye gaze, head orientation, and body orientation. Hietanen (1999, 2002) describes his findings as best explained by a hierarchical referencing model. On this model, eye gaze direction is referenced to head turning direction, and head-turning direction is referenced to body turning direction. In keeping with Perrett and Emery’s social attention detector (Perrett & Emery, 1994), the finding that incongruent head and body orientations shift attention faster than congruent cues is thought to reflect reflexive orienting of social attention, which is triggered by directional codes. Initially, these codes are formed in an allocentric-based frame of reference, where eye gaze supersedes head orientation and head orientation is superseded body orientation (see Table 1.2).

On account of this, if another agent’s head, eye and body are all oriented to the left, the viewer is less likely to shift their attention to the location the agent is attending to because there is no implied social valence to congruent cues. That is, the congruently aligned agent is not related to the viewer; in a sense, the agent has not made a shift of attention away from the viewer,
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whereas when the head and body are misaligned, with the head facing the viewer this suggest an attentional shift with respect to the viewer.

The second model proposed by Langton (2000) conceptualizes the effects of each cue as independent rather than hierarchical, such that the direction of social attention is computed by separate analysis of each cue’s directional salience. Each cue is analysed in parallel with the final product resulting from the additive effects of each cue. Langton (2011) suggests that the Perrett and Emery (1994) model should include the attenuation rather than the complete inhibition of cells coding cues further down the social attention hierarchy. For example, cells coding upward gaze do not completely inhibit head orientation cells coding downward head orientation. If, like in the macaque STS, there are heterogeneous populations of neurons in portions of the human STS that code both eye gaze and head orientations, then gaze direction should be influenced by adaptation, prolonged exposure, to head orientation and vice versa. In a truly hierarchical fashion, adapting to gaze direction should inhibit cells coding head orientation but adaptation to head orientation should not inhibit perception of gaze direction.

Indeed, separable visual coding of left and right eye gaze directions (Calder, Jenkins, Cassel, & Clifford, 2008; Jenkins, Beaver, & Calder, 2006; Kloth & Schweinberger, 2010), head orientations (Lawson, Clifford, & Calder, 2011), and body orientations (Lawson, Clifford, & Calder, 2009) was reported in behavioural experiments that employed visual adaptation. Psychologists study visual adaptation by using aftereffects. As explained more fully in Chapter 2, aftereffects are changes in the perceived properties of objects
experienced as a result of exposure to an unchanging stimulus (Webster, 2011). Adaptation aftereffects manifest as perceptual biases that are induced after exposure to a stimulus and are thought to reflect a reduction in the response of neuronal cells tuned to specific features of that stimulus (discussed in detail in the preamble to Chapter 2). A typical orientation adaptation experiment involves a baseline discrimination task where participants judge the direction of, for example eye gaze, as direct, left or right. They then view a continuous stream of eye gaze stimuli oriented in one direction, for example left. Afterwards participants’ discrimination of eye gaze direction becomes biased. Participants no longer accurately judge eye gaze stimuli as oriented slightly to the left and become more likely to judge these stimuli as looking straight ahead.

Unpublished research by Jenkins, Keane and Calder (2007), presented at ECVP, describe a cross adaptation study where participants both adapted to averted eye gaze or to head orientation, and were subsequently tested on their perception of eye gaze direction. This method was employed to examine if adapting to a different directional cue, head orientation, influenced cells coding eye gaze direction. In line with the hierarchical model of social attention (Perrett & Emery, 1994; Perrett et al., 1992), Jenkins et al. (2007) do not report cross adaptation such that cells coding head orientation do not influence the perception of the primary cue eye gaze direction. The authors’ abstract, also mentioned in Calder et al. (2008), states that no cross cue adaptation was observed. However, the reverse was not examined, that is perception of head orientation was not tested after adaptation to eye gaze direction. Cross cue adaptation in one direction would provide evidence of
social attention cells, tuned to the same orientation of head and eye gaze direction, but that follow the hierarchical inhibitory structure that Perrett and Emery (1994) proposed.

Bayliss, Bartlett, Naughtin, and Kritikos (2011) employed a novel technique that combined spatial cueing of attention and adaptation to examine the relationship between the perception of eye gaze direction and reflexive orienting of attention to eye gaze direction. If the mechanisms responsible for reflexive orienting of attention to eye gaze are stimulus specific, then attention cueing should be impaired after adaptation to eye gaze direction. Adapting to the direction of eye gaze did impair spatial cueing of attention to that particular eye gaze direction. This was further supported in a control experiment where adaptation to a different, yet highly salient directional cue, hand pointing, did not elicit the same effect on eye gaze cueing. This suggests that eye gaze and hand pointing direction are coded separately as cues to social attention.
### Table 1.2

*Summary of Method and Mechanisms Proposed to Account for the Integration of Directional information from Cue Combinations*

<table>
<thead>
<tr>
<th>Directional cue type combination</th>
<th>Experimental Method</th>
<th>Social attention mechanism</th>
<th>Key References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eye gaze direction &amp; Head orientation</td>
<td>Attention cueing <em>Posner</em></td>
<td>Hierarchical</td>
<td>(Hietanen, 1999)</td>
</tr>
<tr>
<td></td>
<td>Attentional interference <em>Stroop effect</em></td>
<td>Bidirectional</td>
<td>(Langton, 2000; Laube et al., 2011; Seyama &amp; Nagayame, 2005)</td>
</tr>
<tr>
<td>Eye gaze direction &amp; Body orientation</td>
<td>Attention cueing <em>Posner</em></td>
<td>Hierarchical</td>
<td>(Hietanen, 2002)</td>
</tr>
<tr>
<td></td>
<td>Orientation discrimination</td>
<td>Bidirectional</td>
<td>(Seyama &amp; Nagayama, 2005)</td>
</tr>
<tr>
<td>Head orientation &amp; Body orientation</td>
<td>Attention cueing <em>Posner</em></td>
<td>Hierarchical</td>
<td>(Hietanen, 2002)</td>
</tr>
<tr>
<td></td>
<td>Spatial Compatibility <em>Simon effect</em></td>
<td>Bidirectional</td>
<td>(Moors et al., 2016; Pomianowska et al., 2012)</td>
</tr>
<tr>
<td>Eye gaze direction &amp; Pointing direction</td>
<td>Visual Adaptation &amp; Attention Cueing</td>
<td>Hierarchical</td>
<td>(Bayliss et al., 2011)</td>
</tr>
</tbody>
</table>

*Note. This table refers to experiments that examined responses to one directional cue when another conflicting cue was also present oriented congruently or incongruently with the cue of interest.*  

Hierarchical and Bidirectional refer to the proposed way that directional information from the cue combinations is processed. *Italics* denote the name of the method used.
1.6 Perception of Pointing

1.6.1 Developmental trajectory

The majority of the developmental research concerning joint visual attention has examined infant responses to eye gaze direction and hand pointing. There are two competing views to describe the relationship between joint attention and pointing. According to one account, infants’ comprehension of social directional cues is initially given by changes in the orientation of the signallers head, and direction of eye gaze. It is only after this that pointing comprehension is observed nearing the end of the first year of infancy (Butterworth & Jarrett, 1991; D’Entremont et al., 1997; D’Entremont & Seamans, 2007; Hood et al., 1998; Scaife & Bruner, 1975).

The opposing view asserts that joint attention requires mental state attribution, and suggests that infant comprehension and perception of these social cues, head, gaze and pointing, develops in parallel closer to the end of the first year (Corkum & Moore, 1998; Tomasello, Carpenter, & Liszkowski, 2007).

Mental state attribution concerns representation of the perceptual experience of the communicative partner or co-attender (Gallagher & Hutto, 2008). A slightly richer interpretation holds that to direct and respond to the attention of another you must have some epistemic comprehension of the co-attender’s mental state. Theory of Mind (ToM) lays its foundations on the suppositions that we can mentally simulate the thoughts, desires, and feelings of another (Baron-Cohen, 1991, 1997; Premack & Woodruff, 1978). Seen as a cornerstone for the development of social cognition, ToM involves making inferences about the internal drives of observable actions such as a
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person’s goals, intentions, preferences and personality (Koster-Hale & Saxe, 2013). If a conversational partner averts their eye gaze towards the door, does this mean that they want to leave, that they want to leave together, or that they are bored or distracted? Reasoning about the possible motives for this shift in attention is called having ‘a theory of mind’ (Baron-Cohen, 1995b). If, instead, the conversational partner pointed with their hand to the door the meaning is arguably more explicit and ascertained by a primarily perceptual representation rather than abstract reasoning about the other person’s epistemic state. Here, is where pointing with the eyes and pointing with the hand differs.

Both developmental accounts assume that pointing production and comprehension do not emerge until the end of the first year. Eye gaze following is traditionally understood to develop much earlier than pointing, with evidence to suggest that infants follow eye gaze as young as 3 months (D’Entremont et al., 1997; Farroni et al., 2000; Gredebäck & Melinder, 2010). However, a recent study reported infants as young as 4 months shift their visual attention in response to hand pointing stimuli to a peripheral target (Bertenthal, Boyer, & Harding, 2014; Rohlfing, Longo, & Bertenthal, 2012). Rohlfing et al. (2012) tested 4 and 6-month-old infants’ ability to follow a pointing gesture. They employed an adaptation of the Posner (1980) spatial cueing paradigm where images of hands, pointing to the left or right, at or away from a peripheral target, were presented centrally and served as spatial cues. Infants oriented their visual attention faster to a target that appeared in the location that the pointing hand was positioned pointing towards than to targets that appeared in the opposite, incongruent location to
where the pointing hand was pointing. Static pointing cues, however, did not cue attention. The authors then controlled for motion cues by presenting a dynamic pointing cue where the hand moved in the opposite direction to the pointing finger. They found that while movement is necessary to orient the infants’ attention, movement alone did not shift attention (Rohlfing et al., 2012).

Later Bertenthal et al. (2014) tested the specificity of infants’ selective attention to the pointing cue by comparing responses to a pointing hand, an arrow and a stimulus that had the same holistic configuration of the pointing hand but with the internal features removed. Infant studies of pointing comprehension and production often present or produce the gesture with accompanying infant directed speech as this has been assumed to be a prerequisite to effectively capture the infants attention (Daum, Ulber, & Gredebäck, 2013; Senju & Csibra, 2008). In contrast, Bertenthal et al. (2014) did not require infant directed speech to trigger the infants’ attention to the target as the pointing cue alone facilitated this. The findings of Bertenthal et al. (2014) indicate exceptionally early attention to the pointing gesture without a communicative context. Infants spent significantly longer looking at social rather than non-social stimuli. Infants as young as 4 months could perceptually discriminate between a hand pointing cue, a foil which was the hand pointing cue minus the internal features and an arrow cue of similar colour to the pointing cue. This is evidence of high-level perceptual discrimination that influences the very early development of the cognitive scaffolding required for triadic communication. Such early demonstration of
selective attention and perceptual discrimination of hand pointing supports selective representation of this gesture (Materna et al., 2008a, 2008b).

1.6.2 Pointing and joint attention

The traditional distinction between imperative and declarative triadic coordination in the joint attention literature is also evident in the pointing development literature. Imperative behaviour in joint attention contains requesting exchanges whereas declarative exchanges involve sharing interest or awareness of a place or object (Liszkowski & Tomasello, 2014; Mundy & Newell, 2013; Tomasello & Carpenter, 2007). A number of authors describe a third type of triadic exchange that has an interrogative function (Begus & Southgate, 2012; Southgate, Van Maanen, & Csibra, 2007). In producing attention-orienting cues such as pointing, the frequency of pointing at 10 months is positively correlated with vocabulary expansion (Brooks & Meltzoff, 2008). Objects that infants point at are the objects that are more likely to enter the child’s vocabulary (Goldin-Meadow, 2007).

Individuals with Autism Spectrum Disorder ASD have impairments in both imperative and declarative triadic exchanges (Charman et al., 1997), with the most severe deficits in declarative exchanges and initiating joint attention (Charman, 2003). Following eye gaze and producing and following pointing gestures are key components in screening for ASD (Charman et al., 1997). Children with ASD and typically developing (TD) show different patterns of social orienting towards people and objects (Swettenham et al., 1998). This is consistent with Baron-Cohen’s (1995b) mindreading model. Children with ASD have a specific impairment or delay in attending to social stimuli
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(Swettenham et al., 1998). This may reflect a deficit in brain regions responsible for processing stimuli that facilitate joint and shared attention, in particular eye gaze direction. A recent study employed the same head and body cue stimuli and paradigm as Hietanen (2002) and found that adults with ASD integrate information about head and body orientation to judge the direction of someone’s attention in a way that is qualitatively different to typically developing adults (Ashwin, Hietanen, & Baron-Cohen, 2015).

1.6.3 Function of pointing

Pointing is primarily a deictic gesture that functions to direct the attention of others. A precursor to linguistic development, pointing requires that the pointer and co-attender share the same visual space (Liszowski, Brown, Callaghan, Takada, & de Vos, 2012). Further, the pointer must understand that the other person is a potential co-attender, which involves an appreciation that another person’s attentional state can be manipulated (Young, Kaufman, & Nanay, 2013). The index finger pointing gesture involves expression and problem solving that is accomplished via perceptual representation and develops separately from the grasping action (Cappuccio, Chu, & Kita, 2013; Kita, 2003). A recent study observed that infants first exhibit pointing production because of haptic exploration of objects. They argue that it is only after touching objects and positive reinforcement from caregivers that infant pointing begins to serve a social function (Carpendale & Carpendale, 2010).

Bates, Camioni and Volterra (1975) proposed that pointing in infancy is not initially a communicative act and that the communicative feature of
pointing only emerge later. The authors made a distinction between proto declarative and proto imperative pointing. Both imperative and declarative pointing are intentional signals, just with different emphasis, to either request or to show/point out (Bates et al., 1975). Baron–Cohen (1989) extended this distinction and defined proto imperative pointing as a non-intentional signal, and proto declarative pointing as an intentional act.

1.6.4 Geometrical cues in pointing perception

Pointing production delivers geometrical information on gaze direction such that the position of the pointer’s attention is mapped on to a set of performative hand-based and postural motor skills that permit alignment of index finger, hand, arm, torso and body with the orientation of eyes (Kita, 2003). Cappuccio et al. (2013) note that the production of pointing requires that the pointer divide their attention between the line of regard at the object and towards their index finger that works to delineate the line of regard for the co-attender. In this case, the index finger draws the trajectory of the pointers attention and functions to calibrate the co-attenders perceptual field.

There are a number of reasons to produce a point. These include - requesting an object, to request information about an object, to share interest on an object or location, and to communicate in order to help by sharing information about the location of an object. In all instances, the pointer and the prospective co-attender must be mutually aware of each other’s line of sight. That is they must be sensitive to the orientation of the other person’s direction of gaze with respect to the environment (Young et al., 2013). In order to produce a successful point the co-attender eyes must become
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oriented toward the object of interest (Wilmut, Wann, & Brown, 2006). In addition, if the point is unsuccessful such that the co-attender misjudges the location of the intended object the pointer will need to be sensitive to the co-attenders misperception and produce a more precise point again to specify the object (Young et al., 2013). This involves online monitoring of the spatial relations between the co attenders line of sight and the intended object, and their current line of sight on the incorrect object. As the pointers hand and index finger moves the co attender’s trajectory of line of regard shifts via eye, head, and even full body movements to accommodate this triangulation (Butterworth, Franco, McKenzie, Graupner, & Todd, 2002; Butterworth & Jarrett, 1991; George Butterworth & Itakura, 2000).

Pointing then, particularly the production of pointing, involves a high level of accuracy and sensitivity to another’s line of sight. Is this sensitivity as high for the comprehension of pointing? While the pointer is sensitive to the co attenders’ line of sight at each stage, before, during, and after the point is made (Wilmut et al., 2006), the co-attenders comprehension of the location of the point requires awareness of the pointers line of sight once the point is executed. Unlike the pointer, the co-attender has additional orientation cues from the hand extended with the palm down, with index finger extended, to enable accurate estimation of the line of regard and from this the localization of the point in space, and thus the attentional focus of the pointer (Ariga & Watanabe, 2009; Cochet & Vauclair, 2013). The trajectory of the pointers’ hand controls precisely where the co-attender should orient their gaze. How precise are we at following the hand pointing gesture? While perceptual acuity for discriminating the direction of eye gaze has been studied
extensively, the question of how proficient we are at estimating the direction and locus of a hand point has not been addressed.

A number of studies have reported that hand pointing direction, like eye gaze direction exerts automatic control on the observers visual attention (Ariga & Watanabe, 2009; Belopolsky et al., 2008; Fischer & Szymkowiak, 2004). The limited amount of research on pointing comprehension in adults has almost exclusively employed attention orienting paradigms (Ariga & Watanabe, 2009; Gregory & Hodgson, 2012; Langton & Bruce, 2000; Materna, Dicke, & Thier, 2008; Sato, Kochiyama, Uono, & Yoshikawa, 2010) such as the Posner spatial cueing task (1980), Stroop type interference paradigms and eye movement tracking, in order to examine how pointing modulates attention.

An index finger and right hand advantage for hand pointing have been reported (Ariga & Watanabe, 2009; Cochet & Vauclair, 2013; Jacquet, Esseily, Rider, & Fagard, 2012). During conversation adults tend to point with the index finger to disambiguate objects of interest from their surround, usually with the palm down rather than vertical (Kendon & Versante, 2003). Ariga and Watanabe (2009) showed that hands pointing with the index finger are superior at directing attention than hands pointing with the middle or little finger.

When observing pointing gestures participants respond faster to hand pointing stimuli that match their own dominant hand (Fischer & Szymkowiak, 2004). Similarly, where pointing and other gestures have been used in the hand laterality task, participants are faster to identify hands seen in
egocentric than in allocentric perspective and reaction times are also modulated by participants’ own handedness (Brady, Maguinness, & Ní Choisdealbha, 2011; Ní Choisdealbha, Brady, & Maguinness, 2011). A preference for right-handed index finger pointing may be related to the precision required to clearly identify a referent to the communicative partner. The extent of this precision is not known, nor how accurate the looker is in discerning exactly where the referent of the point rests in space.

1.7 Summary of Literature Review & Thesis Objectives

In summary, converging evidence supports covariance between specific social features of stimuli and cortical function. Neurophysiological, neuroimaging and behavioural experiments have provided evidence of neural tuning to the direction of socially salient cues in the visual system. The developmental trajectory of human sensitivity to social cues illustrates the intimate link between perception of these cues and the emergence of joint attention.

The primary visual cues that influence how we discern another individual’s locus of attention are the direction of eye gaze, head orientation, body orientation, and hand pointing. However, the majority of research that has examined social cues that facilitate joint attention have focused almost exclusively on the perception of eye gaze direction. Some consideration has been given to body and head orientation but with the exception of adaptation studies the research efforts have been primarily focused on cue integration from the perspective of how the turning direction of these two other salient social cues modulate the perception of eye gaze direction. There is a debate
about how directional information from head, body and eye gaze is integrated with two different models proposed to account for this.

Research that examined cue integration using reflexive attention orienting tasks has provided evidence that supports an integrative hierarchical model, such that eye gaze is referenced to head orientation and head orientation is referenced to body orientation (Hietanen, 1999, 2002). This is in line with Perrett and Emery (1994) who postulated that information from the eyes inhibits neurons coding incongruent information from the head direction but not vice versa. Perrett and Emery (1994), to explain how social attention is detected from eye gaze, head and body cues, proposed a top down hierarchy of social attention cues. The Direction of Attention Director (DAD) combines multimodal social attention cues, in order to determine the direction of another’s social attention (Perrett & Emery, 1994). Eye gaze information is at the top of this hierarchy, superseding all other body cue information. However, this model is not consistent with studies that found a bidirectional interference effect whereby information from eye gaze did not completely inhibit information from head orientation (Langton 2000; Laube et al., 2011). The direction of the interference effects reported are proposed to reflect the independent nature of both cues to social attention and are consistent with a parallel processing model, whereby head orientation and eye gaze direction cues are processed separately, yet have additive effects on the discrimination of social attention (Langton, 2000).

Visual adaptation studies have revealed orientation mechanisms that code left and right body orientations (Lawson et al., 2009) and head orientation
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(Fang & He, 2005; Lawson et al., 2011). These studies provide evidence of neuronal populations tuned to specific orientations of the human form that are in accord with single cell recordings of monkeys showing separate coding of gaze, head and body orientations (Ashbridge et al., 2000; Perrett & Emery, 1994; Perrett et al., 1985, 1992; Wachsmuth et al., 1994). These orientation aftereffects are specific to the stimulus presented and reflect adaptation at the global representation of the stimulus in high-level vision. However, an outstanding question regarding whether or not these perceptual aftereffects are indicative of separate body and head orientation remains. The experiment presented in Chapter 2 employs cross category adaptation to address this question.

To date very different research paradigms have been employed to examine perception of cues to social attention. Given the importance of hand pointing direction for social interaction, and the fact that gaze and pointing play similar roles in the development of shared attention, Chapter 3 examines for the first time, the visual representation of hand pointing direction. We employ same and cross category adaptation to examine if this social directional cue is represented in high-level vision.

Mounting evidence suggests that we orient our attention reflexively towards the direction of eye gaze and follow this cue to the same spatial location (Birmingham & Kingstone, 2009; Friesen & Kingstone, 1998; Friesen, Moore, & Kingstone, 2005; Frischen, Bayliss, & Tipper, 2007; Hayward & Ristic, 2015; Diver et al., 1999; Langton, 2000; Ristic, Friesen, & Kingstone, 2002). The findings from Chapter 2 and 3 are discussed in
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relation to those from research that has used spatial cueing of attention as an index of selective attention to different social cues. One way to address concerns about drawing parallels between the two methodologies is to see if social directional stimuli from Chapter 2, head and body orientation, like eye gaze direction produce spatial cueing effects in a standard adaptation of the Posner cueing paradigm (Chapter 4). That is, will a centrally presented, averted head or body cue facilitate spatial attention in the direction that the cue is oriented, even when the cue is task irrelevant?

The majority of research on the subject of pointing has looked at the development of referential gestures in infants, the utility of the pointing gesture and its association with verbal communication. Despite the considerable attention this deictic gesture has received in the developmental and comparative literature, little is known about how this visual cue is analysed and integrated in the visual system. What perceptual information is used to determine where someone is pointing? How accurate are people at estimating the focus of a pointing gesture? What role does eye gaze direction play in discerning where in space someone is pointing? The study presented in Chapter 5 uses traditional psychophysical method of constant stimuli to discern perceptual acuity for pointing direction.
Preamble to Chapter 2: Visual adaptation

The studies presented in Chapters 2 and 3 employed visual adaptation, an experimental technique described in detail below, to examine visual representation of three social cues; head orientation, body orientation (Chapter 2) and hand pointing direction (Chapter 3). The study reported in Chapter 2 comprises two experiments that address the important question of how visual information from head and body orientation are combined in gauging social attention. Chapter 2 describes evidence supporting hierarchical integration of cues from the human body and is consistent with evidence from single-cell recording studies in nonhuman primates showing that information about head orientation can override information about body posture when both are visible. Chapter 3 reports the second study that employed a visual adaptation paradigm to explore whether two cues to social attention, index finger pointing gesture and a symbolic arrow, are coded separately in the visual system or in common. The study provides novel evidence of adaptation to hand pointing direction revealing separate mechanisms for coding right and leftward pointing directions. The precise stimulus features driving adaptation is still an open question as the cross adaptation effects suggest that adaptation may not be to the biological dimension of the stimulus but driven instead by simple orientation cues contained in the morphological structure of the pointed hand. To further address this issue, visual acuity for pointing perception and its relationship to spatial perception and eye gaze direction is examined later in Chapter 4.
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The following describes the function and application of adaptation as a tool to examine visual perception and representation of a wide range of perceptual phenomena. I describe in detail what visual adaptation is, its functional properties, and how the experimental technique of visual adaptation has been used to investigate the neural coding of both ‘low level’ (e.g., line orientation) and ‘high level’ (e.g., face viewpoint) properties of objects and scenes. This includes a review of the seminal findings from high level orientation adaptation research that support employing this paradigm to investigate visual perception and integration of social cues in high level vision (for reviews see Clifford et al., 2007; Webster, 2012, 2011).

Visual Adaptation

Humans have a visual system that has the remarkable capacity to make rapid sensitivity adjustments to persistently varying viewing contexts. The process by which these sensitivity adjustments are achieved by our sensory systems is called adaptation. Adaptation has been described as an essential property of neuronal plasticity that has a prevailing impact on our perception of the world (Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003), for much of our perceptual experience is relative to our recent sensory history (Kohn, 2007). Defining adaptation is a delicate endeavour. In general, terms, adaptation is any adjustment of a system or organism to change. In sensory terms, adaptation extends the dynamic range of a system, thus permitting the organism to function efficiently over a wide range of environmental conditions (Clifford et al., 2007). In perceptual terms, adaptation involves a shift or change in the perceived properties of objects as a direct result of
exposure to a constant stimulus. Adaptation is a general property of the visual system such that our perceptual experience is mediated by continuous adjustments in neural sensitivity that reflect the recent history of what we are looking at (Webster, 2012). In order to maximize the efficiency of a system, adaptation is considered selective for specific features of a stimulus. This stimulus specificity led to the procedure of sensory adaptation being labelled the 'psychophysicist’s microelectrode' (Frisby, 1980).

**Perceptual Aftereffects**

Psychologists study adaptation by using aftereffects. Aftereffects are changes in the perceived properties of objects experienced as a result of exposure to an unchanging stimulus. Adaptation aftereffects manifest as perceptual biases that are induced after exposure to a stimulus and are thought to reflect a reduction in the response of neuronal cells tuned to specific features of that stimulus. The perceptual change experienced can relate to sensitivity as with light and dark adaptation, biases in perception such as the motion and tilt aftereffects described below or adjustments in sensorimotor coordination (Anstis, Verstraten, & Mather, 1998; Clifford et al., 2007; Webster, 2012). The first description of the visual illusion known as the waterfall illusion or motion aftereffect, MAE, is attributed to Aristotle in his *Parva Naturalia* (Ross, 1931). After prolonged exposure to a moving stimulus such as looking at the cascade of water tumbling vertically downward from a height such as that found in a waterfall, one’s perception of a stationary stimulus will shift. For example the fixed face of a rock by the shore will no longer appear static and instead the features of the rock will
appear to move in an upwards direction. This perception of motion of a static object is the motion aftereffect, MAE (Anstis et al., 1998).

While first described in antiquity, studies of adaptation first began in the nineteenth century (Addams, 1834). From this point, visual adaptation has had a rich and varied history in vision science and psychology. The reason for this is that the aftereffects of adaptation further our understanding of how our visual system encodes and represents the changing environment (Webster, 2012). From this, there are many different types of visual adaptation, which occur along many different parts of the visual stream from the retina (light and dark adaptation), to early visual processing areas (V1), with varying degrees of complexity.

From low to high-level vision, visual adaptation is employed to characterize neural processing and perceptual organization of features in the environment. The measurement of aftereffects provides a way to explore the neural coding of various stimulus dimensions from low level attributes such as colour, shape, contrast, orientation, to mid-level features such as motion, and to more conceptual or abstract high level properties such as facial identity (Ghuman, McDaniel, & Martin, 2010; Jeffery, Rhodes, & Busey, 2006; Rooney, Keyes, & Brady, 2012), facial viewpoint (Balas & Valente, 2012; Fang & He, 2005), emotional expression and gender (Javadi & Wee, 2012).

Most pertinent to the first two studies presented here is the tilt aftereffect (TAE). This occurs when constant exposure to lines that are tilted to the right or to the left leads to a perceptual shift in how subsequently viewed
vertical lines appear (Gibson & Radner, 1937). The phenomena has been reported to be dependent on the angle differentiation between adapting and test stimuli (Clifford, 2002; O'Toole & Wenderoth, 1977). Clifford (2005) summarizes the functional basis of the TAE as follows; adapting to orientations between 0˚ and 50˚ result in a repulsive aftereffect such that subsequent vertical test stimuli are judged as oriented, and tilted away from vertical in the opposite direction to the adaptor. The strongest adaptation aftereffect occurs at angles between 10˚ and 20˚. For larger variation in angle, 75˚ and 80˚, a smaller attraction aftereffect has been reported where vertical test stimuli are judged as tilted in the same direction as the adapting stimulus (Clifford, 2005).

The TAE reflects separate orientation tuned neurons that code left and right orientations. Cells, with receptive fields sensitive to particular orientations, have been shown to appear in a number of visual processing regions, in the primary visual cortex V1 (Hubel & Wiesel, 1962), the lateral geniculate nucleus LGN (Ben-Yishai, Bar-Or, & Sompolinsky, 1995; Soodak, Shapley, & Kaplan, 1987) and extrastriate areas V2, V3, V4 (Boynton & Finney, 2003; Fang & Murray, 2005). However, orientation tuning is sharpest in the primary visual cortex V1 (Dragoi, Sharma, & Sur, 2000). How does adaptation to the feature of a stimulus such as the orientation of a line predispose us to the perception of the opposite? Normalization theory proposed by Gibson (Gibson, 1937; Gibson & Radner, 1937) posits that our perception of line orientation is dependent on adjustment to any deviations from the norms of vertical and horizontal in visual space. For example, viewing a line oriented ten degrees clockwise from vertical will cause the
nearest norm (vertical) to tilt in the direction of the adapting line. After adaptation a vertical line, the original norm, will appear tilted from this new shifted norm in the opposite direction. The larger the angle increases towards horizontal the more likely you are to see an attractive effect.

The fatigue model of adaptation has been the dominant model to offer a functional account of neuronal mechanisms responsible for adaptation aftereffects. According to this model neurons tuned to the particular attribute, e.g. left tuned orientation neurons, fatigue after prolonged exposure (Gibson & Radner, 1937). Once the adaptation phase has completed the response of these cells remains suppressed (Clifford et al., 2007) thus producing a perceptual bias away from the adapting orientation in the population of cells sensitive to this orientation (for full review of functional accounts of orientation adaptation Clifford, 2002; Clifford et al., 2007).

**High-level Adaptation to Social Cues**

So far, I have discussed classic perceptual illusions and aftereffects, such as a perceptual bias in what looks vertical after exposure to tilted lines, the TAE, or a change in what is perceived as stationary after exposure to movement, the MAE. These are simple perceptual aftereffects to basic stimulus attributes, orientation, and motion. More recently, particularly since the turn of the century, attention has shifted to using visual adaptation to examine more complex stimulus attributes.

Over the past decade, visual adaptation has been reported for far more complex and socially salient stimuli that provide insight into the later stages of visual processing. In particular, face related aftereffects have been
reported for such abstract dimensions as the perception of gender (Ghuman et al., 2010; Javadi & Wee, 2012; Kessler, Walls, & Ghuman, 2013; Palumbo, D'Ascenzo, & Tommasi, 2014), identity (Fang, Ijichi, & He, 2007; Leopold, O'Toole, Vetter, & Blanz, 2001) emotional expression (Webster, Kaping, Mizokami, & Duhamel, 2004) and attractiveness (Rhodes et al., 2003; Rhodes, Watson, Jeffery, & Clifford, 2010). Perceptual adaptation to features of faces enables the visual system to flexibly adjust its otherwise limited neural response range to specific attributes as described above and even more abstract categories of faces (Webster, 2011). From moment to moment neural fine-tuning continuously regulates what features of faces are perceived as normal or average (Leopold, Rhodes, Müller, & Jeffery, 2005). Once a norm is established, adaptive recalibration helps us to discriminate even subtle deviations from the norm. This is thought to play an integral role in face recognition and identity discrimination (Leopold, Rhodes, Müller, & Jeffery, 2005; Leopold et al., 2001; Rhodes et al., 2010), with better identity discrimination around an average than a non-average face.

High-level adaptation aftereffects have also been found for complex representations, particularly facial cues such as eye gaze direction (Jenkins et al., 2006). Selective adaptation to eye gaze direction has provided evidence for separate mechanisms coding leftward and rightward gaze. Adapting to faces with eye gaze directed 25˚ left (or right) results in an increased tendency to judge 5˚ and 10˚ eye gaze directions as oriented towards the viewer, straight ahead, whereas the perception of eye gaze in the opposite direction to the adapting 25˚ gaze stimulus often sharpens. For
example, after adapting to leftward gaze, rightward gaze is more likely to be perceived as rightward.

Using neuroimaging, fMRI adaptation, separate pools of cells tuned to left and right eye gaze directions were identified in the anterior portion of the superior temporal sulcus, aSTS adapting to leftward 25° eye gaze direction, activation of this region was reduced when presented with 10° left stimuli (Calder et al., 2007). More recently, researchers examined the role of head orientation in the discernment of eye gaze direction in this region and found finely tuned coding of gaze direction in aSTS that are invariant to head orientation (Carlin et al., 2011).

**Perceptual Frameworks: Multichannel and Opponent**

There are two perceptual frameworks used to conceptualize how neural coding represents object properties, multichannel and opponent coding. Opponent coding is associated with the representation of colour (Webster & MacLeod, 2011) and facial identity (Rhodes, Jeffery, Boeing, & Calder, 2013). One way to distinguish between the two coding models is to compare predictions about perceptual aftereffects e.g., whether adaptation should occur to gaze of a specific orientation. Under an opponent coding framework stimulus features are represented by two distinct channels that are broadly tuned to opposite ends of a continuum (Nummenmaa & Calder, 2009, p.135). Taking eye gaze direction as an example, under an opponent-coding framework direct, front facing eye gaze at 0° has no separate channel for coding direct gaze. Instead equal activation of right- and left-tuned channels results in the perception of direct gaze, this represents ‘the null point or
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central tendency’ (Calder et al., 2008, p.245). Adaptation to direct gaze here would involve equal attenuation of the right and left channels. As direct gaze is the result of the combined and equal activation of neurons coding left and right orientations, no change in the perceived direction of the front facing eye gaze should occur. That is no aftereffect.

In contrast, multichannel coding may involve a number of separate channels that are tightly tuned to code different orientations, for example 20°, 15°, 10°, and 5°, left and right and 0°. Or there may be three broadly tuned channels tuned to left, right, and direct gaze. After adaptation, the output of a channel is reduced in response to the adapting stimulus. The reduction in the firing rate within that channel is in direct proportion to the output evoked by the adapting stimulus. For direct facing gaze, under a three channel multichannel account, the perception of direct gaze results from increased activation of the 0° channel and equal attenuation of the right and left channels. Adaptation to direct gaze under a multichannel model results in a disproportionate decrease in cells coding direct gaze in the direct channel relative to the activation in right and left channels, such that a perceptual shift, aftereffect, is observed whereby small angles of left and right gaze are perceived as oriented more in that direction (more averted) in both left and right channels (Calder et al., 2008; Nummenmaa & Calder, 2009).

Calder et al. (2008) tested these coding models with respect to eye gaze direction using different adaptation conditions, adapting to an averted left or right gaze at 25° deviation and 10° from direct 0°, adaptation to direct gaze 0°, and to alternating left and right averted gaze at 25°. Participants’
discrimination of 0°, 5°, and 10° gaze directions was tested before and after adaptation. Adaptation was measured by the difference between baseline and post adaptation of the percentage of direct categorization of these test stimuli. Calder et al. (2008) found strong evidence to support a multichannel coding system of eye gaze direction. In line with the multichannel-coding framework after adapting to direct gaze, participant’s perception of left and right gaze directions shifted, with more accurate categorization of left and right compared to baseline (less confusion as straight ahead). If only two channels were coding left and right gaze directions, no aftereffect would occur, as both left and right channels would attenuate at the same rate thus leaving no change in the central tendency. After adapting to an averted 25° gaze direction, there was an increased tendency to judge the adapted side test stimuli as direct, i.e. after adapting to the left, 5° and 10° degree left test stimuli were more likely to be perceived as direct facing. In contrast, the non-adapted side test stimuli were less likely to be judged as direct facing and more likely to be correctly categorized as their respective orientation. Under an opponent model, adaptation to averted stimuli should result in equal adaptation aftereffects on both adapted and unadapted sides. And finally, after adaptation to alternating left/ right stimuli, participants were more likely to judge left and right gaze stimuli as direct gaze (Calder et al., 2008). Under an opponent model, no adaptation should occur after left right adaptation.

While eye gaze direction is best represented by a multichannel coding model (Calder et al., 2008; Carlin & Calder, 2013), other high level stimulus attributes are coded by opponent channels. Facial identity is coded with
respect to two different channels positioned along a continuum, referred to as norm based coding (Leopold et al., 2005; Susilo, McKone, & Edwards, 2010). The identity aftereffect paradigm involves adaptation (repeated exposure) to a particular facial configuration such as a face with widely spaced eyes and a thin nose. Subsequent perception of a test face with averaged proportions shifts away from the adapting configuration towards its opposite, so that a face previously perceived as normal, typical or average is now perceived to have narrowly spaced eyes and a broad nose (Leopold et al., 2005; Webster & MacLin, 1999). An opponent-coding framework implements this type of coding. Here, an average face functions as the norm, with deviations from the norm coded and perceived as identity changes (Leopold et al., 2005; Rhodes et al., 2010) Two neural channels, or pools of cells, are tuned to above- and below-average values on each dimension in a multidimensional space (Leopold et al., 2005). Similarly, adapting to a distorted face that is either contracted or expanded causes an undistorted face (average face) to be perceived as appearing in the opposite manner to the adapting face; either contracted if they adapted to an expanded face or expanded if they adapted to a contracted face (Rhodes et al., 2003). Thus, there is strong evidence to support distinct representational frameworks coding facial identity and gaze direction.

**Face Viewpoint Aftereffect**

Particularly pertinent to visual cues that facilitate social attention the face viewpoint aftereffect is considered as a three-dimensional variant of the TAE. Just as our perception of simple line orientation is altered by continual
exposure to lines of a specific orientation, so too can the perceived 3D tilt of complex, socially relevant stimuli such as heads and bodies. The face viewpoint aftereffect (Bi, Su, Chen, & Fang, 2009; Chen, Yang, Wang, & Fang, 2010; Culham, 2005; Daar & Wilson, 2012; Fang & He, 2005; Fang, Murray, & He, 2007; He, Kersten, & Fang, 2012) first observed by Fang and He (2005), occurs following adaptation to side views of a face. The aftereffect manifests as a shift in perception, such that test stimuli oriented towards the frontal view are perceived as oriented in the opposite direction to the adaptor. Like eye gaze direction, adaptation to face viewpoint is best accounted for by a multichannel system (Lawson et al., 2011) with separate channels representing separate pools of cells coding left, right and front facing head views as well as on the vertical plane, up and down. A multichannel coding system predicts that the further the adaptor is from the test view the weaker the adaptation aftereffect will be because each pool of cells responding to that particular orientation are finely tuned with a graded response to different angles within that orientation, such that adapting to an angle that is very far from the test orientation will have less effect on channels that code angles of an image closer to front facing. In contrast, an opponent-coding model predicts that the farther the adaptor is from the test view the greater the activation of the left or right channel. This would then, after adaptation, result in greater suppression in the preferred channel, resulting in larger aftereffects (Calder et al., 2008). Indeed, a reduction in the magnitude of the face viewpoint aftereffects as a function of angular difference between adaptor and test viewpoints has been reported (Chen et al., 2010; Fang & He, 2005).
Chen et al. (2010) examined how the magnitude of the face viewpoint aftereffect varies depending on the angular difference between the angle of adaptor viewpoint and test stimuli. Participants adapted to either left or right adaptors at one of seven side view face orientations, 0°, 15°, 30°, 45°, 60°, and 75°. They found that the angular tuning function of the viewpoint aftereffect had some similarities to the angular tuning function of the TAE (Chen et al., 2010). For example, similar to adapting to line orientation after adapting to face viewpoint, the magnitude of the aftereffect increases quickly, peaks at 30° and then begins to decrease gradually. Adaptation to a 30° profile view of a face induces much stronger adaptation than that of a 60° side view (Chen et al., 2010; Fang & He, 2005). Adapting to line orientation also results in impairment in discriminating subsequent line orientations, although the maximum impairment is induced after adapting to a line orientation that is approximately 10° away from the test stimulus orientation (Clifford, Wyatt, Arnold, Smith, & Wenderoth, 2001). The TAE and viewpoint aftereffect differ in respect to the capacity of large angles, such as 80°, can result in attractive orientation TAE. However, the face viewpoint aftereffect does not induce attractive aftereffects even at 90° (Chen et al., 2010).

The face viewpoint aftereffect is not only a robust aftereffect; it is also a valuable technique that has the potential to reveal how particular types of perceptual aftereffects reflect a beneficial and functional role for high-level visual adaptation. Chen et al. (2010) provided the first evidence to support high-level face viewpoint functions to optimize the limited dynamic range of neural responses for coding visual stimuli by calibrating coding mechanisms to the visual environment. Face view selective neurons have very similar
tuning curves to orientation tuning curves in primary visual cortical area V1 (Perrett et al., 1992, 1985). Furthermore, the model proposed by Clifford et al., (2001) describes the TAE as occurring as a result of inhibition of orientation cells near the adapting orientation combined with bandwidth change away from the adapting orientation. Based on this model, Chen et al. (2010) applied their own computational model to examine viewpoint discrimination optimization. At baseline, participants’ discrimination of face view was established. Face viewpoints ranged from left 5° to right 5° in 0.25° steps. After adaptation to one of five face views, 0° up as far as 90°, participants viewed two successive face viewpoints, direct and left or right. They were required to judge the direction of the second test stimulus. Chen et al. (2010) found that after adapting to the front view 0°, viewpoint discrimination improved for test angles close to the angle of the adapting stimulus. However, after adapting to face stimuli averted by 30° this heightened discrimination of the angles of the test stimuli disappeared and was replaced with typical impairment of viewpoint as expected with the viewpoint aftereffect. From this, the adaptation aftereffect decreased as the adapting angles increased.

How does the face viewpoint aftereffect reflect processing further down the visual stream? The initial observations of the viewpoint aftereffect used adaptors and test stimuli of the same identity. Does the configuration of the face modulate the viewpoint aftereffect? Fang et al. (2007) investigated if the configuration of a face, as manipulated by changes in facial identity and by changes in both facial identity and gender can modulate the viewpoint aftereffect. By employing face morphing along both gender and identity
dimensions, Fang et al. (2007) found strong transfer of the aftereffect after adapting to faces of different identity and gender. The greater the difference between adapting and test stimuli the further the magnitude of the aftereffect diminished. Similarly, in a separate experiment adaptation to side views of inverted faces resulted in reduction of the face viewpoint aftereffect (Fang, Ijichi, et al., 2007). The strong but incomplete transfer of the face viewpoint aftereffect from adaptation to different faces suggests that some face viewpoint-selective neurons in the human visual system are also tuned to face structures (e.g., identity and gender). To control for low-level retinotopic adaptation researchers using adaptation to examine face viewpoint vary the size, shape, identity and position of the adapting and test stimuli (Calder et al., 2008; Chen et al., 2010; Fang, Ijichi, et al., 2007). The perceptual shift persists regardless, demonstrating that these aftereffects reflect high-level selective adaptation to face viewpoint and have important implications about the representation of face viewpoint in the visual system.

High level adaptation aftereffects that show separable coding of eye gaze direction and head orientation in humans confirm the seminal findings of work by Perrett and colleagues (Perrett et al., 1985, 1992) who examined the question of how these social directional cues are processed and combined from the perspective of individual cell activity. They discovered cells in anterior STS of macaques preferentially tuned to different eye gaze and head orientations. As both human adaptation and monkey neurophysiological studies have provided evidence for separate neural cells tuned to eye gaze direction (Jenkins et al., 2006) and head orientation (Fang & He, 2005; Lawson et al., 2011) an important question concerns the extent
gaze direction modulates the perception of face viewpoint. It has recently been reported that changing the direction of eye gaze exerts more of an influence on the face viewpoint aftereffect than changing the identity of a face (Bi et al., 2009; Fang, Ijichi, et al., 2007). Much of the initial research examining face viewpoint aftereffects did not remove eye gaze cues from the adapting and test stimuli. To dissociate the role of eye gaze direction adaptation from the face viewpoint aftereffect Bi et al., (2009) manipulated both of these cues independently. The adapting face stimuli included adaptor with congruent eye gaze direction, or direct eye gaze (incongruent). They report a 33% reduction in the magnitude of the face viewpoint aftereffect after adapting to incongruent (direct gaze). This indicates a close relationship between the neural representation of face view and gaze direction. Interestingly, vertical inversion of face images eliminated this modulation. Face identity adaptation has also been reported to be modulated by gaze direction (Kloth, Jeffery, & Rhodes, 2015). Adapting to stimuli with averted gaze resulted in larger aftereffects than adaptors with direct gaze. In line with attention research (discussed later), our perceptual analysis of these cues as demonstrated through adaptation studies support the primacy of eye gaze direction and face orientation in stimulating social attention.

While there is substantial research that uses adaptation paradigms to examine face perception, remarkably little is understood about the perception of the rest of the human body. At the single cell level, Perrett et al. (1992) found that cells in monkey aSTS are also tuned to particular quadrupedal and bipedal body postures when the head was occluded from view. This
indicates that socially salient orientation information contained in body postures that imply attention is oriented either downwards (quadrupedal posture) or towards the horizon (bipedal posture) is selectively coded. Pertinent to the research presented here, one study that has used visual adaptation to explore the perception of body orientation in humans. Lawson et al. (2009) report a viewpoint aftereffect in the perception of body orientation, such that after adapting to bodies that are oriented either to the right or to left, participants perceive forward facing test bodies as turned in the opposite direction. The pattern of aftereffects is consistent with a multichannel model in which separate mechanisms code the direction of left, right and forward facing bodies.

Similar to face identity and configure aftereffects described above, a recent study tested if adapting to body shape would produce a shift in the perception of slim and heavy bodies and, if so, whether these ‘body shape’ aftereffects transfer across viewpoint of adaptors (Sekunova, Black, Parkinson, & Barton, 2013). Similar to face shape aftereffects (Rhodes et al., 2003), Sekunova et al. (2013) provide initial evidence of a body form representation in the visual system with neural channels coding slim body and heavy body shapes. In contrast to face identity aftereffects (Jeffery et al 2006; Jiang et al 2006), these aftereffects reported were largely view invariant.
Cross Adaptation

In order for visual adaptation to occur in the primary visual cortex (V1), the adaptor and test stimuli must share similar simple attributes such as orientation, spatial frequency and temporal frequency (Kohn, 2007). Using cross-category adaptation, Fang and He (2005) found that the viewpoint aftereffect does not transfer between object groups. Specifically, adapting to faces oriented to the right or left did not produce a perceptual shift in judging the orientation of a selection of non-biological control stimuli including cars and paperclips. Perceptual aftereffects were found within all these object categories but not between categories. Although the potential of this technique to reveal shared or separate neural representations is considerable, cross-category adaptation has not been extensively employed to study the representation of the human body. Fang and He (2005) concluded that neurons selective for viewpoint are also selective for object categories.

To examine cross category adaptation as well as direction selectivity we (Chapter 2, this thesis; Cooney, Dignam, & Brady, 2015) employed a standard left and right adaptation paradigm. This study presents the first evidence of cross-category adaptation to head and body orientation by way of a novel direction-specific perceptual aftereffect.
Chapter 2


2.1 Abstract

Determining where another person is attending is an important skill for social interaction that relies on various visual cues, including the turning direction of the head and body. This study reports a novel high-level visual aftereffect that addresses the important question of how these sources of information are combined in gauging social attention. We show that adapting to images of heads turned 25° to the right or left produces a perceptual bias in judging the turning direction of subsequently presented bodies. In contrast, little to no change in the judgment of head orientation occurs after adapting to extremely oriented bodies. The unidirectional nature of the aftereffect suggests that cues from the human body signalling social attention are combined in a hierarchical fashion and is consistent with evidence from single-cell recording studies in nonhuman primates showing that information about head orientation can override information about body posture when both are visible.
2.2 Introduction

Facilitated by a number of visual cues, such as eye-gaze, pointing gestures, head orientation and body posture, the ability to discriminate the direction of another person’s attention is an important skill in social interaction. The fast and efficient discernment of where someone else is attending permits joint attention, an ability that emerges early in human development and that is integral to the development of theory of mind (Emery, 2000).

Psychophysical studies that address how the various cues from the body signal the direction of one’s attention can be divided methodologically; those that employ attention orienting and interference paradigms (Driver et al., 1999; Hietanen, 1999, 2002; Langton, 2000) and those that use visual adaptation to examine the representation of eye-gaze direction, head orientation and body orientation (Fang & He, 2005b; Jenkins et al., 2006; Lawson et al., 2009, 2011). Studies employing visual adaptation almost invariably examine these cues in isolation, while studies investigating the important question of how these cues are integrated typically employ cueing and interference paradigms. Here we use a cross-category adaptation paradigm in what is, to our knowledge, the first study to use this method to ask how the cues of head and body orientation interact in signalling the direction of social attention. Our results provide clear evidence for a hierarchical model of cue combination initially proposed to explain single cell data (Perrett et al., 1992).
Perrett et al. (1992) propose a top down hierarchy of cues to social attention in which a Direction of Attention Director (DAD) combines cues of eye-gaze, head orientation, and body posture in order to determine where another person is attending. As eye-gaze is most informative about the direction of attention in cases of cue conflict, it is placed at the top of this hierarchy and supersedes information about head orientation, which, in turn, supersedes information about body posture. The likely site of the DAD is the superior temporal sulcus (STS) where cells responsive to both gaze direction and head orientation are found. These cells respond optimally when eye-gaze and head turning are in the same direction and their responses are modulated by gaze direction in the case of conflicting cues from the head (De Souza, Eifuku, Tamura, Nishijo, & Ono, 2005; Perrett et al., 1992).

Experimental support for this hierarchical model of cue combination is, however, somewhat mixed. Research using the modified Posner cueing paradigm – which measures the time to shift attention - supports an integrative hierarchical model such that eye-gaze is referenced to head orientation and head orientation is referenced to body orientation (Hietanen, 1999, 2002). In contrast, studies using Stroop-like tasks report a bidirectional interference effect whereby information from eye-gaze does not completely inhibit information from head orientation nor vice versa (Langton, 2000; Laube et al., 2011). The asymmetry of the interference effects are consistent with a parallel processing model, whereby head orientation and eye-gaze direction cues are processed separately, yet have additive effects on the discrimination of social attention (Langton, 2000).
One explanation for the discrepant findings is the task requirements, such that visual information for attention orienting (as studied in the spatial cueing paradigm) is processed differently than for overt direction discrimination (as is used in the Stoop-like task). Here we employ a visual adaptation paradigm in which participants are asked to explicitly discriminate head and body turning direction to examine how these cues are integrated by the visual system.

Adaptation is a general property of the visual system such that our perceptual experience is mediated by continuous adjustments in neural sensitivity that reflect the recent history of what we are looking at (Webster, 2012). Aftereffects manifest as perceptual biases that are induced after exposure to a stimulus and that are thought to reflect a reduction in the response of cells tuned to specific features of that stimulus. Therefore, the measurement of aftereffects provides a way to explore the neural coding of various stimulus dimensions (Kohn, 2007). For example, exposure to lines that are tilted to the right or to the left leads to a perceptual shift such that subsequently viewed vertical lines appear to tilt in the opposite direction (Gibson & Radner, 1937), thus revealing the operation of neural ‘channels’ tuned to orientation. Visual adaptation has been employed to explore the neural coding of ‘low level’ stimulus properties such as colour, motion, orientation and curvature, as well as ‘high level’ properties such as facial identity and emotional expression, see (Clifford et al., 2007; Webster, 2012) for reviews.
Pertinent to the current research are a number of studies that have used visual adaptation to explore the perception of body and head orientation. Lawson et al. (2009) report a viewpoint aftereffect in the perception of body orientation such that after adapting to bodies that are oriented either to the right or left participants perceive forward facing test bodies as turned in the opposite direction. And a very similar viewpoint aftereffect is reported in the perception of human heads (Lawson et al., 2011). In both studies the pattern of aftereffects is consistent with a multichannel model in which separate mechanisms code the direction of left, right and forward facing bodies or heads. For example, adapting to an alternating sequence of heads oriented 20° to the right and to the left leads to an increased tendency to judge heads that are oriented a little to the right or left as ‘forward facing’. In contrast, adapting to forward facing heads sharpens orientation tuning, so that faces that are oriented a little to the right or left are now more likely to be correctly categorized as such. This result is consistent with a multichannel but not opponent coding model (Lawson et al., 2009).

Using cross-category adaptation, Fang and He (2005) found that the viewpoint aftereffect does not transfer between object groups. Specifically, adapting to faces oriented to the right or left did not produce a perceptual shift in judging the orientation of a selection of non-biological control stimuli including cars and wireframe objects. Perceptual aftereffects were found within all these object categories but not between categories. Although the potential of this technique to reveal shared or separate neural representations is considerable, cross-category adaptation has not been extensively employed to study the representation of the human body. An
exception is recent research on the representation of gender, with reports that adapting to images of male or female bodies elicits an aftereffect such that the perception of faces is then biased toward the opposite gender (Ghuman et al., 2010; Kessler et al., 2013). Similarly, recent research on preference for facial shape shows that viewing heavy bodies enhances preferences for facial adiposity (Re et al., 2011). Given the considerable physical difference between heads and bodies, such ‘cross-category’ aftereffects must reflect particularly high-level representations.

The experiments reported below investigate whether adapting to images of heads (or bodies) presented in side view produces a perceptual bias in judging the direction of orientation of bodies (or heads). Experiment 1 measured participants’ perception of body orientation before and after adapting to bodies or heads, which were extremely oriented to the right or left. Strong aftereffects were expected in the same-category condition given previous findings (Lawson et al., 2009). While previous research shows that viewpoint aftereffects do not transfer across object categories (Fang & He, 2005) cross-category adaptation has not been previously tested using different parts of the body. Assuming different cues to social attention are commonly coded at some level of visual processing (Perrett et al., 1992) we expected that adapting to extremely oriented heads would influence the perception of body orientation. Experiment 2 measured participants’ perception of head orientation before and after adapting to heads or bodies extremely oriented to the right or left. Again, strong aftereffects were expected in the same-category condition. Assuming a hierarchical coding of cues to social attention such that cues from head orientation override those
from body orientation processing (Perrett et al., 1992) the effects of cross-category adaptation were expected to be weaker or absent.

2.3 Methods

Sample size was chosen in advance of data collection, is comparable to that used in research on high level aftereffects (Lawson et al., 2009, 2011) and is consistent with sampling in psychophysics where all participants typically show the effect (Anderson & Vingrys, 2001). Each participant’s data were checked to ensure they showed adaptation and no observations were excluded from the analyses.

2.3.1 Participants

Three distinct groups of twelve (6 female, 6 male) right-handed volunteers from the UCD student population participated in Experiments 1, 2 and 2(a). All were naïve to the purpose of the experiments, had normal or corrected-normal vision, and received ten euros for their participation. Mean [and SD] age was 21 [0.95] years, 27 [5.87] years and 22.6 [5.5] years for the three groups. The study was approved by the UCD Research Ethics Committee; in accordance with the Declaration of Helsinki all participants gave written, informed consent and were advised of their right to withdraw from the study at any time without prejudice.

2.3.2 Stimuli

The stimuli were computer-generated images of human bodies and heads created using Poser http://poser.smithmicro.com. The bodies were cropped at the neck, just below the hips and at the wrists so as to remove orientation cues that may be provided by the hands or legs. The heads were generated
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without hair, were cropped at the neck and had the eyes closed so as to remove any eye-gaze cues to orientation.

In Experiment 1 the test stimuli depicted bodies of 10 identities, 5 male and 5 female, each positioned at $8^\circ$ left, $4^\circ$ left, $0^\circ$, $8^\circ$ right and $4^\circ$ right. For same-category adaptation, the adapting stimuli were the same 10 bodies oriented $25^\circ$ left and $25^\circ$ right. For cross-category adaptation, the adapting stimuli comprised 10 different identities of heads (5 female, 5 male) with similar variation in shape and skin tone as in the bodies, each oriented at $25^\circ$ left and $25^\circ$ right (Figure 2.1).

![Figure 2.1](image1.png)

*Figure 2.1.* Test and adapting stimuli. Examples of the test bodies (Experiment 1) middle panel and test heads (Experiment 2) bottom panel at angles of $8^\circ$ and $4^\circ$ left, $0^\circ$, $4^\circ$ and $8^\circ$ right and of adapting heads and bodies oriented $25^\circ$ right and left (top panel).
In Experiment 2 heads (at 4° and 2° left, 0°, 2° and 4° right) served as the test stimuli, and heads (bodies) at 25° right and left served as the adapting stimuli in the same (cross) category variants. We chose smaller angles for the test stimuli in Experiment 2 because participants’ discrimination of head orientation was finer than their discrimination of body orientation in Experiment 1. For completion, we also present the results of a preliminary study, Experiment 2(a), as supporting information, in which heads (at 8° left, 4° left, 0°, 8° right and 4° right) served as the test stimuli, and heads (bodies) at 25° right and left served as the adapting stimuli.

Images were rendered in colour at 756 x 756 pixels and subtended, vertically, ~21.2° of visual angle at a viewing distance of 60cm. To avoid retinotopic adaptation in the same-category conditions adaptors were made 15% larger than the test stimuli. The stimuli were presented and participants’ responses recorded using Presentation running on a Dell XPS-8300 PC with a screen size of 19 inches and display resolution of 2048 by 1152 at 60 Hz.

2.3.3 Procedure

The procedure followed that of published research (Lawson et al., 2009, 2011). In both the same-category and cross-category adaptation variants participants completed 3 experimental phases, a pre-adaptation (baseline) phase and an adaptation phase, which was repeated for the 25° left and 25° right adaptors, and a test phase during which participants were also exposed to top-up adaptation. To ensure no carry over adaptation effects participants had a 10-minute break between right and left adaptation phases, and completed the same and cross category variants at least 1 day apart.
In the pre-adaptation phase of Experiment 1 all 10 bodies were shown at each of the 5 orientations for 50 trials. Baseline trials began with a central fixation cross (750ms), followed by a test body (300ms). The screen was then blanked until the participant responded using the number pad keys 1, 2 and 3 to indicate whether they perceived the body orientation as “left”, “direct” or “right” respectively. Presentation order was pseudo-randomized.

The adaptation phase started with an adaptation period of ~ 4mins where the 10 adaptation stimuli (5 male and 5 female bodies or heads, oriented 25° to the right or left) were presented 5 times each for 4000ms followed by a blank 750ms ISI. Trial order was pseudo-randomized and participants stated the gender of each stimulus to maintain attention. Adaptation orientation was counterbalanced so that half the participants adapted to leftward and half to rightward oriented stimuli first.

The adaptation was immediately followed by a block of 50 test trials during which adaptation was topped up. Each top up adaptor was presented for 6000ms followed by a test for 300ms with the word ‘RESPOND’ printed beneath it. Participants indicated whether the test bodies were oriented left, direct or right using the number pad. The procedure was identical in Experiment 2, except that heads served as the test stimuli and bodies as the adaptors. Please refer to Appendix A for graphic representation of adaptation procedure.

2.4 Results

The percentage of ‘straight ahead’ responses was analyzed in R (R Development Core Team, 2010) using ANOVA with within-subjects factors of
stimulus Orientation (5 levels), Adaptation (3 levels), and Condition (same/cross-category). Greenhouse-Geisser corrections were used when Mauchly’s Test for Sphericity was significant and effect sizes are given by generalized eta squared ($\eta^2_G$) (Bakeman, 2005). Following Cumming (2014), significant interactions are explored by plotting and reporting point estimates and associated confidence intervals in lieu of significance testing.

### 2.4.1 EXPERIMENT 1: Same (Body-Body) and Cross (Head-Body) Category Adaptation

The percentage of ‘straight ahead’ responses is plotted by body orientation in Figure 2 where there is evidence of strong adaptation in the same-category condition. At baseline participants show high accuracy in judging the facing direction of bodies oriented at 0° and 8°, but often (~40% of trials) judge bodies oriented 4° left and right as facing straight ahead. After adapting to bodies orientated 25° right or leftward, the response curves shift in the direction of the adapting stimulus, so that the percentage of straight-ahead responses now peaks at 4° right or left respectively. This shift in the ‘neutral point’ is characteristic of many forms of adaptation (Webster & McLeod, 2011). Note also that tuning is sharpened for bodies oriented in the opposite direction to the adapting stimulus, i.e., after right (left) adaptation participants are more likely to correctly perceive 4° left (right) bodies as oriented to the left (right). See also Table 2.1.

There is similar evidence of adaptation in the cross-category condition. Although with no obvious shift in the neutral point, the same characteristics of negative aftereffects outlined by Webster and McLeod (2011) are present, with bodies oriented in the same direction of the adapting head stimuli now
perceived as facing straight ahead. And tuning is sharpened for bodies oriented in the opposite direction to the adapting heads, i.e., after right (left) adaptation participants are more likely to correctly perceive 4° left (right) bodies as oriented to the left (right). See also Table 2.1.

**Figure 2.2.** Same and cross category adaptation experiment 1. Top Panel: The percentage of straight-ahead responses is plotted by test body orientation with separate traces for pre-adapt, post-adapt right and post-adapt left. Error bars show +/-1 S.E.M. Bottom Panel: Mean difference in the percentage of straight ahead responses pre- and post-adaptation by test body orientation, with separate traces for adaptation to rightward and leftward facing adaptors. Error bars show 95% confidence intervals around the point estimates, the dotted black line marks an effect size of zero.

As expected from these observations the omnibus ANOVA test showed a significant 3-way interaction, Orientation* Adaptation* Condition, F(8,88) =
16.93, \( p \sim 0.00, \eta^2_G = 0.20 \), so separate analyses for the same- and cross-category adaptation conditions were run. Both ANOVAs showed significant main effects of Orientation and of Adaptation whose interpretation is qualified by significant Orientation*Adaptation interactions, \( F(8,88) = 50.95, p \sim 0.00, \eta^2_G = 0.66 \) for same-category, and \( F(8,88) = 15.79, p < 0.01, \eta^2_G = 0.28 \) for cross-category adaptation.

These interactions were explored using planned contrasts of the percentage of straight ahead responses prior to and after adapting at each of the five test body orientations. In interpreting these results we follow the ‘new statistics’ approach (Cumming, 2014) and plot point estimates of effect sizes (the mean difference in the percentage of straight ahead responses pre- and post-adaptation) with associated 95% CIs in the lower panel of Figure 2.2. In Table 2.1 we note with an asterisk those rows in which the effect is in the expected direction, where the absolute effect size is substantial and where the 95% CIs do not include zero.
### Table 2.1

*Experiment 1 Response Change Post Adaptation Compared to Baseline*

<table>
<thead>
<tr>
<th>Test</th>
<th>Body</th>
<th>Change</th>
<th>Percent SA</th>
<th>Response</th>
<th>Percent SA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Adapt Right: Baseline</td>
<td>Adapt Left: Baseline</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8° L</td>
<td>↓° L ↑L</td>
<td>-2.92 [-8.89:3.06]</td>
<td>↑2.9 ↓L</td>
<td>55.42 [39.02:71.81]*</td>
<td></td>
</tr>
<tr>
<td>4° L</td>
<td>↓° L ↑L</td>
<td>-31.67 [-45.03:-18.30]*</td>
<td>↑31. ↓L</td>
<td>50.83 [36.25:65.41]*</td>
<td></td>
</tr>
<tr>
<td>0°</td>
<td>↓°.8 ↑L</td>
<td>-27.92 [-48.21:-7.62]*</td>
<td>↓27. ↑R</td>
<td>-26.25 [-47.24:-5.26]*</td>
<td></td>
</tr>
<tr>
<td>4° R</td>
<td>↑° R ↓R</td>
<td>46.25 [29.32:63.18]*</td>
<td>↓6.2 ↑R</td>
<td>-27.92 [-41.08:-4.75]*</td>
<td></td>
</tr>
<tr>
<td>8° R</td>
<td>↑° R ↓R</td>
<td>56.25 [42.36:70.14]*</td>
<td>↓6.2 ↑R</td>
<td>-6.25 [-13.56:1.06]</td>
<td></td>
</tr>
</tbody>
</table>

**Experiment 1 Cross Adaptation (Head to Body)**

<table>
<thead>
<tr>
<th>Test</th>
<th>Body</th>
<th>Change</th>
<th>Percent SA</th>
<th>Response</th>
<th>Percent SA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Adapt Right: Baseline</td>
<td>Adapt Left: Baseline</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8° L</td>
<td>↓° L ↑L</td>
<td>-2.92 [-5.04:-0.79]</td>
<td>↑2.9 ↓L</td>
<td>5.42 [-2.18:13.01]</td>
<td></td>
</tr>
<tr>
<td>4° L</td>
<td>↓° L ↑L</td>
<td>-11.67 [-21.56:-1.77]*</td>
<td>↑11. ↓L</td>
<td>28.33 [13.79:42.88]*</td>
<td></td>
</tr>
<tr>
<td>0°</td>
<td>↓°.3 ↑L</td>
<td>-2.08 [-18.25:14.08]</td>
<td>↓2.0 ↑R</td>
<td>-2.09 [-9.05:4.88]</td>
<td></td>
</tr>
<tr>
<td>4° R</td>
<td>↑° R ↓R</td>
<td>32.5 [20.72:44.27]*</td>
<td>↓2.5 ↑R</td>
<td>-9.17 [-18.03:-0.30]*</td>
<td></td>
</tr>
<tr>
<td>8° R</td>
<td>↑° R ↓R</td>
<td>8.75 [1.19:16.31]</td>
<td>↓.75 ↑R</td>
<td>-2.92 [-5.44:-0.39]</td>
<td></td>
</tr>
</tbody>
</table>

*Note.* SA = Straight Ahead responses; L = Left responses; R = Right responses.

* Substantial effect in the expected direction, and the 95% CIs do not include zero.
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For same-category adaptation these effect sizes run between a low of 26.25% and a high of 56.25%. For cross-category adaptation, these effect sizes run between a low of 9.17% and a high of 32.5% and occur after both rightward and leftward adaptation for test stimuli of 4°L and 4°R. Effect sizes and associated 95% CIs are reported in lieu of significance tests given the high sampling variability of p-values (Cumming, 2014). Cumming notes that ‘only very small p-values give a reasonable basis for rejecting a null hypothesis’ (Cumming, 2014, p.134-135), and that in these cases effect sizes are typically large and unequivocal. We note that where our effect sizes are largest (>30%) paired t-tests all return p-values < 0.001.

To summarize, while the effect sizes are greater after same category (body-to-body) adaptation, there is also clear evidence of robust adaptation in the cross category (head to body) case.

**2.4.2 EXPERIMENT 2: Same (Head-Head) and Cross (Body-Head) Category Adaptation**

Experiment 2 measured participants’ perception of head orientation before and after adapting to heads or bodies oriented 25° to the right or left. In our preliminary study, Experiment 2(a), the test heads were presented at the same angles as the test bodies in Experiment 1, namely 8° and 4° left, 0°, 8° and 4° right. Here same-category adaptation was strong whereas there was no evidence of cross-category adaptation. (See Figure 2.3)

This lack of cross-category adaptation may reflect the proposed hierarchy whereby cues to social attention from the head may override those of the body. However, the lack of adaptation may, in part, reflects participants’ finer discrimination of head orientation than of body orientation for the stimuli as
rendered here, e.g., participants are making ~40% errors for bodies oriented at 4° in the baseline condition (Fig 2.3) whereas their baseline error rate for heads oriented at 4° is ~ 20%.

Using a range of smaller head orientations, namely 4° and 2° left, 0°, 2° and 4° right, had the desired effect with participants perceiving heads oriented at 2° as pointing straight ahead on ~40% of baseline trials. The pattern of responses after head-to-head adaptation is very similar to that seen for body-to-body adaptation in Experiment 1 (Figure 2.3 and Table 2.2). Specifically, after adaptation to heads oriented to the right (left) the neutral stimulus appears to face in the opposite direction. Secondly, heads that are physically oriented in the same direction as the adaptor are more often perceived as facing straight ahead after adaptation, so that there is a clear shift in the neutral point. Finally, tuning is sharpened for heads oriented in the opposite direction to the adapting stimulus. While this pattern of adaptation is evidence in the cross-category (body to head) condition, the effects are much weaker and the pre-adaptation and post-adaptation curves in Figure 2.3 are largely overlapping.

The omnibus test showed a significant Orientation*Adaptation*Condition interaction (p~0). ANOVA for same-category adaptation showed a significant Orientation*Adaptation interaction, F(8,88) = 31.33, p ~ 0.00, $\eta^2_G = 0.50$, as did ANOVA for cross-category adaptation, F(8,88) = 9.64, p ~ 0.00, $\eta^2_G = 0.09$. These interactions are explored in Table 2.2 and the lower panel of Figure 2.3. For head-to-head adaptation the effect sizes in the table cells with an asterisk run between a low of 15.42% and a high of 59.58%
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after rightward adaptation at 2°L, 0°, 2°R and 4°R, and after leftward adaptation at 2°R, 2°L and 4°L. The effect sizes are smaller at 0°, -16.67% after rightward and -9.17% (with the 95% CI including zero) after leftward adaptation, when compared to the effects found for body-body adaptation in Experiment 1. Again, perception of forward facing heads is particularly robust.

In the cross-category condition, the evidence for adaptation is much weaker with smaller effect sizes and fewer 95% CIs that do not include zero (Figure 2.3, Table 2.2). There is a small and unexpected increase in the percentage of straight ahead responses at 0° following both rightward and leftward adaptation; viewing extremely oriented body stimuli appears to strengthen the perception of forward facing heads. In summary, Experiment 2 shows clear evidence of head to head adaptation but little or no evidence of body to head adaptation.
Figure 2.3. Same and cross category adaptation experiment 2. Top Panel: Percentage straight-ahead responses by test head orientation in Experiment 2. Error bars show +/-1 S.E.M. Bottom Panel: Mean difference in the percentage of straight ahead responses pre- and post-adaptation by test body orientation. Error bars show 95% confidence intervals around the mean.
Table 2.2

Experiment 2 Response Change Post Adaptation Compared to Baseline

<table>
<thead>
<tr>
<th>Test</th>
<th>Adapt Right: Baseline</th>
<th>Adapt Left: Baseline</th>
</tr>
</thead>
<tbody>
<tr>
<td>Head</td>
<td>Change</td>
<td>Percent SA</td>
</tr>
<tr>
<td></td>
<td>Response</td>
<td>Change [95% CI]</td>
</tr>
<tr>
<td>4° L</td>
<td>↓° L ↑L</td>
<td>-4.17 [-11.69:3.36]</td>
</tr>
<tr>
<td>0°</td>
<td>↓° .6 ↑L</td>
<td>-16.67 [-30.50:2.83]*</td>
</tr>
<tr>
<td>2° R</td>
<td>↑° R ↓R</td>
<td>47.92 [24.13:71.71]*</td>
</tr>
<tr>
<td>4° R</td>
<td>↑° R ↓R</td>
<td>44.58 [20.45:68.72] *</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Test</th>
<th>Adapt Right: Baseline</th>
<th>Adapt Left: Baseline</th>
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<tbody>
<tr>
<td>Head</td>
<td>Change</td>
<td>Percent SA</td>
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<tr>
<td></td>
<td>Response</td>
<td>Change [95% CI]</td>
</tr>
<tr>
<td>4° L</td>
<td>↓° L ↑L</td>
<td>-3.75 [-8.06:0.56]</td>
</tr>
<tr>
<td>2° R</td>
<td>↑° R ↓R</td>
<td>13.75 [0.26:27.24] *</td>
</tr>
<tr>
<td>4° R</td>
<td>↑° R ↓R</td>
<td>8.75 [1.07:16.43]</td>
</tr>
</tbody>
</table>

Note. SA = Straight Ahead responses; L = Left responses; R = Right responses.
* Substantial effect in the expected direction, and the 95% CIs do not include zero.
2.5 Discussion

This study presents the first evidence of cross-category adaptation to head and body orientation by way of a novel direction-specific perceptual aftereffect. Adapting to images of extremely oriented heads produces a perceptual bias in judging the turning direction of subsequently presented bodies. In contrast, little to no change in the judgment of head orientation occurs when participants adapt to extremely oriented bodies. The unidirectional nature of the aftereffect suggests that head orientation modulates the perception of body orientation but that information about body orientation does not inhibit the perception of head orientation, a finding consistent with the idea that cues from the human body signalling social attention are combined in a hierarchical fashion whereby cues to social attention from the head may override those of the body (Perrett et al., 1992).

As expected and in line with previous research (Fang & He, 2005; Lawson et al., 2009, 2011) adapting to side views of human bodies and heads biases the perceived direction of subsequently viewed bodies and heads respectively, and these strong viewpoint aftereffects provide support for the existence of view-selective neurons in the visual system. The aftereffects are unlikely to reflect low-level adaptation as the adaptor and test stimuli varied in shape, in size and in gender and identity. Secondly, the relatively short presentation of test stimuli (300ms) suggests that the aftereffects do not follow from an extended cognitive analysis of individual face or body features but is based on fast global processing as, like faces, bodies are processed configurally (Reed et al.,
Finally, in the specific case of cross-category adaptation, the adapting and test stimuli did not share the same configuration of local features. Therefore, an interpretation of these results as reflecting high-level adaptation to head and body orientation is warranted, with the cross-adaptation effects having important implications for understanding the neural coding of head and body viewpoint.

Our results also point to a particularly robust representation of forward facing heads. First, participants’ judgments that a head is oriented ‘straight ahead’ are less susceptible to same-category adaptation (Experiment 2) than are bodies (Experiment 1) so that there is a much less obvious shift in the neutral point for head to head than for body-to-body adaptation. Secondly, adaptation to extremely oriented bodies in Experiment 2 strengthens rather than weakens the perception of forward facing heads as facing ‘straight ahead’. As our heads were rendered with eyes closed, this is unlikely to reflect the recently reported expectation bias that gaze is usually directed at the observer (Mareschal, Calder, & Clifford, 2013).

Previous research on the viewpoint aftereffect (Fang & He, 2005) found no cross adaptation between images of human heads and of other objects and concluded that neurons selective for viewpoint are also selective for object categories. However, the stimulus categories used by Fang and He were biological and non-biological. In contrast, we used heads and bodies that are two categories of the one biological form. While cross adaptation between different viewpoints of these two social
signals has not been previously examined, cross adaptation aftereffects have been reported for faces and bodies along the higher order dimension of gender. Interestingly, unlike our viewpoint aftereffects, which are directional in nature, the gender aftereffects transfer both ways. Continuous viewing of male or female bodies (Ghuman et al., 2010) or heads (Palumbo et al., 2014) leads to the opposite gender bias in the perception of subsequently presented faces or bodies respectively. Coupled with reports that gender aftereffects can also be induced by continuous viewing of gender-specific objects (e.g., lipstick, shoes, items of clothing etc.), it is likely that these effects evidence neuronal populations tuned to the higher order, learned, concept of gender (Javadi & Wee, 2012).

In the case of the viewpoint aftereffects reported here, adaptation likely occurs at neuronal sites where information about the human face and body are integrated. Single cell recordings from the anterior region of macaque STS reveal whole body selective cells tuned to both orientation and size (Ashbridge et al., 2000). While cross-category viewpoint invariant responses – via response pooling across orientation-tuned cells – may be necessary for object recognition, the authors argue that the retention of information about viewpoint is crucial for interpreting social signals. Indeed, neuroimaging research points to human anterior STS in coding both head orientation and eye-gaze direction (Ashbridge et al., 2000; Laube et al., 2011). The fusiform gyrus is also implicated in processing head (Laube et al., 2011) and body facing direction (Vangeneugden, Peelen, Tadin, & Battelli, 2014).
As described above, behavioural studies examining cue integration provide conflicting accounts as to how cues to social attention are combined, with different experimental paradigms supporting different accounts. For example, both Langton (2000) and Laube et al. (2011) use a Stroop-like task and report that cues from the head and from the eyes influence each other in a bidirectional manner. In Langton (2000) study, participants were shown images of a head turned to the right or left with the eyes gazing in the same or opposite direction. In separate blocks, they made speeded responses to indicate the direction of eye gaze or the turning direction of the head whilst ignoring the second cue. The study reported symmetrical interference effects such that judgments of both eye gaze and head orientation were slowed when the to be ignored cue was incongruent with the cue participants were attending to. This suggests that social cues to attention are processed in parallel and later combined in an additive manner such that one cue can inhibit the other and vice versa.

In contrast, research using the modified Posner paradigm supports a hierarchical model of cue integration. In Hietanen (1999, 2002) participants made speeded responses to indicate whether a peripheral target appeared to the right or left of a central fixation with each response trial preceded by a brief, centrally presented directional cue. When Hietanen (1999) used heads as the directional cue, they only served to speed up response times when the eye gaze and head turning direction were in different directions. Specifically, a frontally facing head with eye gaze averted to the right or left led to faster responses when
eye gaze direction was predictive of target location. In contrast, heads which were turned to the right or left with eyes gazing back to the participant did not speed up response times when head turning predicted target location. And somewhat surprisingly, when both head turning and eye gaze were in the same direction and predictive of target location, they did not serve to speed response times. Interestingly, this identical stimulus (head turned to the right or left with eyes gazing in the same direction) did lead to significantly faster response times when combined with a body that was facing the observer (Hietanen, 2002).

Together these two studies suggest, first, that social cues to attention are judged with reference to the perspective of the person we are looking at. When observing another person, averted eyes (relative to their head orientation) or a turned head (relative to their body orientation) are strong cues to a shift in that person's attention and they draw our attention in the same direction. Secondly, these results suggest that cues are combined hierarchically such that eye gaze is referenced to head orientation and head orientation is referenced to body orientation. A recent study using a novel ‘representational momentum’ paradigm, in which participants judged the endpoint of a just viewed rotating head also points to the strong influence of eye-gaze information on the perception of head orientation in a dynamic task (Hudson, Liu, & Jellema, 2009).

The unidirectional nature of the cross adaptation aftereffects observed in the current study supports an integrative hierarchical model of cue
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combination. To put our findings in the context of other research in this area, we note, first, that they are consistent with predictions based on the seminal single cell studies of Perrett et al. (1992). As adaptation offers a non-invasive and direct way to study the neural coding of visual information, it stands as a straightforward test of the DAD model of cue integration. Secondly, although our study involves an overt direction discrimination task our results are consistent with findings from the spatial cueing research (Hietanen, 1999, 2002) which points to the primacy of eye-gaze over head orientation and of head over body orientation when these are placed in conflict. It could be argued, as suggested by a reviewer, that our findings measure cue integration at the level of perceptual processing rather than at the level of attentional cueing. In response, we note our assumption, in linking our findings to those from the spatial cueing research that the attentional system draws directly on underlying perceptual mechanisms. This issue has been addressed recently for the case of single cues to social attention (Bayliss et al., 2011), where it was shown that the effectiveness of eye gaze as a directional cue may be diminished as a direct result of perceptual adaptation to eye gaze direction. This paradigm, which combines perceptual adaptation with spatial cueing offers a way to further explore the links between perceptual and attentional mechanisms and to addresses the important question as to the role of social perception in social cognition, e.g., deficits in the following of eye gaze has been posited to underlie deficits in joint attention and social cognition in autism (Ashwin et al., 2015).
In summary, our findings show cross adaptation between two cues integral to social attention, head and body orientation. The asymmetrical nature of the aftereffects we observe have important implications for understanding how these cues integrate in the visual system and support the hierarchical model of cue combination.
Preamble to Chapter 3: Perception of pointing

The preceding Chapter looked at two perceptual cues that facilitate social attention, head orientation and body orientation. Using cross adaptation we found evidence to support separate pools of cells that code for these directional social cues. Perceptual representation of head and body orientation is coded in a fashion analogous to a hierarchical organization of ‘social attention’ cells reported in macaque aSTS (Perrett et al., 1992). Chapter 3 presents research that also employs the method of cross adaptation to examine visual perception of another highly salient visual directional cue, index finger hand pointing.

Pointing differs from head and body orientation in the extent to which the effector can extend laterally into space (Butterworth, Franco, McKenzie, Graupner, & Todd, 2002; Butterworth & Itakura, 2000). It is arguably a more powerful directional cue than head and body orientation, depending on the magnitude of the extension. Pointing differs from eye gaze direction, head orientation, and body orientation in that the purpose of a point is always communicative; it invites rather than requires inference from the communicative partner (Cappuccio et al., 2013). While a shift in the position of a person’s eyes, head and body can indicate that their attention has transferred to a new location (e.g., Bayliss et al., 2004; Hietanen, 1999; Langton, 2000; Ristic et al., 2002), this location can be internal or external as we often move our eyes, head and body position to consider or reflect on information, for postural
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reasons, and for reasons other than making another person aware of a precise place or object in the surrounding environment.

An interesting question is whether this social cue is represented in high-level vision. Like face (Haxby et al., 2000; Kanwisher et al., 1997) and body recognition regions (Downing et al., 2001; Peelen & Downing, 2005; Taylor et al., 2007) there is evidence to support representation of the human hand in extrastriate areas (Bracci et al., 2010; Orlov et al., 2010). Hands play a significant role in expression, communication, and purposeful action. Simultaneous visual monitoring of hand actions is required for accurate performance (e.g., to direct attention and in order to manipulate objects).

Behaviourally, it has been shown that hands attract attention over other objects (Morrisey & Rutherford, 2013). Morrisey and Rutherford (2013) presented pairs of photographs of a variety of objects including hands, bodies, feet, hand tools, ovens, toasters and other animals such as dogs. Then a target appeared in one of the two locations where the images had been. Participants were faster to respond to targets on the same side that a hand, body or foot stimulus had appeared compared to other animate (dogs, starfish) and inanimate objects (oven, toaster, tool). However, there was no difference in selective attention to the category of body object (hands, feet, bodies). Similar to previous research that reported face inversion effects (Farah, Tanaka, & Drain, 1995) and body inversion effects (Bosbach, Knoblich, Reed, Cole, & Prinz, 2006; Brandman & Yovel, 2010; Reed et al., 2003), inversion of the hands, feet
and bodies eliminated the attentional bias. Morrisey and Rutherford (2013) provide first evidence of a hand inversion effect.

Previous research showed that sensitivity to manipulations of hand laterality (Brady et al., 2011; Conson, Aromino, & Trojano, 2010; Ní Choisdealbha et al., 2011) is modulated by visual perspective. Participants are faster and more accurate at discriminating hand laterality when the image of the hand approximates an egocentric perspective (Brady et al., 2011).

Viewpoint and identity of hand stimuli have also been shown to modulate neural regions involved in body perception (Chan, Peelen, & Downing, 2004; Myers & Sowden, 2008; Saxe et al., 2006). Chan et al. (2004) examined the role of viewpoint in differentiating between self and others by manipulating visual perspective between egocentric and allocentric views of the human body. They found that activity in the right EBA was stronger in response to allocentric views of the human body than to egocentric views; however, the authors report no identity discrimination in this region. A similar finding, reported by Saxe et al. (2006), found activity in right EBA increased as stimuli of hands and feet moved towards an allocentric view, a view that approximates the orientation of another person. Using repetition suppression or adaptation with fMRI, Myers and Sowden (2008) examined coding of hand identity in body selective regions. Participants viewed hand stimuli from an egocentric visual perspective, a view that approximates the visual perspective one has of their own hand. The stimuli of hands were
images of the participants’ own hand and those of an unfamiliar person (Myers & Sowden, 2008). The authors report that identity modulated activity in right EBA, particularly for images of hands that belonged to another person, as significantly less adaptation was observed in conditions where the participant’s own hand was presented.

Hand pointing is a deictic gesture that illustrates the power of the hand to instigate and manipulate joint attention by identifying a referent to a communicative partner (Cappuccio et al., 2013). Indeed, many non-human species use pointing to achieve group coordination on a target (Gómez, 2007). Joint attention, by definition, requires a target object or event. In the preceding study described in Chapter 2, we presented the social directional cues oriented to the left or right of centre, or direct facing, without a target object. The target object, in a sense, is the viewer as the stimuli faced either directly at or away from the viewer from an allocentric perspective. In consideration of the features of joint attention, the study presented in Chapter 3 addresses these concerns by inclusion of a target object. In contrast to other studies that have looked at high level representation of hands (Bracci et al., 2010), social attention to hands (Morrisey & Rutherford, 2013; Ní Choisdealbha et al., 2011) and hand pointing (Ariga & Watanabe, 2009; Daum & Gredeback, 2011; Fischer & Szymkowiak, 2004), in this study the hand pointing gesture is not presented as a disembodied suspended hand. Instead, the hand and arm are positioned extending from an egocentric visual perspective at or away from an object positioned in depth.
What manner of pointing does the pointing stimulus used in Chapter 3 denote? Traditional accounts of pointing in infancy have distinguished two functions of pointing imperative or declarative (Tomasello et al., 2007). In the stages of infant development, imperative pointing is associated with a first step towards social reciprocity in that it used to obtain objects, usually food, from a caregiver. In theory declarative pointing is dissociated from imperative pointing as it involves mental state attribution, and further involves understanding that the mental states of others can be manipulated through the use of this gestural behaviour (Liszkowski & Tomasello, 2014; Tomasello & Carpenter, 2007; Tomasello et al., 2007). Some theorists have described imperative pointing as a purely selfish non-communicative act (Baron-Cohen, 1989). However, requesting an object by orienting another person’s attention in space towards a proximal or distal target is a communicative act that requires a considerable level of perceptual and attentional coordination between co-attenders. Southgate et al. (2007) argue that pointing in infancy may be primarily interrogative, information requesting, i.e. to get the co-attender to do something, rather, as Tomasello et al. (2007) have argued, to get the adult co-attender to know something.

When adults were asked to respond verbally and gesturally to hypothetical scenarios delineated by imperative and declarative requests, it was imperative requests to distal targets that encouraged index finger pointing the most (Cochet & Vauclair, 2013). This makes sense when you consider that requesting something, such as the car keys or the remote control for the television, involves a high degree of
precision in both locating and discriminating the object of interest apart from the variety of competing objects that surround it. Southgate et al. (2007) argue that the imperative /declarative distinction has encouraged a false dichotomy and contend that imperative pointing does involve estimation of the attentional state of another and the prosocial motive behind declarative pointing has been overstated. For the purpose of the study reported here we describe the type of pointing as proto declarative, however as there is no explicit communicative context the type of pointing can also be understood as imperative or interrogative.
Chapter 3


3.1 Abstract

Of the many hand gestures that we use in communication, pointing is one of the most common and powerful in its role as a visual referent that directs joint attention. While numerous studies have examined the developmental trajectory of pointing production and comprehension, very little consideration has been given to adult visual perception of hand pointing gestures. Across two studies, we use a visual adaptation paradigm to explore the mechanisms underlying the perception of proto-declarative hand pointing. Twenty-eight participants judged whether 3D modelled hands pointed, in depth, at or to the left or right of a target (test angles of 0°, 0.75° and 1.5° left and right) before and after adapting to either hands or arrows, which pointed 10° to the right or left of the target. After adaptation, the perception of the pointing direction of the test hands shifted with respect to the adapted direction, revealing separate mechanisms for coding right and leftward pointing directions. While there were subtle yet significant differences in the strength of adaptation to hands and arrows, both cues gave rise to a similar pattern of aftereffects. The considerable cross category adaptation found when arrows were used as adapting stimuli and the asymmetry in aftereffects to left and right hands suggests that the adaptation aftereffects are likely driven by simple orientation cues, inherent in the morphological structure
of the hand, and not dependent on the biological status of the hand pointing cue. This finding provides evidence in support of a common neural mechanism that processes these directional social cues, a mechanism that may be blind to the biological status of the stimulus category.
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3.2 Introduction

With relative ease and little reflection, we readily follow numerous cues that direct our focus of attention. These directional cues can be biological such as hand gestures, head orientation and eye gaze or symbolic non-biological cues, like arrows. Of the various biological cues to social attention that people use, hand pointing is a meaningful social gesture that can convey a variety of communicative intentions (Tomasello et al., 2007). Comprehension of pointing gestures provides an integral foundation for developing social reciprocity. The intention of the gesture is often aligned with the type of communicative point: imperative pointing is used to request an object whereas declarative pointing is used to direct another’s attention upon an object or event in the environment (Cochet & Vauclair, 2013; Tomasello et al., 2007).

Producing declarative pointing gestures with the index finger begins to emerge toward the end of the first year of infancy (Daum et al., 2013; Goldin-Meadow, 2007; Gómez, 2007; Tomasello et al., 2007), is predominantly right handed (Jacquet et al., 2012) and is predictive of positive vocabulary acquisition (Begus & Southgate, 2012; Brooks & Meltzoff, 2008). Infants as young as 4.5 months have been shown to be sensitive to pointing direction towards a distal referent (Rohlfing et al., 2012). A developmental delay in producing and comprehending pointing gestures is often used as a diagnostic marker for Autism Spectrum Disorder (ASD) (Swettenham et al., 2013). Pointing, like eye gaze, is a deictic gesture that permits the signaller to indicate to a recipient an object or target of interest. The resulting convergence of eye gaze
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between the two interacting parties facilitates a mutual understanding of a common focus of interest, understood as joint attention (Baron-Cohen, 1989; Kita, 2003).

Numerous studies have examined the developmental trajectory of pointing production and comprehension. By comparison, very little consideration has been given to adult perception of hand pointing gestures. While interacting with others, our visual system is constantly processing a number of biological directional cues that serve to establish and maintain joint attention (Bangerte, 2004). Converging evidence suggests that some of these biological cues, such as eye gaze direction (Jenkins et al., 2006), body orientation (Lawson et al., 2009) and head orientation (Lawson et al., 2011), are represented at a relatively high-level of visual processing. This paper asks if the visual system selectively codes for hand pointing direction. If so, is this done at a high level of visual processing? To determine if a selective population of neurons represents hand-pointing direction in the brain we employ visual adaptation. Visual adaptation provides a well-established method (Clifford et al., 2007; Fang & He, 2005; Lawson et al., 2009; Webster, 2011) to study how the visual system codes for these directional cues.

When repeatedly presented with a stimulus, adaptation aftereffects manifest as perceptual biases that result from reduced neuronal sensitivity to specific features of that stimulus (Webster, 2011). For example, adaptation to a leftward tilted line changes our perception of the orientation of a subsequently presented vertical line so that it
appears to tilt in the opposite direction. The tilt aftereffect (Gibson, 1937) and visual adaptation aftereffects in general reflect the continuous adjustment or recalibration of the response properties of neurons tuned to specific stimulus features in the environment (Clifford et al., 2007; Webster, 2011). Perceptual aftereffects have been found for basic stimulus features such as motion (Levinson & Sekuler, 1975) and orientation (Gibson, 1937) and to higher level qualities such as face identity (Leopold et al., 2005), face viewpoint (Fang & He, 2005; Lawson et al., 2011) and gender (Javadi & Wee, 2012; Kessler et al., 2013). For instance, after participants adapted to a side view of a human face their judgments of forward facing test stimuli shifted in the opposite direction (Lawson et al., 2011). Fang and He (2005) found that the face viewpoint aftereffect did not transfer between object groups, such that adapting to a face did not produce a perceptual shift in judging the viewpoint of a selection of non-biological control stimuli such as cars and abstract wireframe objects. However, cross category aftereffects have been reported for the representation of gender, such that adapting to a male face results in a perceptual shift in the perception of body gender away from the gender of the adaptor and vice versa (Kessler et al., 2013).

Interpretation of this cross category aftereffect as evidence of neuronal populations tuned to the higher order concept of gender are supported by further research (Javadi & Wee, 2012) where prolonged viewing of gender-specific non biological objects (e.g., lipstick, shoes, items of clothing etc.), induced a shift in the perception of face gender. There is considerable potential of cross category adaptation aftereffects
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to examine neural sensitivity to high-level stimulus features. Here, we use the technique to examine visual coding of hand pointing direction, a biological directional cue, and ask whether this type of directional cue is visually coded by a separate neural mechanism than arrows, a non-biological directional cue.

The limited amount of research on pointing comprehension in adults has almost exclusively employed attention modulation paradigms (Ariga & Watanabe, 2009; Gregory & Hodgson, 2012; Langton & Bruce, 2000; Materna et al., 2008a; Sato et al., 2010) such as the Posner visual cueing task (1980), Stroop type interference paradigms and eye movement tracking, in order to examine how pointing along with other social cues can modulate attention. With particular consideration given to the biological versus non-biological features of the social cues, a number of studies have reported that hand pointing direction, like eye gaze direction (Langton & Bruce, 2000) exerts automatic control on the observers visual attention (Ariga & Watanabe, 2009; Belopolsky et al., 2008; Fischer & Szymkowiak, 2004). It is not only biological hand pointing and eye gaze cues that have been shown to modulate visual attention; social symbols such as arrows and directional words have been found to produce comparable attentional effects (Langton et al., 1996; Sato, Kochiyama, Uono, & Yoshikawa, 2009). These studies provide evidence of a common neural mechanism that processes these social cues that may be blind to the biological status of the stimulus category.
In contrast, studies that have employed more complex attention-orienting paradigms that require a heavier cognitive load, to examine the influence of biological versus non-biological cues in capturing visual attention have provided evidence to support separate attentional processing of eye gaze direction, hand pointing direction, and arrows (Bayliss et al., 2011; Gregory & Hodgson, 2012). One study (Bayliss et al., 2011) combined visual adaptation with attention orienting to examine the influence gaze perception and hand-pointing perception has on attentional shifts in the direction of observed gaze. They found that repeated exposure to averted gaze but not to hand pointing direction resulted in subsequent weakened gaze cueing in the adapted direction while gaze cueing in the unadapted direction remained at normal attention cueing levels. This suggests that eye gaze and hand pointing direction are coded separately as cues to social attention.

Here we employ an adaptation paradigm rather than an attentional cueing paradigm to explore whether two cues to social attention, index finger pointing gesture and a symbolic arrow, are coded separately in the visual system or in common. Both same-category and cross-category adaptation are used to examine, for the first time, the visual representation of hand pointing direction. We ask two main questions, does adapting to hand pointing direction like other biological cues to joint attention such as eye gaze, head orientation and body orientation elicit a perceptual aftereffect? And, if so, are the aftereffects indicative of separate groups of neurons that code for this particular directional body cue or does the directional information alone elicit a perceptual shift? If
hand-pointing direction is represented in high-level vision then cross adapting to a non-biological directional cue such as arrows should not elicit a shift in the perception of hand pointing direction.

3.3 Methods

3.3.1 Participants

Twenty-eight (14 female) right-handed volunteers from the UCD student population (mean age of years, 25.54, SD = 6.30 years) received fifteen euros for their participation. All were naïve to the purpose of the experiments and had normal or corrected to normal vision. The study was approved by the University College Dublin, Human Research Ethics Committee, Humanities (HREC); in accordance with the Declaration of Helsinki all participants gave written, informed consent and were advised of their right to withdraw from the study at any time without prejudice.

3.3.2 Stimuli

The stimuli were computer-generated images of left and right hands with a portion of the forearm visible, positioned in a pointing gesture, with the index finger pointing in depth at an object, a kitchen skillet. All stimuli were created using 3D animation software Poser® http://poser.smithmicro.com.

In both the same-category and cross-category variants of the adaptation experiment the test stimuli depicted 10 hands in total (5 right and 5 left hands) pointing directly at the handle of the skillet (0°) and 0.75° and 1.5° to the left or right of the skillet. These angles were chosen after a pilot study to gauge participants’ ability to discriminate pointing
direction in this task. In the same-category adaptation variant, the adapting stimuli were 1 left and 1 right hand pointing in depth 10° to the left or right of the skillet. In the cross-category adaptation variant, the adaptor was changed to an arrow pointing in depth 10° to the left or 10° to the right of the skillet (See Figure. 3.1).

All images were rendered in colour at 978 x 978 pixels and subtended, vertically, ~27° of visual angle at a viewing distance of ~60cm. The distance from the tip of the finger (when in the 0° position) to the skillet handle was ~5.2° of visual angle. The stimuli were presented and participants' responses recorded using Presentation® (http://neurobs.com) running on a Dell XPS-8300 PC with a screen size of 19 inches and a display resolution of 2048 by 1152 at 60 Hz.
**Figure 3.1.** Stimuli and protocol. Top Panel: Examples of test stimuli (pointed hands), and adaptors, (arrow and pointed hands) at different orientations. Bottom Panel: Sample of the experimental protocol. This included a baseline phase where participants judged the pointing direction of test hands at 5 orientations 0°, 0.75° right, 0.75° left, 1.5° right, 1.5° left. Followed by a long adaptation phase where participants viewed a series of adaptors (either hands or arrows). The long adaptation period, ~ 4mins, was immediately followed by a post-adapt top up and test block. Each top up adaptor - left and right hands (same-adaptation) or arrows (cross-adaptation) pointing 10° left or right of the skillet - was presented for 6000ms followed by a test stimulus for 400ms.
3.3.3 Procedure

In both the same category and cross category adaptation variants of the experiment participants completed 2 experimental phases, a baseline phase and an adaptation phase, which were repeated for the 10° left and 10° right adaptors. To ensure no carry over adaptation effects participants had a 10-minute break between the right and left adaptation phases, and they completed the same category and the cross category adaptation variants of the experiment at least 1 day apart. Running order was also counterbalanced so that half the participants completed the same category variant of the experiment first and half completed the cross category first.

In each of the two baseline phases (one each before adaptation to right and to left pointing adaptors) all 10 hands (a right and left hand, each shown at 1.5º and 0.75º left, 0º, 0.75º and 1.5º right) were repeated 5 times for 50 trials, so that the combined number of baseline trials was 100. Baseline trials began with a central fixation cross for 750ms followed by a test hand for 400ms. The screen was then blanked until the participant responded using the number pad keys 1, 2 and 3 to indicate whether they perceived the hand as pointing to the left of, directly at or to the right of the skillet handle respectively. Presentation order was pseudo-randomized.

The adaptation phase started with an adaptation period of ~ 4mins during which the adaptation stimuli (a left and a right hand pointing 10° to the right or left of the skillet handle) were presented 25 times each for
4000ms each followed by a blank 750ms ISI. Adaptation direction was counterbalanced so that half the participants adapted to leftward pointing stimuli first and half to rightward pointing stimuli first. The adaptation period was immediately followed by a post-adapt top up and test block of 50 trials. Each top up adaptor - left and right hands (same-adaptation) or arrows (cross-adaptation) pointing 10° left or right of the skillet - was presented for 6000ms followed by a test stimulus for 400ms. The word ‘RESPOND’ was printed beneath each test stimulus and participants judged whether the test hands were pointing to the left of, directly at or to the right of the skillet using the keys on the number pad. The order of the 50 test trials was pseudo-randomized.

3.4 Results

The percentage of ‘direct’ responses was analysed in R (R Development Core Team, 2010) using ANOVA with within-subjects factors of test hand Pointing Direction (5 levels), Adaptation Condition (pre-adapt, post-adapt right, post-adapt left), and Adaptation Type (same-category, cross-category) and a between-subjects factor of Order of Adaptation (adapt to hands first, adapt to arrows first). Greenhouse-Geisser corrections were used when Mauchly’s Test for Sphericity was significant and effect sizes are given by generalized eta squared ($\eta^2_G$) (Bakeman, 2005). Following Cumming (Cumming, 2014), significant interactions are explored by plotting and reporting point estimates and associated confidence intervals (Figure 3.2). In addition, significant interactions were further analysed using planned comparisons with Bonferroni-correction.
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In the omnibus test the main effect of Order of Adaptation was not significant, $F(1,26) = 3.55$, $p = 0.07$, $\eta^2_G = 0.03$, and none of the higher order effects involving Order of Adaptation were significant, e.g., for the 4-way interaction of Order of Adaptation*Direction*Condition*Type, $p = 0.80$. Therefore the data are collapsed across the two groups of participants (those who adapted to hands first and those who adapted to arrows first) in Figure 3.2.
**Figure 3.2.** Adaptation to hand pointing and Arrow direction. Top Panel: Percentage direct responses plotted by hand pointing direction with separate traces for pre-adapt (blue), post-adapt right (red) and post-adapt left (black). Error bars show +/-1 S.E.M. Bottom Panel: Mean difference in the percentage of direct responses pre- and post-adaptation by pointing direction, with separate traces for adaptation to rightward (red) and leftward (black) pointing adaptors. Error bars show 95% confidence intervals around the point estimates, the dotted black line marks an effect size of zero. Same and cross category variants of the experiment are shown in the left and right panel respectively.
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The percentage of trials on which participants perceived the test hands as pointing directly at the skillet handle, is plotted by hand pointing direction in the top panel of Figure 3.2. There is evidence of strong adaptation in the same-category condition. At baseline participants show high accuracy in judging the direction of hands which are pointing directly at the skillet and 1.5° to its left or right, but often judge hands pointing 0.75° to the left or to the right as pointing directly at the target. After adapting to hands pointing 10° to the right or to the left of the target, the response curves shift in a way that is indicative of negative aftereffects as outlined by Webster and McLeod (2011).

First, hands that are pointing in the same direction as the adapting stimulus are now more likely to be perceived as pointing directly at the target, and this is particularly marked for the smallest pointing angle (0.75°). Secondly, and in contrast, hands that are pointing in the opposite direction to the adapting stimulus are now more likely to be correctly perceived as pointing in that direction. These characteristics of adaptation are also evident in the lower panel of Figure 3.2 in which we plot point estimates of effect sizes (the mean difference in the percentage of straight-ahead responses pre- and post-adaptation) with associated 95% CIs. The effects are positive for test hands that point in the same direction as the adaptors and negative for test hands that point in the opposite direction to the adaptors.

There is similar evidence of strong adaptation in the cross-category condition where arrows pointing to the right or left of the skillet handle
serve as the adapting stimuli. Test hands that are pointing in the same
direction as the adapting arrows are now more likely to be perceived as
pointing directly at the target. And accuracy is sharpened a little for test
hands pointing in the opposite direction to the adapting arrows, i.e., after
right (left) adaptation participants are more likely to correctly perceive
0.75° left (right) pointing hands as pointing to the left (right).

Statistical analyses confirm these observations. The omnibus test
showed that the 3-way interaction of Pointing Direction*Adaptation
Condition*Adaptation Type, $F(8,208) = 5.39, p < 0.001, \eta^2_G = 0.03$, was
significant. This suggests that the strength and pattern of adaptation
varied with the type of adaptation, hand-to-hand or arrow-to-hand.
Further analyses were performed on the same-category and cross-
category data sets separately.

ANOVA for the same-category data showed significant main effects of
Pointing Direction, $F(4,108) = 134.93, p \sim 0, \eta^2_G = 0.61$, and of
Adaptation Condition, $F(2,54) = 27.50, p \sim 0.0, \eta^2_G = 0.06$, whose
interpretation is qualified by a significant Pointing Direction* Adaptation
Condition interaction, $F(8,216) = 53.35, p \sim 0.0, \eta^2_G = 0.42$. Planned
comparisons showed a significant change in the percentage of ‘pointing
directly at’ responses at 0.75° right, $t(27) = 6.38, p \sim 0.0, \text{ES} = 37.5\%
[29.88, 45.12]$ and at 1.5° right $t(27) = 7.28, p \sim 0.0, \text{ES} = 36.07\%
[25.90, 46.24]$, between baseline and adaptation to rightward pointing
hands. Planned comparisons between baseline and adaptation to
leftward pointing hands showed a significant change in the percentage of
‘pointing directly at’ responses at 1.5° left, t(27) = 6.32, p ≈ 0.0, ES = 32.32% [21.83, 42.82], at 0.75° left, t(27) = 11.33, p ≈ 0.0, ES = 40.89% [33.49, 48.30] and at 0.75° right, t(27) = -4.07, p = 0.0004, ES = -12.5% [-18.79: -6.20].

ANOVA for the cross-category data likewise showed significant main effects of Pointing Direction F(4,108) = 186.06, p ≈ 0, η²G = 0.67 and of Adaptation Condition, F(2,54) = 11.69, p ≈ 0.0, η²G = 0.02 whose interpretation is qualified by a significant Pointing Direction* Adaptation Condition interaction, F(8,216) = 30.94, p ≈ 0, η²G = 0.30. Planned comparisons showed a significant change in the percentage of ‘pointing directly at’ responses at 0.75° right, t(27) = 4.78, p = 0.00005, ES = 21.25% [12.13, 30.37], and at 1.5° right, t(27) = 3.47, p = 0.0017, ES = 15.17% [6.22, 24.14], between baseline and adaptation to rightward pointing arrows. Planned comparisons between baseline and adaptation to leftward pointing arrows showed a significant change in the percentage of ‘pointing directly at’ responses at 1.5° left, t(27) = 4.39, p = 0.0002, ES = 16.25% [8.65, 23.85], at 0.75° left, t(27) = 8.09, p ≈ 0.0, ES = 36.96% [27.59, 46.33] and at both 0.75° right, t(27) = -4.13, p = 0.0003, ES = -16.25% [-24.32: -8.18], and 1.5° right, t(27) = -3.77, p = 0.0008, ES = -6.25% [-9.65: -2.85]. A comparison of these planned comparisons results across the same-category and cross-category adaptation conditions, along with inspection of the lower panels of Figure 3.3 reveals the rather subtle effect of the Adaptation Type * Adaptation Condition * Pointing Direction interaction, i.e., same-category (hand-hand) adaptation generally leads to slightly higher changes in the
percentage of 'pointing straight at' responses than does cross-category (arrow-hand) adaptation.

Figure 3.3. Same and cross adaptation pointed hand direction. Percentage direct responses are re-plotted by hand pointing direction in the hand-to-hand (top panel) and arrow-to-hand (bottom panel) tasks, separately for left and right test hands. These plots illustrate an asymmetry in baseline (blue) performance such that participants are more accurate in judging the pointing direction of leftward pointing right hands and rightward pointing left hands when the task is most difficult. Error bars show +/-1 S.E.M.
Figure 3.3 re-plots the percentage of direct responses by hand pointing direction separately for left and right test hands to explore the role of hand shape in participants’ judgments of hand pointing direction. At baseline, and when the task is most difficult (0.75°), participants are more accurate in judging the direction of leftward pointing right hands than of rightward pointing right hands and, similarly, they are more accurate in judging the direction of rightward pointing left hands than of leftward pointing left hands. This perceptual bias is also seen in the post-adaptation profiles where the shift in the ‘neutral point’ (the shift in which hand is most often perceived as pointing directly at the target) is hand specific, with a leftward shift for left hands and a rightward shift for right hands. This suggest that task performance is not based on a simple vernier acuity cue but that participants take both hand shape and index finger orientation into account in judging where the hand is pointing relative to the object.

3.5 Discussion

This study presents, for the first time, evidence of rapid visual adaptation to hand pointing direction. Adapting to hands pointing away from an object resulted in a shift in the perception of the direction of subsequently presented hand pointing stimuli away from the direction of the adaptor, a key characteristic of negative aftereffects (Webster & MacLeod, 2011).

The novel direction specific high level adaptation aftereffect reported here has, to date, been observed for three other types of visual social
cues; eye gaze direction (Jenkins et al., 2006), head orientation (Fang & He, 2005; Lawson et al., 2011) and body orientation (Lawson et al., 2009). In concluding that these aftereffects reflect the operation of relatively high-level visual processing, researchers typically adjust either the size (Lawson et al., 2009) or the orientation (Rhodes et al., 2003) of the adapting stimuli relative to the test stimuli so as to rule out low-level, retinotopic effects. Here the adapting stimuli (hands or arrows pointing 10° to the right or left of the target) differ in orientation to and are non-overlapping with the test stimuli (hands pointing 0° or 0.75° and 1.5° to the right or left of the target). As such, the aftereffects we report are unlikely to reflect retinotopic adaptation. Instead, this strong aftereffect provides initial evidence for the existence of neurons in the visual system tuned to hand pointing direction.

In response to a reviewer, we note that the pattern of responses before and after adaptation cannot be explained by a stimulus response compatibility effect, such as the Simon effect. According to the Simon effect, responses should be more accurate when participants press a response key that is located on the same side as the stimulus. In this study participants used the number pad, which is located to the right of the keyboard, yet the same pattern of accuracy is seen for rightward and leftward pointing hands. In fact, examination of Figure 3.3 shows that participants are more accurate at judging the direction of right hands pointing leftward and left hands pointing rightward and find the task more difficult for right hands pointing rightward and left hands pointing...
leftward. This suggests that the overall shape of the hand is important to the task.

Given that the directional information present in the adapting stimulus is paramount to this aftereffect, we asked whether it is the specific configuration of the pointed hand that is responsible or whether adaptation to a non-biological cue to direction elicits a comparable perceptual shift in the perception of hand pointing. The results show that when adapting to an arrow oriented away from the object, participants subsequent perception of hands pointing in the same direction were also repelled away from the direction of the arrow adaptor. Both arrows and pointed hands serve as adaptors and change perception of the pointing direction of test hands. However, the strength of the adaptation attenuated a little when participants adapted to arrows, showing a small yet significant difference between same and cross category adaptation. The finding that adaptation varies according to the type of adaptor confirms that pointed hands are a more effective adaptor than arrows, as evidenced by generally greater effect sizes.

The cross category adaptation observed suggests that a relatively simple orientation cue is driving the aftereffects here. The inclusion of a referent object to the scene increases the number of potential cues that participants could use in judging the pointing direction of the hand. These include the orientation of the index finger, the overall shape of the hand and forearm and additionally, vernier acuity – the misalignment of the tip of the skillet handle and the fingertip or tip of the arrow. In the
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case of vernier acuity, this misalignment is identical for leftward pointing left hands and leftward pointing right hands but participants are more accurate in the latter than former case, thus suggesting that vernier acuity is not the dominant cue for the adaptation aftereffect.

When executing index finger pointing gestures a greater tendency to move the dominant right hand to extend further into contralateral space than the non-dominant left hand towards the right side of space has been reported (Jacquet et al., 2012). Similarly, when observing pointing gestures participants respond faster to hand pointing stimuli that match their own dominant hand (Fischer & Szymkowiak, 2004). Similarly, where pointing and other gestures have been used in the hand laterality task, participants are faster to identify hands seen in egocentric than in allocentric perspective and reaction times are also modulated by participants’ own handedness (Brady et al., 2011; Ní Choisdealbha et al., 2011). In contrast, attention orienting to pointed hands has been shown to be independent of visual perspective, where response latency to same dominant hand pointing stimuli was not moderated when the viewpoint was switched from egocentric to allocentric visual perspectives (Fischer & Szymkowiak, 2004). While the participants in the present study did not produce the pointing gesture, the stimuli were shown from an egocentric, first person visual perspective.

While the dominant hand preference is pertinent in the context of observation of hand pointing it does not fully explain the finding of the present study that participants were more accurate at judging the
direction of hands pointed toward the contralateral side of space than to those pointed towards the ipsilateral side of space. Further experimentation is needed to determine the exact cues that observers are using, and if superior accuracy for contralateral directed hand pointing stimuli is found in left-handers. However, our results show that we are incredibly accurate and can resolve pointing direction at very small angles and this fine-tuned discrimination is likely gauged from both the structure of the pointed hand and the extent that the stimulus extends diagonally into contralateral space.

Our findings are in line with a study (Ariga & Watanabe, 2009) that found fine-tuned visual discrimination of the morphological structure of the pointed index finger. Ariga and Watanabe showed that hands pointing with the index finger are superior at directing attention than hands pointing with the middle or little finger. This advantage in manipulating the viewer’s direction of attention was shown not to be limited to the position of the index finger relative to the thumb or to the length of the index finger but from a holistic visual analysis of the morphological structure of the indexical gesture as a whole. Furthermore, when the accuracy and speed of directional judgments of index, middle and little finger at different lengths were measured, participants were fastest and most accurate at discriminating shortened index finger pointing stimuli. Interestingly, the type of indexical point did not always correlate with discrimination of direction, highlighting a partial dissociation between the cues we use to orient our attention to index finger pointing and those that we use to discriminate the direction of
indexical pointing. However, both the present study’s finding of cross category adaptation to arrow direction and those of the study described above provide evidence that it is likely low-level cues that drive both the attentional shift and direction discrimination.

A parallel can be drawn with the cues used to discriminate eye gaze direction. Studies of eye gaze perception have emphasized the importance of processing simple geometric cues such as scleral contrast, the relative position of the iris to the white matter of the eye (Anstis et al., 1969). Other studies have demonstrated the high resolution of gaze acuity (Bock et al., 2008; Cline, 1967; Symons et al., 2004) reported very fine-tuned sensitivity to detecting small changes in eye gaze direction, as small as 1.4˚ from as far as 1 metre away. Given the importance of discerning eye gaze and hand pointing direction to social interaction, and the fact that gaze and pointing play similar roles in the development of shared attention and language acquisition, it is perhaps unsurprising that our perception of these cues is subserved by simple cues. However, it is important to note that in the case of eye gaze perception, using simple geometric cues alone only works under restricted settings as head orientation also contributes to the detection of eye gaze direction (Langton et al., 2000). Similarly, the position of the index finger relative to the hand and the position of the forearm relative to the hand and body are further configural cues that we use to judge the direction of the point. Like eye gaze direction, it is likely a combination of simple geometric cues and configural processing at work in judging pointing direction.
The findings of the present study are unlike previous research that reported no transfer of aftereffects across categories (Fang & He, 2005). Fang and He employed cross category adaptation to examine the face viewpoint aftereffect and found no cross adaptation between images of human heads and of other non-biological objects, concluding that neurons selective for viewpoint are also selective for particular object categories. Similar to the present study the stimulus categories used were biological (faces) and non-biological (wire like objects and cars). However, unlike Fang and He (2005), we observed cross adaptation between a non-biological directional cue (arrows) and a biological directional cue (pointed hands) presented oriented at or away from an object. Cross category orientation adaptation aftereffects between biological stimuli, heads and bodies, have been reported, where adapting to head orientation produces a perceptual bias in judging the turning direction of subsequently presented bodies. In contrast, little to no change in the judgment of head orientation occurs after adapting to extremely oriented bodies (Cooney et al., 2015a). Similar cross category aftereffects have been reported along the higher order dimension of gender and shown to be independent of stimulus orientation (Kessler et al., 2013). In the case of the cross adaptation aftereffects reported here, cross-category adaptation to these two directional cues likely occurs at an early stage of visual processing.

Our finding that adapting to an arrow causes a shift in the perception of pointed hands suggests that it may not be the biological dimension of the stimuli per se that is producing the effects. Through experience, we
learn that both biological and non-biological cues contain salient directional information, so that our response to these cues is based on the directional information and not the semantic features of the stimulus. However, Bayliss et al. (2011) findings suggest otherwise, as adapting to a hand pointing stimulus did not result in weakened gaze cueing in the adapted direction while adapting to averted gaze did, which implies that it is the perception of the specific biological stimulus dimensions that modulates attention cueing. A strict comparison between studies that employed attention orienting and the present study’s use of perceptual adaptation is difficult; however, by combining adaptation with subsequent measurements of attentional cueing, Bayliss et al. (2011) demonstrate a direct link between perceptual cues and attentional shifts.

To date very different research paradigms have been employed to examine the interaction of cues to social attention. Studies that employed attention cueing paradigms have shown that pointing elicits a spatial cueing effect in the same way as arrows and other directional cues. For example, Langton and Bruce (2000) examined the relationship between the information present in the social directional cues; pointing gestures, head-gaze orientation and spoken directional information. Using a cross-modal interference paradigm, where the pointing gesture was either congruent or incongruent with the verbal stimulus “up” or “down” and the head orientation was congruent or incongruent with the pointing gesture, they observed bi-directional interference effects. Interestingly, in a control experiment they examined whether interference effects would be observed between head direction and non-social
directational cues. The pointing stimuli were replaced with non-biological directional cues; arrows and participants were required to respond to the arrow and, in separate blocks, to the orientation of the head. The to-be-ignored head orientation cues were found to interfere with judgments of the direction of the arrow stimuli. This provides evidence that it is the directional meaning rather than the biological dimension of the stimulus that is encoded at this early stage of processing. Using a very different paradigm, our finding of strong cross-category adaptation is consistent with this interpretation.

Some neuroimaging studies point to a common neural mechanism for processing both biological and non-biological directional cues. An fMRI study that compared responses to passively viewed directional biological and non-biological stimuli showed similar response in the occipital temporal cortex to arrow and hand pointing stimuli (Sato et al., 2009). Consistent with (Materna et al., 2008a) where participants were required to actively follow either hand pointing or eye gaze stimuli, there was no differentiation in the response of STS to these stimuli, supporting the suggestion that STS could be involved in automatic attentional orienting towards the cued direction, regardless of the biological dimension of the stimulus.

The current study provides novel evidence of adaptation to hand pointing direction revealing separate mechanisms for coding right and leftward pointing directions. The precise stimulus features driving adaptation is still an open question as the cross adaptation effects
suggest that adaptation may not be to the biological dimension of the
stimulus but driven instead by simple orientation cues contained in the
morphological structure of the pointed hand.
The first two studies presented here, Chapter 2 and 3, use perceptual adaptation to measure the representation of a number of directional social cues (head and body orientation and hand pointing). Social attention involves using such cues to infer the direction of another’s attention and to direct our attention to where they are attending (Nummenmaa & Calder, 2009). Establishing joint attention in this way is a necessary basis for social cognition, which involves inferring the intentions and goals of others (Mundy & Newell, 2013; Baron-Cohen, 1991; Tomasello & Carpenter, 2007).

As discussed in Chapter 2 perceptual adaptation provides insight into the neural basis of social perception. Other methodologies, especially the Posner cueing paradigm, are used to investigate social attention. Below, the findings from research that has used spatial cueing of attention as an index of selective attention to different social cues are introduced. Chapter 3 asks if the social directional stimuli from Experiment 1, head and body orientation, produce spatial cueing effects in a standard adaptation of the Posner cueing paradigm. That is, will a centrally presented, averted head or body cue facilitate spatial attention in the direction that the cue is oriented, even when the cue is task irrelevant?
Posner Spatial Cueing Paradigm as an Index of Social Attention

In order to gain insight into the intentions of others, we need to first be able to perceive the direction of their attention, but importantly we must relocate our own attention with a shift in theirs. Traditionally, it is understood that attention can be overt or covert (Posner, 1980). Posner described overt orienting as involving a discernible shift in the observer, for example an eye movement or head movement to a particular spatial location in order to better examine a particular stimulus. Covert attention, on the other hand, is achieved without a discernible or overt change in the position of the observer's sensory receptors. The spatial cueing paradigm (Posner & Cohen, 1984; Posner, 1980) has been central to the study of covert orienting of visual attention. In the original paradigm, a central fixation is presented with two placeholders positioned to the left and right of central fixation. Participants are required to make a speeded response when a target appears in one of the placeholders. The presentation of a target is preceded by a cue, for example the illumination of one of the placeholders' borders or the appearance of a centrally presented arrow position oriented towards the left or right placeholder. A typical spatial cueing effect is found when participants RTs to targets in the placeholder that were cued, in this example an arrow head pointed towards one of the placeholders that flashed, are faster than when targets appear in the uncued location (Jonides, 1981; Posner, 1980).
There are two different types of attention orienting, exogenous and endogenous. For example when the placeholder flashes, attention is automatically oriented (exogenous attention) as RTs are faster to targets that are presented in the placeholder that flashed even when the illumination of the placeholders does not predict where the target will be presented, (the target is presented with equal probability in either placeholder). In contrast, the centrally presented arrow head oriented to the left or right has traditionally been described as facilitating voluntary shifts of attention (endogenous) because facilitation of attention was assumed to only occur when the arrow predicts the location of the target (e.g., the target is presented in the cued placeholder 80% of the time, and in uncued placeholder 20% of the time). That is central cueing was thought to be spatially non predictive (Jonides, 1981).

**Eye Gaze Cueing**

More recently an adapted version of the paradigm has been employed extensively to study the type of orienting facilitated by social cues particularly the direction of eye gaze (Bayliss, di Pellegrino, & Tipper, 2005; Daum, 2011; Driver et al., 1999; Friesen & Kingstone, 1998; Friesen et al., 2005; Qian, Song, & Shinomori, 2013; Ristic et al., 2002; Ristic & Kingstone, 2005; Sato et al., 2009). Following Driver et al. (1999) a typical experimental procedure includes a central eye gaze cue presented looking to the left or right. The participant is asked to respond to a target that might appear either at the same location to which the eye gaze was directed (valid) or the opposite invalid location. Faster
reaction times for validly cued targets are taken as evidence for a shift of attention to the gazed-at location. Participants shift their attention in the direction of the eyes gaze even when they are told that these cues do not reliably predict the location of an upcoming target. This finding was surprising as standard endogenous central cueing effects were understood as volitional because centrally presented arrow heads that are spatially uninformative do not produce spatial facilitation (Jonides. 1981; Posner, 1980).

Unlike a peripheral cue, such as illumination, a symbolic central cue’s direction of attention requires some interpretation or cognitive appraisal of the positional information present in the stimulus. Central spatial cueing is generally understood as involving a voluntary, top down attention orienting mechanism (see Birmingham & Kingstone, 2009; Frischen et al., 2007 for reviews). However, gaze cueing was initially labelled ‘reflexive’ because spatial facilitation was observed to spatially non predictive cues (Friesen & Kingstone, 1998) or even counter predictive of the target location (Driver et al., 1999; Friesen et al., 2005). Possessing signatures of typical covert exogenous orienting, gaze cueing was in some of the original studies shown to emerge quickly at short intervals between presentation of cue and subsequent presentation of the target, referred to as stimulus onset asynchronies (SOAs) of 150ms, peaking at 300ms and disappearing with longer SOAs of 1,005ms (Driver et al., 1999; Friesen & Kingstone, 1998; Langton & Bruce, 1999) (see Appendix B for schematic representation of typical eye gaze cueing procedure).
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In the case of eye gaze cueing, mounting evidence suggests that we orient our attention reflexively towards the direction of eye gaze and follow this cue to the same spatial location (Birmingham & Kingstone, 2009; Driver et al., 1999; Friesen et al., 2005; Frischen et al., 2007; Hayward & Ristic, 2015; Langton, 2000; Ristic et al., 2002). The gaze cueing effects are reported to be resilient to the demands of working memory load (Hayward & Ristic, 2013) and more recently have been reliably reported for up to long cue target intervals of 1440 ms (McKee, Christie, & Klein, 2007). Further, social orienting to central eye gaze cues has rarely (but see Frischen & Tipper, 2004) been reported to involve inhibition of return (IOR), a phenomenon whereby the cueing effect is short lived and at longer cue target intervals is replaced by delayed responding to targets at the cued location as attention to previously attended regions becomes inhibited (McKee et al., 2007).

A vast amount of research has examined attentional capture by uninformative eye gaze direction, with the debate generally focused on identifying the type of attentional control, exogenous or endogenous, responsible for the gaze cueing effect. Exogenous attentional control involves a fast automatic response and is primarily stimulus driven whereas endogenous orienting of attention is top down, involving a voluntary, goal driven, shift of attention (Frischen et al., 2007). Orienting to eye gaze direction has been shown to be independent of endogenous control (Hayward & Ristic, 2013). However, eye gaze cueing does not follow the standard template usually prescribed by exogenous attentional
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control with early reaction time validity effects followed by IOR (Posner, Rafal, Choate, & Vaughan, 1985).

**Stimulus Onset Asynchrony**

With centrally presented eye gaze cues, Friesen and Kingstone (1998) observed spatial facilitation early at 105ms SOA depending on the type of response condition. Cueing effects at very short SOAs of 105ms were found using a target detection response task, whereas indicating the location of the target or the identity of the target occurred later at SOA of 300ms. In the first examination of eye gaze cueing Friesen and Kingstone did not observe cueing at the later SOA of 1005ms. Although, when Driver et al. (1999) used photographs of faces instead of line drawings used by Friesen and Kingstone they found eye gaze facilitated attention at cued locations faster than uncued locations at SOAs of 300ms and 700ms but not at 100ms. Frischen and Tipper (2004) conducted an extensive set of experiments and observed cueing at SOAs as late as 1200ms. Frischen and Tipper also report IOR at 2400ms. In a set of experiments designed to examine the time course of IOR with different types of eye gaze cue McKee et al. (2007) found cueing up to 1440ms. Further, McKee et al. (2007) did not find evidence of IOR at any SOA up to 2880ms.

A considerable amount of eye gaze cueing experiments have used SOAs between 500ms and 1200ms (Alwall, Johansson, & Hansen, 2010; Bayliss et al., 2005a; Deaner, Shepherd, & Platt, 2007; Friesen et al., 2005; Hayward & Ristic, 2015; Driver et al., 1999; McKee et al., 2007;
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Qian et al., 2013; Ristic et al., 2002; Ristic & Kingstone, 2005; Sato et al., 2009) and reported significant cueing effects up to 1200ms. In most studies the cueing effect for eye gaze cues decreases as the SOA increases (Friesen et al., 2005; Ristic et al., 2002; Ristic & Kingstone, 2005), with the maximum facilitation effect, largest difference between uncued RT and cued, occurring around 300 – 600ms (McKee et al., 2007).

Cue Type

Spatial cueing has also been reported with centrally presented head orientation cues (Langton & Bruce, 1999) and pointing hands (Sato et al., 2010). It is important to note that an ongoing debate persists regarding social orienting, as biologically irrelevant cues, arrows have been shown to produce equivalent cueing effects to eye gaze direction (Bayliss et al., 2005; Daum, 2011; Guzzon, Brignani, Miniussi, & Marzi, 2010; Ristic et al., 2002; Ristic & Kingstone, 2006; Sato et al., 2009). Even a protruding tongue has been shown to produce comparable orienting effects to eye gaze (Downing, Dodds, & Bray, 2004), suggesting that it is the spatial compatibility between cue and target that produce shifts in the observers attention and not necessarily the uniqueness of the eye gaze cue as a powerful social communicative tool. However, recent research has found that participants expectancies induced by the standard adaptation of the Posner (1980) spatial cueing paradigm parameters, such as overall readiness to respond and
voluntary temporal preparation within trials, are differentially modulated by arrows and eye gaze cues (Hayward & Ristic, 2015).

**Gender Differences in Eye Gaze Cueing**

When gender differences were examined in response to eye gaze cues, the gaze cueing effect was found to be significantly weaker in males than females (Alwall et al., 2010; Bayliss et al., 2005; Deaner, Shepherd, & Platt, 2007; Feng, Zheng, Zhang, Song, & Luo, 2011). While both male and female participants exhibited faster RTs to valid versus invalid targets when a central eye gaze cue is presented, the magnitude of the cueing effect was significantly larger in females (Bayliss et al., 2005). The difference in attentional cueing between males and females was evident at 700ms SOA and not the shorter 100ms and 300ms cue target intervals. When arrows were used instead of eye gaze cues the gender difference persisted, female participants demonstrate a markedly greater cueing effect than males (Bayliss et al., 2005) even at very long cue target intervals of 1000ms (Merritt et al., 2007).

In summary, attentional orienting in response to centrally presented eye gaze cues is robust, has been demonstrated at both early and late SOAs, is modulated by the response task given (Friesen & Kingstone, 1998), by gender (Alwall et al., 2010; Bayliss et al., 2005) and in general the longer the SOA the smaller the eye gaze cueing effect (Friesen et al., 2005; Ristic & Kingstone, 2005). The study presented in Chapter 4 examines, in
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separate studies, central spatial cueing of attention to three cues, head orientation, body orientation, and eye gaze direction.
Chapter 4

Text as it appears in Cooney, S., Ryan, K., & Brady, N. (Revised and Resubmitted to Experimental Brain Research). Spatial orienting of attention to social cues is modulated by cue type and gender of viewer

4.1 Abstract

Gender differences have been documented in how selective attention is deployed with respect to eye gaze direction. In three separate spatial cueing experiments, this study examines gender differences in the deployment of spatial attention to three potent cues from the body that signal the direction of attention, eye gaze direction, head turning direction and body orientation. Results replicate and extend previous findings of gender differences in the eye gaze cueing effect whereby female but not male participants responded significantly faster to validly cued targets than to invalidly cued targets. A robust cueing effect with unequivocal cueing for both male and females participants was found when head turning direction was used as the central cue, whereas no cueing effect and no gender difference were observed when a body cue oriented left or right was employed. Results suggest that head turning direction is the most potent cue in directing spatial attention at longer cue target intervals. Gender differences in spatial orienting to social cues are discussed with reference to the broader literature on how males and females differ in spatial abilities and in their empathizing and systematizing skills.
4.2 Introduction

The ability to quickly discriminate where someone is attending involves reading changes in that person’s physical orientation, which include shifts in their eye gaze and in the turning direction of their head and body. Humans are remarkably good at detecting small changes in both eye gaze direction (Symons et al., 2004) and head orientation (Wilson et al., 2000), and perceiving where someone is attending is usually followed by a redeployment of one’s own attention to that location (Nummenmaa & Calder, 2009). Men and women are reported to differ in how they deploy attention in space (Merritt et al., 2007), with females orienting their attention in the direction of another’s eye gaze more readily than males (Alwall et al., 2010; Bayliss et al., 2005). Here we investigate the potency of eye gaze, head turning and body orientation, by examining the effect they have on the deployment of attention during a spatial cueing task. In addition, we aim to replicate the reported gender difference in eye gaze cueing and, to see if eye gaze is special in this regard, we investigate if spatial cueing by head turning and body orientation cues are also modulated by gender.

The spatial cueing paradigm (Posner, 1980), originally developed to study how attention is deployed in space in response to non-social cues, has become central to the study of social orienting. An adapted version of the paradigm has been employed extensively to study how attention is captured by social and symbolic cues. A typical experimental procedure involves presenting a central eye gaze cue looking to the left or right. The participant is asked to respond to a target that appears either at the same (validly cued) location to which eye gaze was directed or at the opposite (invalidly cued)
location. Faster reaction times for validly cued targets are taken as evidence for a shift of attention to the gazed-at location. In the case of eye gaze cueing, a large number of studies have reported evidence suggesting that we orient our attention reflexively towards the direction of eye gaze and follow this cue to the same spatial location (Driver et al., 1999; Friesen & Kingstone, 1998; Friesen et al., 2005; Ristic et al., 2002). The reflexive or automatic nature of eye gaze cueing is evidenced by the fact that it engenders both covert (Friesen & Kingstone, 1998) and/or overt (Driver et al., 1999) shifts in attention to the cued location even when participants are fully aware that the cue carries no information about the likely location of the target.

An important parameter in the Posner cueing paradigm is the stimulus-onset-asynchrony (SOA), which refers to the time between the onset of the cue and the appearance of the target, and early studies of attentional cueing made an important distinction between exogenous and endogenous cues with reference to their time course. Exogenous cues, such as a bright flash presented at a peripheral location, reflexively or automatically draw attention to their location so that a target which appears there within a narrow time frame (SOA ~ 50-150ms) will be detected more rapidly than targets appearing at an un-cued location (Jonides, 1981; Posner, 1980). At longer SOAs the advantage wanes and is replaced by an inhibitory effect (SOA > ~150-200ms) such that targets at the cued location now take longer to detect than those at the un-cued location, a phenomenon now referred to as ‘inhibition of return’ or IOR (Posner & Cohen, 1984).
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As reviewed by Frischen et al. (2007) gaze cueing also emerges early, being established by ~300ms, but distinguishes itself from peripheral cueing in that it extends up to 700ms and beyond and shows no evidence of IOR, at least in the convention variant of the paradigm in which the cue remains on until the appearance of the target. Gaze cueing effects have been reported as early as 300ms but increasing in strength at 700ms (Driver et al., 1999), as early as 105ms, still present at 600ms but dissipated at 1005ms (Friesen & Kingstone, 1998), and as extending out to 1005ms (Friesen et al., 2005; Ristic et al., 2002). In summary, gaze cueing shares one important aspect of exogenous, peripheral cueing, namely its automatic or reflexive nature, but it is particularly robust and flexible in its time course.

Research on the cueing effects of other social cues, namely heads and bodies, is less extensive than research on gaze cueing. Where head turning direction has been studied as a cue to shifting social attention, it has been in conjunction with eye gaze direction, with emphasis placed on the effect head orientation has on attentional shifts to the direction of eye gaze cues. Langton and Bruce (1999) report evidence of a combined head and gaze cueing effect using a variant of the Posner paradigm in which a centrally positioned head stimulus was oriented toward one of four possible target locations – up or down, right or left with respect to the centre cue. Stimulus eye gaze direction was always congruent with the head turning direction. When the central cue predicted the axis on which the target would appear (up-down, or right-left) but not the actual target location, cueing effects were found for an SOA of 100ms but not for SOAs of 500ms or 1000ms. And when the central cue predicted neither the target location nor the axis of
location, a cueing effect was still found for an SOA of 100ms but not for an SOA of 1000ms. Only when the cue predicted the target location with high probability were cueing effects significant at both 100ms and 1000ms, the authors suggesting that the effects at 100ms are due to a type of exogenous, reflexive shift in attention and the effects at 1000ms reflecting a type of endogenous cueing under volitional control. The time course of these effects is markedly different from those reported for gaze-cueing, being very short-lived.

Hietanen (1999) manipulated eye gaze and head orientation independently and found, in contrast to Langton and Bruce (1999), that when the head and eye orientations were congruent and turned horizontally by 30° there was no cueing effect whereas a frontally facing head with eyes gazing right or left by 30° produced the standard gaze-cueing effect. Similarly, a head facing right or left by 30° with frontally directed gaze (i.e., gaze directed back to the observer) produced a reverse validity effect, such that responses were fastest for targets located opposite to the turning direction of the head. These results show that stimuli in which gaze direction and head turning direction are in opposite directions (‘incongruently combined’ cues) are much more effective in shifting attention than those in which gaze direction and head turning direction are ‘congruently combined’. Hietanen (1999) suggests that observers first compute the direction of attention in an allocentric reference frame (e.g., ‘the model is looking to their left’) and then with respect to their own position in space (e.g., ‘the model’s direction of attention is to my right’). The result also speaks to the dominance of the eye gaze cue over that of head orientation. Under the classic hierarchical model of social
cue integration, which is based in part on modelling the response properties of cells in superior temporal sulcus (STS) which are sensitive to directional cues from the body, the direction of eye gaze takes precedence over head orientation and head orientation dominates over body orientation (Perrett et al., 1992). See also (Cooney et al., 2015a).

In a follow up study, Hietanen (2002) examined head and gaze orientation and their relationship to upper body orientation. Again cueing effects were observed when cues were combined incongruently (e.g., body facing forward, head and gaze facing to the right or left) but not congruently (e.g., body, head and gaze all facing to the right or left). Again, only relatively short SOAs of 150ms and 250ms were tested. The importance of how social cues are combined was confirmed in a study employing a Simon task (Pomianowska et al., 2011), where incongruently combined cues (e.g., body oriented to the right or left with head and gaze oriented back to the observer) generated spatial compatibility effects consistent with Hietanen's (1999) proposal of how cues are combined to extract information on the direction of another's attention. To summarize, studies of body orientation as cues to attention have mainly focused on cue combination, and the strength of body turning direction to produce a shift in the observers’ attention has not examined independently of head and eye gaze direction previously.

There is some evidence to suggest that males and females allocate selective attention to central cues differently (Merritt et al., 2007). When gender differences were examined in response to eye gaze cues, the gaze cueing effect was found to be significantly weaker in males than females in
two studies (Alwall et al., 2010; Bayliss et al., 2005), while in a third study females showed significantly larger cueing effects than males when the gaze cues were modelled by familiar faces but not when modelled by unfamiliar faces (Deaner et al., 2007). This gender difference in the gaze cueing effect does not appear to depend on the gender of the cue as studies have observed this asymmetry between genders when the cue has been male (Deaner et al., 2007), female (Alwall et al., 2010) and when both male and female alternating cues have been presented (Bayliss et al., 2005).

Regarding the time course, while both male and female participants exhibited faster RTs to valid versus invalid targets the magnitude of the cueing effect was significantly larger in females at an SOA of 700ms but not at shorter SOAs of 100ms and 300ms (Bayliss et al., 2005). When arrows replaced eye gaze as central cueing stimuli the gender differentiation in the cueing effect persists, female participants demonstrate a markedly greater cueing effect than males for 300ms and also at 700ms (Bayliss et al., 2005). Using targets that could appear at four possible locations and a central arrow cue, Merritt et al. (2007) report a cueing advantage to females at 100ms, 250ms and 500ms. Further, no difference in validity effects between males and females was observed in a non-social peripheral cueing task in which possible target locations were cued by peripheral brightening (Bayliss et al., 2005; Merritt et al., 2007).

The current study has two objectives. The first is to examine the relative strengths of three primary directional cues, eye gaze direction, head turning and body orientation, in orienting observers’ spatial attention. Given
previous findings that the body appears to inform initial estimates of a person’s facing direction, with attentional cues then read from head tuning and eye gaze (Hietanen, 2002; Pomianowska et al., 2011), an oriented body alone may not serve as an effective cueing stimulus. The second objective is to explore gender differences in the effectiveness of these cues in the deployment of spatial attention. We chose to examine the spatial cueing effects of all three stimuli at longer SOAs of 700ms and 1100ms based on piloting and on evidence from previous experiments that show reliable eye gaze cueing effects at these longer SOAs (Driver et al., 1999; Friesen et al., 2005; Ristic et al., 2002). Notably, Bayliss et al. (2005) found the largest gender difference in the cueing effect at an SOA of 700ms.

4.3 Methods

4.3.1 Participants

A total of 120 participants from the University College Dublin (UCD) student population took part in the study. Each participant was randomly assigned to one of three experimental groups, eye gaze, head and body, with each group balanced for gender resulting in three groups of 40 right-handed volunteers, 20 females and 20 males. All were naive to the purpose of the experiments and all had normal or corrected-to-normal vision. The mean age [and SD] in years of female and male participants was 23.6 [4.26] in the gaze group, 20.8 [1.54] and 24.5 [6.23] in the head group, and 24.95 [7.56] and 27.2 [8.75] in the body group. The study was approved by the UCD Research Ethics Committee; in accordance with the Declaration of Helsinki all participants gave written, informed consent and were advised of their right to withdraw from the study at any time without prejudice.
4.3.2 Apparatus and Materials

The experimental stimuli were computer-generated, full-colour images of human bodies, heads with eyes closed and heads with eyes open, created using 3D animation software Poser® http://poser.smithmicro.com. These computer-generated images provide fine-grained control of the rendered view of the stimulus. The body cue was a male torso cropped below the hips and at the neck, with arms positioned close by the model’s torso and cropped at the wrists so as to remove any additional orientation cues that may be provided by the hands. The head cues were front facing, female avatars generated without hair, cropped at the neck and with the eyes closed so as to remove any eye-gaze cues to orientation. The eye gaze cues were female faces of avatars generated without hair and cropped at the neck with eyes closed in the pre-cue stimulus and open for the cue stimulus. See Figure 4.1. All of the stimuli were modelled on a black background at 0° (pre-cue stimuli) and at 25° to the right and left (cue stimuli) for use as directional cues as explained below.
Figure 4.1. Central spatial cues body orientation, eye gaze direction, head orientation. Pre cue stimuli are in the centre column. Left and right body cue (top panel), head cue (centre panel) and eye gaze cue (bottom panel).
The body stimuli were 9.5 cm in height and 6.4 cm in width and subtended 10.85° and 7.32° of visual angle at a viewing distance of 50 cm. The corresponding values for the head stimuli were 6.5 cm or 7.44° (height) and 4.5 cm or 5.15° (width). The same sized heads were used in the gaze condition with the open eye region measuring 0.4 cm or 0.46° (height) by 1 cm or 1.15° (width). Targets were the capital letters T and L, sans serif Arial font, positioned in a 1 cm² (1.15°) text box and positioned 12.5 cm (14.25°) from the central fixation. The stimuli were presented and participants’ responses recorded using Presentation® software running on a Dell XPS-8300 PC with a screen size of 19 inches and display resolution of 2048 by 1152 at 60 Hz.

4.3.3 Design and Procedure

The same design and procedure was used in all three experiments with each participant completing a practice block of 32 trials followed by 5 experimental blocks of 64 trials. The 320 experimental trials comprised 160 valid and 160 invalid trials in which the target either appeared on the same side (valid trials) or on the opposite side (invalid trials) of the screen as cued by the social stimulus, an oriented body, head or gaze stimulus in Experiments 1, 2 and 3 respectively. The 160 valid and 160 invalid trials each comprised 80 trials with an SOA of 700 ms and 80 trials with an SOA of 1100 ms, where the SOA or stimulus onset asynchrony refers to the time between the onset of the cue (the oriented body, head or gaze cue) and the appearance of the target. SOA times were chosen after careful piloting of three participants. The two targets, the capital letters ‘L’ and ‘T’, appeared with equal frequency across trials and were positioned an equal number of
times to the right or left of the screen. Trial order was pseudo-randomized across blocks. Each block took ~4mins to run and participants took a 2min break between blocks.

Participants were seated 50cm from the monitor with their head positioned in a chin rest and were asked to fixate centrally on the screen. Each trial began with the appearance of a centrally positioned fixation cross which was displayed for 675ms and then replaced by a forward facing (0° oriented) pre-cue stimulus for 900ms. The pre-cue stimulus was then replaced by a cue stimulus, which was oriented to the left or right. The pre-cue stimuli and cue stimuli used in each experiment are shown in the central and side columns of Figure 4.1. After a variable SOA of 700ms or 1100ms, the target letter ‘T’ or ‘L’ was presented to the right or left of the centrally positioned cue stimulus and participants pressed buttons marked ‘T’ or ‘L’ (the B and H buttons on the keyboard covered by a labelled sticker) to indicate which target they perceived. The cue stimulus and target remained onscreen until the participant responded and (Driver et al., 1999; Friesen & Kingstone, 1998) participants were instructed that the central cues did not predict the location of the target.

4.4 Results

A small number of correct reaction times (RT) less than 200ms were removed from the data as ‘anticipation errors’ (0%, 0.05% and 0.11% for body, head and eye gaze experiments). Following recent studies with a comparable design and a range of SOAs (Alwall et al., 2010; Bayliss et al., 2005) we also clipped RTs at the upper end removing those which were
greater than 1500ms. The percentage of RTs removed was very small (0.24%, 0.13%, 0.21%, and for the body, head and gaze experiments respectively) and including them in the data analyses does not change the results reported below. As reported in previous studies of this kind (Driver et al., 1999) overall error rates were very low at 3.6%, 4.1% and 3.5% respectively for the body, head and gaze cue variants of the experiment. The data were analysed using ANOVA with within-subjects factors of cue Validity (valid, invalid) and SOA (700ms, 1100ms) and a between-subjects factor of Sex of participant. ANOVA effect sizes are given by generalized eta squared ($\eta^2_g$) (Bakeman, 2005). Following best practice (Cumming, 2014) means ($\bar{X}$) and associated 95% confidence intervals [95CI] are graphed and reported.

Figures 4.2 to 4.4 plot the mean reaction times for valid and invalid trials at SOAs of 700ms and 1100ms for the body, head and eye gaze cues, with the data for males and females plotted in separate panels. For all three cue types participants are generally faster at responding to the targets at the longer 1100ms SOA. As the SOA measures the time lag between the onset of the oriented body, head or eyes and the appearance of the target, this suggests that participants may be still processing these complex social directional cues at the shorter time lag.
Figure 4.2. Mean RT for invalid (blue) and valid (red) body cues at SOAs of 700ms and 1100ms are shown for male (left) and female (right) participants. Error bars show 95% CIs.

Figure 4.3. Mean RT for invalid (blue) and valid (red) head cues at SOAs of 700ms and 1100ms are shown for male (left) and female (right) participants. Error bars show 95% CIs.
Figure 4. Mean RT for invalid (blue) and valid (red) gaze cues at SOAs of 700ms and 1100ms are shown for male (left) and female (right) participants. Error bars show 95% CIs.

Of primary interest is the cueing effect, the RT difference between valid and invalid trials with the expected pattern of faster responses to validly cued targets. Turning first to the body cues (Figure 4.2), the only graphical trend toward a cueing effect is at the longer SOA of 1100ms and only then for male participants. For the oriented head cues (Figure 4.3), responses are generally faster for validly than invalidly cued targets and this is particularly marked in the graph at the longer SOA of 1100ms and for both genders. Finally, Figure 4.4 shows the expected pattern for the eye gaze cueing effect at both SOAs but only for female participants. Statistical analyses confirm these observations.

4.4.1 Body Cue

For the body cue experiment, there was a significant effect of SOA only, $F(1,38) = 21.02, p < 0.0001, \eta^2_G = 0.006,$ with longer RTs at 700ms, $\bar{X} =$
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536.88ms, 95CI = [533.37, 540.38], than at 1100ms, $\bar{X}$ = 524.66ms, 95CI = [521.21, 528.11].

4.4.2 Head Cue

For the head cue experiment, there were significant effects of Validity, $F(1,38) = 15.21, p < 0.001, \eta^2_G = 0.008$, and of SOA, $F(1,38) = 30.18, p \sim 0.001, \eta^2_G = 0.009$, whose interpretation is qualified by a significant Validity * SOA interaction, $F(1,38) = 5.88, p = 0.02, \eta^2_G = 0.002$.

Post-hoc comparisons showed that the effect of validity was not significant at the shorter SOA of 700ms, $F(1,39) = 2.56, p = 0.18, \eta^2_G = 0.002$, but was significant at the longer SOA of 1100ms, $F(1,39) = 21.91, p < 0.001, \eta^2_G = 0.016$. At the 1100ms SOA RTs were shorter on valid trials, $\bar{X} = 498.80$ms, 95CI = [495.91, 501.70], than on invalid trials, $\bar{X} = 508.54$ms, 95CI = [505.59, 511.48].

4.4.3 Gaze Cue

For the gaze cue experiment, there was a significant effect of SOA, $F(1,38) = 40.99, p < 0.001, \eta^2_G = 0.012$, with longer RTs at 700ms, $\bar{X} = 535.31$ms, 95CI = [531.73, 538.88], than at 1100ms, $\bar{X} = 519.21$ms, 95CI = [516.04, 522.38]. Additionally, there was a significant (‘borderline’ by conventional approaches) Sex*Validity interaction, $F(1,38) = 4.07, p = 0.0501, \eta^2_G = 0.001$. Post-hoc comparisons showed that the effect of validity was not significant for male participants, $F(1,19) = 0.21, p = 0.65, \eta^2_G = 0.0001$, but was for females, $F(1,19) = 10.75, p = 0.004, \eta^2_G = 0.004$. Female participants showed shorter RTs on valid trials, $\bar{X} = 527.56$ms, 95CI = [522.63, 532.48], than on invalid trials, $\bar{X} = 538.57$ms, 95CI = [533.74, 540.38].
While the Sex*Validity*SOA interaction did not reach significance at conventional levels (p = 0.15) Figure 4.4 suggests a smaller cueing effect at 1000ms than 700ms. A further analysis of the female data showed a significant effect of validity at 700ms, F(1,19) = 10.84, p = 0.004, $\eta^2_G = 0.01$, but not at the later SOA of 1100ms, F(1,19) = 1.44, p = 0.24, $\eta^2_G = 0.001$.

Figure 4.5 plots the mean ‘validity effect’ for the three different cues - the validity effect being calculated as the difference between the RT on invalid and valid trials for each participant separately for the two SOAs (Alwall et al., 2010). Positive values indicate faster RTs to valid cues. The plots serve to summarize the findings concisely with the significant effects of validity that are reported above occurring where the 95% confidence intervals do not cross the zero line in Figure 4.5, i.e., for both male and female participants’ responses to the head cue at the longer SOA and for female participants’ responses at the shorter SOA only for the gaze cue. A further ANOVA with the validity effect as dependent variable and between-subjects factors of Cue (body, head, gaze) and Sex, and a within-subjects factor of SOA (700ms, 1100ms) showed a significant main effect of Cue, F(2,114) = 3.16, p = 0.046, $\eta^2_G = 0.028$, and a Cue*SOA interaction ‘approaching’ significance as defined conventionally, F(2,114) = 2.59, p = 0.07, $\eta^2_G = 0.021$. 
Figure 4.5. Mean validity effects for male and female participants. Male (blue) and female (red) participants are plotted for SOAs of 700ms and 1100ms with separate plots for body, head and gaze cues. Error bars show 95% CIs.

Pairwise comparisons between cue types showed a significant difference in the validity effect between body and head at an SOA of 1100ms, $F(1,78) = 4.76, p = 0.032, \eta^2_G = 0.057$, but not at 700ms ($p = 0.16$), and between body and gaze at an SOA of 700ms, $F(1,78) = 4.14, p = 0.045, \eta^2_G = 0.05$, but not at 1100ms ($p = 0.96$). The difference in the validity effect for head and gaze cues was not significant at an SOA of 700ms ($p = 0.46$) but was at 1100ms ($F(1,78) = 6.54, p = 0.012, \eta^2_G = 0.08$).

4.5 Discussion

The key findings are as follows. First, a spatial cueing effect was observed for two of the three cues examined, eye gaze direction and head turning direction. Participants were faster to detect the presence of a target when it
was immediately preceded by a valid head or eye gaze cue than when preceded by an invalid head or gaze cue. In keeping with the seminal studies of eye gaze cueing (Driver et al., 1999; Friesen & Kingstone, 1998), both eye gaze and head cueing effects occurred despite the fact that participants were instructed that the cues were uninformative of the target location. Secondly, no difference in RTs to invalid versus valid cues was found in response to a centrally presented body orientation cue. Thirdly, a gender difference in the cueing effect was observed only for eye gaze cues, whereby oriented gaze served as a strong cue for females but not for males at an SOA of 700ms, with neither sex showing significant cueing effect to eye gaze at 1100ms. No gender difference was observed in the head turning experiment, with both sexes showing strong cueing effects at an SAO of 11000ms but not at 700ms, nor in the body orientation experiment where the oriented bodies proved ineffectual as cues to attention for both males and females at both SOAs tested.

4.5.1 Attention cueing and cue type

As predicted and in line with numerous other studies (Driver et al., 1999; Friesen & Kingstone, 1998; Friesen et al., 2005; Hietanen, 1999) eye gaze direction serves as a reliable cue to target location generating fasted response times to validly cued than invalidly cued locations. While this pattern was observed at both 700ms and 1100ms cue-target intervals the validity effect was statistically significant at the 700ms SOA only, and then only for female participants. With regard to the time course, these findings
are in line with previous reports which show the gaze cueing effect established by 300ms but stronger at 700ms (Driver et al., 1999), while at the upper end there are mixed reports of effects extending out to an SOA of 1005ms (Friesen et al., 2005; Ristic et al., 2002) and of dissipating at 1005ms (Friesen & Kingstone, 1998). As reviewed above, the time course of exogenous, peripheral cueing - usually studied via a brightening cue in the vicinity of potential targets - is well documented and replicated across many studies (Jonides, 1981; Posner & Cohen, 1984; Posner, 1980). In contrast, gaze cueing, while sharing the essential characteristic of automaticity with peripheral cueing, is more flexible in its time course. One possible explanation for the difference in the time course reported in different studies is that there is a form of perceptual adaption to the SOA, so that studies using a broad range of SOAs may report a different time course than those using a narrow range of SOAs focused at the shorter or longer end. Modifying the experimental procedure to include a blocked design whereby different SOAs are not intermixed may be useful in future studies.

As noted in the Introduction the study of head turning direction - a salient cue to where another person is attending when eye gaze cues are unavailable - is confounded by the presence of gaze direction cues in previous studies (Hietanen, 1999; Hietanen, 2002; Langton & Bruce, 1999). In contrast, our head stimuli, presented with eyes closed, led to robust cueing effects at an SOA of 1100ms for both male and female participants. While a direct comparison with Hietanen (1999, 2002) is not possible as he only tested at relatively short SOAs of 150ms and 250ms, our results stand in marked contrast to those of Langton & Bruce (1999) who report reflexive,
automatic cueing to head turning only at the shortest SOA of 100ms and not for longer SOAs of 500ms or 1000ms. An obvious difference between the studies is that we used a stimulus that engenders apparent motion with a sudden shift in head orientation when the pre-cue, a front facing head, is replaced by the cue, a head oriented to the right or left. In contrast, the oriented heads in Langton & Bruce (1999) appear suddenly without a pre-cue. To address the issue of whether our effects might simply reflect the operation of low-level motion sensitivity, whereby the cue is the directional signal rather than the social characteristics of the stimulus, we make the following observations. First, using the same methods in our body experiment, a forward facing body pre-cue followed by an oriented body cue that will similarly generate apparent motion, we found no cueing effect at the same SOAs. Secondly, as well studied in the change blindness literature the sudden appearance of a stimulus onscreen causes a visual transient (O’Reagan, Rensink, & Clark, 1999), and in the case that the oncoming stimulus is biased toward one side of space (e.g., a centrally positioned upper body with head clearly oriented to the right or left) it is questionable whether the sudden onset method reliably excludes the role of low level visual signals. Finally, real world shifts of attention involve actual movement of eyes and heads. Nonetheless, it would be useful in future studies using the present set of stimuli to disambiguate the role of low level motion cues from the social nature of these cues by controlling with non-social stimuli that re-orient in space.

Our body stimuli failed to produce reliable cueing effect at either SOA although there is a trend toward faster response times to validly cued target
locations at the longer cue-target interval of 1100ms. Why might an oriented body stimulus fail to shift attention in space? As reviewed above, a number of studies suggest that for more naturalistic stimuli - using the torso and head (Hietanen, 2002) or the full body including head, trunk, arms and legs (Moors et al., 2016; Pomianowska et al., 2011) – the body serves to indicate a person’s facing direction in an allocentric reference frame with the direction of attention then read from head and gaze cues. With respect to these cues, we note that human ability to discriminate eye gaze direction is remarkably good (Symons et al., 2004). The primary visual cues used to determine the direction of gaze are the contrast between iris and sclera and the geometrical information present in head orientation (Olk et al., 2008; Ricciardelli, Baylis, & Driver, 2000; Sinha, 2000; Todorović, 2006), and neuroimaging research points to the anterior portion of superior temporal sulcus, for processing left and right eye gaze direction unaffected by head position (Carlin et al., 2011). Likewise, head orientation is an effective social signal independent of eye gaze direction, with infants reported to use head orientation as the primary attention-following cue before head-independent eye gaze following emerges around 12 months (Butterworth & Jarrett, 1991). Adults can perceive a change in the direction of head orientation of as little as 1.9 degrees from direct facing, a threshold value not disrupted by removal of the internal features of the face or the outline of the head contour (Wilson et al., 2000).

4.5.2 Gender differences

Our finding of a gender difference in eye gaze cueing is consistent with the seminal finding of Bayliss et al. (2005) who report than females show a significantly greater eye gaze cueing effect than males. In their study, gender
differences in the cueing effect were not significant at SOAs of 100ms and 300ms but were at the later SOA of 700ms, and in our study gender differences in the cueing effect were also significant at an SOA of 700ms but not at the later SOA of 1100ms. The fact that males and females showed comparable cueing effects for head turning direction in our study and that the oriented body stimuli failed to effectively cue attention in either males or females might seem, at first glance, to strengthen that conclusion that there is something special about gaze and gender. However, the story is complicated by the finding that females also show stronger cueing effects than males when centrally positioned and non-predictive arrow cues are used in lieu of eye gaze cues (Bayliss et al., 2005). More generally, the idea that reflexive or automatic cueing by centrally positioned stimuli is the prerogative of social stimuli is countered by numerous reports of cueing by symbolic cues such as arrows (Guzzon et al., 2010; Hommel, Pratt, Colzato, & Godijn, 2001; Ristic et al., 2002), directional words (Hommel et al., 2001) and even by a protruding tongue (Downing et al., 2004).

Two explanations have been offered to account for the gender difference in eye gaze cueing. First, Bayliss et al. (2005) had a subset of participants complete the Autism Spectrum Quotient (AQ), an inventory used to screen for common autistic traits in research populations (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001), and found these scores to negatively correlate with the magnitude of the cueing effect in the eye gaze experiment but not in the arrow experiment. This suggests that participants who report less empathizing skills and an enhanced tendency to systematize may also be less likely to engage in joint attention via eye gaze following.
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This explanation is informed by the ‘extreme male brain’ theory of autism where difficulties in empathizing and a preference for systematizing and repetitive behaviours are emphasized in autism (Baron-Cohen, 2002). Alwall et al. (2010) also report a stronger gaze cueing effect for females than males, a difference most marked at an SOA of 300ms. While gaze cueing scores in this study were not predicted by scores on either the Empathizing Quotient (on which females scored higher than males) or by the Systemizing Quotient (on which males scored higher than females), further analysis revealed a relationship between the gaze cueing effect and a subset of inventory items that related predominantly to empathizing.

The second explanation of gender differences in gaze cueing suggests that they reflect differences in performance strategies. Using arrows as cues and a task which included neutral or un-cued trials in addition to validly and invalidly cued trials Merritt et al. (2007) show that while both genders demonstrated faster RTs on validly cued trials relative to un-cued trials, males exhibited a different response signature to females on invalidly cued trials. Specifically, females showed the typical costs expressed by slower RTs to invalidly cued targets than to un-cued targets, whereas males showed the opposite pattern of faster RTs on invalidly cued compared to un-cued trials. Interestingly, the gender difference in gaze cueing reported here (for the SOA of 700ms) shows that pattern, i.e., males and females show comparable RTs on valid trials (females, $\bar{X} = 532.68ms$, 95CI = [525.42, 539.93], and males, $\bar{X} = 529.02ms$, 95CI = [521.79, 536.93]) but very different RTs on invalid trials (females, $\bar{X} = 549.07ms$, 95CI = [541.77, 556.37], and males, $\bar{X} = 530.49ms$, 95CI = [523.69, 537.31]). Males appear
to discount invalid gaze targets more quickly than females. In our study, as in almost all (e.g., Bayliss et al., 2005; Driver et al., 1999; Friesen & Kingstone, 1998), RT decreases with increasing SOA so that at a cue-target interval of 1100ms females reaction time on valid trials is $\bar{X} = 522.46$ ms, 95CI = [515.79, 529.12] and the increase for invalid trials ($\bar{X} = 528.3$ ms, 95CI = [521.74, 534.34]) is considerably less than for the SOA of 700ms (~8ms versus ~16ms). Females appear to find it easier to discount invalid cues at longer cue-target intervals. Testing at a range of SOAs in future studies could be particularly informative, as males may find it less easy to disengage from invalid locations at shorter SOAs, as would the inclusion of non-cued trials for a more formal investigation of this approach to understanding gender differences.

In summary, the present study examined the efficacy of three cues from the human body to communicate the direction of the model’s attention and to shift the observer’s attention. Given ongoing debate as to whether social and symbolic cues generate similar or different types of cueing, the present results are equivocal on the exact type of attentional orienting facilitated by eye gaze, head and body orientation cues. Nevertheless, for the specific SOAs tested, they show that the directional information of eye gaze, head turning and body orientation direct spatial attention in different ways that are modulated by the gender of the observer and the amount of time the cue is presented for.
Chapter 5

Text as it appears in Cooney, S.M., Brady, N. & McKinney, A (in preparation). Pointing Perception is Precise; Sensitivity to the direction of the hand pointing is modulated by pointed hand but not by eye gaze.

5.1 Abstract

As adults, we can effortlessly read other people’s eye gaze and pointing gestures as cues to where they are attending, and this ability to follow gaze and pointing are closely linked in infant development. Yet while there is substantial research on the exquisite accuracy with which we perceive gaze, there is little research on the perception of hand pointing. Across two studies, we measured psychophysical thresholds for discerning where another person is pointing and investigated the cues that underlie this ability. In Experiment 1 observers judged whether a live pointer was pointing to the left or right of a target dowel positioned at three locations – left, centre and right space. In separate blocks, the pointer used her left and right hand to point. Perceptual acuity for discerning where another person is pointing is remarkable accurate, between 0.5° and 1.5° of visual angle at best, and is modulated by the target’s location in space, the hand used to point, and by an underlying attentional bias to left space. In Experiment 2 thresholds were measured under conditions in which the pointer’s eyes were occluded from view, and in which embodiment cues were either enhanced or minimized. Results indicate that humans are remarkably sensitive to the direction of
the extended index finger point, with the direction of eye gaze used minimally to discern the precise location of the point.

5.2 Introduction

Joint focus of attention is a state of intersubjective engagement that is achieved when two people are mutually aware that they are both attending to the same location or object in space at the same time (Butterworth & Jarrett, 1991; Mundy & Newell, 2013). For most, joint attention is established via an automatic computation that precedes social interaction and does not require much reflection. However, difficulty in following the visual cues that facilitate joint attention are directly related to social deficits that characterize developmental disorders such as autism spectrum disorder, ASD (Ashwin et al., 2015). Pointing is a powerful directional cue that facilitates joint attention (Cappuccio et al., 2013). Described as a foundational building block of human communication pointing is a preverbal developmental milestone (Kita, 2003), as both production and comprehension of pointing gestures predict early vocabulary acquisition (Goldin-Meadow, 2007) and the development of theory of mind (Baron-Cohen, 1991). Understanding how this pervasive gesture is perceived and integrated in the visual system is key to expanding our knowledge of the precise features of joint attention.

5.2.1 Pointing perception

The production of pointing gestures emerge in the first year of life with some variability of onset ranging from 8 to 15 months (Carpenter, Nagell, Tomasello, Butterworth, & Moore, 1998; Tomasello et al., 2007) and is predominantly right handed in infants (Butterworth et al., 2002; Cochet & Vauclair, 2013). Following pointing gestures is usually observed by the end
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of the first year of life (Carpendale & Carpendale, 2010; Carpenter et al., 1998; Von Hofsten, Dahlström, & Fredriksson, 1998). However, recent reports have provided evidence that pointing comprehension may emerge much earlier (Bertenthal et al., 2014; Daum et al., 2013; Gredebäck & Melinder, 2010; Rohlfing et al., 2012) in concert with eye gaze perception, which usually emerges around 4-6 months (D'Entremont et al., 1997; Farroni et al., 2000; Hood et al., 1998). Research has demonstrated a cross cultural preference for index finger pointing over other body parts (Liszkowski et al., 2012) with some evidence to suggest that hand pointing is a more salient social cue than eye gaze direction in preschool children (Triesch, Teuscher, De, & Carlson, 1998).

Pointing is the principal deictic gesture as it directs a looker’s attention towards a specific referent in the distal or proximal environment (Cochet & Vauclair, 2013). Imperative pointing is used to request an object or that an action be taken on an object. Declarative pointing can have two functions; first, to express an interest in a particular object or event in the environment and second, to provide information to the recipient regarding an object relating to the communicative context (Tomasello et al., 2007). During conversation adults tend to point with the index finger to disambiguate objects of interest from their surround, usually with the palm down rather than vertical (Kendon & Versante, 2003). Couchet and Vauclair (2013) described hypothetical communicative situations to adult participants and recorded the type of pointing that participants used to respond to the communicative situation. They examined handedness for pointing production between imperative and declarative pointing gestures and found
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that imperative points at hypothetical distal targets were most frequently
accomplished with right-handed index finger pointing. This may be related to
the precision required to clearly identify a referent to the communicative
partner. It is not yet known the extent of this precision or how accurate the
looker is in discerning exactly where the referent of the point rests in space.

5.2.2 Spatial shifts of attention to pointing gestures

Of the limited research that has investigated adult comprehension of
pointing the majority has employed some variant of a spatial cueing or
interference paradigm as an index of selective attention to pointing cues. A
common finding is that participants reflexively orient attention toward the
direction of a pointing gesture, even when the gesture is irrelevant to the task
at hand (Ariga & Watanabe, 2009; Belopolsky et al., 2008; Daum &
Gredeback, 2011; Fischer & Szymkowiak, 2004; Langton & Bruce, 2000;
Langton et al., 1996). Using a Stroop type interference paradigm, Langton et
al. (1996) found that viewing static images of pointing gestures influences
analysis of spoken directional words. Participants were shown images of
hands pointing up, down, left and right. Visual presentation was paired with
auditory cues of spoken words of these directions that were either congruous
or incongruous to the visual cue. When required to respond to the direction
of the auditory cue RTs increased when an incongruent to-be-ignored
pointing stimulus was presented. The interference was bidirectional such
that spoken directional information also influenced how pointing gestures are
processed. In a further study Langton and Bruce (2000) showed that
incongruent head/gaze cues also modulate attention to pointing gestures
and, again, the interference effect was bidirectional.
The superior temporal sulcus and inferior parietal lobule are implicated in processing directional information from social cues including eye gaze direction, arrows and pointing (Materna et al., 2008b; Sato et al., 2009). The fronto-parietal network sub serving reflexive shifts of social attention (Cazzato, Macaluso, Crostella, & Aglioti, 2012) is particularly sensitive to the relationship between the type of directional cue and the effector used to respond to the stimulus (Porciello, Crostella, Liuzza, Valentini, & Aglioti, 2014). When participants were required to either point with their index finger or make an eye movement towards a target, while ignoring task irrelevant distractors of eye gaze, arrow and pointing stimuli, different parts of the fronto parietal cortex were activated (Porciello et al., 2014). Using TMS stimulation of the right posterior parietal cortex, Porciello et al. (2014) observed increased reflexive orienting of attention to pointing cues but not to arrows or eye gaze.

The neuroimaging and behavioural experiments mentioned above generally employed static images of either photographs or avatars of disembodied pointing hands (but see Belopolsky et al., 2008). Pointing involves extending the hand and forearm dynamically into space. To discern where and at what someone is pointing a complex amount of visual information is presented to the viewer including, dynamic bisection of space that is either contralateral or ipsilateral to the hand that is used to point. It is essential to examine this strongly dynamic cue in real-time with a live pointer. Classic studies of perceptual acuity for eye gaze direction employed naturalistic paradigms and found that acuity for the perception of eye gaze...
direction is remarkably high (Anstis et al., 1969; Bock et al., 2008; Cline, 1967; Gibson & Pick, 1963; Moors, et al., 2016; Symons, et al., 2004).

5.2.3 Acuity for perception of eye gaze

Based on classic work by Gibson and Pick (1963), Symons et al. (2004) used a live looker to examine the threshold for detecting where someone is looking in three-dimensional space. An important distinction is made between dyadic gaze, which primarily functions to engage eye contact in face-to-face interaction and triadic gaze, which involves computing the direction of regard at an object or place in the environment. Both involve estimation of the asymmetry in iris scleral contrast, but triadic gaze requires the observer to compute further geometrical information by triangulating convergence of line of sight from both eyes at an object. Acuity was defined as the amount of shift in degrees of visual angle at the objects gazed at relative to a central target. Symons et al. (2004) showed that the thresholds for detecting shifts in eye gaze are exceptionally low. Resolution for acuity was ~30 seconds arc, 1.3 degrees of visual angle. Both Bock et al. (2008) and Symons et al. (2004) found that initiating eye contact with the participant did not modulate perceptual acuity at targets and acuity is reduced when only one of the lookers’ eyes is visible. Whereas when the participant used monocular vision this did not affect the participants precision in identifying targets (Bock et al., 2008)

5.2.4 The current study

The majority of research that has examined pointing has looked at the emergence of referential actions in infants, the origins of the pointing gesture and its relationship to verbal communication. Despite the considerable
attention this referential action has been given in the developmental and comparative literature, little is known about how this visual cue is analysed and integrated in the visual system. What perceptual Information is used to determine where someone is pointing? How accurate are people at estimating the focus of a pointing gesture?

One study that included pointing as a cue (Butterworth & Itakura, 2000) examined infant and adult visual joint attention and the visual cues that serve to establish it; head orientation, eye gaze and pointing. Accuracy for correctly discerning the object the experimenter was attending to was compared across four visual cue combinations that were combined in a hierarchical fashion; eyes gaze only, head orientation and eyes gaze direction combined, head orientation only and pointing, eye gaze direction, and head orientation combined. Butterworth and Itakura (2000) found that it is not until 15 degrees of angular separation (70 cm gap from target centre to centre at a viewing distance of 2.7m) that all cue combinations are sufficient to accurately detect a target. The inclusion of the pointing cue provided an advantage for discerning peripheral targets even at the smallest distance, 4 degrees (19cm target centre to centre at 2.7m viewing distance) between objects. Participants tended to inaccurately estimate the location of the experimenter’s attention to the left of the object the experimenter was actually attending to and this bias depended both on cue type and whether they were seated to the left or right of the experimenter. It is important to note that pointing was not isolated from the other cues and participants only had a profile view of the experimenter as they were seated side by side.
Following methodology employed to examine accuracy in detecting where and at what someone is looking (Bock et al., 2008; Symons et al., 2004) this study uses a live pointer to investigate, for the first time, adult visual perception of hand pointing. There are three main objectives. The first, to examine visual acuity for triadic pointing comprehension via threshold estimation across visual field location, second to compare acuity for left handed versus right-handed points, and third to examine the influence of eye gaze direction and embodiment cues on the estimation of where someone is pointing in space.

5.3 Experiment 1

5.3.1 Methods

Participants

Twenty volunteers (10 female) from the student population at UCD, with a mean age = 27.10 years, SD = 10.43 years, and range =18 to 50 years, participated in Experiment 1. All had normal or corrected to normal vision with an average hand laterality score of +0.49 (SD = 0.22), range -0.50 to +0.90, on the McManus Brief Handedness Questionnaire (http://www.ucl.ac.uk). A score of 1.00 on the questionnaire indicates extreme right-handedness, -1.00 indicates extreme left-handedness, and 0 indicates ambidexterity. Two participants were left handed with laterality scores of -0.5 and -0.18. The study was approved by the UCD Research Ethics Committee; in accordance with the Declaration of Helsinki all participants gave written, informed consent and were advised of their right to withdraw from the study at any time without prejudice.
Apparatus

Participants sat at a table of length 1820mm and width 2130mm with their head positioned in a chin rest and facing a purpose built wooden apparatus of length 1820mm, width 60.5mm and height 40mm in which cylindrical dowels of height 150mm and diameter 18mm were placed. Three groups of test dowels were positioned at locations referred to as left space (LS), centre (C) and right space (RS) defined with respect to the participant’s position as shown in Figure 5.1. There were 7 test dowels at the centre location and 9 test dowels at the left and right locations. The entire apparatus, base and dowels, was painted in an off white colour with the central target dowel at each location marked by a coloured sticker that was clearly visible to the participant. A white cloth covered the table to remove any texture cues to orientation than might be available from the wooden table top.

The target dowel at C was positioned at the midpoint of the apparatus, 910mm from the left edge and the target dowels at the LS and RS locations were positioned 31mm and 1789mm from the left edge respectively. The distance between the target dowel at C and the target dowel at both LS and RS was 600mm. The 7 dowels at the central location were placed side by side so that the centre-to-centre distance for a neighbouring pair was 18mm, whereas at both the left and right locations, LS and RS, the centre-to-centre distance for a neighbouring pair was 36mm. The three locations on the apparatus and the spacing between the dowels were chosen to generate useable psychometric functions after piloting of three participants.
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With their head positioned in a chin rest, the participant’s eyes were 1000mm from the target dowel at C. The target dowel subtended 1.03° of visual angle in width and 8.58° in height and the centre-to-centre distance between neighbouring dowels was 1.03°. For locations LS and RS the distance between the participant’s eyes and the target dowel was 1166.19mm, and the participant’s line of sight was no longer perpendicular to the stimulus plane. Visual angles were calculated accordingly. The visual angles separating the flanking dowels from the target dowel at the centre locations were +/-3.09°, +/-2.06°, +/-1.03° and 0° where negative and positive values indicate dowels to the left and right of the target dowel. In left space the corresponding values were -5.68°, -4.33°, -2.94°, -1.49°, 0°, +1.54°, +3.13°, +4.77°, +6.45°, and in right space they were -6.45°, -4.77°, -3.13°, -1.54°, 0°, +1.49°, +2.94°, +4.33°, +5.68°.

The pointer, a female research assistant aged 21 years with normal visual acuity, stood with hands by her side on the opposite side of the apparatus facing the observer and positioned so that the eye-to-eye distance between pointer and observer was 2000mm. The pointer was extremely right-handed with a laterality score of 1.0. The experimenter sat behind the participant, so as not to be visible to them, and, for each trial, wrote the order of presentation (pointing hand, dowel number and location) on a whiteboard for the pointer to see.
Figure 5.1. Schematic of the apparatus and experimental set up. The lower panel contains a close up representation of centre space and right space including the target dowels and the visual angle in degrees of each dowel. The upper panel shows the position of the participant, seated facing the apparatus with the pointer on the other side. The pointer’s right hand is labelled in blue and left hand labelled in red.

Pointer and looker were positioned at either end of a table, apparatus placed in between them. Ninety-nine dowels were positioned along the wooden platform, one exactly at the centre point, and 49 positioned either side. Along the apparatus three zones of space Left Space, Centre Space and Right Space are shown in Figure 5.1. Each zone, marked here for illustration purposes, has a centre target. The actual delineation of zones along the apparatus was not visible to the participant only the target in each
zone was visible via the green sticker. Figure 5.1 also provides a close up of centre space and right space, which shows the dowels that the pointer was pointing to and the visual angle in degrees of each dowel.

**Procedure**

The experiment involved 6 blocks, 2 pointing hands by 3 locations. At the beginning of each block the pointer was instructed by the experimenter to point with either the left or right hand to a particular region; left, centre or right space. Then, on every trial within that block –140 trials (70 each with left and right hand) for central space and 180 trials for both left and right space (90 each with left and right hand) - the pointer was instructed by the experimenter to point to a particular dowel. The order of the blocks was counterbalanced across participants and the order of the dowels was pseudorandomized within each block.

In making each point, the pointer first looked to the target dowel. Then, extending her arm and hand with extended index finger in the required direction (see Figure 5.2), she fixed the point at 100 mm below the top of the test dowel, this location was clearly marked on her side of the apparatus with a coloured sticker. The pointer held the point until the participant responded to say whether the pointer was pointing to the left or right of the target dowel, which was marked with a green sticker. The 2 alternative forced choice verbal response was recorded by the experimenter.
Figure 5.2. Visual representation of the pointer pointing with her right hand towards the observer’s Left Space, Centre Space and Right Space, reading from left to right. The left image is an example of an ipsilateral point, whereas the right image is an example of a contralateral point.

The participant’s head was oriented toward centre space via the use of the chin rest but they were free to make eye movements to follow the points to their resting locations. The participant’s hands rested on the table to either side of the chin rest. At the beginning of each block, the experimenter instructed the participants to which region the pointer would point. Participants had a 2-3 minute break between blocks and a 20-minute break at the halfway point. Each block took approximately 10 minutes.

5.3.2 Results

The psychometric functions were fit using quickpsy in R, a package which estimates parameters using a maximum likelihood procedure (Linares & López-Moliner, 2015). Thresholds, estimated at the 0.5 probability point on the psychometric functions, were saved for analysis in R (R Development
Core Team, 2010) using ANOVA with within-subjects factors of Pointing Hand (left, right) and Location (left space, centre, right space). Greenhouse-Geisser corrections were used when Mauchly’s Test for Sphericity was significant and effect sizes are given by generalized eta squared ($\eta^2_G$) (Bakeman, 2005) (see Appendix C for example of curve fitting for one participant).

Figure 5.3 and Table 5.1 show the absolute threshold in degrees of visual angle for both pointing hands at all three locations. A number of observations can be made. First, thresholds are lower and perceptual acuity higher in the centre relative to the left or right side of space. Second, at the central location participants’ acuity is higher when the pointer uses her left than her right hand. Third, in both left and right space thresholds are notably higher when the pointer has to move her arm across the midline of her body to point to the target. Thus, participants’ perceptual acuity is much greater when observing the right-handed than the left-handed gesture in left space, the pointer’s right hand being in the observers’ left space. In contrast, acuity is greater when observing the left-handed than the right-handed gesture in right space, the pointer’s left hand being in the observers’ right space. Finally, looking at the thresholds at all three locations, perceptual acuity for discerning where another person is pointing is remarkable accurate with best performance of 1.42°, 0.46° and 1.45° degrees of visual angle at left, centre and right spatial locations respectively, see Table 5.1.
Figure 5.3. Absolute thresholds are shown in degrees of visual angle for left, centre and right space where these are defined with respect to the observer’s central seating position. The red and blue bars indicate thresholds when the pointer used her left or her right hand respectively to point. These are positioned on the graph according to the observer’s perspective, the pointer’s right and left hand appearing in the observer’s left and right visual field when they centre their gaze on the pointer. Error bars show the 95% CIs.
Table 5.1

*Absolute threshold by spatial location and pointing hand*

<table>
<thead>
<tr>
<th>Location</th>
<th>Pointing Hand</th>
<th>Threshold</th>
<th>Lower 95% CI</th>
<th>Upper 95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Left Space</td>
<td>Right Hand</td>
<td>1.42°</td>
<td>0.88°</td>
<td>1.96°</td>
</tr>
<tr>
<td></td>
<td>Left Hand</td>
<td>2.92°</td>
<td>2.22°</td>
<td>3.62°</td>
</tr>
<tr>
<td>Centre</td>
<td>Right Hand</td>
<td>1.15°</td>
<td>0.83°</td>
<td>1.47°</td>
</tr>
<tr>
<td></td>
<td>Left Hand</td>
<td>0.46°</td>
<td>0.28°</td>
<td>0.64°</td>
</tr>
<tr>
<td>Right Space</td>
<td>Right Hand</td>
<td>3.39°</td>
<td>2.51°</td>
<td>4.28°</td>
</tr>
<tr>
<td></td>
<td>Left Hand</td>
<td>1.58°</td>
<td>1.13°</td>
<td>2.03°</td>
</tr>
</tbody>
</table>

*Note.* CI = confidence intervals.

Repeated measures ANOVA showed significant main effects of Hand, F(1, 19) = 6.82, p = 0.017, η²G = 0.02, and of Location, F(2, 38) = 27.49, p < 0.0001, η²G = 0.28, whose interpretation is qualified by a significant Location*Hand interaction, F(2, 38) = 14.42, p < 0.001, η²G = 0.26.

Post-hoc comparisons showed significant differences between the left-hand and right-hand thresholds at all three locations; left space (F(1, 19) = 11.91, p < 0.01, η²G = 0.25), centre (F(1, 19) = 12.13, p < 0.01, η²G = 0.29),
and right space (F(1,19) = 15.29, \( p < 0.001, \eta^2_G = 0.28 \)). Thresholds were lower (acuity higher) for the left than for the right hand in both right space and at the central location, but lower for the right than for the left hand in left space. See Table 5.1. A planned post-hoc comparison to test whether the ‘best performance’ threshold (right hand in left space, and left hand in centre and right space) differed by location showed a significant difference, F(2,38) = 11.12, \( p < 0.001, \eta^2_G = 0.24 \). The best performance threshold was significantly lower at the centre location than in either left space, F(1,19) = 14.48, \( p < 0.01, \eta^2_G = 0.25 \), or right space, F(1,19) = 20.87, \( p < 0.001, \eta^2_G = 0.38 \), whereas there was no difference in ‘best performance’ threshold in left and right space (\( p = 0.57 \)).

Figure 5.4, which plots the signed thresholds or ‘points of subjective equality’ illustrates how participants’ perception of pointing direction is clearly influenced by the hand used by the pointer (See also Table 5.2). At all three locations the point of subjective equality is pulled leftward when the pointer uses her right hand, which falls in the participants’ left space, and is pulled rightward when the pointer uses her left hand, which falls in the participants’ right space. This ‘spatial pull’ is particularly strong in left and right space when the pointer has to shift her hand across her body to point.

Repeated measures ANOVA showed significant main effects of Hand, F(1,19) = 145.95, \( p \sim 0, \eta^2_G = 0.38 \), and of Location, F(2,38) = 14.36, \( p \sim 0, \eta^2_G = 0.36 \), whose interpretation is qualified by a significant Location*Hand interaction, F(2,38) = 29.30, \( p \sim 0, \eta^2_G = 0.07 \).
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Post-hoc comparisons showed significant differences between the left-hand and right-hand thresholds at all three locations; left space (F(1,19) = 133.15, $p \approx 0$, $\eta^2_G = 0.35$), centre (F(1,19) = 29.67, $p < 0.0001$, $\eta^2_G = 0.44$), and right space (F(1,19) = 119.30, $p \approx 0$, $\eta^2_G = 0.46$).

Figure 5.4. Signed thresholds or points of subjective equality are shown in degrees of visual angle for left, centre and right space where these are defined with respect to the observer’s central seating position. The red and blue bars indicate thresholds when the pointer used her left or her right hand respectively to point. Negative and positive values on the x-axis indicate space to the left and right of the target dowels respectively, the target dowel being positioned at 0° in all three locations. Error bars show the 95% CIs.

Finally, planned comparisons were used to test whether, in each condition, the signed thresholds were significantly different from zero. Using t-tests with Bonferroni correction of alpha = 0.008 for 6 comparisons, this
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was the case for LS, left hand, $t(19) = 6.87$, $p < 0.0001$, but not for LS, right hand $t(19) = 1.12$, $p = 0.28$. At the centre location, the signed threshold was significantly different from zero for the left hand, $t(19) = 4.37$, $p < 0.001$, and for the right hand, $t(19) = -3.75$, $p = 0.001$. And at the right location, the signed threshold was not significantly different from zero for the left hand, $t(19) = 1.39$, $p = 0.18$, and was for the right hand, $t(19) = -6.48$, $p < 0.0001$.

Table 5.2
Signed thresholds by spatial location and pointing hand

<table>
<thead>
<tr>
<th>Location</th>
<th>Pointing Hand</th>
<th>Threshold</th>
<th>Lower 95% CI</th>
<th>Upper 95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Left Space</td>
<td>Right Hand</td>
<td>-0.20°</td>
<td>-1.07°</td>
<td>0.66°</td>
</tr>
<tr>
<td></td>
<td>Left Hand</td>
<td>2.60°</td>
<td>1.65°</td>
<td>3.55°</td>
</tr>
<tr>
<td>Centre</td>
<td>Right Hand</td>
<td>-1.01°</td>
<td>-1.42°</td>
<td>-0.60°</td>
</tr>
<tr>
<td></td>
<td>Left Hand</td>
<td>0.25°</td>
<td>-0.01°</td>
<td>0.50°</td>
</tr>
<tr>
<td>Right Space</td>
<td>Right Hand</td>
<td>-3.40°</td>
<td>-4.28°</td>
<td>-2.51°</td>
</tr>
<tr>
<td></td>
<td>Left Hand</td>
<td>-0.02°</td>
<td>-0.91°</td>
<td>0.86°</td>
</tr>
</tbody>
</table>

Note. CI = confidence intervals
5.3.3 Discussion

Looking at the thresholds at all three locations, perceptual acuity for discerning where another person is pointing is remarkable accurate with best performance of 1.42°, 0.46° and 1.58° degrees of visual angle at left, centre and right spatial locations respectively, see Table 5.1 and Figure 5.3. Also evident from the point of subjective equality plot (Figure 5.4) is a response asymmetry that likely reflects an underlying attentional bias to left space that is commonly observed in the line bisection task (Jewell & McCourt, 2000). To understand this bias we refer to ‘ipsilateral points’ as those in which the pointer points to a target by extending her hand into space without crossing the midline of her body. These include using the right hand to point into the observer’s left space and the left hand to point into the observer’s right space. Conversely, ‘contralateral’ points involve pointing to a target while crossing the body midline; using the left hand to point into the observer’s left space and the right hand to point into the observer’s right space as shown in Figure 5.1 and 5.2 for targets that are positioned in the observer’s right and left space, ipsilateral points lead to a point of subjective equality that is closer to the true position of the target dowel that do contralateral points which serve to bias the point of subjective equality in the opposite direction. But there is an additional asymmetry such that contralateral points into the observer’s right space leads to a greater bias in the point of subjective equality than do contralateral points into the observer’s left space. This could reflect an underlying bias toward left space on the part of the observers. Similarly, for points made to targets in the observer’s centre space (which are neither contralateral nor ipsilateral as the pointer is pointing
straight ahead) there is an asymmetry such that the blue bar is longer than the red bar.

5.4 Experiment 2

It is clear from experiment 1 that acuity for the perception of pointing is remarkably high. What cues are driving this precision? To what extent do shifts in eye gaze direction made by the pointer facilitate this precision? Experiment 2 examines the influence of eye gaze direction and embodiment cues on the estimation of where someone is pointing in space.

From Experiment 1 a right response bias is evident where participants inaccurately determine the centre dowel as to the right of centre thus pushing perception of midpoint into left space. The asymmetrical pattern in the threshold results suggests an attentional bias to left space. As described in the introduction, in their study of the perception of the referent of pointing, Butterworth and Itakura (2000) observed a leftward bias whereby participants tended to inaccurately estimate the location of the experimenter’s attention to the left of the object the experimenter was actually attending to. This leftward bias is echoed in some studies that required participants to complete a baseline direction discrimination task where they were required to judge the direction of social cues as; direct facing, to the left, or to the right (Calder et al., 2008; Jenkins et al., 2006; Lawson & Calder, 2015; Lawson et al., 2011). Upon close inspection of baseline direction discrimination tasks an apparent asymmetry in judging the direction of social cues is evident, with a slight leftward spatial bias reported for eye gaze (Jenkins et al., 2006), head orientation (Lawson & Calder, 2015; Lawson et al., 2011) and pointing
direction (Cooney et al., 2015b). Participants had less accurate
categorization of right relative to left gaze directions, and even when the
mirror image was used to remove extraneous cues the asymmetry persisted
(Calder et al., 2008). Calder et al. (2008) note that this may reflect a general
left spatial bias as evidenced in pseudoneglect (Benwell, Harvey, & Thut,
2014; Jewell & McCourt, 2000; McCourt & Jewell, 1999), where, on average
people bisect a horizontal line slightly to the left of the veridical midpoint,
such that the perception of centre shifts into left space. An interesting
question is whether the bias in judging the direction of these social cues is
correlated with general leftward spatial bias as demonstrated in
pseudoneglect. To examine this bias, participants in experiment 2 were also
given a standard pen and paper line bisection task to determine the
presence of pseudoneglect.

5.4.1 Methods
The methods (ethics, apparatus, etc.) were identical to those in
Experiment 1 except where specified below.

Participants
Thirty volunteers participated in Experiment 2, none of whom had
participated in Experiment 1. One participant did not complete the task and
another’s data were unusable, as they could not be fit with psychometric
functions due to the high number of rightward responses. Of the remaining
28 participants (23 female, mean age = 20.82 years, SD = 2.92 years, range
= 18 to 30 years), all had normal or corrected to normal vision with an
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average laterality score of 0.60, SD = 0.22, range 0.09 to 1.00, on the McManus Handedness Questionnaire.

Procedure

Experiment 2 measured participants’ acuity for hand pointing direction over four conditions, referred to as Baseline, Eyes Occluded, Point Back and Disembodied Point. To accommodate the extra three conditions without overtiring observers, data were collected at just two of the three locations used in Experiment 1, centre, CS, and right space, RS, and the pointer pointed with her right hand only.

The Baseline condition was identical to that described in Experiment 1, the observer seated centrally using the chin rest but free to move their eyes. To investigate whether eye gaze direction influenced participants’ judgments of hand pointing direction, the pointer wore opaque sunglasses that occluded their eyes from the observer’s view in the Eyes Occluded condition. To examine if visual acuity improved when the observer was allowed to copy the pointer’s gesture, the Point Back condition required participants to point with their own right hand towards the dowel they perceived the pointer to be pointing at before responding. The Disembodied Point condition was employed to control for the influence that ‘embodiment’ – via the simulation or internal preparation of a pointing gesture – might have on perceptual acuity. This was accomplished by restricting the observer’s ability to produce or imagine producing a hand pointing gesture by placing their hands in a configuration that limited the ability to point, wrapping the hands in cloth and placing them out of the observer’s view on their lap.
The experiment involved 8 blocks in total, 4 experimental conditions (Baseline, Eyes Occluded, Point Back and Disembodied Point) by 2 locations (CS and RS). At the beginning of each block the pointer and participant were instructed which condition the block required and to which region the pointer would be pointing; CS or RS. Then, on every trial within that block - 70 trials for CS and 90 trials for RS - the pointer was instructed by the experimenter to point to a particular dowel, resulting in 640 experimental trials in total. The order of the blocks was counterbalanced across participants and the order of the dowels was pseudorandomized within each block.

The procedure followed by the pointer in making the point was identical to that described above for Experiment 1 and the observer’s head was oriented toward centre space via the use of the chin rest but they were free to make eye movements to follow the points to their resting locations. Except in the Disembodied Point condition, the participant’s hands rested on the table to either side of the chin rest. Participants were given a 2-3 minute break between blocks and a 20-minute break at the halfway point. Each block took ~10 minutes.

**Line Bisection Task**

A line bisection task was administered to each participant to investigate to what extent the perceptual thresholds in the pointing task reflect spatial bias in allocating attention in space.
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**Materials**

The stimuli were black lines of four lengths (220mm, 180mm, 140mm and 100mm) and of uniform thickness, 4mm. The four lines were printed horizontally at three locations (centre space, left space and right space) in landscape orientation on A4 sheets of paper. The four lines at centre space were placed centrally on the page with the midpoint of each line falling on the midpoint of the page. The four lines at left space were positioned extending into the centre of the sheet flush to the left margin 2.5cm from sheet edge extending towards the centre of the sheet. The four lines at right space were positioned flush to the right margin 2.5cm from edge extending from right towards centre of the sheet. The order of presentation the lines from top to bottom on page was randomized. The stimulus lengths chosen are within the same range as published work (McCourt & Jewell, 1999; Milner, Brechman & Pagliarni, 1992). A total of 96 line bisection trials, 32 trials per location, half of these were bisected with the left hand, half with the right hand.

**Procedure**

Participants sat at the centre point of the long side of the same table as used in the pointing task and they maintained alignment with the centre point throughout the bisection task. Each stimulus sheet was placed directly in front of the participant. The experimenter stood behind the participant and passed each sheet with both hands overhead to the participant. An A4 card with a rectangular window cut out was positioned over the stimulus sheet so that it revealed one line while occluding the other three and the experimenter
instructed the participant where to locate it on each trial, the order of the trials being pseudorandomized in this manner. Participants were instructed to bisect the line at the perceived midpoint with a black marker. Each line length was presented at each location 8 times and the participant bisected with the right hand on half the trials and with the left hand on the other half. Ninety-six trials were administered in total.

5.4.2 Results

Thresholds for pointing

Starting with the pointing task Figure 5.5 shows the absolute threshold in degrees of visual angle for all 4 conditions at the two locations, centre and right space (see Appendix D for psychometric fit of one participant). While thresholds are clearly lower (acuity higher) at the central than at the right space location as expected from Experiment 1, there is little evidence of any difference in thresholds across the conditions. This is confirmed by statistical analyses. Repeated measures ANOVA showed a significant main effects of Location, $F(1,27) = 32.34, p < 0.0001, \eta^2_G = 0.26$. Neither the effect of Condition, $F(3,81) = 0.90, p = 0.44, \eta^2_G = 0.003$, nor the Condition*Location interaction, $F(3,81) = 0.88, p = 0.45, \eta^2_G = 0.002$, were significant. Figure 5.6 shows the signed thresholds in degrees of visual angle for centre and right space where these are defined with respect to the observer’s central seating position.
Figure 5.5. Absolute thresholds are shown in degrees of visual angle for centre and right space where these are defined with respect to the observer’s central seating position. The different colour bars indicate thresholds in the various conditions: baseline (white), with pointer’s eyes occluded (light grey), with observer’s hands restricted (dark grey) and with observer pointing back (black). Error bars show the 95% CIs.
**Figure 5.6.** Signed thresholds Experiment 2. Signed thresholds are shown in degrees of visual angle for centre and right space where these are defined with respect to the observer’s central seating position. The differently bars indicate thresholds in the various conditions: baseline (white), with pointer’s eyes occluded (light grey), with observer’s hands restricted (dark grey) and with observer pointing back (black). Error bars show the 95% CIs.

**Line Bisection**

Figure 5.7 shows clear bias or deviation toward left space evident across all three spatial locations and for all 4 line lengths with the magnitude of the deviation generally increasing with increasing line length and reaching a maximum for the longest lines of 220mm.
Figure 5.7. Line bisection deviations at each region. Left bias in the Bisection task shows mean deviation in millimetres on the x axis, for each of the four line lengths, y axis, where the longest line is line 4, the shortest line is line 1, from veridical midpoint at each location on the page (Left Space, Centre Space, Right Space). Error bars show the 95% CIs.

A repeated measures ANOVA was carried out with factors of Hand Used (Left, Right), Region (Centre space, Left Space, Right space) and Line Length in ascending order (1, 2, 3, 4) as within subjects factors and the deviation in millimetres as the dependent variable. Greenhouse-Geisser corrections were used when Mauchly's Test for Sphericity was significant and effect sizes are given by generalized eta squared ($\eta^2_G$) (Bakeman, 2005). A main effect for Line Length $F(3, 84) = 4.50, p = 0.01, \eta^2_G = 0.013$, and for Hand Used $F(1,28) = 13.00, p = 0.001, \eta^2_G = 0.007$. This is qualified by a significant Hand Used*Region interaction $F(2, 56) = 4.77, p = 0.012, \eta^2_G = 0.007$. Further interaction Line Length*Hand Used*Region, $F(6,168) = 4.48, p = 0.003, \eta^2_G = 0.011$. 
Correlations Within and Between Tasks

As the data from Experiment 1 suggest an underlying bias in attention to the left side of space in the pointing task, the line bisection task was used here to make an independent measure of this attentional bias and to explore whether it correlates with the bias seen in the pointing task. As any spatial bias in attention will vary across participants, we start by examining correlations within the line bisection task and within the pointing task and follow as a prelude to looking at how performance correlates across these two diverse tasks.

Correlations within bisection task

Figure 5.8 illustrates the relationships between participants’ spatial biases in the line bisection task across line lengths (left panel) and across regions of space (right panel). Pearson's product-moment correlations show positive correlations of bisection deviation across line lengths. Taking line length 1 as example a strong, positive correlation was found between Line Length 1 and Line 2, \( r = 0.92 \), \( n = 26 \), \( p < 0.0001 \), Line 3, \( r = 0.85 \), \( n = 26 \), \( p < 0.0001 \), and Line 4, \( r = 0.82 \), \( n = 26 \), \( p < 0.0001 \). Correlations between the measured bias across these conditions are very strong, showing consistent performance within the task. Pearson correlations for mean deviation at Centre Space is positively correlated with mean deviation at Right Space, \( r = 0.80 \), \( n = 26 \), \( p < 0.0001 \), and at Left Space, \( r = 0.94 \), \( n = 26 \), \( p < 0.0001 \).
Figure 5.8. Line bisection deviation by region and line length. Left panel shows how deviations in the line bisection task for line lengths of 2, 3 and 4 correlate with deviations for line length 1, the data being collapsed across the three spatial locations (right panel) shows how deviations in the line bisection task for right and left space correlate with deviations for centre space, the data being collapsed across the four line lengths.

Correlations within pointing task

Next, we looked at how the performance of same group of participants correlated across the 4 different conditions (baseline, eyes occluded, point back and disembodied point) in the pointing task. Pearson’s correlations are shown below separately for centre and right space. As in the line bisection task, the spatial bias, here measured in terms of the participants’ signed thresholds, is strongly correlated across the conditions.
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In Centre Space, signed thresholds between the three conditions and baseline are strongly positive; these are for Eyes Occluded, \( r = 0.77 \), \( n = 26 \), \( p < 0.001 \), for Hands Restricted, \( r = 0.65 \), \( n = 26 \), \( p < 0.001 \), and for Point Back, \( r = 0.49 \), \( n = 26 \), \( p = 0.01 \). In Right Space, Pearson’s correlations are for Eyes Occluded, \( r = 0.84 \), \( n = 26 \), \( p < 0.0001 \), for Hands Restricted, \( r = 0.86 \), \( n = 26 \), \( p < 0.0001 \), and for Point Back, \( r = 0.82 \), \( n = 26 \), \( p < 0.0001 \).

**Figure 5.9.** Graphs for the correlations in pointing thresholds across conditions, separately for right and centre space. On each plot the signed thresholds for 3 conditions (eyes occluded, hands restricted, point back) are plotted against signed threshold for baseline performance. Correlations with baseline are strong and positive as the coloured regression lines are largely parallel (especially in Right Space).
Correlation between tasks

Despite strong correlations within each of the separate tasks, pointing and line bisection, there is little obvious correlation between line bisection deviations and signed pointing thresholds. A Pearson’s product-moment correlation coefficient was computed to assess the relationship between the mean bisection deviations at centre space collapsed across line length and the mean pointing thresholds in centre space. There was no correlation between the two variables, \( r = -0.21, n = 26, p = 0.28 \). At right space no correlation between mean deviation in the bisection task at right space and mean threshold at right space for the pointing task was observed, \( r = -0.15, n = 26, p = 0.56 \).

**Figure 5.10.** Correlations for pointing thresholds Baseline Condition and Bisection Deviation, separately for right and centre space. On each plot the signed thresholds for baseline condition (y axis) are plotted against the mean leftward deviation on the bisection task (x axis).
5.4.3 Discussion

It is clear that the thresholds for perception of pointing do not vary from baseline when eye gaze cues are removed, when the participant can point back to the object they perceive the pointer to be pointing at or when the participants’ ability to produce a point is inhibited. Again a right response bias is demonstrated where the point of subjective equality shifts to the left of the veridical centre target for each region. This marked right response bias is most evident when the pointer is pointing with her right hand to the participants’ right space. It is interesting that the right response bias is consistent across both regions and within subjects.

On the line bisection task participants show a typical left bias in determining the midpoint of a series of horizontal lines. In line with previous research, this is most pronounced for the longest line (Jewell & McCourt, 2000; McCourt & Jewell, 1999) and is modulated by the hand used to bisect the line. The pattern of results is consistent across the three regions of lines presented to the participants. While participants show pseudoneglect, neglect of a portion of the right side of space, such that the midpoint is pushed into the left side of space, no relationship is apparent between the spatial bias evident in the thresholds for pointing and the spatial bias evidenced on the line bisection task. We must therefore limit our interpretation to the basic fact that participants show a form of pseudoneglect in both tasks. It is worth noting that the right response bias reported here could be explained by hemispheric asymmetry in social processing rather than hemispheric asymmetry in general attention allocation. There is a right
hemisphere bias for processing social stimuli (Greene, Mooshagian, Kaplan, Zaidel, & Iacoboni, 2009; Greene & Zaidel, 2011).

5.5 General Discussion

The present work examined acuity for pointing perception by a live pointer in a naturalistic setting. In addition, we examined the influence of the hand used to point, eye gaze direction cues, and embodiment cues on discerning where someone is pointing in space. Participants demonstrate remarkable acuity for discerning where the pointer is pointing with best performance at targets in the centre region of 1.42°, 0.46° and 1.58° degrees of visual angle at left, centre and right spatial locations respectively (Experiment 1). In both experiments, the point of subjective equality shifts to the left of the true midpoint for both central and right and left space (Experiment 1) and central and right space (Experiment 2).

The thresholds are very accurate, with best performance in centre space comparable to resolution of eye gaze cues in centre space (i.e., the research on ‘being looked at’) (Anstis et al., 1969; Cline, 1967). Further, thresholds are higher (acuity lower) when the pointer points to peripheral space – again there is comparable to results on eye gaze acuity such that the turning direction of the head biases the perceived direction of eye gaze in that direction (Cline 1967; Gibson & Pick, 1963; Pomianowska et al., 2011; Moors et al., 2016). Here, it appears that the extended arm/hand plays a similar role in pointing perception such that the extension of the arm across the bodies midline pulls the observers attention further into their right space and
thus biases the perceived direction of hand pointing in that direction. Consequently, the observer judges the locus of the point to be further to the right of the veridical centre target than it is.

The threshold for determining the object of the point is clearly modulated by the hand the pointer uses to point with. Perception of points that cross the midline of the pointer’s body into contralateral space (i.e. the pointer’s right hand pointing towards targets in the participant’s right space) result in increased right responses to the centre target and to objects to the immediate left of the centre target such that the perception of the centre position in right space on the apparatus shifts leftwards along the horizontal. Manual midline crossing occurs when a person moves their hand across their midline into contralateral hemi space (van Hof, van der Kamp, & Savelsbergh, 2002). During development, the ability to cross the body midline into contralateral space has been shown to increase with age, is a marker of typical perceptual-motor development and has been linked to both the development of hand preference and bimanual coordination (Scharoun & Bryden, 2014; van Hof et al., 2002).

What about the perception of contralateral points i.e., points made across the midline of the body? In an earlier study, we used visual adaptation to examine the representation of this directional cue in the visual system, and found that adapting to a hand pointing to the left or right of an object resulted in a subsequent shift in perception of the direction of test hand stimuli, such that, perception shifted in the opposite direction to the adapting stimulus (Cooney et al., 2015b). Prior to adapting to a directional hand pointing cue,
an asymmetry at baseline judgments was observed where participants were more accurate in judging the pointing direction of leftward pointing right hands, and rightward pointing left hands, when the task is most difficult. This perceptual bias is also seen in the post-adaptation profiles, where the shift in the ‘neutral point’ (the shift in which hand is most often perceived as pointing directly at the target) is hand specific, with a leftward shift for left hands and a rightward shift for right hands. Hand pointing stimuli were presented from an egocentric viewpoint so that observers were looking at a computer-generated image that approximated the position of their own hand pointing out in space from their body. Here, observers are facing a live pointer, an allocentric visual perspective. While in the adaptation study (Cooney et al, 2015b) this manifested experimentally as more accurate judgments of where the hand was pointing at or away from an object, in this task it results in more right responses as the right hand crosses the midline into the viewers right space and perception is pulled more into peripheral right space. The asymmetry observed in both cases suggests that regardless of perspective, the extension of the hand/arm serves as a cue and modulates the perception of the spatial relationship between the index finger and the referent.

In contrast to this study, the pointing hands in Cooney et al. (2015b) were static computer generated images presented from an egocentric viewpoint towards or away from an object positioned in depth. Belopolsky et al (2008) used video recordings of pointing gestures at objects and manipulated viewpoint to examine the role of egocentric and allocentric visual perspective on the allocation of attention to observed points and found that, contrary to previous accounts, the allocation of attention was not modulated by visual
perspective. It is the hands’ lateral extension into contralateral space that
was driving the asymmetry in the adaptation study (Cooney et al., 2015b)
much like the bias reported in this study where contralateral points made by
the pointer viewed from an allocentric perspective drive the viewers’
perception into the periphery.

Butterworth and Itakura (2000) reported that participants tended to
inaccurately estimate the location of the experimenter’s attention to the left of
the object that the experimenter was actually attending to and this bias
depended both on cue type and whether they were seated to the left or right
of the experimenter. Inclusion of the pointing gesture as a cue combined
with head and eye gaze direction resulted in more misallocation errors to the
left of the correct target than to the right of the correct target. The errors
were consistent from both seating positions to the left of experimenter and
right. From the right seating position, there was a left bias for all other cue
combinations, eyes only and head and eyes. Similar to Experiment 2 of the
present study pointing was always right handed. In contrast to the present
study, participants were best at correctly identifying the object to which the
experimenter was attending when the experimenter pointed to objects in the
periphery. There is considerable difference between the experimental set up
used by Butterworth and Itakura (2000) and ours. In their study, the
participants were seated side by side with the experimenter, thus limiting the
view the participants had of the experimenter to a profile view. Further, as
eye gaze cues from a profile view are monocular at best, it is difficult to
assess the contribution of eye gaze direction.
Butterworth and Itakura (2000) conclude that vector extrapolation alone is not used to determine where someone’s attention is because accuracy for pointing varied between peripheral and intermediate positions. If vector extrapolation was primarily used to extract this information performance should not vary. In the present study, pointing is clearly modulated by the hand the pointer uses, more specifically, whether that hand crosses the midline of the body into contralateral space. Our findings suggest that vector extrapolation is paramount in accurately discerning where and at what someone is pointing. This is confirmed further by the fact that removal of eye gaze information did not alter the participants’ response significantly from baseline.

An alternative approach used to study this topic is to look at the role of pointing in naturalistic tasks that involve communication between participants about the location of objects in interpersonal space. One study reported that as distance between referent and observers decrease, pointing gestures replace speech localisation (Bangerter, 2004). Here, we show that perception of pointing to distal targets is accomplished with incredible precision by the visual system. Acuity is so fine-grained that it is comparable to the acuity observed for the direction of gaze reported by Symons et al. (2004). We often request that a communicative partner look at an object or act upon a specific object, this can require a considerable amount of precision even if the object is located a few metres from the conversation. From this, pointing does not only function to locate a general zone of space but also acts to specify with precision referents within a general zone of space.
We did not control for the contribution of head and body orientation information. The torso of the pointer moved with respect to the head, gaze and hand position. This is most evident when pointing to peripheral regions.

Of the visual cues that facilitate joint attention, research has focused almost exclusively on examining eye gaze direction and the influence that head orientation (Carlin et al., 2011; Hietanen, 1999; Kluttz et al., 2009; Langton, 2000; Langton & Bruce, 1999; Langton, Honeyman, & Tessler, 2004; Laube et al., 2011; Moors et al., 2016) and body orientation (Moors et al., 2015; Pomianowska et al., 2011; Seyama & Nagayama, 2005) has on judgments of eye gaze direction. Gaze perception is not only controlled by geometrical extrapolation of information about the position and size of the sclera and iris but can also be mediated by the orientation of the head (Todorović, 2006). A robust overshoot effect has been demonstrated, when eye gaze direction and head orientation are incongruently oriented, perceived gaze direction shifts in the opposite direction to the incongruent head orientation (Anstis et al., 1969; Moors et al., 2016; Ricciardelli & Driver, 2006; Seyama & Nagayama, 2005; Todorović, 2006). In the current study, the pointers eyes, head, hand, and torso were congruently oriented once fixated on the target. At that distance head orientation may facilitate demarcation between centre, left and right space, but it is unlikely that head orientation alone would produce similar thresholds.

Gaze estimation is also influenced by the orientation of the body. Recently, an overshoot effect was reported by Moors et al. (2015), where the discord between head and body orientation resulted in perceived gaze direction in the direction opposite to the body orientation. In general, in that
study, participants overestimated at which object the avatar was gazing when viewing an array of objects positioned in the foreground. Interestingly, when the head was aligned with the orientation of the body this resulted in participants underestimating where the gazer was looking. Pointing at centre space in this study produced some incongruence, in that, the body was completely front facing and the head, hand and eyes shifted laterally to the central targets with slight incongruence between torso orientation and head orientation of the pointer. Future studies could incorporate manipulation of body orientation into naturalistic studies of pointing perception.

5.6 Conclusion

The results of this study provide novel evidence of the remarkable acuity for eye gaze perception. Acuity is highest when looking at a person pointing to objects located directly in front of viewer and pointer. Thresholds increase as the target objects move into left and right peripheral zones. The hand used modulates the accuracy for discerning the spatial location of a pointing gesture. This is explained by a bias in the perception of manual midline crossing. At this distance, eye gaze cues have little to no effect on estimating where in space someone is pointing. In line with some recent developmental research, pointing accuracy in perceiving where someone’s attention is located is comparable to eye gaze acuity. Pointing is a primary deictic visual cue that facilitates attentional orienting not just to zones of space but facilitates focused attention on particular objects of interest. Unlike eye gaze, pointing is primarily used to communicate, and is arguably a more salient communicative cue than gaze because of the large amount of dynamic information provided. From this, future studies examining adult
social perception and attention should consider this cue as of comparable importance to eye gaze and head orientation.
6.1 Introduction: Revisiting the theoretical background

6.1.1 Models of social attention perception

In order to facilitate social interaction via joint attention, the visual system must represent postural cues from the body which signal the direction of attention (Ashbridge et al., 2000). Classic single cell research with monkeys found separate cell populations tuned to specific social directional cues; eye gaze, head turning direction and body orientation in anterior superior temporal sulcus (aSTS) (Barraclough & Perrett, 2011; Perrett & Emery, 1994; Perrett et al., 1985, 1992). The fact that particular neural populations in aSTS show such directional selectivity indicates that social signalling is represented in high-level vision. Most accounts of social attention place eye gaze as the privileged medium to convey and receive social information. The primary example is Baron-Cohen’s (1995a, 1995b) proposed Eye Direction Detector (EDD). The EDD singles out eyes from other features in the environment, as looking at the observer, and then processes the direction that eye gaze is oriented. From this, the EDD ascribes ownership or agency to the cue (Baron-Cohen, 1995a). Recent behavioural adaptation research have shown that, similar to monkey studies, humans have functionally distinct mechanisms that code left and right gaze directions (Calder et al., 2008; Jenkins et al., 2006), head orientations (Fang & He,
However, Perrett et al. (1992) also observed that some of the cells in the monkey aSTS responded to more than one cue type. For example, in some cells, head and body stimuli oriented in the same direction produce similar firing rates. These cells were termed ‘social attention cells’ because they were selective to a specific direction of cue irrespective of the type of social cue. These cells may function to discern the locus of another individual’s attention. To account for when multiple cues are visible simultaneously or situations when one cue is unavailable due to impoverished viewing conditions, Perrett and Emery (1994) proposed a hierarchical social attention model, a ‘direction of attention detector’, DAD, that detects the direction of another’s attention via a hierarchical ordering of cues. On this model, information coded about the direction of eye gaze would always, via inhibitory connections, override incongruent information about head orientation, and both eye and head direction information would inhibit information about incongruous body posture (Perrett et al., 1992; Perrett & Emery, 1994). Accordingly, when presented with a number of cues that are incongruently oriented, body orientation would not override information from head orientation and head orientation would not override information from eye gaze.

Experimental support for this hierarchical model of cue combination is, however, somewhat mixed. A number of different behavioural techniques have been employed to examine how social directional cues, specifically those from eye gaze and head orientation, are integrated. Some support for
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A hierarchical model comes from spatial cueing and spatial compatibility studies (e.g., Hietanen, 1999, 2002; Seyama & Nagayama, 2005; Pomianowska et al., 2012). Such studies show that the directional information provided by a person’s eye and head is more salient when the cues are oriented in opposite directions, e.g., a forward facing head with eyes oriented to the right or left or a head oriented to the right with eyes directed back to the observer. In marked contrast, in research using spatial interference paradigms directional information has been found to be more salient when different directional cues (i.e., head and gaze) are oriented in the same direction than when they point to opposite directions (Langton, 2000; Langton & Bruce, 2000). The second model, a parallel processing account, proposed by Langton (2000) conceptualizes the effects of each cue as independent rather than hierarchical, such that the direction of social attention is computed by separate analysis of each cue’s directional salience. Each cue is analysed in parallel with social attention deduced from the additive effects of each.

6.1.2 Why is hand pointing a special social cue?

Following the direction of others’ point gestures appears several months before the development of language (Gredebäck & Melinder, 2010). Delays in the ability to follow another’s gaze and pointing gestures, and failures to use proto-declarative pointing, are among the earliest symptoms of autism, a neurodevelopmental disorder characterized by impairments in social and communicative functioning (Swettenham et al., 2013). Indeed, pointing meets all the criteria of a marker of biological function as it is acquired.
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without learning (Daum et al., 2013: Gredeback et al., 2010) and is
universally used by humans (Bates et al., 1975; Tomasello et al., 2007)

Combined with eye gaze, body posturing and head turning, pointing
indicates where and at what another person is attending to, thus permitting
the observer to make inferences about another person’s knowledge,
thoughts or feelings (Tomasello et al., 2007). Pointing serves to establish
joint attention, which is defined as the experience of openly sharing with
others a common focus of interest (Mundy & Newell, 2013). On some
accounts eye gaze and hand pointing are important precursors to theory of
mind, the ability to understand others’ beliefs, intentions and goals (Ashwin
et al., 2015; Swettenham et al., 2013; von dem Hagen, Stoyanova, Rowe,

Indeed, pointing, like eye gaze, is a deictic gesture that permits the
signaller to indicate to a recipient an object or target of interest (Butterworth &
Jarrett, 1991; Butterworth & Itakura, 2000). The resulting convergence of eye
gaze between the two interacting parties facilitates a mutual understanding of
a common focus of interest (von dem Hagen et al., 2013). As the pointing
gesture is a fundamental tool for manipulating joint attention, pointing is linked
to the development of the uniquely human capacity for shared intentionality
(Tomasello & Carpenter, 2007). With the exception of developmental studies
of infant pointing (Tomasello et al., 2007), there is remarkably little research
on the perception of hand pointing. Given its importance in language
development (Kita, 2003), joint attention (Fischer & Szymkowiak, 2004) and
its likely importance in the development of theory of mind (Swettenham et al.,
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2013) an examination of the visual representation of pointing is needed to elucidate our understanding of the processes that facilitate joint attention.

The main conclusion to be drawn from the present work is that cue specific directional information from visual signals further down the proposed hierarchy of social attention perception is represented at a high level in the visual system. Yet directional judgments are likely moderated by low-level geometric cues. In the following sections, the specific findings of the work are discussed and integrated with one another and with the wider field of research.

6.2 Summary of findings

A broad review of the relevant literature regarding social attention perception in Chapter 1 identified the link between perceptual analysis and representation of specific social cues, extraction of directional information and subsequent orienting of the viewer’s attention to the direction of these cues. Particular consideration was given to research that supports high-level sensitivity to social cues. The debate pertaining to the organization of social attention perception was outlined and the methodologies employed thus far to examine the unresolved question of how social cues are integrated in the visual system were described. The review identified a gap in knowledge concerning the perception of pointing which highlights a need for a clearer understanding of how the pointing gesture is perceived and subsequently attended to. Particular note was made of how, traditionally, perception of these cues and attention towards them are studied with various methods, usually in isolation. However, recent findings address and empirically
explicate the tacit connection between perceptual analysis of directional information inherent in the configuration of these social cues and subsequent facilitation of attentional shifts in the viewer. The following section summarizes the main empirical findings from each of the four studies presented.

6.2.1 Hierarchical integration of cues to social attention

Adaptation offers a non-invasive and direct way to study the neural coding of visual information. As described in Chapter 2, we employed a cross adaptation paradigm to investigate whether aftereffects reflect functionally distinct (adaptable) mechanisms that are stimulus specific. Alternatively, if adapting to one directional cue produces an aftereffect in a different cue, this would be consistent with the existence of ‘social attention cells’ as described in the single cell studies with macaques that code for the direction of attention irrespective of cue (Perrett & Emery, 1994; Perrett et al., 1992).

We report a novel cross-category perceptual aftereffect. After adapting to images of a head oriented to the left or right by 25° participants show a perceptual bias in judging the turning direction of subsequently presented test bodies at smaller angles. In contrast, adaptation to body turning direction, a cue further down the proposed social cue hierarchy, did not result in a perceptual aftereffect for head orientation. The unidirectional nature of the aftereffect suggests that head orientation modulates the perception of body orientation but that information about body orientation does not inhibit the perception of head orientation. These findings support a hierarchical model of cue combination.
6.2.2 Evidence that pointing is represented in high-level vision

Research described in Chapter 3 presents, for the first time, evidence of rapid visual adaptation to hand pointing direction. Adapting to hands pointing away from an object resulted in a shift in the perception of the direction of subsequently presented hand pointing stimuli away from the direction of the adaptor. A second experiment tested the extent that the directional information alone drives the perceptual aftereffect by replacing the hand pointing adaptor (a social cue) with an arrow (a symbolic cue) to see if this elicits a comparable perceptual shift in the perception of hand pointing.

The results show that when adapting to an arrow oriented away from the object, participants subsequent perception of hands pointing in the same direction were also repelled away from the direction of the arrow adaptor. Directional information inherent in the cue likely drives adaptation aftereffects. However, the strength of the adaptation attenuated a little when participants adapted to arrows, showing a small yet significant difference between same and cross category adaptation. The finding that adaptation varies according to the type of adaptor confirms that pointed hands are a more effective adaptor than arrows, as evidenced by generally greater effect sizes.

6.2.3 Spatial cueing of attention: cue type and gender of viewer

The Posner cueing paradigm has been central to the study of attention cueing and in the past 15 years has been employed to examine spatial cueing towards socially salient cues, particularly eyes gaze direction and arrows (e.g., Driver et al., 1999; Ristic et al., 2002). In separate experiments,
the research described in Chapter 4 examined the potency of eye gaze direction, head direction, and body orientation to facilitate shifts in spatial attention, by specifically examining the power they exert on the deployment of attention during a central spatial cueing task.

In line with previous research a spatial cueing effect was observed for two of the three cues examined, eye gaze direction and head turning direction (Driver et al., 1999; Langton & Briuce, 2000), with a difference in how males and females orient their attention to eye gaze (Bayliss et al., 2005). Participants were faster to detect the presence of a target when it was immediately preceded by a valid head or eye gaze cue than when preceded by an invalid head or gaze cue. No difference in RTs to invalid versus valid cues was found in response to a centrally presented body orientation cue. A gender difference in the cueing effect was observed only for eye gaze cues, whereby oriented gaze served as a strong cue for females but not for males at an SOA of 700ms, with neither males nor female participants showing significant cueing effect to eye gaze at 1100ms. Body orientation proved to be an ineffectual cue to attention for both males and females. From this, directional information of eye gaze, head turning and body orientation direct spatial attention in different ways that are modulated by the gender of the observer and the amount of time the cue is presented for.

The experiment presented in chapter four was the only experiment that included gender as an a priori factor of interest. This was due to previous research that found a gender difference in how men and women orient spatial attention in response to eye gaze (Bayliss et al., 2005) Where
possible experiments were balanced for gender. Data from all experiments were subject to an examination of any gender effects and none was present except for the study presented in chapter 4.

6.2.4 Perceptual acuity for pointing

As described in Chapter 5, observers' accuracy in determining where a live model is pointing was tested in two experiments. We report that perceptual acuity for discerning where another person is pointing is remarkably accurate, akin to perceptual acuity for eye gaze direction (Symons et al., 2004). Acuity was highest, thresholds lowest, for targets located centrally between viewer and pointer, and thresholds increased as targets moved horizontally into left and right spaces. Accuracy also varied asymmetrically, such that the hand that the pointer uses to point modulates acuity. Specifically, the observer’s perceptual acuity is much greater when observing the right-handed than the left-handed gesture in left space, the pointer’s right hand falling in the observer’s left space. In contrast, acuity is greater when observing the left-handed than the right-handed gesture in right space, the pointer’s left hand falling in the observers’ right space. The best performance thresholds were 1.42°, 0.46° and 1.45° of visual angle at left, centre and right spatial locations respectively.

Study 2 further examined the visual cues employed to gauge pointing direction by comparing performance in the baseline condition, which was identical to Study 1, to performance; when eye gaze cues were removed, when participants could use their own hand to point to where they perceived the pointer to be attending, and when this ability was restricted by having the
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observer hold their hand in a posture incompatible with making a point. Within these conditions, participant’s acuity did not differ significantly from baseline, with thresholds similar to Study 1. Participants evidenced, via a line bisection task, typical pseudoneglect, a bias where on average people judge the centre point of a line to the left of veridical centre (Jewell & McCourt, 2000). This was not correlated with the accuracy thresholds for the pointing task.

These results indicate that humans are remarkably sensitive to where another person is pointing in space, utilizing perceptual information from the extended arm, hand and index finger and that, at a distance of 2 metres, eye gaze information contributes minimally to discern the precise location of the point. Pointing not only directs attention towards a general spatial region but the fine grained morphological structure of the pointing hand extending into space is also used to discern with greater precision the location of the pointer’s attention.

6.3 Theoretical implications

6.3.1 Social attention perception

**Hierarchy of social cues.** One of the main concerns of this thesis was to examine perception of and attention towards what are described in the field as social cues. The social feature of these cues is ascribed based on the utility of these cues to communicate socially relevant information pertaining to the direction and locus of another person’s interest or attention. Converging evidence has shown that eye gaze, in particular, is a ‘special’ cue, and as such is preferentially processed by the visual system. A raft of
neurophysiological, behavioural, neuroimaging and psychophysical studies support selective representation of eye gaze direction (e.g., Allison et al., 2000; Carlin & Calder, 2013; Emery, 2000). These findings not only complement our intuitions about the eyes, as windows to the soul, but also reinforce the primacy of detecting the direction of eye gaze and its key role in Baron-Cohen’s (1995b) ‘mindreading model’. Indeed, much of the foundation for the experiments described here was laid by psychophysical and behavioural work that has revealed the incredible accuracy with which we can discern a shift in eye gaze direction (Anstis et al 1969; Bock et al., 2008; Cline, 1967; Gibson & Pick, 1963; Symons et al., 2004), and head orientation (Wilson, et al., 2000), and the cues we use to estimate these changes (Ando, 2004; Todorović, 2006). Developmental research has revealed early emergence of preference for eyes and eye contact in infancy (Batki et al., 2000; Farroni et al., 2000; Senju et al., 2015).

Replication of the eye gaze cueing effect in Chapter 4 further supports the primacy of this cue in its ability to capture the viewers’ attention. While perception of eye gaze has received substantial attention over the past number of decades, (see Carlin & Calder, 2013; Itier & Batty, 2009; Langton et al., 2000), more recently, diverse research groups have considered the rest of the body both as a special category of object (Downing & Peelen, 2007) and as a socially salient directional cue (Lawson et al., 2009; Seyama & Nagayama, 2005) whose postural configuration can communicate valuable information regarding the affective states of a person (de Gelder, 2006; de Gelder et al., 2015).
In Chapter 2 we present evidence for directionally selective cells tuned to body orientation (Cooney et al., 2015a; Lawson et al., 2009) and head orientation (Carlin et al., 2012; Lawson et al., 2011). We present a novel finding of cross category adaptation between head and body orientation (Cooney et al., 2015a; Chapter 2, this thesis). Cross category adaptation was employed to examine if adapting to a different directional cue, head orientation, influenced cells coding body direction. Similarly the reverse was tested to check if cross adaptation occurs in one direction, and if so if this direction is top-down, i.e. more salient social directional cues such as head orientation may adapt body orientation, but social cues further down the hierarchy will not influence (adapt) perception of head orientation. Cross category adaptation in one direction supports existence of human ‘social attention cells’, tuned to the same orientation of head and body direction, our finding of unidirectional cross category adaptation follows the hierarchical inhibitory structure of the DAD that Perrett and Emery (1994) proposed.

Since beginning the research for this thesis, Lawson and Calder (2015) have also published work that inspected cross category adaptation between head and body orientation as well as with a control test object (chair). In contrast to the type of adaptation method used in Chapter 2 and Chapter 3 participants in the Lawson and Calder (2015) study adapted to an alternating sequence of left and right heads or bodies. In Chapter 2, participants adapted to a continuous stream of heads or bodies in one direction, either left or right. The predicted aftereffects, following alternating adaptation to left and right adaptors, would cause the observer to display an increased
tendency to judge the smaller left and right angles of the test stimuli as
direct. This approach is an efficient time saving method as there is a single
adaptation condition rather than two. Remarkably, using an alternating
adaptation paradigm, no transfer of the direction aftereffect was observed for
cross category head or body or control object orientation, such that adapting
to an alternating sequence of 20° heads did not produce a shift in the
perception of body orientation and vice versa.

Lawson and Calder (2015) conclude that body orientation and head
orientation are represented in the brain at a category specific level. The
aftereffects observed for both head and body orientations, in their account,
are strictly facilitated by the specific social cue type and not by populations of
cells tuned to the direction of attention or ‘social attention cells’. Similarly,
they argue that the aftereffects observed do not reflect simple orientation
cells tuned to left and right as evidenced by no cross adaptation after
adapting to a non-social control adaptor, i.e., no shift in perception of body or
head orientation was observed after adapting to left and right oriented chairs.

What could explain the discrepancy between Lawson and Calder (2015)
and the cross category adaptation study reported in Chapter 2 (Cooney et
al., 2015a)? Other than the type of adaptation method used there are a
number of comparisons to be made between the two studies in terms of task
parameters. First, the time course of adaptation phase differed between
studies. Participants in our study were exposed to a longer adaptation phase
compared to Lawson and Calder (2015) (~4 minutes, compared ~2
minutes). The second notable difference in task and experimental
parameters is in how each study presented the test and adapting stimuli.
While Lawson and Calder (2015) presented greyscale images of head and body stimuli, we used full colour images. Furthermore, their body stimuli were full bodies with legs and hands. We used just torso orientation, as limbs, particularly hands, provide additional cues to orientation. In consideration of converging evidence that supports high-level representation of hand shape in high-level vision (Bracci et al., 2010; Orlov et al., 2010), we removed this additional social cue. There is also an appreciable difference in the size of the stimuli presented. Head, body and chair stimuli in the Lawson and Calder (2015) study subtended a visual angle of 3° at viewing distance of 57cm, whereas our (Chapter 2, this thesis; Cooney et al, 2015a) stimuli subtended, vertically, ~21.2° of visual angle at a viewing distance of 60cm, such that they were approximately 7 times larger.

Finally, to ensure no carry over adaptation effects participants in our study (Chapter 2, this thesis) completed the same and cross category variants at least one day apart, whilst Lawson and Calder (2015) did not. Participants in their study completed each of the three adaptation conditions and baselines, same social, other social, and control object in a single experimental session, all in one hour, with breaks limited to request-only. A within-subjects comparison of the two types of cross adaptation protocol to these particular cues could be used in future studies in order to further explicate the basis of these somewhat conflicting findings.

**Support for social attention cells from neuroimaging.** The existence of ‘social attention cells’ in humans is further supported by neuroimaging research that has focused its efforts on identifying view invariant and stimulus specific responses along the large swathe of STS. As
described and defined by Allison et al. (2000) the STS region extends far beyond the anatomical banks of the sulcus, to include parts of the cortex on the surface of the posterior middle temporal gyrus as well as cortex within STS. Classic single cell studies with macaques primarily identified cells in anterior STS that coded for directions of cue types, eye gaze, head, and body (Perrett et al., 1985; Perrett, et al., 1992; Wachsmuth et al., 1994).

Further, the subset of cells that responded to the direction conveyed by more than one cue type were also located in small regions of aSTS (Perrett et al., 1985). However, until recently, research efforts with humans using conventional fMRI focused on the posterior portion STS.

When passively viewing shifts in eye gaze direction the posterior portion of STS is preferentially activated (Hoffman & Haxby, 2000; Pelphrey et al., 2003). A more recent study showed that it is not only passive viewing of someone's eyes that activates pSTS, spatial shifts of attention in response to the direction of gaze also activates this region. Using spatial cueing with eye gaze direction as the central cue, the only area that showed differential activation to congruent and incongruent gaze direction was pSTS (Materna et al., 2008a). Importantly, this activation was dissociated from activation in a region involved in spatial attention, the intraparietal sulcus IPS (Materna et al., 2008a). This demonstrates that it is not the reallocation of spatial attention that exclusively drives the response in STS. However, when neural response to following two different social cue types to a target, were compared (photographs of pointing cues and eye gaze cues presented simultaneously) no significant difference was found in brain activation in pSTS. The authors conclude that this is evidence that pSTS processes
socially relevant directional cues rather than the direction of eye gaze exclusively (Materna et al., 2008b).

Improvement of techniques used to analyse fMRI data has permitted researchers to examine the graded response and representational overlap of cells selective for left and right eye gaze and dynamic head views in functionally heterogeneous regions such as STS. Carlin et al. (2011) report view invariant coding of eye gaze direction in human aSTS. Using dynamic stimuli of head turns, Carlin et al. (2012) found a region of right aSTS sensitive to dynamic shifts of head direction. Indeed, using a model predictor, researchers could accurately predict if activity in the region is predicted by exposure to a left or right oriented head turn. To summarise, neuroimaging studies point towards a particular portion of aSTS that codes for the direction of attention. Sensitivity of a population of neurons in pSTS to different head views has been reported (Fang et al., 2007). There is convincing evidence that head and eye gaze direction are coded hierarchically in STS, with static head view represented in pSTS, possibly dynamic head view in portions of aSTS, and left and right eye gaze direction in aSTS.

Most research efforts and subsequent models of social attention perception emphasise eye gaze direction and head view. Further down this hierarchy we show for the first time, from behavioral adaptation, cross adaptation aftereffects that may reflect not just separate coding of these directional cues but subsets of cells tuned to the direction of these cues.
6.3.2 Neurocognitive model of pointing perception

**Commonalities and differences with eye gaze.** Like eye gaze, pointing perception stimulates a number of high-level socio-cognitive processes, including but not limited to; attention orienting, perceptual sensitivity to biological cues, and joint attention. Chapter 3 provides initial support of perceptual sensitivity to hand pointing direction in high-level vision. Chapter 5 extends this to show the remarkable fine-grained precision with which people can judge the object or focus of the hand gesture. Accuracy at this distance was not conferred by the salience of the pointer’s eye gaze direction. In one of the few studies that have addressed adult perception of pointing, Materna et al. (2008b) found no difference in accuracy for detection of a target that was either looked at or pointed at by eye gaze and hand pointing respectively. Nor did cue type differentially engage a region associated with social attention, STS. To speculate, one of the reasons no difference in both accuracy and neural response was observed may be due to the unusual pointing cue they used, which did not reflect the expected view of a pointing gesture. As described in Chapter 1, humans have a preference for index finger points with the palm down such that it affects accuracy in following a pointing gesture (Ariga & Watanabe, 2009; Cochet & Vauclair, 2013). Further, we show that it is at much smaller visual angles between target objects that we may begin to see the relative strength of each cue to direct attention upon an object emerge (Chapter 5). Both eye gaze and pointing were shown by Butterworth and Itakura (2000) as useful cues to direct attention towards general zones of space. Our results show that precision is far greater within zones of space than previously expected, and
this precision relies on using hand pointing as the referent rather than eye
gaze direction. This precision is modulated to a large degree by the hand
the pointer uses and the extent to which it moves across the midline and
draws the observers attention towards the contralateral side of space.

In terms of a hierarchy of visual cues that facilitate joint attention where
does hand pointing fit in this hierarchy? Combined evidence from three
strands of investigation - developmental, perceptual, and selective attention -
reflect three core processes in pointing comprehension traditionally
considered in eye gaze processing. Early development and attention toward
the cue favours reflexive attentional orienting that supports preferential
processing of social attention to this salient cue type. Acuity for discerning
where someone’s attention is focused in space is supported from our study
with adults (Chapter 5) who displayed greater accuracy and low perceptual
thresholds when following pointing gestures to a target. Indication of the
neurological correlates of pointing comprehension, indexed by spatial cueing,
have been described by Gredeback et al. (2010) where static hand pointing
cues were presented indicating the same location as a preceding object had
appeared at, or the opposite, incongruent direction to where the object had
appeared. Gredeback and colleagues found differential neural processing of
the pointing gesture that was modulated by the congruency between the
point and location of object over posterior temporal areas. As with eye gaze,
reflexive orienting of attention via pointing gestures has been shown by a
number of groups (Belopolsky et al., 2008; Fischer & Szymkowiak, 2004;
Sato, et al., 2010). Pointing and eye gaze also share some attentional
properties as indexed by interference studies (Langton & Bruce, 2000).
Some studies have not found any dissociation between attention orienting to pointing, eye gaze, and other directional stimuli arrows (Sato et al., 2009). The attention orienting task perhaps only taps into the referential nature of the eye gaze and pointing cue (Birmingham & Kingstone, 2009). Other studies support distinct neural substrates such as Bayliss et al. (2011) which showed that orienting of attention to shifts in eye gaze direction were not modulated by visual adaptation to hand pointing direction.

Both pointing with the eyes and pointing with the hand are referential actions. A number of authors, including Tomasello et al. (2007) and Kita (2003), suggest that the emergence of pointing perception in infancy reflects cognitive changes that are directly related to the development of representational thinking. While eye gaze perception and pointing both focus the observer’s visual attention on a place or thing in the environment, pointing is in all cases explicitly referential. The primary goal of a hand point is to refer, whereas an observer can infer different reasons for discrete changes in a person’s eye gaze (Baron-Cohen, 1995b; Conty, George, & Hietanen, 2016). From this, eye gaze perception differs from pointing in the direct link between perception of eye gaze direction and the inferences that observers can then make about the looker’s epistemic and emotional states. Referential index finger pointing may facilitate mental state attribution in a more preliminary fashion.

6.4 Directions for future research

According to Baron-Cohen (1995b), accurately detecting that someone is looking at you is a necessary precursor to establishing a state of shared
attention. With the exception of the study presented in Chapter 5, all experiments in this thesis presented the social directional cues in isolation. None of the studies employed eye contact as a cue. This was because the primary aim of this thesis was to examine representation of cues further down the direction of attention hierarchy (Perrett & Emery, 1994).

Furthermore, initiation of eye contact is well understood to modulate a host of perceptual and cognitive processes that include attentional capture, face processing, self awareness, pro-social actions and appraisal of others (see Conty et al., 2016 for review). Most pertinent to the research presented here, as mentioned throughout this thesis, attention capture by direct gaze is indicative of highly specialized regions of the brain responsible for eye gaze perception (Itier & Batty, 2009).

Behaviourally, eye contact can ameliorate performance on a number of tasks, particularly target discrimination (Böckler, van der Wel, & Welsh, 2015) and slow down detection of peripheral targets (Senju & Hasegawa, 2005). The hold that direct gaze has over attentional capture results in greater performance in face processing tasks but interferes with tasks that require analysis of simultaneously presented visual stimuli (Conty et al., 2016). From this, orienting to social directional cues would be affected by initial eye contact, particularly in the experiments described in Chapter 5. Understandably, this reduces the naturalistic setting of the experiment, as establishing eye contact often precedes producing a point, and in turn the co-attender following a pointing gesture, at a given distance (Wilmut et al., 2006). Future studies could assess the impact eye contact has on subsequent accuracy in judging the locus of the pointing gesture. In
addition, increased use of experimental settings that include live social interaction would prove beneficial in social perception research, particularly considering the physiological effect live eye contact has on the viewer, and the finding that this is modulated by whether or not the observer believes the looker can see them (Myllyneva & Hietanen, 2015).
Geometric cues that drive pointing perception

Accuracy in determining where someone is looking, as described in the introduction (Chapter 1), is driven by low-level visual cues, including the distribution of luminance cues across the eye region (Ando, 2004), iris scleral contrast (Kobayashi & Kohshima, 2001) and the position of the rotation of head relative to direction of eye gaze (Kluttz et al., 2009). Perception of head orientation is driven by deviation of the contour of the head from bilateral symmetry (direct facing) and deviation of the nose from vertical (Wilson et al., 2000).

From the findings presented in Chapters 3 and 5, the degree to which the hand and forearm extend ipsilaterally or contralaterally in space with respect to the observer, are the primary cues that encourage the line of sight of the observer towards a general zone in space. From this, the true location of the point is estimated, via vector extrapolation, on the basis of the position of the index finger relative to the object or location within the zone of space. The subtle configuration of hand shape and finger used to point are the cues that drive attentional orienting to hand pointing. Reflexive orienting of attention to hand pointing cues is modulated by the configuration of the hand gesture, with a significant advantage for indexical pointing (Ariga & Watanabe, 2009). It would be particularly useful to examine the effects of combinations of these configural cues on pointing perceptual thresholds. As the contribution of body orientation and head orientation to pointing perception was beyond the scope of the four studies presented in this thesis, a comparison of the relative strengths of these cues, with regards to ascertaining pointing perception, would provide information regarding integration of these powerful
socially salient cues. Do we require information from head and body orientation to accurately determine where someone is pointing? Similarly, how are these pointing cues extracted? What cortical circuits are involved?

There is some evidence that extraction of dyadic information relative to self, for example social directional visual cues that are presented looking at the viewer, such as a photograph of a person looking at and pointing in the direction of the participant viewer, are integrated ~200ms after stimulus onset in the right premotor cortex (Conty, Dezecache, Hugueville, & Grezes, 2012).

**Spatial biases in social attention perception**

Also evident from the thresholds for pointing, Chapter 5, and baseline discrimination of pointing gesture, Chapter 3, is an asymmetry in directional judgments of these social stimuli. When asked to judge the direction social stimuli are facing, a number of studies revealed a slight leftward spatial bias reported for discrimination of the direction of eye gaze (Jenkins et al., 2006) and head orientation (Lawson & Calder, 2015; Lawson et al., 2011).

Do these asymmetries reflect the same process? For the perception of hand pointing direction, while participants demonstrate a typical spatial bias on a pseudoneglect task, this was not correlated with the thresholds for discerning where someone was pointing in space. For the pointing response bias (Chapter 5), it is more likely the hand and arm moving across the pointer’s body into the observer’s right space that draws their attention further into right space. This likely precipitates a mislocation of the point more to the right of the centre target object than it actually is, thus shifting the point of subjective equality leftwards. However, this does not explain the
bias seen at centre space, where a right bias persisted even when using the left hand, a hand the does not cross the body midline of the pointer. Conty et al. (2012) report a dissociation between self-directed gaze and pointing cues and averted gaze and pointing cues and propose that this may be indicative of a right hemisphere dominance for processing the actions of others (Decety & Chaminade, 2003; Jackson et al., 2006).

Further questions regarding spatial asymmetry in the perception of social directional cues include: Does the response bias asymmetry reported in this thesis and in other studies mentioned above reflect an attentional bias? If so, is this bias a space-based bias or an object-based bias? Is the cue type driving the bias? Alternatively, is a general attention orienting mechanism responsible such as that for pseudoneglect? Is this related to hemispheric asymmetry found when shifting attention to social stimuli compared to non-social stimuli (Greene et al., 2009; Greene & Zaidel, 2011)?

6.5 Conclusions

The research conducted as part of this thesis employed behavioural and psychophysical measures to examine visual representation and visual acuity of specific social directional cues, and the potency of these cues to direct spatial shifts of attention. Results show that the perceptual information regarding the direction of head and body orientation is integrated in a unidirectional manner, which supports hierarchical processing of these two cues, such that perception of head orientation influences our perception of body orientation but the reverse does not. Unlike eye gaze direction and head orientation, averted body direction seems to have little effect on the
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observer’s spatial attention. The main conclusion to be drawn from the present work is that visual representation of cue specific directional information from cues further down the proposed hierarchy of social attention is represented at a high-level in the visual system, while directional judgments, particularly to pointing direction, are likely moderated by a number of low-level geometric cues. From this, pointing perception should be considered more systematically, both in the broader context of covariance between specific social features of stimuli and cortical function, and in dedicated psychophysical experiments to further disambiguate the precise visual components of pointing perception.
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Appendices

Appendix A
Experimental Protocol Cross Adaptation

Baseline discrimination of head orientation top panel and cross adaptation to body orientation procedure (bottom panel) used in Chapter 2, experiment 2.
Appendix B

Schematic of Eye Gaze Cueing Protocol

Protocol of eye gaze cueing experiment Chapter 4. Fixation appeared centrally for 675ms, followed by the pre cue stimulus for 900ms. The eye gaze cue was presented for either 700ms or 1100ms, until the target appeared either to the left or right of the cue. The cue stimulus and target remained onscreen until the participant responded. The cues were non-predictive, and were presented either looking to the left or right with equal probability.
The psychometric functions were fit using quickpsy in R, a package that estimates parameters using a maximum likelihood procedure. Thresholds are estimated at the 0.5 probability point on the psychometric functions.

In the legend, LS = left space, C = centre, RS = right space, LH = left hand, and RH = right hand.
Appendix D

Psychometric Fit of One Participant Experiment 2 Chapter 5

The pointer pointed with right hand only at two regions Centre Space and Right space over four conditions. In the legend CS = Centre Space, RS = right space. The psychometric functions were fit using quickpsy in R, a package which estimates parameters using a maximum likelihood procedure. Thresholds are estimated at the 0.5 probability point on the psychometric functions. Degrees in visual angle are shown on the x-axis.