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From vision to touch : the cortical and behavioural effects of viewing others in pain

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From vision to touch:
The cortical and behavioural effects of viewing others in pain

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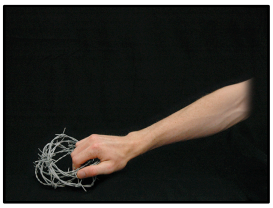

And, to my helping hand, with love.

Contents

Thesis Summary

The observation and experience of actions, emotions, touch, and pain activates overlapping cortical regions. However, the aetiology and function of these so-called "mirrored" representations is unclear. By focusing on the effects of viewing others in pain, this thesis extends our understanding of both the underlying mechanisms and behavioural consequences of vicarious cortical activity.

We used multi-voxel pattern analysis to explore whether the type of viewed pain, for example stinging or stabbing pain, was represented by the observer. Our findings demonstrate that only the general experience of pain, rather than the precise sensory consequences of an action, can be accurately identified in regions outside of visual cortex.

We predicted that viewing others in pain goes beyond cortical representation, to selective behaviour change in the observer. In a series of experiments, participants viewed a hand either grasp, or avoid, objects that were potentially painful or not painful, whilst detecting tactile stimulation delivered to their right index finger. Participants were faster and more biased to report touch on their own body when viewing someone else in pain. Two further control experiments demonstrated that the "painful grasp effect" was both sensory specific, and could not be explained by attentional effects. These data suggest that shared representations of pain enable the prediction of the sensory consequences of a painful grasp, leading to potentially adaptive behaviour change in the observer.

Interestingly, the effects of viewing others in pain are not automatic, but are mediated by tasks demands and relevance of the stimuli to self. Only when participants made judgements about the appropriateness of an action (engaging self referential thought), or viewed the actions from a first person perspective, was the "painful grasp effect" revealed. In contrast to understanding the actions of others, our data support a system that utilises one's own motor repertoire to represent actions similar to, or relevant to, self.

Chapter 1

Shared representations of pain

1.1 Summary

Research has revealed that viewing someone else in pain activates brain regions which are similar to those recruited during the first-hand experience of pain. This chapter explores the possible underlying mechanisms that give rise to these shared cortical representations, focusing on the prominent account of an evolved system to understand the actions of others, and an alternative account which posits that mirror neurons are a result of associative learning.

The literature investigating shared representations of pain is reviewed. We highlight methodological differences that might account for disparate findings: for example, differences in cortical activation between experienced and observed pain may, in part, be due to the different pain stimuli (such as heat pain and pricking pain) used in each condition. Similarly, the inconsistent activation of both sensory and affective pain processing regions may be a consequence of task demands.

Activation of somatosensory processing regions during the observation of others in pain raises the question of whether an observer's tactile perception is modified during pain perception. We review the evidence that vision of bodies and touch does indeed alter tactile processing, but a lack of relevant research leaves the effects of viewing others in pain on touch unknown. However, the literature investigating the direct experience of pain on tactile processing is suggestive that observing pain may alter the tactile processing of the observer.

The aims and structure of the thesis are outlined, namely to further our understanding of the cortical and behavioural effects of viewing others in pain. For the first time, we investigate whether the type of pain being viewed is encoded by the observer, and whether viewing someone else in pain modifies an observer's ability to detect touch. The research not only generates novel findings, but also clarifies the effects of potential methodological confounds in the literature. Our research is discussed in relation to the underlying mechanisms that most parsimoniously account for our data.

1.2 Introduction

Observing the world around us provides us with a rich source of information that goes beyond vision alone. When we view someone grasp an apple, not only do we perceive the actor's hand and the colour of the apple, but also, the muscles in our own arm become active, as if we were performing the action ourselves. A seminal study by Di Pellegrino, Fadiga, Fogassi, Gallese, and Rizzolatti (1992) provided the seemingly unequivocal evidence, that perception and action are intimately linked at the cortical level. The authors reported single cell recordings in the macaque brain that responded to both the observation and performance of goal-directed actions, so-called "mirror neurons" (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). Following this discovery in non-human primates, numerous studies have provided indirect evidence that such a system exists in humans: viewing others perform actions (Buccino et al., 2001), display emotions (Wicker et al., 2003), and encounter touch (Keysers et al., 2004) and pain (Bufalari, Aprile, Avenanti, Di Russo, & Aglioti, 2007; Singer et al., 2004) elicits activation of cortical regions that are similarly recruited when we experience these phenomena first-hand. However, despite the abundance of studies reporting such effects, the underlying mechanisms and functional role of these shared representations remains unclear.

There are many theories purporting the aetiology of mirror neurons, however one view remains prominent: mirror neurons evolved to understand the actions and intentions of others. However, other authors suggest mirror neurons develop throughout the life of an organism as a result of learnt associations between experience and observation[1.1]. Mirror neurons are believed to be a consequence of these associations, rather than an innate mechanism with a role in inferring the mental states of others (Heyes, 2010; Keysers & Perrett, 2004). It may seem trivial to want to distinguish between these theories - if both acknowledge that mirror neurons exist, why does it matter how they come into existence? - but each theory makes different predictions, albeit sometimes subtle, about how such a system will function, and how dysfunction might affect an individual (see Chapter 6). Important to note is that many authors now use the phrase "mirror neurons" or "mirror systems" to explain their effects without stating to which underlying mechanism they ascribe. This has led to mirror neurons and mirror systems describing data without the mechanism

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[1.1] I acknowledge that there are a plethora of mirror neuron theories, creating a continuum from an innate to learnt mechanisms, the boundaries of which are sometimes blurred. However, a complete discussion of mirror neuron theories is beyond the scope of this thesis. I have selected the most dichotomous mirror neuron theories to more clearly distinguish between the alternative predictions that each makes about behaviour.

itself being explained (Uithol, Haselager, & Bekkering, 2008). How is it that mirror neurons enable the understanding of others' actions and intentions?

1.3 Shared representations: Innate or acquired?

1.3.1 Mirror neurons: An evolved system

Evolved theories of mirror neuron function suggest that perception and action share a common code (Iacoboni, 2009). Rather than unimodal neurons becoming bi-modal as a consequence of associative learning (Heyes, 2001, 2010), evolved accounts suggest mirror neurons are present from birth (Gallese, Gernsbacher, Heyes, Hickok, & Iacoboni, 2011). Mirror neurons are said to be of "great evolutionary importance" (Rizzolatti & Craighero, 2004), enabling the understanding of others' actions and intentions. The "direct-matching hypothesis" states that a viewed goal-directed action is understood because the same mirror neurons fire as if the action were being performed by the observer (Rizzolatti, Fogassi, & Gallese, 2001). The direct-matching of viewed actions is thought to be automatic (Rizzolatti & Craighero, 2004), and therefore resistant to top-down modulation (Iacoboni et al., 2005).

Umiltà et al. (2001) provided evidence suggesting that it is not only the action, but also the goal that is represented during observation. Single cell recording in the macaque monkey demonstrated that mirror neurons continue to fire even when the grasping component of an action is hidden from view, behind an occluder. Crucially, this mirror activity does not occur with pantomimed actions. For example, when the experimenter performs an identical reaching action, but there is no object behind the occluder. Iacoboni et al. (2005) extended these findings further from goal representation to the inference of intentions.

Human participants viewed video clips pertaining to different contexts, actions and intentions (Iacoboni et al., 2005). In the crucial intentions condition, participants viewed a hand grasping a cup, but the cup either contained a drink and was surrounded by items ready for a meal, or the cup was empty, and surrounded by what looked like the remnants of a meal. As such, the goal of the action in both conditions was to grasp the cup, but the intention was either to drink or to wash up. Iacoboni et al. (2005) report differential activation in the inferior frontal region, analogous to area F5, the region where mirror neurons were originally identified by Di Pelligrino et al. (1992), when participants viewed the slide where the intention was to drink, compared to actions where the intention was to clear away[1.2].

Since the discovery of mirror neurons, their potential functional role has continually expanded, encompassing imitation (Iacoboni, 2009), language (Rizzolatti & Craighero, 2004) and other higher level social constructs. For example, Iacoboni states mirror neurons are the "prerequisite for experiencing empathy" (Gallese et al., 2011, p. 395). Indeed, mirror neuron activation has been shown to correlate with empathic concern (Kaplan & Iacoboni, 2006; Singer et al., 2004). Given that mirror neurons are said to "represent the specific mental states of others" (Gallese & Goldman, 1998, p. 495), it is perhaps not surprising that disorders typified by an apparent deficit in understanding others, such as autism (Dapretto et al., 2006) and psychopathy (Fectaeu, Pascual-Leone, & Théoret, 2008), have, in part, been attributed to mirror neuron dysfunction.

However, although mirror neurons have been credited with explaining a range of psychological functions, the precise manner in which motor resonance achieves these is not known. The consistent failure of proponents of evolved mirror neuron function to explain how the cells can perform such wide-ranging roles has led to fundamental criticisms of the theory (Dinstein, Thomas, Behrmann, & Heeger, 2008; Gallese et al., 2011; Heyes, 2010).

1.3.2 Mirror neurons: Alternative accounts

Critics of evolved theories of mirror neuron function do not believe mirror neurons are necessary for action understanding, mindreading, inference of intentions, or provide the biological basis of empathy (Csibra, 2007; Heyes, 2001, 2010; Hickok & Hauser, 2010). Indeed, Hickok (2009) states there is no evidence that shared representations have a role in understanding actions, emphasising that actions outside an animal's motor repertoire are understood and that regions beyond those endowed with mirror neurons play a more critical role in action understanding. Instead, mirror neurons are said to be a by-product of associative learning (Heyes, 2010). As such, these alternative accounts do not posit that mirror cells are specialised for, or unique to, higher beings, but rather, that they would be found in lower organisms too. Indeed, mirror neurons have been discovered through single cell recordings in swamp sparrows (Prather, Peter, Nowicki, & Mooney, 2008).

Associations, and subsequently mirror neurons, are ostensibly created when observation

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[1.2] Note however, that the alternative comparison (wash-up > drink) did not reveal activation in the inferior frontal region. As such, these results again demonstrate the importance of goals, but not intentions. The finding that a cup containing a liquid to drink activates shared representations is similar to the animal research, which suggested that mirrored activity only occurs when food is involved (Gallese et al., 1996) ie. when the goal is relevant to the observer.

and performance of events are temporally congruent and predictive of each other (Heyes, 2010). Importantly, these associations can be made when viewing one's own actions being performed, or during the observation of others performing actions. For example, facial expressions are not frequently viewed directly, however, caregivers and other conspecifics will often imitate such expressions simultaneously with the actor (Heyes, 2010; Ray & Heyes, 2011). The notion that pairings of perception and action through the life history of an organism develops mirror neurons, leads to specific predictions about how such a system functions and could be modified. For example, an interesting prediction based on an associative account of mirror neuron function would be that the system crucially relied on vision and action occurring in synchrony, whereas an innate common code for action and observation would predict the system could be modified through vision or performance of actions alone (Heyes, 2010). By learning incongruent pairings between vision and action, "counter-mirror" activations should be possible, for example viewing a hand movement could evoke cortical activity previously associated with performing an action with the foot (Heyes, 2010). Important to note is that an evolved system to understand the actions of others would not accommodate such a prediction.

To test the counter-mirror prediction, Catmur, Walsh, and Heyes (2007) asked participants to view clips of a hand make an index finger or little finger movement whilst performing either congruent or incongruent actions. Participants in the congruent condition imitated the actions as they were seen on screen, whereas participants in the incongruent condition were instructed to make the opposite movement to the visual stimulus, such that when they viewed a little finger movement, the participant made an index finger movement. After a period of training, motor evoked potentials (MEPs) were recorded from the participants' index finger and little finger whilst they merely observed the actions. The participants who had previously performed congruent actions evoked congruent MEPs, whereas the group trained to make incongruent actions actually evoked muscle activity in the limb they would move, not the limb they viewed. These data suggest that mirror activation is not due to direct matching of the observed action, but rather sensorimotor learning. In stark contrast to understanding the actions of others, these effects provide evidence that visual perception evokes motor responses relevant to self, not what is being observed.

Although we provide only a brief summary of the direct-matching and associative accounts of mirror neuron function in the above section, we will return to each throughout the thesis. By reviewing the available literature and investigating the cortical and behavioural effects of shared representations, we hope to provide evidence to help differentiate between the two accounts. More specifically, we will investigate the effects of shared representations of pain on cortical activity and behaviour.

1.4 The cortical effects of viewing others in pain

Research examining the effects of viewing others in pain provides a unique opportunity to investigate, in unison, the proposed action, emotion, tactile, and noxious mirror systems. Understanding another person in pain involves interpretation of the action that has been performed, the affective state of the individual experiencing pain, and the sensation that the person may be feeling. Importantly, cortical areas commonly activated during the experience and observation of pain do involve motor processing regions including the cerebellum, sensory processing regions including the secondary somatosensory cortex (SII) and less consistently, primary somatosensory cortex (SI), as well as affective processing regions, including the anterior insula (AI), midcingulate cortex (MCC), and anterior cingulate cortex (ACC; Keysers, Kaas, & Gazzola, 2010; Lamm, Decety, & Singer, 2011).

Although overlapping cortical activity during the observation and experience of pain is suggestive of shared representations of pain, evidence of "mirror neuron" activity in humans is indirect. The majority of techniques used to investigate mirrored activity in humans lack the spatial resolution which single cell recordings provided during action observation in monkeys (see however, Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010). It is therefore possible that a separate and unique set of neurons respond to the observation of pain, and these do not overlap with the experience of pain. If this were the case, these separate populations could not be distinguished from each other using standard functional magnetic resonance imaging (fMRI), and electroencephalography (EEG) analysis techniques (Dinstein, Thomas, Behrmann, & Heeger, 2008). More direct evidence for the existence of mirror neurons in humans is therefore necessary, yet single-cell recording remains impractical. However, recent advances in neuroimaging analysis techniques, such as repetition suppression and multi-voxel pattern analysis (MVPA), have begun to provide evidence that overlapping cortical activity may indeed be the product of mirror neurons (Haxby et al., 2001; Kilner, Neal, Weiskopf, Friston, & Frith, 2009).

Standard fMRI univariate analysis techniques examine differences and similarities in cortical activity in a cluster of voxels between experimental conditions. However, a limitation of this analysis technique with regards to mirror neuron activity is that, even if the magnitude or location of a cluster of cortical activity is the same in different conditions, the underlying pattern of neuronal activity may differ. In contrast, MVPA enables a finer-grained analysis of the data by exploring the pattern of activity amongst individual voxels in response to different stimuli (Mur, Bandettini, & Kriegeskorte, 2009), improving both the sensitivity and spatial resolution of fMRI data analysis (Norman, Polyn, Detre, & Haxby, 2006; see Chapter 2).

The first, and to our knowledge, only study to investigate shared representations of pain using MVPA was carried out by Corradi-Dell'Acqua, Hofstetter, and Vuilleumier (2011). Female participants experienced painful and non-painful heat stimulation delivered to their right hand whilst being scanned. In a separate session, participants viewed images of hands in painful and non-painful situations. Participants were instructed to indicate whether the hand they saw in the picture was a left or a right hand. The results of the MVPA analysis reveal patterns of activity corresponding to the affective aspects of pain in the insula and middle cingulate cortex. However, there was no evidence for shared representations in somatosensory processing regions, such as SI or SII. Their findings replicate those of a seminal study by Singer et al. (2004), where female participants were scanned whilst viewing painful and non-painful electrical stimulation delivered to their own hand, or their partners' hand. With the application of univariate analyses only, Singer et al. (2004) also revealed shared activity in emotional pain processing regions and not cortical regions involved in processing the sensory aspects of pain.

The findings of Corradi-Dell'Acqua et al. (2011), alongside those of Singer et al. (2004), suggest mirrored activation only occurs for affect, and not somatosensation, during observation of another person's pain. The potential significance of such findings utilising MVPA could raise doubt about previously reported sensory activation during pain perception in studies only utilising univariate analysis techniques. However, this interpretation of the Corradi-Dell'Acqua et al. (2011) data may be inaccurate. A fundamental weakness in the study is that the type of pain stimulus differs between the experienced and observed pain conditions. Therefore, a lack of sensorimotor resonance may be due to different types of pain being encoded in somatosensory processing regions during the experience and observation of pain. Indeed, many studies have not engaged with the possibility that the type of pain may also be represented during pain observation. As such, many authors collapse across different types of pain during viewing (Jackson, Meltzoff, & Decety, 2005; Morrison, Peelen, & Downing, 2007; Vachon-Pressau et al., 2012), and use incongruent pain stimuli during the experience and observation of pain (Vachon-Pressau et al. 2012; Zaki, Ochsner, Hanelin, Wager, & Mackey, 2007).

A further limitation of the Corradi-Dell'Acqua et al. (2011) study is that participants experienced pain on their right hand, but viewed pain in left and right hands, from both egocentric and allocentric perspectives. Although the boundary conditions surrounding shared representations of pain are poorly understood, we propose that viewpoint in particular may be an important mediating factor. Therefore, the role of somatosensory mirrored activity during the observation of others in pain cannot be ruled out by the findings of Corradi-Dell'Acqua et al (2011).

Important to note is that disparate findings in the literature are not necessarily due to confounds in a particular study, but may be resolved by contrasting the different methodological approaches. For example, the involvement of somatosensory regions during the observation of others in pain may be mediated by task demands. In the study by Singer et al. (2004), participants were asked to passively view an abstract cue whilst experiencing pain, or knowing their partner was in pain. In contrast, in a study by Bufalari et al. (2007), somatosensory cortical involvement during the observation of others in pain was revealed. Participants viewed videos of a hand being penetrated by a syringe or touched by a cotton-wool bud whilst receiving electrical stimulation on their own wrist, and answered questions about the stimuli after every experimental block (63 seconds). The questions included the number of cotton wool buds or needles shown, the gender of the hands, and whether the participants were able to ignore the electric stimulation delivered to their wrist in the previous block. In order to answer these questions, attention must be drawn to the distinction between pain evoking and non-painful objects, there must be careful consideration of the physical properties of the hand, and perhaps inadvertently, awareness brought towards the tactile sensation on the participant's own body. Indeed, the EEG recordings of the somatosensory evoked potentials (SEPs) elicited by the tactile stimulation at the wrist differed in the pain and non-pain condition. During the observation of others in pain, the amplitude of the P45 component, analogous to SI, exhibited greater amplitude than viewing non-painful hand-object interactions.

Interestingly, evidence that somatosensory and affective processing during the observation of others in pain may be dependent on task demands, suggests that the vicarious activations are not automatic. Establishing the boundary conditions under which shared representations do occur will enable better understanding of the functional role vicarious activations may have. In turn, this will provide more information to help distinguish between the two alternative accounts of mirror neuron function.

Another factor mediating the extent of shared representations of pain may be the visual stimuli which are used. Singer et al. (2004) used an abstract cue to signify when pain would occur to the participant or their partner. Although the participant could see their own and their partner's hand, the painful stimulus was delivered by an electrode which meant the onset and delivery of the painful stimulus could not be seen. In contrast, Bufalari et al. (2007) showed videos of a cotton wool bud approaching and touching the hand, or a needle puncturing the skin on the hand. The suggestion from these findings is that knowledge of a pain evoking stimulus and vision of the hand is not sufficient to evoke somatosensory co-activation, but vision of a hand penetrated by a needle is. However, the individual contribution of action understanding, object knowledge and the observed painful experience on vicarious activations have not been thoroughly explored. Indeed, several of the studies previously discussed have focused on the broad distinction between pain and no pain conditions (Bufalari et al. 2007; Jackson, Meltzoff, & Decety, 2006). In some cases this means that the reported effects of viewing others in pain may be due to vision of a pain-evoking stimulus, such as the needle compared to the cotton wool bud (Bufalari et al., 2007), rather than the experience of pain per se. Similarly, some studies compare the observation of pain with the observation of a "no-touch" condition (Lamm, Nusbaum, Meltzoff, & Decety, 2007; Jackson, Meltzoff, & Decety, 2005; Vachon-Pressau et al., 2012). The cortical regions involved in processing pain are not uniquely activated by pain perception (i.e., SI and SII are involved in both the direct experience of touch and pain; Coghill et al., 1994), therefore any vicarious activations evoked by viewing others in pain, may be due to contrasting this activation with a no touch condition.

In a recent study by Morrison, Tipper, Fenton-Adams, and Bach (2012), a novel paradigm enabled the action properties, object properties, and hand-object interactions to be investigated independently within the same task. Participants were asked to view hands either grasp, or withdraw from, potentially painful and non-painful objects whilst being scanned. On a trial-by-trial basis, in a delayed response task, participants had to combine action and object information in order to judge whether the hand-object interaction they had just seen was appropriate or inappropriate. For example, a hand grasping a painful object required the response "inappropriate". The imaging data provide an important extension to the previous literature of shared representations of pain, demonstrating that areas within somatosensory cortical processing regions, often attributed to pain processing, are in fact selectively encoding the action, the object painfulness, and the appropriateness of an action. For example, the postcentral gyrus and inferior parietal lobule were more active during the observation of painful compared to non-painful objects, and the observation of grasping actions (touch) versus withdrawals (no touch). Interestingly, two distinct subregions of SI (BA1/3b and BA2) and SII, were preferentially active during the observation of painful actions compared to all other conditions. These data demonstrate that not only the action and object properties are encoded, but also the painful consequence of the action during the observation of others in pain.

Selective recruitment of primary and secondary somatosensory processing regions during the observation of others in pain raises the question as to the functional role of such vicarious activations. Proponents of mirror neuron theory, underlying the understanding of others, propose that shared representations of pain enable humans to empathise with others and promote helping behaviour (Preston & de Waal, 2002). However, vicarious activations of core sensory processing regions may be more self centred, altering the observer’s own ability to respond to touch or pain, in a similar manner as if they themselves were at threat (Avenanti, Bueti, Galati, & Aglioti, 2005). However, evidence of cortical activations alone cannot discriminate between these alternative accounts. Firstly, the reported changes in cortical activity during action observation may not be sufficient to elicit detectable behaviour change. Secondly, changes in cortical activity may reflect inhibitory and not excitatory responses. In order to explore the functional role of shared representations beyond the suggestion of empathy, the effects of observing others in pain on behaviour must be investigated. Yet, despite the large literature of imaging studies supporting vicarious activations during pain observation (for review see Lamm et al., 2011), very little is known about the possible effects these activations have on the observer’s own behaviour. The experiments in this thesis aim to bridge this gap in the literature by directly testing how an observer’s ability to detect touch is mediated by viewing others in pain.

1.5 The effects of vision on touch

Research investigating the behavioural effects of viewing bodies and touch suggest it is not inconceivable that vision of others in pain may also modify our ability to detect tactile stimuli. For example, Tipper et al. (1998) asked participants to make a speeded response to a vibrotactile stimulus delivered to their arm, whilst viewing either their stimulated arm, or their unstimulated arm on a video monitor placed in front of them. Participants’ reaction times to the detection of touch were facilitated when they viewed their stimulated arm, but not when they viewed their unstimulated arm; suggesting a visual enhancement of touch (VET) specific to the limb being stimulated. Interestingly, and in line with sensorimotor learning accounts of shared representations, the effects of viewing body parts on touch were greater for those body parts viewed more often, such as the hand, compared to the back of the neck (Tipper et al., 2001). However, Press, Taylor-Clarke, Kennett, and Haggard (2004) failed to replicate the effect of speeded reaction times to above threshold tactile stimuli during observation of one's own body. Rather, Press et al. (2004) suggest that VET can only be discerned in more difficult tasks involving ambiguous stimuli, such as a two-point discrimination task. The level of stimulation is therefore a consideration when testing tactile processing during the observation of others in pain. However, the increased salience of viewing painful actions, compared to body parts, may negate the need for such sensitive measures.

During a two-point discrimination task, participants judge whether a tap, for example on their forearm, was made by two spatially distinct, or one stimulator. The distance between the stimulators is varied to assess the participant's tactile acuity by measuring their two-point discrimination threshold: the distance at which the tap from two stimulators is perceived as being made by one. Taylor-Clarke, Kennett, and Haggard (2002) combined a two-point discrimination task with recordings of SEPs. Participants viewed their own arm, or an inanimate object, whilst they performed the task. The simultaneous recording of SEPs enabled the association between somatosensory activation and changes in tactile perception to be made. When participants viewed their own arm, their two-point discrimination threshold was lower and ERP components, analogous to SI and SII processing, had greater amplitude than when they viewed the object. Similarly, ERP amplitude related to primary somatosensory activation is greater when viewing others in pain (Bufalari et al., 2007), suggesting pain observation may indeed influence tactile processing.

Fiorio and Haggard (2005) demonstrated a causal role for SI activation in VET. Whilst receiving transcranial magnetic stimulation (TMS) to SI or SII, participants judged the orientation of gratings (parallel ridges and troughs) on the base of a small object touched against their finger. Participants viewed either their own hand or a neutral object, followed by a dark period including TMS, and then performed the grating orientation task (GOT). TMS during the dark period was designed to interfere with any change in tactile processing that may occur after vision, but prior to the touch instant. In line with previously cited research, when no TMS was applied, participants were more accurate at judging the orientation of gratings when they viewed their own hand, compared to the object. However, compared to the no TMS condition, TMS over SI, but not SII, reduced the accuracy of orientation judgements whilst viewing hands, but improved accuracy when viewing objects. The lack of effects of TMS over SII is interesting because this higher level processing region is also affected by attention, often more so than SI (Johansen-Berg & Lloyd, 2000). Consequently, it may have been assumed that SII would be a candidate region for enhancing tactile perception, due to the difference in self-relevance (ergo attention) between viewing one's own hand and an inanimate object (Fiorio & Haggard, 2005), yet the TMS results suggest VET is only mediated by primary somatosensory cortex.

Importantly for the current research, evidence supporting visual enhancement of touch is not restricted to the observation of one's own body. Haggard (2006) demonstrated that similar effects are found when viewing others' bodies. Participants performed the GOT whilst viewing their own hand, an object, or an experimenter's hand. When the participants viewed their own hand or the experimenter's hand, they were more accurate at judging the orientation of the gratings compared to when they viewed the object. Further, viewing other people being touched improves tactile detection (Serino, Pizzoferrato, & Làdavas, 2008). For some people, known as mirror-touch synaesthetes, viewing others being touched actually results in the percept of touch on their own body (Banissy & Ward, 2007). Interestingly, these mirror-touch sensations have been attributed to increased activation of somatosensory processing regions including SI, SII and the anterior insula (AI), compared to normal control subjects (Blakemore, Bristow, Bird, Frith, & Ward, 2005).

Although studies investigating the effects of vision on touch may provide some insight into the possible consequences of viewing others in pain, pain is arguably a distinct sensation from touch (Craig, 2003). For example, Bufalari et al. (2007) demonstrated that although viewing touch decreased ERP amplitudes, analogous to SI activation, observation of pain increased SI activity. Therefore predicting the effects of viewing others in pain on touch may be best guided by research investigating the direct experience of pain.

1.6 The direct experience of pain

The direct experience of noxious stimulation leads to the perception of pain, yet how pain is perceived, and the consequences of pain perception are complex and context dependent (Treede, Kenshalo, Gracely, & Jones, 1999; Wall, 1978). For example, repeated exposure to pain may result in sensitisation to pain, or habituation to pain (Kleinböhl, Trojan, Konrad, & Hölzl, 2006) and the direct experience of pain has been shown to reduce the ability to detect tactile stimulation (Apkarian, Stea, & Bolanowski, 1994), whereas the direct experience of touch is thought to reduce pain perception (Wall, 1978). The anticipation of pain can also lead to seemingly conflicting percepts. For example, Hsieh, Stone-Elander, and Ingvar (1999), demonstrated that anticipation of expected pain resulted in decreased activation of ACC, potentially reducing the unpleasantness of the upcoming stimulation, whereas ACC responses to unpredictable noxious stimuli were increased. Similarly, the adaptive response to the perception of pain may differ when escape from a pain-evoking stimulus is possible, in comparison to a situation where the pain is unavoidable (Petrovic & Ingvar, 2002).

The complex and seemingly dichotomous responses to pain suggest that experimental paradigms and task demands are critical in mediating findings. Important to note also is that the effects of direct experience of pain may differ from those of viewing pain. Although theories supporting shared representations of pain posit overlapping cortical activations, a distinction must be made between representations of directly experienced and observed pain; otherwise viewing pain would evoke the sensation of pain (see however, Bradshaw & Mattingley, 2001).

More directly related to our research, Valeriani et al. (2008) investigated the effects of viewing others in pain whilst the observer was in pain. Participants experienced painful laser stimulation delivered to their hand whilst viewing videos of hands, feet and a tomato being touch by cotton wool buds, or penetrated by needles. Participants were asked to imagine that the hands and feet they viewed were their own. Participants received laser stimulation every time they viewed the action videos, but the onset time of the laser varied between trials. Interestingly, laser evoked potentials (LEPs), analogous to somatosensory processing, were reduced when participants viewed a hand being penetrated by a needle. Note that the reduction in cortical activity when viewing others in pain is opposite to that reported by Bufalari et al. (2007), when participants concurrently received non-painful tactile stimulation. However, in neither study were the effects of viewing others in pain on tactile or pain perception investigated, therefore the consequence of contrasting amplitude change on behaviour remains unknown. Valeriani et al. (2008) did ask participants to rate the intensity and unpleasantness of the laser stimulation, however, this occurred at the end of each experimental block and consequently did not reveal any differences between conditions.

A recent study by Höfle, Hauck, Engel, and Senkowski (2012) provides a more sensitive measure of the effects of viewing pain on one’s own somatosensory perception. Important to note is that the viewed hand was incorporated into the participant’s own body schema by requiring the participant to place their own hand directly beneath a screen displaying the visual display of the hand, therefore potentially limiting the findings to understanding pain in self, not others. In contrast to the studies by Bufalari et al. (2007) and Valeriani et al. (2008), participants experienced both painful and non-painful stimulation, reporting the intensity and unpleasantness of the stimulation on a trial-by-trial basis, whilst viewing a hand being penetrated by the needle, or touched by the cotton wool bud. Alongside the subjective ratings, participants' pupil dilation was also recorded using an eye tracker. Unsurprisingly, participants rated the direct experience of pain to be more unpleasant and more intense than the experience of touch. Ratings of the unpleasantness and intensity of electrical stimulation were also higher when participants viewed needles penetrating hands compared to cotton wool buds. Pupil dilation followed the same distribution, with greater dilation during the experience of pain and the observation of needles penetrating skin. The highest intensity rating was given when the hand penetrated by the needle, was combined with the experience of the painful electrical stimulation. These data appear to suggest that viewing pain increases the intensity of one's own pain perception. However, it is possible that the intensity ratings of own pain and viewed pain were combined; although participants were instructed to rate only the intensity on their own body, it is possible they took account of the intensity of the pain in the visual image on-screen. Ratings of perceived pain intensity are by definition subjective, and an objective measure would be needed to make a claim about the actual effect of viewing pain on tactile perception. Consequently, the behavioural effects of viewing others in pain remain poorly understood.

1.7 Conclusions

Converging evidence has demonstrated that somatosensory and affective cortical regions are activated when we view someone else in pain (Lamm et al., 2011), yet surprisingly little is known about the functional role of such vicarious representations. Although opposing mechanisms have been suggested to underlie the cortical responses of viewing others in pain, including the direct-matching hypothesis (Rizzolatti et al., 2001) and the associative learning account (Heyes, 2001; 2010), the current evidence does not allow for a distinction to be made between the two. The aim of this thesis is therefore to further our understanding of the effects of observing others in pain on behaviour, focusing in particular on tactile perception. By testing the boundary conditions within which shared representations of pain occur, we hope to provide evidence that can help to elucidate the mechanism underlying such effects.

This thesis contains four experimental chapters. The literature directly relevant to the experiments will be reviewed at the beginning of each chapter. Chapter 2 utilises fMRI and MVPA to explore the specificity of shared representations of pain, directly comparing the cortical processing of pricking and stinging pain. Chapter 3 provides the first objective measures of sensory specific behaviour change caused by viewing others in pain. The boundary conditions for such behavioural change are explored further in Chapters 4 and 5. Chapter 4 investigates whether the effects of viewing others in pain on behaviour are automatic or mediated by task demands. Chapter 5 clarifies the role of viewing perspective on shared representations of pain, controlling for the visual confounds previously seen in the literature. In the final chapter, the experimental findings are discussed in relation to a specialist system designed to understand the actions of others, and the associative learning account of shared representations of pain.

Chapter 2

Exploring the specificity of vicarious cortical representations of pain

2.1 Summary

Overlapping cortical regions are involved in the direct experience and observation of pain. However, it is not known whether the type of viewed pain is encoded by the observer. In an fMRI study, participants viewed two frame sequences of hands grasping potentially painful (holly & nettle) and non-painful (ivy & balsam) plants. Critically, grasping the painful plants would evoke two distinct sensations: holly, a pricking pain, and nettle, a stinging pain.

Standard univariate analysis techniques were used to identify regions in the brain that were differentially active during the observation of painful and non-painful actions, and responded differently to the observation of pricking and stinging pain. We also utilised multi-voxel pattern analysis to explore the representational content of evoked cortical responses. Using a whole-brain searchlight approach we were able to identify patterns of activity that accurately represented the painfulness of an observed action, but not the specific type of pain experienced by the actor.

The experiment is an initial attempt at addressing the question of specificity in shared representation of pain, and our results provide the first evidence that the sensory aspects of observed pain can be accurately decoded using MVPA. Further research will need to be carried out to assess the efficacy of our findings.

2.2 Introduction

Viewing others in pain activates regions of the cortex that are similarly involved in processing the direct experience of pain (Lamm, et al., 2011). Such vicarious activations have been related to mirror neuron theories, which state that the same neurons are active during both the observation and performance of actions (Rizzolatti et al., 2001). The purpose of this bimodal activity is ostensibly to enable the understanding of others' actions and emotions (Iacoboni & Dapretto, 2006). Although brain imaging data analysed with standard univariate techniques has provided a burgeoning literature in support of these claims (Lamm et al., 2011), the efficacy of the interpretation of these data can be challenged (Dinstein et al., 2008).

Functional imaging data is credited with high spatial resolution, yet even a 1mm^3 voxel contains thousands of individual neurons. Consequently, significant activation in a spatially smoothed cluster of voxels, during both the observation and performance of an action, may not reflect activity in the same neuronal population, but rather spatially distinct neurons (Kriegeskorte, Goebel, & Bandetti, 2006). Further, univariate analyses depend on differences in magnitude of evoked cortical responses, which means that if a region is equally activated by two different conditions, the assumption is often that they are processed equivalently in that region, and hence not discriminated. Again, it may be the case that although the degree of activation is the same, the pattern of neuronal activation within the regions differs (Mur et al., 2009).

Recent advances in neuroimaging analysis techniques, such as multi-voxel pattern analysis (MVPA), have provided the opportunity to extract more detailed information from functional imaging data. Rather than taking the average activation within a cluster of voxels, MVPA reveals the pattern of activity across voxels in response to a certain condition (Mur et al., 2009). In a seminal study by Haxby et al. (2001), the authors demonstrated that patterns of voxel-based activity within ventral temporal cortex could discriminate different categories of object. The activation evoked by viewing a particular category, such as houses, in the first and second half of the experiment was correlated within this category, and between different categories of objects (such as shoes, cats and faces). The correlations both within and between categories were then compared, and an identification accuracy score was calculated. If the within-category correlations between the separate halves of the experiment were greater than the between category correlations, the pattern of activity was deemed to represent information specific to that particular category of object (For a more detailed explanation see section 2.3.1 Searchlight Analysis). Thus, in a region of visual cortex typically attributed to representing different categories of object in similar or overlapping cortical activations, distinct patterns of activity for each category were revealed.

To our knowledge, there is only one study that has investigated shared representations of pain using MVPA. Corradi-Dell'Acqua et al. (2011) investigated the activation associated with directly experienced thermal pain and cortical activity evoked when viewing others in pain. The authors utilised univaritate and multi-variate analysis techniques to explore their data. As expected, the univariate analysis revealed cortical activity common to both the direct experience and observation of pain, including postcentral gyrus, anterior insula, and midcingulate cortex. However, MVPA only revealed similar representations of felt and seen pain in the middle and anterior insula, and middle cingulate cortex.

The accurate decoding of pain via MVPA in affective processing regions, and not sensory processing regions, fuels a discrepancy in the literature to the extent of shared representations of pain. For example, Morrison, Peelen et al. (2007), and Singer et al. (2004), alongside Corradi-Dell'Acqua et al. (2011), provide evidence of cingulate cortex activity during the observation of others in pain, suggesting only the emotional aspects of pain are encoded by the observer. In contrast, Morrison et al. (2012), Bufalari et al. (2007), and Lamm et al. (2007) highlight somatosensory activity, and hence sensory encoding, during the observation of others in pain. As the study by Corradi-Dell'Acqua et al. (2011) is the only experiment to have utilised MVPA, it may be considered that although the aforementioned studies do show sensory regions are active during the observation of others in pain, these may be distinct from the neuronal activity associated with the direct experience of pain. However, we propose two alternative explanations, not mutually exclusive, that may account for the lack of shared somatossensory representations of pain in the study by Corradi-Dell'Acqua et al (2011).

Firstly, during the observation task, participants judged whether the hand they had viewed was a left or a right hand. This judgement task did not require the physical aspects of the visual scene to be processed, and, as such, the sensory consequences of the observed image were task-irrelevant. Although the more general affective aspects of the scene may be automatically encoded by the observer, the specific sensory aspects of pain may require directed attention (This specific issue is engaged with in Chapter 4 of this thesis). For example, when participants merely judge whether there is contact made between an object and a limb, somatosensory regions are not significantly activated (Morrison, Peelen, et al., 2007). In contrast, when participants judge the intensity and painfulness of an observed action the sensory aspects of pain are encoded (Bufalari et al., 2007). Further, the images used by Corradi-Dell'Acqua et al. (2011) contain stimuli of others from both a first person perspective and third person perspective. Although evolved mirror neuron theories suggest shared representations of pain enable the understanding of others' actions (Lamm et al., 2011), perhaps with a preference for the more typical "other" viewpoint, alternative hypotheses suggest that vicarious activity arises predominantly as a consequence of viewing one's own actions from an egocentric perspective (Heyes, 2010). If either of these hypotheses is correct, both suggest that shared representations of pain may not be equivalent in the first person and third person viewing perspective (see Chapter 5). Consequently, a failure to reveal discrimination of shared representations of pain in somatosensory regions may be due to a loss of power caused by collapsing across viewpoint.

The second alternative explanation for no accurate discrimination of pain in tactile processing regions pertains to the difference between the experienced and observed painful stimuli. Participants experienced thermal pain, but viewed stabbing pain, cuts and abrasions. Yet these various types of pain evoke distinct first-hand sensory experiences. If indeed shared representations of pain activate the same neurons that are active during the experience of pain, then it must also be possible that different types of pain are represented at the cortical level in the observer. This would then also explain why the sensory aspects of felt and seen pain failed to be revealed in the study by Corradi-Dell'Acqua et al. (2011). Surprisingly, this issue has not been engaged with in the literature. Indeed many studies investigating shared representations of pain collapse across different types of pain. For example, Jackson et al. (2005) showed participants images containing thermal, compression and cutting pain, and Morrison, Peelen et al. (2007) collapsed their data across pricking, cutting and hammering pain. Similar to the study by Corradi-Dell'Acqua et al., Zaki et al. (2007), and Vachon-Pressau et al. (2012) administered thermal pain to their participants, but participants then viewed videos of legs being broken or a person hit by a train, or images of cutting and compression pain, respectively. Each of these studies highlights the similarities and differences between felt and seen pain, yet some of these differences might be explained by the discrepancy between the type of experienced and observed pain.

Indeed, it has recently been suggested that distinct representations of observed touch are encoded in somatosensory processing regions (Meyer, Kaplan, Essex, Damasio, & Damasio, 2011). Participants viewed five-second videos of pairs of hands haptically exploring a set of keys, a tennis ball, a light bulb, a ball of wool, and the leaves of a plant

(Meyer et al., 2011). On average, across all two-way discriminations, the different textured objects were decoded above chance in the postcentral gyrus region of interest. However, identification accuracy for the discrimination of tennis ball and light bulb in this region was not significant. Although the texture of the tennis ball and light bulb are significantly different, the shape of these objects is similar. Critically, this suggests that accurate decoding of so-called observation of touch in postcentral gyrus may actually be driven, to some extent, by the observed manual actions, rather than tactile information per se. Thus, proprioceptive information, known to be processed in primary somatosensory cortex (Keysers et al., 2010), may provide an alternative explanation for these findings.

The current study was designed to address two questions: i) Can shared representations of pain be accurately decoded in somatosensory processing regions during the observation of others in pain? and, ii) Is the type of pain experienced by the actor encoded by the observer? To this end, participants viewed two-frame sequences of a hand approaching and grasping potentially painful (holly & nettle) and non-painful (balsam & ivy) plants. Critically, the pain evoked by touching the painful plants differed; grasping holly would cause a pricking or stabbing pain, whereas nettles would cause a burning or stinging pain. Unlike the videos used by Meyer et al. (2011), we chose highly controlled two-frame static images to reduce the possibility that classification accuracy could be based on activity unrelated to the somatosensory properties within the visual stimuli. All the objects were from the same semantic class (leaves) and the viewed grasps were very similar, hence feedback from motor outputs and feed-forward from object recognition processes were less likely to bias somatosensory representations. To ensure participants engaged with the sensory aspects of the scene, on occasional catch trials participants were required to judge the appropriateness of the viewed action. To make this judgement, participants had to engage with the performed action and the viewed plant, combining the two to predict the sensory consequences of an observed action. For example, a hand grasping a nettle required a button press response corresponding to “inappropriate”. Data were analysed using standard whole-brain and region of interest univariate techniques, and searchlight MVPA.

2.3 Experiment 1. The effects of viewing different types of pain on cortical activity

2.3.1 Methods

Participants

All participants (n = 14) were female, aged 18 years of over (*M* = 24.8, *SD* = 1.9), were right-handed, and had normal or corrected-to-normal vision. Only female participants were recruited because, in general, females have a smaller head size than males, which enabled whole-brain MRI coverage. Further, mirrored cortical activation has been suggested to be greater in females than males (Schulte-Rüther, Markowitsch, Shah, Fink, & Piefke, 2008), thus increasing the power of the experimental design. All participants fulfilled the requirements of the Bangor Imaging Unit safety screening procedure and provided written informed consent to participate in the study. All participants had reported previously touching stinging nettles and holly. The experimental procedures were approved by the Bangor University, School of Psychology Ethics Committee. Participants received £40 for their time.

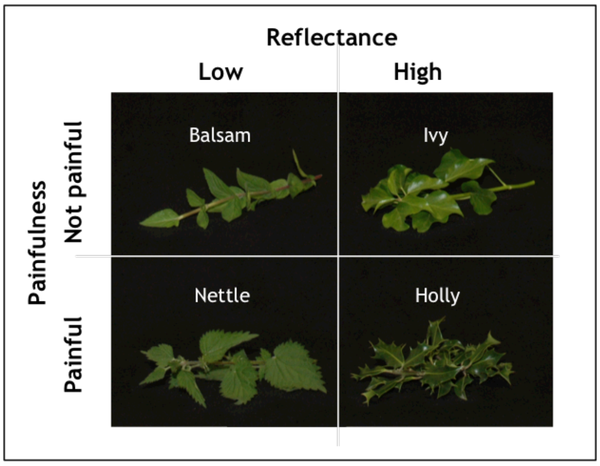

Figure 2.1 Experimental stimuli creating a 2 x 2 design of painfulness (painful/ not painful) by reflectance (low/ high).

Stimuli

Participants viewed two-frame images of a hand approaching and grasping two potentially painful (nettle/ holly) and two non-painful plants (balsam/ ivy; see Figure 2.1 & 2.2). Critically, the sensation evoked by grasping the two painful plants would differ. Holly causes a pricking or stabbing pain, whereas nettles cause a burning or stinging pain. Four exemplars of each plant were used in the experiment. During catch trials, participants viewed the hand grasp and miss the plants (see Figure 2.2).

Design and Procedure

Session 1: Training and Localiser Participants completed two behavioural tasks outside of the scanner and a localiser task inside the scanner.

Task 1: This task was designed to familiarise participants with the plant stimuli and confirm they could accurately identify each plant on the computer screen. On each trial, participants viewed a hand in a neutral position next to a plant (see Figure 2.3a, third frame). Following the presentation of this image, participants were asked to decide whether they had seen balsam, nettle, ivy or holly, by making a self-paced keyboard button press response, using the numbers 1 to 4 respectively. Participants received feedback on every trial. There were 48 trials in total. For the first 16 trials the image of the hand and plant was displayed for 1500ms. However, on the subsequent 32 trials, the image was displayed for 750ms to accurately represent the timings within the scanning session. An experimenter observed the participant make their responses. All participants could accurately name each of the plants by the end of the training session.

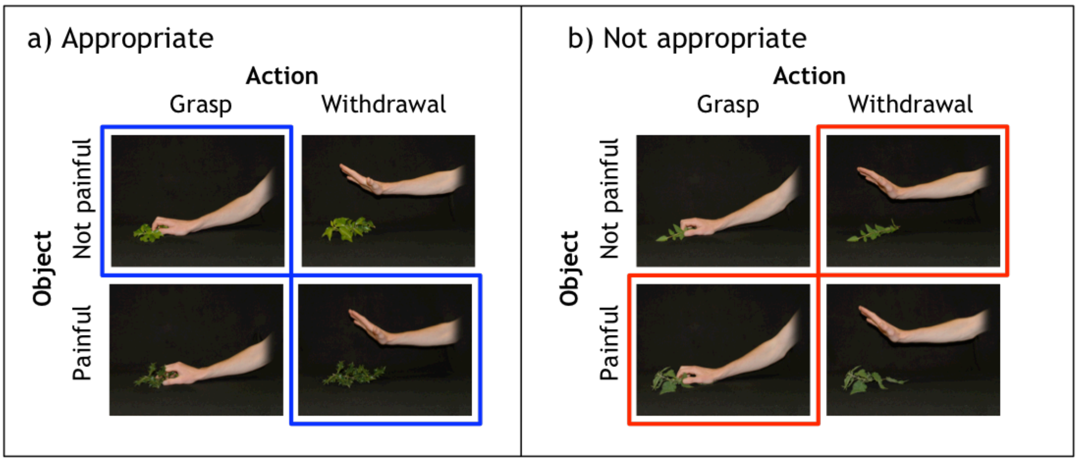

Figure 2.2 During the main experimental trials participants only viewed the hand grasp the plants. On catch trials participants viewed the hand either grasp or miss the plants. At the end of a catch trial they had to judge the appropriateness of the viewed action. a) Examples of correct "appropriate" responses when viewing ivy and holly. b) Examples of correct "inappropriate" responses when viewing balsam and nettle.

Task 2: During Task 2, participants observed the hand either grasp or miss the potentially painful and non-painful plants. At the end of every trial, participants had to judge whether the action they had just seen was appropriate or not appropriate by making a button press response. For example, if the hand grasped a nettle, the correct response was "inappropriate", whereas if the hand missed the nettle, the correct response was "appropriate" (see Figure 2.2). The context for these judgements was given that if a person was doing the gardening with their bare hands, it would be appropriate to grasp and remove the ivy and balsam, but not the holly and nettle. This task served as practise for the catch trials in the main experiment, as such the timing of these trials was identical to those in the main experiment (see Figure 2.3b). There were 32 trials, containing 16 grasping actions and 16 miss actions. Every example of each plant stimulus was viewed once.

On completion of Task 1 and 2, participants were positioned in the scanner bore. However, prior to the localiser task being performed, participants were again asked to name the plant stimuli which were now displayed on a projector behind them and viewed through a rear-view mirror. This brief procedure was designed to ensure the participants could still recognise the plants on the somewhat less clear back projection. All participants were completely accurate at naming each of the plant stimuli in the scanner.

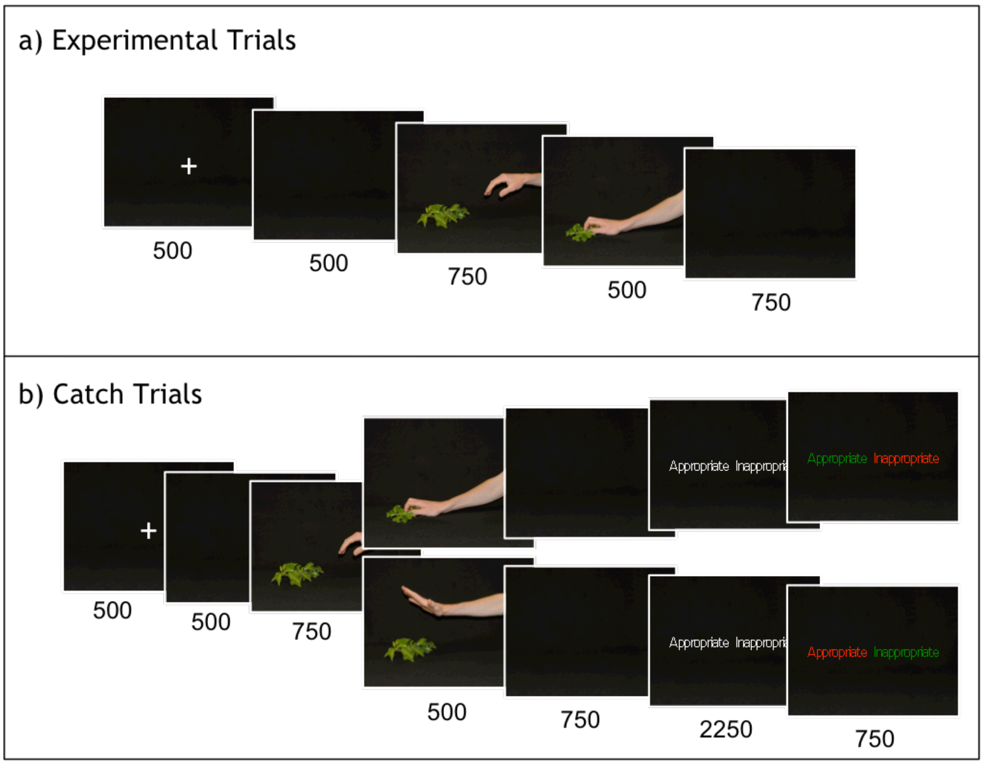

Figure 2.3. Schematic of a) the main experimental trials and b) catch trials. During the main trials participants only viewed grasping actions. In catch trials participants viewed hands grasp or miss the objects and had to judge the appropriateness of the viewed action. Feedback was given after every catch trial. Green indicated the correct response, and red indicated the wrong response. If the participant failed to respond, both words (appropriate and inappropriate) were displayed in red.

Localiser task: The localiser task was designed to activate regions of the brain involved in somatosensory processing, including SI and SII. To this end, participants haptically explored plastic textured balls (tumble drier balls, about the size of a tennis ball) or had their hands and fingers stroked with the same balls by the experimenter. A sheet of paper was placed around the head coil to prevent the participant from viewing their own or the experimenter's actions. In a blocked design, participants performed two runs of haptic exploration, and experienced two runs of passive touch. Each run contained 8 blocks of stimulation to the right hand, 8 blocks of stimulation to the left hand, and 4 rest blocks. The left and right hand order was counterbalanced between sets of four blocks (for example, ABAB or BABA), with a rest block at the end of each set of four. There were also 16 seconds of baseline fixation at the beginning of each run. Each block lasted 20 seconds, containing 16 seconds stimulation, and four seconds preparation time when the experimenter removed the ball, ready to replace it in the appropriate hand in next block. Instructions were projected onto the wall of the scanner room to cue the experimenter to the onset and offset of each block. Participants received auditory cues over the headset to inform them of the beginning and end of each block. The localiser task took approximately 20 minutes.

Session 2: A day after Session 1, participants returned to complete the main experiment. To engage participants with the potential painfulness of the holly and nettle plants, participants were asked to rate how painful they imagined it would be to grasp each plant, and to what degree they judged this from their own experience. Participants also completed two blocks of practise trials (32 trials total) outside the scanner. During the practise trials and main experiment, participants viewed hands grasp the nettle, ivy, balsam and holly. They were instructed to imagine what it would feel like for the actor to grasp the plants. On catch trials only, the participant viewed the hand grasp or miss the plant, and then had to make a button press response to the appropriateness of the observed action (see Figure 2.2 & 2.3). There were one or two catch trials in each block, randomly selected and inserted into the set of 16 experimental trials. There were 8 runs, with 4 blocks of 16 experimental trials per run, and each block was interleaved with 16 seconds baseline fixation, creating 128 trials per condition. The order of trials was counterbalanced within each block. There were 16 seconds baseline fixation at the beginning of each run. An anatomical scan was performed after run 5 to give the participants a break, where they could relax and close their eyes. The scanning session lasted for approximately 60 minutes.

Data Acquisition

The imaging data were acquired using a Philips 3T MRI Scanner, with a SENSE phased-array head coil. Functional data were collected using an echo-planar imaging sequence (T2* weighted, gradient echo sequence, echo time 35ms, flip angle, 90^{o}). Acquisition parameters were as follows: repetition time 2500ms; voxel size 2.5mm x 2.5mm x 2.5mm; 39 off-axial slices. Anatomical data were collected with T1-weighted scans with a matrix size of 288 x 232, 1mm isotropic voxels, TR = 8.4ms, TE = 3.8 ms, and flip angle = 8^o.

Preprocessing

BrainVoyager QX 1.9 (Brain Innovation, Masstricht, The Netherlands) was used to preprocess and analyse all univariate data, and Matlab (The MathWorks, Natick, MA) was used to carry out MVPA searchlight analyses (Script courtesy of P. Downing, Bangor University). Motion artefacts and low-frequency drifts were removed from the data by performing BrainVoyager's automated motion correction and temporal high-pass filter (0.006 Hz). However, two participants' data had to be excluded due to excessive motion that could not be rectified by this procedure. Data for the univariate analyses was spatially smoothed using a 6mm full-width-half-maximum kernel. No smoothing was applied to the data submitted to the searchlight analyses. The preprocessed functional data were coregistered to the anatomical data. The 3D anatomical scans and functional data were transformed into Tailarach space (Tailarach & Tournoux, 1988). General linear models were created for each participant's localiser and main experimental runs. Each condition of interest was modelled by a boxcar predictor convolved with a two-gamma hemodynamic response. Predictors were also created to model the button press response on catch trials, as well as regressors of no interest (essentially accounting for baseline activity). In each voxel, regressors were fitted to the MR-time series resulting in parameter estimates (beta values) that were used to estimate the magnitude of response in each condition.

Regions of Interest Analysis

Functional regions of interest were located by analysing the localiser data, and through selection of peak coordinates previously reported to be activate during the observation of painful grasps (Morrison et al., 2012). Indeed, the paradigm used in the current study was very similar to that utilised by Morrison et al. (2012); participants in their study viewed two-frame sequences of a hand grasping or missing painful and non-painful objects, and were asked to judge the appropriateness of the action at the end of every trial. Morrison et al. (2012) reported preferential activation of IFG, MFG, and IPL/PostCG during the observation of painful grasps. To confirm the role of these regions in encoding the painful consequences of others actions, we also used the peak coordinates of these regions as ROIs in the current study.

The localiser data for both haptic exploration and passive touch were collapsed together to maximise the chance of defining ROIs in each subject. The contrast right hand > left hand stimulation was used to identify regions of interest with a cluster size greater than 93.75 voxels, equivalent to six acquired voxels (each $2.5mm^3$) and $p < .001$. SI and SII were our target regions, however, only SI could be reliably identified across participants, with SII activation apparent in only 7 participants. Consequently, we also created group averaged ROIs for SI and SII. All ROIs were defined by a 9mm cube centred on the voxel with the peak activation.

Searchlight Analysis

The searchlight analysis utilised in this experiment was based on the correlation MVPA method used by Haxby et al. (2001). No spatial smoothing was applied to the data to be analysed with MVPA, however the data was normalised to enable comparison between participants. The beta parameter estimates computed in every voxel, for each condition, for each run, were exported as a matrix to Matlab. A 7mm sphere, serving as a moving window, visited every voxel in this matrix, with the constraint that the sphere had to stay within the boundary of the matrix. Consequently, there was a frame within active cortex where MVPA analysis could not take place. This can be seen in the abrupt edges of, especially posterior visual regions, capable of discriminating stimuli (see Figure 2.6, x = -15 & x = -20).

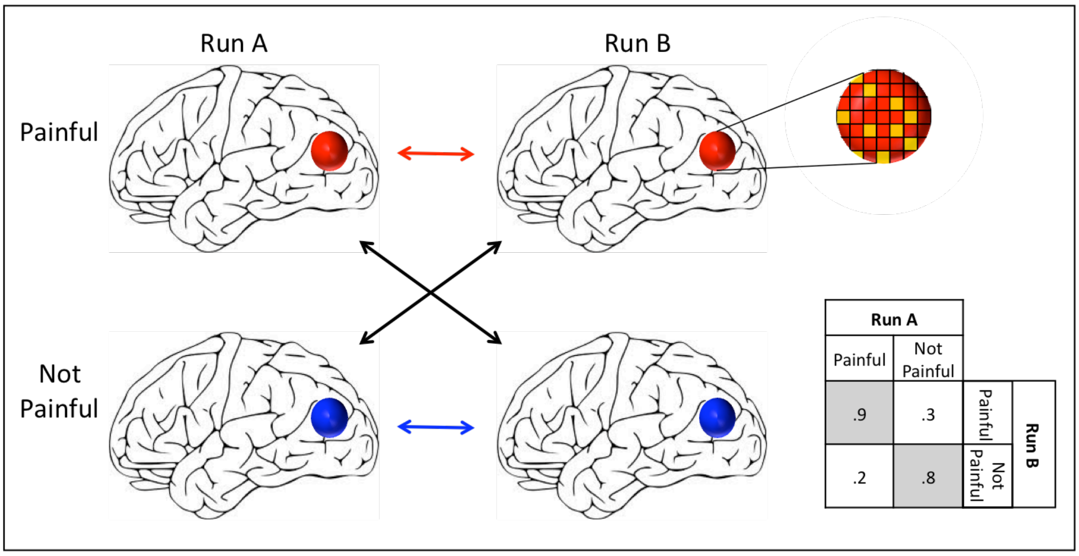

Figure 2.4. Illustration of searchlight MVPA. A 7mm sphere moves through every voxel in the brain. The pattern of activation in each sphere for Run A is correlated with the pattern of activation in Run B. Correlations are performed both within and between conditions. The correlations in the table demonstrate that painful and non-painful stimuli are decoded in this sphere. An accuracy score is calculated by comparing the number of times the off-diagonal correlations (painful/ not painful, and not painful/ painful) are greater than the on-diagonal correlations (painful/ painful, and not painful/ not painful). In this example, the identification accuracy would be 100% as all off-diagonal correlation are lower than the on-diagonal correlations.

Correlations were calculated by correlating the pattern of activation within the sphere in a particular location, both within and between conditions, and runs (see Figure 2.4). Correlations were calculated for every run against ever other run. The identification accuracy score was calculated by comparing the strength of the on-diagonal correlations (within category) with the off-diagonal (between category) correlations. If the on-diagonal correlations were consistently greater than the off-diagonal correlations, the identification accuracy was deemed to be 100%. The identification accuracy score for each location of the sphere was reported at the centre voxel of the sphere. To assess whether the identification accuracy was significantly above chance, the accuracy scores, across all run combinations within a voxel were averaged. The average accuracy score for each voxel, across participants was then compared against 50% using a t-test. The p values from these t-tests were then resubmitted and visualised in BrainVoyager. Voxels that accurately discriminated between categories were considered significantly above chance if $p < .0005$, at a cluster threshold of 93.75mm^3.

2.3.2 Results

Univariate Analysis

Four contrasts, utilising a whole-brain, random effects analysis were carried out. Unless otherwise stated, we used an uncorrected voxelwise threshold of $p < .001$, and a cluster threshold of 6 acquired voxels (equivalent to 93.75mm^3). Four runs were removed from the analysis due to motion artefacts.

To verify the manipulation of pain had been successful, and corroborate previous reports of regions active during the observation of pain, we first contrasted pain-evoking grasping actions (holly & nettle) with non-painful grasping actions (ivy & balsam; see Figure 2.5 & Table 2.1). All significantly active voxels were more active during the observation of painful actions than non-painful actions. This activation not only included visual areas such as lingual gyrus and superior occipital gyrus, but also lateral occipital cortex. Further, inferior parietal lobule, posterior supramarginal gyrus, and precentral gyrus were also were more active when participants viewed painful grasps. Although some of these regions are often reported in studies investigating shared representations of pain (Lamm et al., 2011), the absence of more typically active regions, such as the insula and ACC, led us to explore the data further. Indeed, at a less stringent threshold of $p < .005$ anterior insula activity was revealed to be greater during the observation of painful trials compared to non-painful trials (see Figure 2.5 & Table 2.1).

We performed a further contrast to explore whether there were any differences between cortical activity evoked by the reflectance of the viewed plants (high > low; see Table 2.2). Although we did not predict any differences beyond visual cortex, MFG was significantly more active for plants with low reflectance, compared to high reflectance. Exploratory analyses indicate this main effect may be due to activation associated with processing nettle, rather than low reflectance per se (average betas: nettle = 0.436, balsam = 0.169, ivy = -0.156, holly = -0.069). However, this was not born out by a significant interaction ($p > .05$).

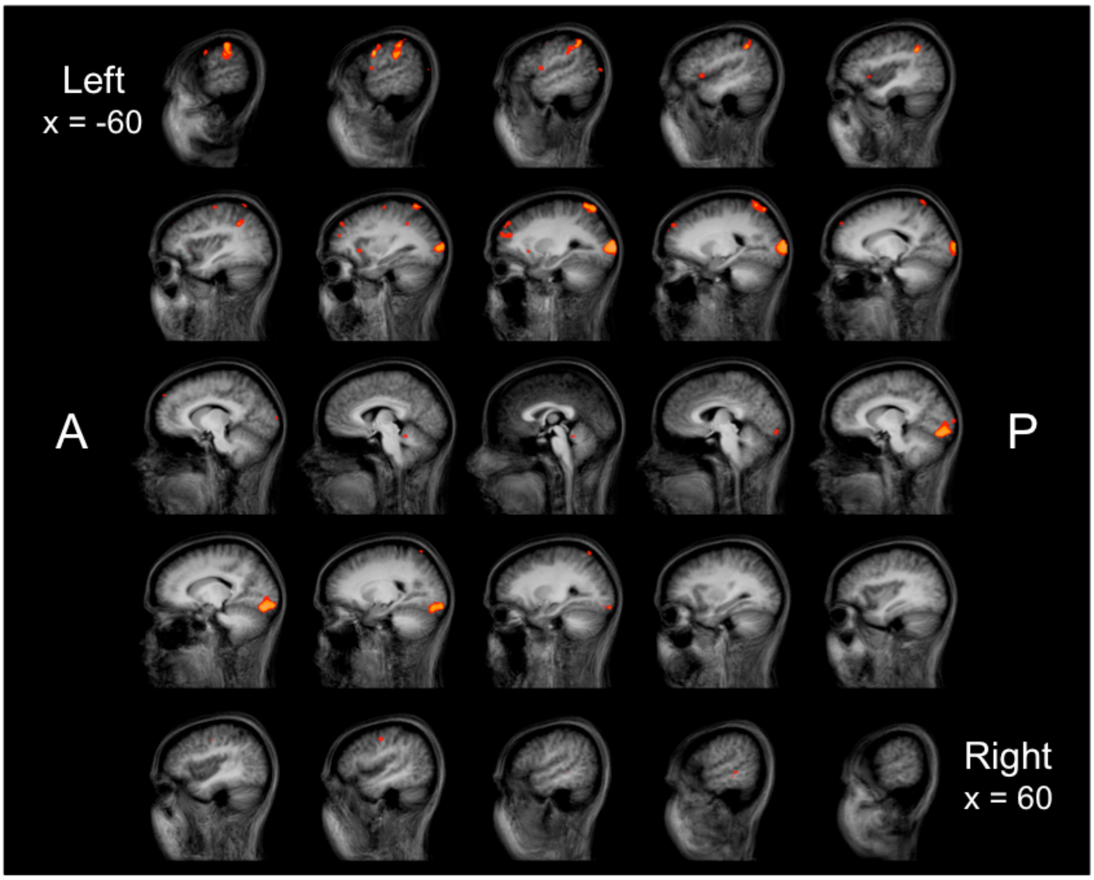

Figure 2.5. Univariate Analysis. Significant activations for the main effect of pain (Nettle +Holly > Balsam + Ivy) for the whole brain, random-effects analysis. Functional data is displayed on the group-average anatomical brain, from x = -60 to x = 60 in steps of 5. Orange = $p < .001$, red = $p < .005$, cluster threshold = 93.75mm^3.

The motivating question for this study was whether the observer encoded different types of viewed pain. To address this question we examined the interaction between painfulness and the reflectance of the plant (Holly + Balsam > Nettle + Ivy; see Table 2.2). Only a region of LOC (distinct from that reported in the analysis of pain > no pain) remained significantly active in this contrast. A 2 by 2 ANOVA of painfulness (painful/ not painful) and reflectance (high / low) did not reveal a main effect of pain ($F < 1$), but did reveal a main effect of reflectance, *F*(1,11) = 20.36, *p* = .001, η^2_p = .65. More importantly, there was a significant interaction between painfulness and reflectance, *F*(1,11) = 27.10, *p* < .001, η^2_p = .71. Pairwise comparisons revealed that this interaction was driven by a significant difference between nettle (average beta = 0.717) and holly (average beta = -0.137; *p* < .001), but no difference in activity between balsam and ivy (*p* = .676).

Table 2.1. *Main effect of pain (Holly + Nettle > Ivy +Balsam). Cluster threshold of 93.75mm^3. Talairach coordinates are given for each peak voxel.*

	Region	**Peak coordinates (x, y, z)**	**Maximum t-score**	**Cluster size (mm^3)**
***p* < .001**				
1	Lingual Gyrus	14, -80, -15	8.19	2633
2	Superior Occipital Gyrus	-22 -98 3	8.49	2669
3	LOC	-22 -71 57	8.33	681
4	IPL/ Posterior SMG	-46, -47, 42	7.11	536
5	Anterior SMG	-61, -29, 45	5.93	851
6	PreCG	-55, 1, 33	8.99	196
***p* < .005**				
7	Middle Temporal Gyrus	53, -29, -9	5.41	214
8	PreCG	44, -8, 42	5.82	178
9	SPL	20, -65, 63	4.71	181
10	Superior Frontal Gyrus	2, 7, 63	3.78	100
11	Cerebellum	-4, -41, -18	5.48	168
12	MFG	-25, 46, 21	6.17	1299
13	Anterior Insula	-28, 22, 0	4.92	254
14	PreCG	-31, -14, 60	5.41	174
15	Insula/ Frontal Operculum	-43, 16, 0	4.70	301
16	PreCG	-49, 4, 12	4.47	297
17	Mid Occipital Gyrus	-52, -77, 9	6.60	187

IPL = Inferior Parietal Lobe
LOC = Lateral Occipital Cortex
SMG = Supramarginal Gyrus
MFG = Middle Frontal Gyrus
SPL = Superior Parietal Lobe
PreCG = Precentral Gyrus

To increase the power of our univariate analyses, we identified functional regions of interest. However, on both an individual subjects and group-averaged basis, neither of the ROIs (SI or SII) revealed any significant activity ($F < 1.5$, for all) [2.1]. In contrast, the ROIs defined by the peak coordinates in the Morrison et al. (2012) study did reveal some interesting findings. Although MFG (x, y, z = -39, 38, 13) did not replicate Morrison et al.'s previously reported increased activation during pain observation, $F(1,11) = 1.81, p = .205, \eta^2_p = .14$ (all other effects, $F < 1$), IFG and PCG/IPL did. The analysis of activation within IFG (x, y, z = -51, 11, 13) revealed a main effect of pain, $F(1,11) = 7.38, p = .020, \eta^2_p = .40$. Greater activation was associated with viewing painful grasps (average betas = 0.675) in comparison to non-painful grasps (average betas = 0.332). There was no effect of reflectance ($F < 1$) and no interaction between the two, $F(1,11) = 2.29, p = .159, \eta^2_p = .17$. Similarly, PCG/IPL (x, y, z = -48, -25, 34) also revealed a main effect of pain, $F(1,11) = 7.40, p = .020, \eta^2_p = .40$ (all other effects $F < 1$), again with greater activation during the observation of hands grasping painful plants.

Table 2.2. *Main effect of reflectance, and the interaction between plant painfulness and reflectance. Cluster threshold of 93.75mm^3, p < .001. Talairach coordinates are given for each peak voxel. For abbreviation meanings see Table 2.1.*

	Region	**Peak coordinates (x, y, z)**	**Maximum t-score**	**Cluster size (mm^3)**
Main effect of reflectance *(Holly + Ivy > Nettle + Balsam)*				
1	Inferior Occipital Gyrus	38, -86, -3	-5.22	209
2	LOC	20, -71, 48	-11.12	4818
3	MFG	26, -11, 51	-5.77	323
4	Lingual Gyrus	-13, -68, -6	-6.07	299
5	Middle Occipital Gyrus	-25, -92, 0	6.32	1223
6	Lingual Gyrus	-22, -50, -9	-7.04	417
Interaction *(Holly +Balsam > Nettle + Ivy)*				
1	LOC	29, -62, 51	-6.02	210

Multivariate Pattern Analysis

Although the univariate analysis of cortical activity is a useful starting point for

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[2.1] It is possible that the localiser contrast of right hand > left hand stimulation removed SII activation associated with right hand stimulation, thus decreasing the likelihood of accurately identifying bilateral SII. In future studies, a localiser task requiring participants to discriminate between two types of tactile stimulation may be more appropriate for localising somatosensory regions involved in tactile discrimination tasks.

investigating shared cortical representations of pain, we wanted to know whether the type of pain is encoded by the observer. Therefore we also utilised the more sensitive searchlight MVPA technique. Further, the consistently greater activation across all significantly active voxels during the observation of painful grasps (as revealed by the univariate contrast, pain > no pain), suggests this activation could be driven by the salience of these stimuli, rather than the perception of pain per se. For example, rather than somatosensory associative regions discriminating between painful and non-painful actions, greater activation during the observation of pain may be due to the increased attention paid to these stimuli. Therefore MVPA not only offers a more fined-grained analysis of the data, but also provides the opportunity to help distinguish between attentional and pain perception accounts of the univariate analyses.

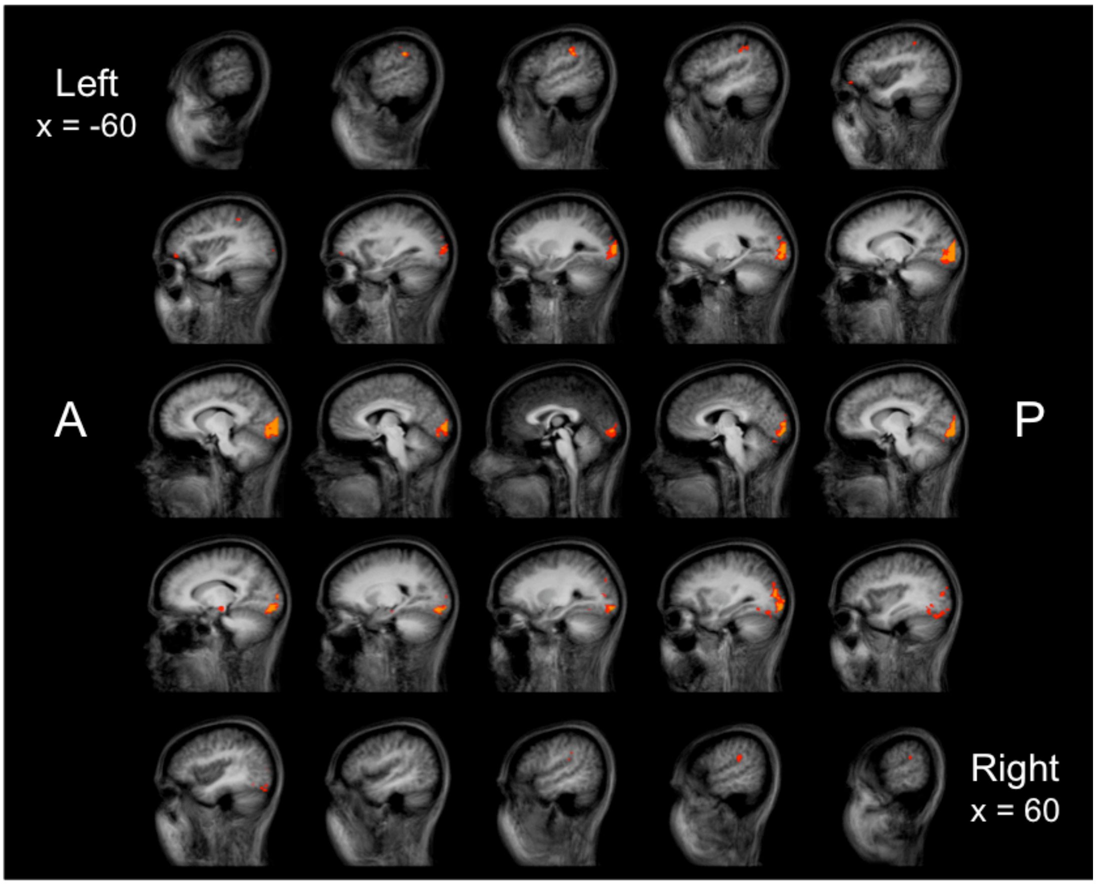


Figure 2.6. MVPA Analysis (painful/ non-painful). Visualisation of regions where painful actions and non-painful actions were discriminated significantly above chance, displayed on the group-average anatomical brain, from x = -60 to x = 60 in steps of 5. Orange = $p < .0001$, red = $p < .0005$, cluster threshold = 93.75mm^3.

We carried out three separate searchlight analyses. Firstly, we investigated where observed painful and non-painful actions were accurately decoded in the brain. The identification accuracy for decoding cortical activity evoked during the observation of hands grasping painful plants (nettle/ holly) and non-painful plants (balsam/ ivy) was significantly above chance across the occipital cortex and in a cluster of voxels encompassing the parietal operculum and SMG (see Figure 2.6 & Table 2.3). Similar to the univariate analyses, we also used a less stringent threshold to explore the data further. At this reduced threshold bilateral parietal operculum, midbrain and orbital frontal gyrus also accurately discriminated painful from non-painful actions.

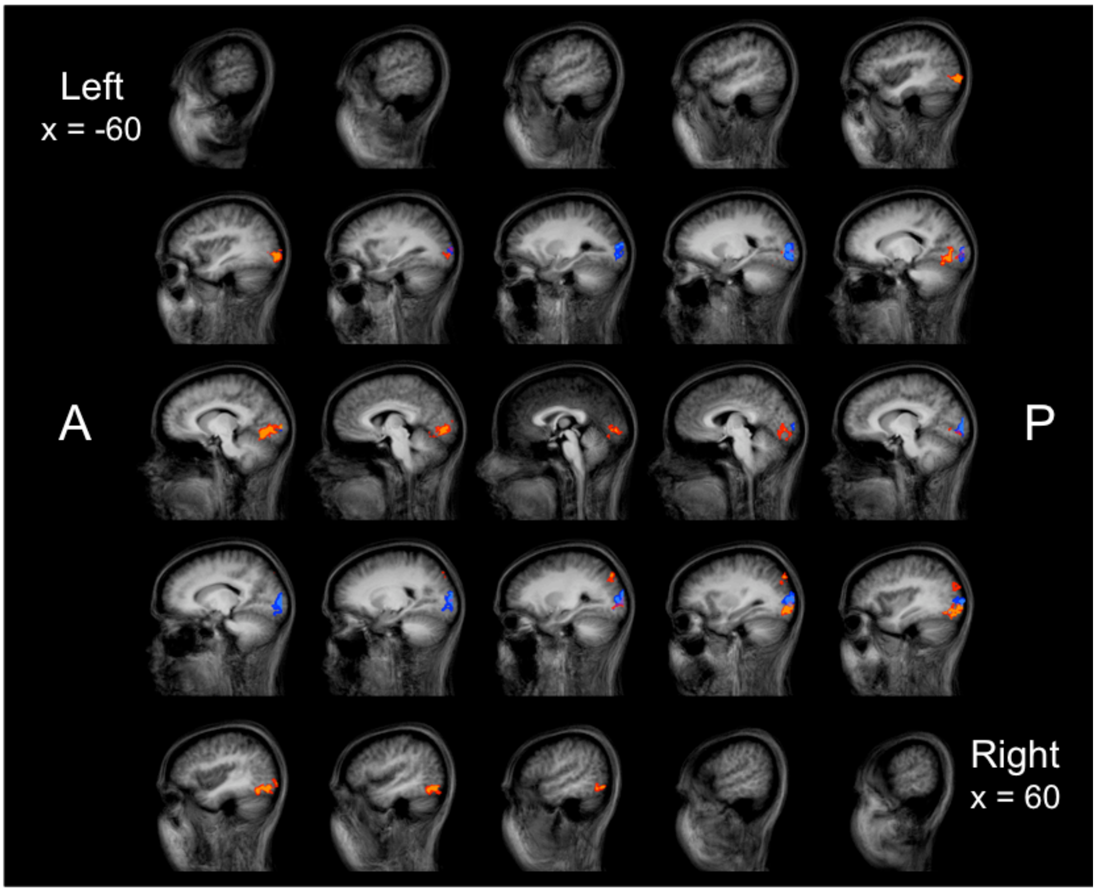


Figure 2.7. MVPA Analysis. Visualisation of regions where types of pain (holly and nettle) or non-painful plants (ivy and balsam) are discriminated significantly above chance, displayed on the group-average anatomical brain, from x = -60 to x = 60 in steps of 5. Cluster threshold = 93.75mm^3. Holly and Nettle: orange = $p < .0001$, red = $p < .0005$; Ivy and Balsam: light blue = $p < .0001$, dark blue = $p < .0005$. Purple = overlap in regions discriminating holly and nettle, and balsam and ivy.

The searchlight analysis for areas capable of decoding holly and nettle unsurprisingly revealed regions in visual cortex including inferior occipital gyrus and lingual gyrus, and also, LOC (see Table 2.3 & Figure 2.7). However, even at a reduced threshold, no regions involved in pain processing, such as somatosensory cortex, insula or ACC provided evidence that accurate decoding of different types of observed pain took place. Similarly, balsam and ivy were only discriminated in visual processing regions (see Table 2.3 & Figure 2.7).

Table 2.3. *Searchlight analyses. Cluster threshold of 93.75mm^3. Talairach coordinates are given for each peak voxel. For abbreviation meanings see Table 2.1.*

	Region	**Peak coordinates (x, y, z)**	**Minimum p value**	**Cluster size (mm^3)**
Painful/ Not painful				
	p < .0001			
1	Occipital Lobe	-13, -89, 6	3.43e-11***	7873
2	Parietal Operculum/SMG	-55, -35, 33	9.17e-08***	276
	p < .0005			
3	SII/Parietal Operculum/SMG	53, -29, 21	2.59e-07**	413
4	Lateral Occipital Temporal Gyrus	29, -71, -15	1.33e-06*	707
5	Midbrain	17, -14, -9	3.21e-06*	323
6	Superior Occipital Gyrus	-19, -83, 21	5.57e-06*	172
7	Orbital Frontal Gyrus	-34, 46, -7	8.78e-06*	244
Holly/Nettle				
	p < .0001			
1	Inferior Occipital Gyrus	38, -71, -12	6.38e-10***	3016
		-40, -80, -3	1.55e-08***	1055
2	LOC	26, -77, 39	2.16e-07**	224
3	Lingual Gyrus	-16, -71, -9	1.30e-08***	2157
	p < .0005			
4	Lingual Gyrus	-16, -71, -9	1.31e-08***	6640
Balsam/Ivy				
	p < .0001			
1	Middle Occipital Gyrus	11, -93, 3	4.79e-07**	3157
2	Middle/Inf/Sup Occipital Gyrus	-22, -86, 9	2.46e-07**	1376

*p < .00001 (1.00e-05)
**p < .000001 (1.00e-06)
***p < .0000001 (1.00e-07); p < .05 Bonferroni corrected

2.4 Discussion

The univariate analysis, contrasting the observation of painful actions with non-painful actions, replicated previous findings of shared representations of pain. For example, regions implicated in the production of avoidance behaviours during the direct experience of pain, such as the precentral gyrus and cerebellum, were more active when participants viewed hands grasp painful plants, compared to non-painful plants (Almeida, Roizenblatt, & Tufil, 2004). Similarly, the observation of painful grasps was related to greater activation in the anterior insula, a region involved in processing the sensory aspects of pain (Peyron, Laurent, & García-Larrea, 2000). The inferior parietal lobule (IPL) was also more active when participants viewed painful grasps. Although IPL recruitment is consistently associated with action observation (Molenberghs, Cunnington, & Mattingley, 2012), it has also been reported during the observation of pain evoking actions (Lamm et al., 2011).

Significant activation of middle frontal gyrus (MFG) was revealed during the observation of painful grasps, but also during the observation of plants with low reflectance. In line with the main effect of pain, there is evidence for a role in MFG during the direct experience and observation of noxious sensations (Ochsner et al., 2008). However, MFG is also involved in naming objects and object recognition (Price, Devlin, Moore, Morton, & Laird, 2005). Therefore, increased activation when viewing balsam and nettle may be due to an increased difficulty in recognising and naming these plants in comparison to holly and ivy. Interestingly, exploratory analyses indicated that the main effect of reflectance may actually be driven by the activation evoked when viewing a hand grasp the nettle.

The lateral occipital cortex was the only region revealed by the univariate contrasts to be active for the main effect of pain, the main effect of reflectance, and the interaction between the two (although the peak voxel varied between these contrasts). Interestingly, the lateral occipital cortex is not normally related to pain processing, but rather object recognition (Grill-Spector, Kourtzi, & Kanswisher, 2001). Thus, the previous explanation for greater MFG activity during the observation of high versus low reflective plants may also hold for LOC activity. However, there is evidence to suggest that LOC may integrate visual and haptic information in order to necessitate both visual and tactile object recognition (Amedi, Malach, Hendler, Peled, & Zohary, 2001), an explanation that perhaps aligns better with recruitment of this region during the observation of painful grasps. Interestingly, the interaction contrast only revealed differential activity within categories of plant in the LOC. The level of activity evoked by viewing a hand grasp a nettle was greater than that evoked by viewing holly, whereas no differences between the non-painful stimuli were revealed. This difference in evoked cortical activity is difficult to interpret because it may be due to a difficulty recognising nettles compared to holly, or the differing sensory qualities of nettle and holly. Further studies will need to be carried out to better understand this interaction.

Despite showing activity in several regions involved in pain processing, primary and secondary somatosensory cortical activity was not evidenced by any of the whole-brain univariate contrasts. However, MVPA provided an opportunity to investigate whether a more fine-grained analysis technique could reveal the involvement of these regions during the observation of painful actions. Recall that the purpose of utilising this sensitive technique was to test if differences in cortical activity evoked by viewing painful and non-painful actions could be revealed at a representational level, rather than in varying magnitudes of cortical activity. Further, we wanted to explore whether different types of pain were represented by the observer.

The observation of hands grasping painful and non-painful plants, holly and nettle, and balsam and ivy were all accurately discriminated in visual cortices. Significant identification accuracies for nettle and holly were also revealed in the LOC. Importantly, painful and non-painful plants were identified significantly above chance in the parietal operculum/ supramarginal gyrus, on the border of SII. At the less stringent threshold of $p < .0005$, this activation was revealed to be bilateral, encompassing SII proper. SII is involved in processing the sensory aspects of directly experienced painful and non-painful stimuli (Coghill et al., 1994), but also has an important role in object recognition through haptic exploration (Reed, Shoham, & Halgren, 2004). At the lower threshold, midbrain and orbital frontal gyrus also contained representational information regarding pain perception. Midbrain responses may reflect processing of different autonomic responses elicited by viewing painful and non-painful actions (Hudson, 2000). Accurate decoding of painful and non-painful actions in orbital frontal gyrus may reflect the functional role this region has in encoding the predicted value of an action (Schoenbaum, Takahashi, Liu, & McDonald, 2011). Further, the orbital frontal gyrus receives direct inputs from primary and secondary somatosensory cortex which may act to reinforce or punish such predictions (Kringelbach & Rolls, 2004).

The accurate identification of observed painful and non-painful actions in SII, midbrain and orbital frontal gyrus, provides the first evidence that vicarious cortical activity represents the sensory aspects of pain. However, regions typically involved in pain processing were not able to discriminate between the type of observed pain. The absence of such findings may seem surprising if one considers that the observation of others' action are directly mapped onto one's own motor system (Rizzolatti et al., 2001). Yet, Veldhuijzen et al. (2009) have demonstrated that even the direct experience of different types of pain does not relate to differential activity in typical pain processing regions. The authors delivered painful burning and pricking stimuli to the feet of participants whilst they were being scanned, and report overlapping activity in anterior insula, thalamus and anterior cingulate cortex for both types of pain. Unexpectedly, hippocampal regions amongst others were more active during the experience of pricking pain, whereas dorsolateral prefrontal cortex was more active during the experience of burning pain. However, a limitation of their findings is that the authors used univariate methods to analyse their data, rather than MVPA. Had the data been analysed using the more sensitive technique, it is possible that burning and pricking pain may have been accurately decoded in pain processing regions that did not reveal significant differences in the magnitude of cortical activity. After all, the sensations evoked by these two types of painful stimuli are experienced as qualitatively different. What is important to consider though, is the point at which this qualitative difference reaches awareness. If shared representations are mediated by an action production system, the rapid identification of threat per se is critical. In contrast, the knowledge of the precise sensory properties that a stimulus might possess is superfluous to appropriate action selection, when that action is simply to withdraw, or escape from pain. Consequently, the perception of pain and the discrimination of types of pain may be processed separately.

The study presented in this chapter is the first to address whether different types of pain are encoded by the observer. Although preliminary findings suggest pain per se, rather than different noxious sensations, are represented by the observer, further studies will need to be carried out to replicate and extend our findings. Crucially, there are a number of limitations in the current design that will need to be refined in future methodologies. For example, participants only viewed hands grasping the plants in the experimental trials. This means that any representation or activation associated with these stimuli might refer only to the object, and not the sensory consequence of grasping the object. In a previous study by Morrison et al. (2012), participants viewed hands both grasp and miss painful and non-painful objects. The elegance of their design was that the action and object effects could be distinguished from the painful consequences of an observed action. Although we were aware of this design, we chose to maximise the power of the critical painful grasp trials to facilitate MVPA analyses by removing the miss trials. Interestingly, we chose three regions of interest from the Morrison et al. (2012) study that were preferentially active during the observation of painful grasps, and not pain per se. Two of these regions, IFG and PCG/IPL, were also significantly more active during the observation of painful grasping actions in our study, providing some evidence that the sensory consequences of observed actions may have been driving our effects.

Overall, cortical activity was greater when participants viewed painful actions compared to non-painful actions. This may have been due to participants paying more attention to the salient painful stimuli in comparison to the non-painful stimuli, rather than a distinct representation of pain per se. The possible attentional effects limit the interpretation of the univariate analyses, but are less problematic for MVPA. Further, despite overall greater activation during the observation of others in pain, the failure to show primary and secondary somatosensory activation in the whole-brain univariate analyses may be considered a limitation of the study. However, overall weak activation of regions typically involved in pain observation is likely due to the controlled nature of our stimuli. We used two-frame still sequences and ensured the performed grasping actions were similar across all conditions. Further, the stimuli were matched as closely as possible to help prevent visual properties of the scene driving accurate classification. Despite these important constraints, MVPA revealed that secondary somatosensory cortex accurately represented painful and non-painful actions. Indeed, no appreciable difference in the magnitude of cortical responses in this region, as evidenced by the univariate analyses, is actually strong evidence that the pattern classification we report is valid. This is because recent studies suggest that differences in cortical activity may actually bias pattern classification accuracy (Smith, Kosillo, & Williams, 2011). As such, this may be a consideration for the accurate decoding of holly and nettle in LOC, as this region was also shown to be significantly more active when viewing hands grasp nettle compared to holly.

The current study provides an initial attempt at addressing the question of the specificity of shared representations of pain. As such, it provides a new direction in the study of vicarious cortical activity. Further, we provide the first evidence that observed pain not only evokes a greater cortical response, but can be accurately discriminated from non-painful actions in midbrain, orbital frontal cortex and SII.

Chapter 3

The behavioural effects of viewing others in pain

3.1 Summary

In a series of four experiments, we investigated whether vicarious cortical representations of pain altered an observer's own ability to detect touch[3.1]. In Experiment 2, participants viewed two frame sequences of a hand either approach and grasp, or withdraw from, potentially painful and non-painful objects. Participants detected a threshold level tactile stimulus, delivered to their right-index finger, whilst viewing the hand-object interactions. Participants detected most tactile stimuli during the observation of others in pain, but were also more biased to report touch in this condition.

In Experiment 3, we investigated whether the effects of viewing others in pain were due to a general arousal, or a sensory specific effect. In a modified version of Experiment 2, participants detected threshold level auditory stimuli, rather than tactile stimulation. Participants' auditory detection was not affected by viewing others in pain, suggesting the effects of viewing others in pain are specific to the tactile modality.

Experiment 4 aimed to extend the findings of Experiment 2, from the detection of threshold level tactile stimuli to above threshold tactile stimulation. That is, participants responded as quickly as possible to the presence of an easily detectable tactile stimulus. The distribution of reactions times was similar to the data reported in Experiment 2. Participants were fastest to respond to a vibration on their finger when they viewed others in pain.

Experiments 2 and 4 suggest participants encode the sensory consequences of an observed action, leading to a "painful grasp effect". However, it is also possible that the hand reaching forward to grasp the object merely draws attention to the painful object. Experiment 5 aimed to control for the alternative attentional account of our findings. Participants observed both bare hands and gloved hands (protected from pain) interact with the objects. Even though attention was drawn to the painful object in the gloved hand condition, participants were only faster to respond to touch when the bare hand, vulnerable to pain, grasped the painful object.

[3.1] The methods and results from Experiments 2 and 3 have been published in Morrison, Tipper, Fenton-Adams, and Bach (2012). Fenton-Adams carried out and produced the text and figures for these behavioural experiments published in Morrison et al. (2012), but did not contribute to the imaging aspects of the manuscript.

3.2 Introduction

Previous research has revealed that broad cortical networks involved in processing one's own pain are also activated during the observation of others in pain. Although shared representations of pain are thought to underlie the understanding of others (Preston & de Waal, 2002), we hypothesised that activation of core tactile encoding regions may fulfil a more functional role. Indeed, in a recent study, Morrison et al. (2012) emphasised the role of primary (SI) and secondary somatosensory (SII) cortex in encoding the sensory consequences of others' actions, in particular, the painful outcome of viewing a hand grasp a noxious object. Morrison et al. (2012) suggested that these somatosensory regions may be responsible for combining action and object information to infer, or create a "sensory expectation", during the observation of painful actions. In this chapter we report the findings of four experiments which aimed to investigate whether an observer's ability to detect touch is mediated by viewing others in pain.

Although there is an abundance of research investigating the cortical effects of viewing others in pain on cortical activity (Keysers et al., 2010; Lamm et al., 2011), there is little direct evidence of these effects on behaviour. For example, previous studies have often relied on subjective measures to infer the behavioural consequences of viewing others in pain (Bufalari et al., 2007; Valeriani et al., 2008). In contrast, the effects of viewing bodies and touch on behaviour have been measured more objectively. These studies provide valuable insight into the possible effects of viewing pain on an observer's tactile processing. As discussed in Chapter 1, these studies demonstrate that viewing ones own or others' bodies causes a visual enhancement of touch (VET), including facilitated reaction times to touch (Tipper et al., 1998) and greater tactile acuity (Taylor-Clarke et al., 2002). Although these effects have been found with supraliminal tactile stimuli (Tipper et al., 1998; 2001), other authors suggest VET can only be revealed with ambiguous stimuli (Press et al., 2004).

Important to note is that in none of the VET experiments did vision of the participant's own body provide information relevant to when or where the tactile stimulation might occur. Therefore VET effects are distinct from crossmodal congruency effects (Spence, 2011) whereby the onset of a visual stimulus that occurs, for example, in a similar time and space to the onset of touch, facilitates tactile processing. However, within a given task, VET and cross-modal congruency effects may occur together and be difficult to disentangle. For example, Serino et al. (2008) investigated the possible visual enhancement of touch when viewing bodies being touched. Unlike previous experiments exploring VET, the visual stimuli in this experiment provided information about the tactile stimulus: not where it would occur, but when it might occur. Participants detected touch on their own cheeks whilst viewing their own face, another person's face, or a house being touched by a finger. Serino et al. (2008) demonstrated that viewing touch of a face improved accuracy of tactile detection. This effect was greatest when participants viewed their own face (rather than another person's face) being touched, compared to viewing a house being touched. Thus, not only vision of a body, but also vision of touch, improves tactile detection.

In the cited papers reporting visual enhancement of touch (VET), and inherent in the name of the effect, is the assumption of a better ability to detect touch. However, in a series of three experiments applying signal detection theory (SDT), Johnson, Burton, and Ro (2006) directly tested whether changes in tactile performance during vision of the body were due to a better ability to detect touch or a bias to report touch. A ring electrode and light emitting diode were attached to the participant's middle finger, which delivered tactile and visual stimuli respectively. On a trial-by-trial basis, participants judged whether they had felt a threshold-level tactile stimulus, seen a light, experienced both light and touch, or neither stimulus. Unlike previous experiments, the authors were able to attribute their results to a bias to report touch during vision and touch trials, and not a greater sensitivity to touch. In contrast to the assumption of previous studies, only when the authors combined the three studies together was an increase in sensitivity between touch alone, and vision and touch trials, statistically significant.

Mirams, Poliakoff, Brown, and Lloyd (2010), extended the findings of Johnson et al. (2006) by directly comparing tactile detection trials where participants viewed their own hand and a light, with those where their hand, but not the light, was occluded. During the study by Mirams et al. (2010), participants only reported the tactile stimulus and not the light stimulus. Participants made more false alarms (erroneous detections of touch) during the concurrent stimulation of light and touch when they could see their own hand, compared to when they could not see their hand. Participants also made more false alarms in light trials, than no light trials when viewing their own hand, but this difference was not observed when the hand was hidden from view. In contrast to previous findings, there was no effect on the number of accurate tactile detections participants made when they viewed their own hand in comparison to an occluded hand. Rather than a better ability to detect touch, differences between viewing conditions were suggestive of a bias to report touch, similar to that reported by Johnson et al. However, in the study by Mirams et al. (2010), the bias measure did not reach significance. The data presented by Mirams et al. (2010) and Johnson et al. (2006)

suggest it would be prudent for future studies investigating VET to analyse their data with the application of SDT, in order to attribute changes in tactile detection to an enhancement, rather than a bias to report touch.

Unlike the effects of vision of the body on tactile detection, the effects of viewing others in pain have not been widely investigated. In general, behavioural research has focused on the effects of physical threat or pain on motor responses and tactile attention, rather than the effects of viewing someone else in pain on tactile processing. For example, Morrison, Poliakoff, Gordon, and Downing (2007) report the differential effects on reaction times in a go/ no go task when viewing a hand or sponge, touched by a cotton wool bud or penetrated by a needle. Participants made both press and release responses to a go signal, which alternated between go signal trials. Overall, press responses were faster than release responses. However, during the observation of a hand penetrated by a needle, reaction times to make a release response were speeded and press responses were slowed. Interestingly, these seemingly adaptive action contingencies (speeded withdrawals and slowed approach movements) during the observation of others in pain are not always reported.

In a combined imaging and reaction time study by Morrison, Peelen, et al. (2007), participants viewed non-painful and painful implements make contact with, or miss, a hand. In separate blocks, participants only ever made speeded button press responses, not release responses, to the detection of hit trials (where the implement made contact with the hand) and miss trials (where the implement missed the hand), regardless of the potential painfulness of the implement. Participants were fastest to make the press response when they saw a painful action (such as a hammer hitting the hand) compared to non-painful hit trials. The seemingly dichotomous results of Morrison, Peelen et al. (2007) and Morrison, Poliakoff et al. (2007) highlight the context dependence of behavioural responses to viewing others in pain, similar to when pain is experienced first-hand (Petrovic & Ingvar, 2002).

In the study by Morrison, Peelen et al. (2007), participants were slower to respond when a painful implement missed the hand, compared to when a non-painful implement missed the hand. The speeded response to painful hits and slowed response to painful misses suggest the reaction times were not driven by the observation of a painful implement per se, but rather the interaction between the implement and the action that was made. These data support the idea that the sensory consequences of others' actions are encoded by the observer and mediate their behaviour. Although these studies provide evidence supporting the motoric effects of viewing others in pain, the possible effects on tactile processing have not been tested directly.

In a closely related area of research, the effects of viewing a threatening image on tactile attention have also been investigated. In a study by Poliakoff, Miles, Li, and Blanchette (2007) participants positioned their hands beneath, and on either side of, a computer monitor. Participants viewed a threatening picture cue (snake or spider) or non-threatening picture cue (mushroom or flower) on the left or right hand side of the monitor, followed by a vibration to their left or right finger. Participants' reaction times were recorded when they made a pedal response to the discrimination between a low and high frequency vibration that had been delivered to their finger. When tactile stimulation occurred 250ms after image onset, participants were faster to respond in congruent trials (visual and tactile stimulation was on the same side of the screen) when a snake was presented, compared to non-threatening images. Interestingly, these effects were not found for the spider stimuli, possibly due to participants having a greater fear of snakes than spiders. These results suggest that viewing a sufficiently threatening image captures tactile attention, speeding the processing of tactile stimuli in the same spatial location.

Van Damme, Gallace, Spence, Crombez, and Moseley (2009) extended the findings of Poliakoff et al. (2007) by asking participants to complete a temporal order judgment (TOJ) task of both tactile and auditory stimuli. The authors added the auditory task to investigate the modality specificity of the effects reported by Poliakoff et al. (2007). Participants viewed images containing physical threat (such as hand brandishing a knife, and a hand close to a meat slice), general threat (including more distant threat, such as a ship sinking and a jet exploding), or no threat (for example, a flower, a boat, and a bus), displayed on either the left or right hand side of a computer monitor. In separate blocks, participants judged which tactile stimulus delivered to their left and right hand, or auditory stimuli emitted from speakers at either side of the monitor, occurred first. It was predicted that, if the effects of viewing threat were modality specific, touch perception would be affected more than auditory perception in the physical threat condition. In contrast, if the effects of viewing threat were due to general attention effects, then both auditory and tactile perception would be mediated by the physical threat condition. The results showed that participants' point of subjective simultaneity (PSS; analogous to bias) was greatest when tactile stimulation followed physical threat pictures, decreasing for general threat pictures, with the lowest PSS for neutral images. In contrast, auditory PSS was greatest for general threat pictures, with lower PSS for physical and neutral pictures. The analysis of just noticeable differences (JNDs) only revealed a main effect for the picture content, with threatening pictures having larger JNDs (analogous to sensitivity) than non-threatening pictures. The authors suggest the data supports a modality-specific shift in attention when viewing physically, compared to general, threatening stimuli. Interestingly, the results also replicate and extend the findings of Johnson et al. (2006) who demonstrated a bias to report touch, when tactile and visual stimuli are combined. Van Damme et al. (2009) demonstrate that vision of physical threat biases tactile detection in addition to the bias caused by a simple visual stimulus. The experiments in this chapter aimed to extend these findings from viewing threat, to the effects of viewing others in pain on tactile processing.

Taking into account previous research, the studies in this chapter were designed to: i) differentiate between a bias to report touch and sensitivity to report touch during the observation of others in pain, ii) investigate the specificity of any observed effects, testing both tactile and auditory modalities, iii) generalise the effects from the detection of ambiguous tactile stimuli to above threshold stimuli, and finally iv) control for alternative attentional accounts of our findings (such as those provided by Van Damme et al., 2009).

In a series of four experiments, participants viewed two-frame sequences of a hand approaching and grasping or avoiding, painful and non-painful objects, whilst detecting tactile or auditory stimuli. In contrast to previous experiments investigating pain perception, rather than the hand being attacked by implements, participants viewed a hand reach forward and grasp the painful objects.

3.3 Experiment 2. The effects of viewing others in pain on the detection of threshold level tactile stimulation

In this experiment, we directly tested whether viewing someone else in pain mediates an observer’s ability to detect touch. Using a modified version of the imaging paradigm utilised by Morrsion et al. (2012), participants detected a vibrotactile stimulus delivered to their right index finger whilst observing a hand either approach and grasp, or withdraw from, potentially painful and non-painful objects. Tactile stimulation occurred 150ms after the onset of the action frame, when the hand either grasped or withdrew from the object. At the end of each trial, participants judged whether the action they had seen was appropriate or not appropriate. For example a hand grasping an object that would cause pain, such as a cactus, required the response “not appropriate” (see Figure 3.1). By making this judgement, participants had to encode both the action and object properties of the stimuli on a trial-by-trial basis. We decided to use a threshold level of stimulation to have a more sensitive measure of tactile detection performance (see Press et al., 2004). By using an ambiguous stimulus, we were also able to analyse the data according to signal detection theory (SDT).

SDT allows the distinction to be made between a person’s ability to detect a stimulus, and a person’s likelihood to report a stimulus (see Section 3.3.1).

Experiments investigating the role of threat on tactile attention might predict that viewing a painful object would enhance or bias tactile detection, regardless of the action performed by the hand (see Van Damme et al., 2009). In contrast, imaging studies have shown selective activation of somatosensory cortical regions during pain evoking actions, when a hand grasps a painful object, rather than merely viewing the pain-evoking object, suggesting the sensory consequences of the interaction are encoded (Morrison et al., 2012; Morrison, Peelen et al., 2007). Hence, the evidence from these studies would suggest that viewing painful grasps may specifically enhance or bias tactile detection.

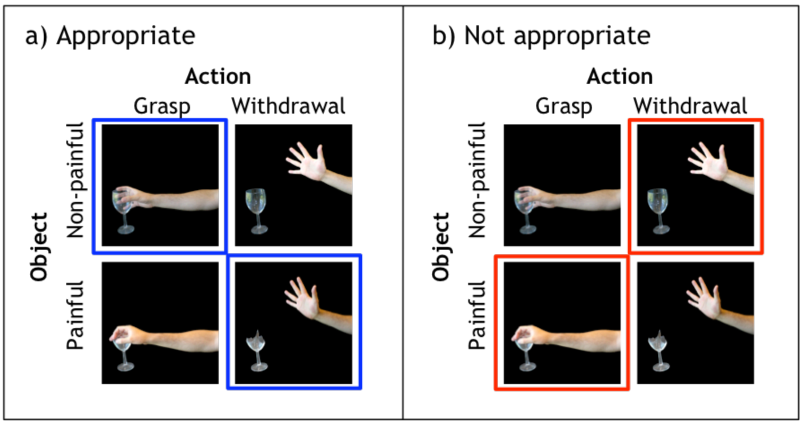
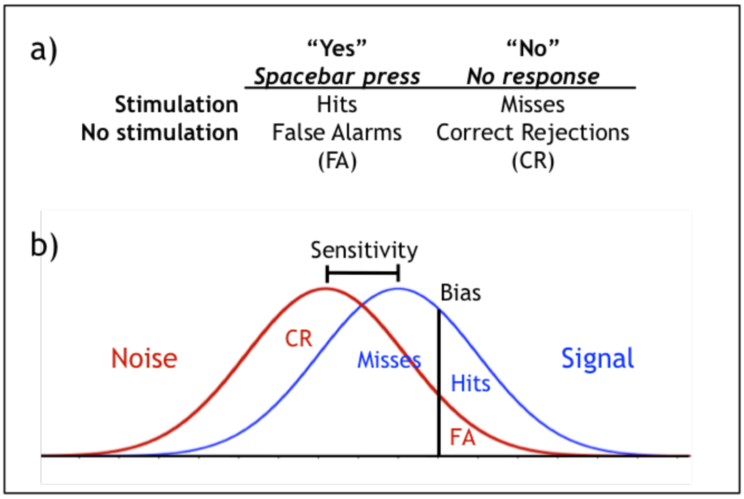


Figure 3.1. Example of a) appropriate (highlighted in blue) and b) inappropriate (highlighted in red) verbal responses.

3.3.1 Signal Detection Theory

Signal Detection Theory (SDT) enables a more detailed analysis of participants’ responses to the detection of a stimulus (Wickens, 2002). Typically, researchers examine the number of correct detections (hits) and erroneous detections (false alarms) in isolation. However, if a participant has a higher level of hits in a particular condition, it is not clear whether this is due to a better ability to detect the stimulus in this condition, or a more liberal criterion to detect the stimulus. In contrast, SDT combines the information from the hits data and false alarm data to discriminate between a person’s sensitivity to detect the stimulus, and their bias to detect the stimulus. SDT can be applied to any situation where there is a degree of uncertainty, i.e. when a signal is to be detected amongst noise. In the current experiment, the signal occurs on trials where the participant receives tactile stimulation (but these trials also inherently contain noise), whereas trials with no tactile stimulation are noise only trials.



a)

	"Yes" *Spacebar press*	"No" *No response*
Stimulation	Hits	Misses
No stimulation	False Alarms (FA)	Correct Rejections (CR)

Figure 3.2. Signal Detection Analysis. a) Participants' responses are coded in one of four categories: hits (correct detections), false alarms (erroneous detections), misses and correct rejections. b) The distribution of signal (blue line) and noise (red line).

The concepts of signal, noise, bias and sensitivity are perhaps best explained pictorially (see Figure 3.2) and by a real-world example (Wickens, 2002). A neurologist looking at a patient's scan has to decide whether the image of the brain they see is normal or contains an abnormality of clinical concern. An experienced neurologist will be adept at making such decisions, being better able to discriminate between normal variants and clinical diagnoses. In contrast, a trainee neurologist may be less able to tell whether what they are looking at is abnormal or not. In this instance, the experienced neurologist has a greater sensitivity than the inexperienced trainee. Both the trainee and experienced neurologist are anxious not to miss any abnormal cases, and are likely to refer cases for further investigation. In this instance, both are less conservative in making a suspected diagnosis, as they would rather have a healthy patient investigated further (resulting in a false alarm) than fail to refer an unwell individual (resulting in a miss).

In order to compute sensitivity and bias measures, the number of hits and false alarms are converted into proportions. The proportion of hits is calculated by dividing the number of correct detections by the number of times the participant did not detect the stimulus (misses). The proportion of false alarms is calculated by dividing the number of erroneous detections by the number of correct rejections. The proportion of hits and false alarms are then used to calculate the bias and sensitivity scores (Wickens, 2002).

a. Sensitivity $= z(H) - z(FA)$ b. Bias $\ln(ß) = -½\,[z(H)^2 - z(FA)^2]$ [3.2]

[3.2] Bias measures were also calculated using the criterion formula, $c = -(z[Hits] + z[FA])/2$, but only ln(ß) are reported in text, in correspondence to Morrison et al. (2012). However, the use of c replicated the effects reported with ln(ß).

It is important to note that sensitivity and bias are independent constructs. As such, two people may have the same sensitivity level, but a different bias to report a stimulus (see example above). The larger the sensitivity score (see Formula a.), the better able a person is to discriminate between signal and noise. The smaller the bias score (see Formula b.), the more conservative a person is to report a stimulus.

3.3.2 Methods

Participants

Participants (*n* = 24, female =15) were recruited through the Bangor University, School of Psychology participation panel. All participants were aged 18 years or over (*M* =26.4, *SD* = 6.1), two participants were left handed, and all participants had normal or corrected-to-normal vision. Participants received course credits or £6 to compensate them for their time. The procedures were approved by the School of Psychology Ethics Committee, Bangor University, Wales[3.3].

Measures

Participants completed a 32-item rating scale questionnaire. Using a 5-point Likert scale (1 = *not at all* to 5 = *very much*), participants were asked to rate each of the 16 objects they would see during the experiment on how painful they imagined it would be to grasp the object, and to what degree they judged this from their own experience. The ratings task was designed to engage participants with the painfulness of the objects, and familiarise them with each of the stimuli prior to the main experiment.

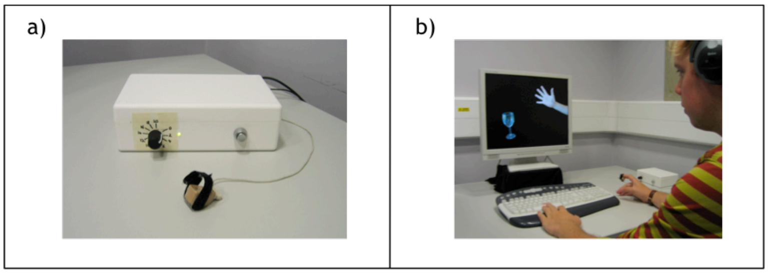


Figure 3.3. a) Tactile stimulation device (custom built), including Oticon bone conductor and manually operated variable transistor. b) Experimental set-up. Participants wore earplugs and ear protectors during tactile detection task.

[3.3] Unless stated otherwise, the recruitment, compensation, and ethical procedures remained the same for all experiments in this thesis.

Apparatus

The stimuli were presented using Presentation (www.neurobs.com) on 3.2 Ghz Pentium computer running Windows XP. The tactile stimulator, an Oticon BC462 bone conductor, was attached to the tip of the participant's right index finger with adjustable tape (see Figure 3.3). The stimulation was a 200 Hz sine wave, overlaid with white noise, lasting 50 ms. The first and last 10ms were faded in and out to prevent sharp transients [3.4]. Participants wore earplugs to prevent them from hearing the tactile stimulation.

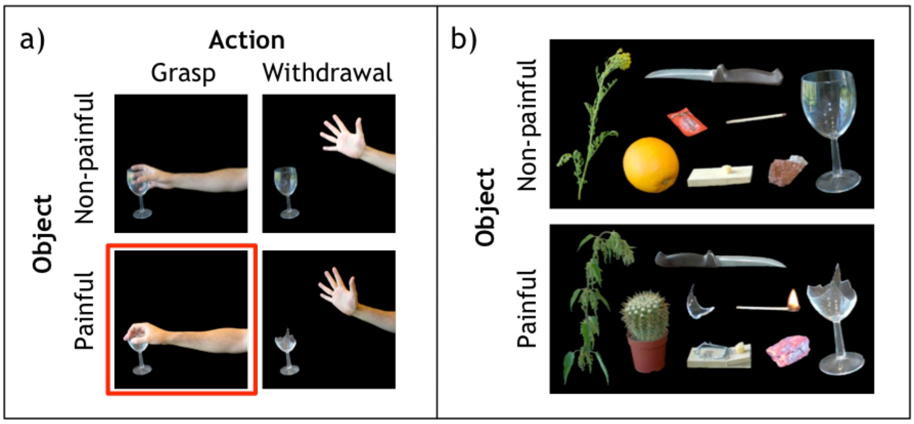


Figure 3.4. a) Example of the four experimental conditions. From top left to bottom right: grasping a non-painful object, withdrawing from a non-painful object, grasping a painful object, and withdrawing from a painful object. The red square highlights the only condition that would result in pain for the actor. b) Experimental stimuli. Non-painful objects: a non-painful plant, knife (handle facing the actor), tomato sauce sachet, orange, unlit match, wooden board with cheese on, a stone and an intact wine glass. Painful objects: a stinging nettle, knife (serrated blade facing the actor), shard of glass, cactus, lit match, loaded mousetrap, hot coal, and a broken wine glass.

Stimuli

Each participant viewed a hand approach and grasp, or withdraw from, eight potentially painful and eight non-painful objects (see Figure 3.4).

Design and Procedure

Participants were seated in a dimly lit room facing a colour monitor at a distance of 60 cm (see Figure 3.3). Participants first completed the 32-item rating scale and then inserted the earplugs and attached the stimulation device to the tip of their right index finger. Participants rested their right arm on the table in front of them, palm facing inwards. A calibration was performed to find the participants approximate detection threshold of the tactile stimuli. The tactile stimuli to be detected in the main experiment were delivered in a constant stream, every 1000 ms. Stimulation began at the lowest intensity and was slowly

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[3.4] Unless stated otherwise, the measures and apparatus remained the same for all experiments in this thesis.

increased until the subject reported to reliably feel the tactile stimuli. This threshold was then validated in a simple tactile detection task lasting for about three minutes. Participants were instructed to press a space bar whenever they detected the stimuli. To match the visual input to the main experiment, participants were instructed to look at their own hand during this procedure. 60 tactile stimuli were delivered in a constant train, every 1500 ms, with 36 null trials randomly interspersed. Stimuli were delivered at 90%, 88%, 86%, 84% and 82% of the threshold intensity established in the first calibration session. The experimenter then analysed the detection probabilities across these intensities. When the data showed a decrease of accurate detection at 90% stimulus intensity to below chance performance at 82% stimulus intensity, the main experiment began. Performance at 82% stimulus intensity was, on average, 19%, whereas at 90% stimulus intensity, participants accurately detected 90% of the tactile targets. If no such decrease was detectable, a new calibration session was performed.

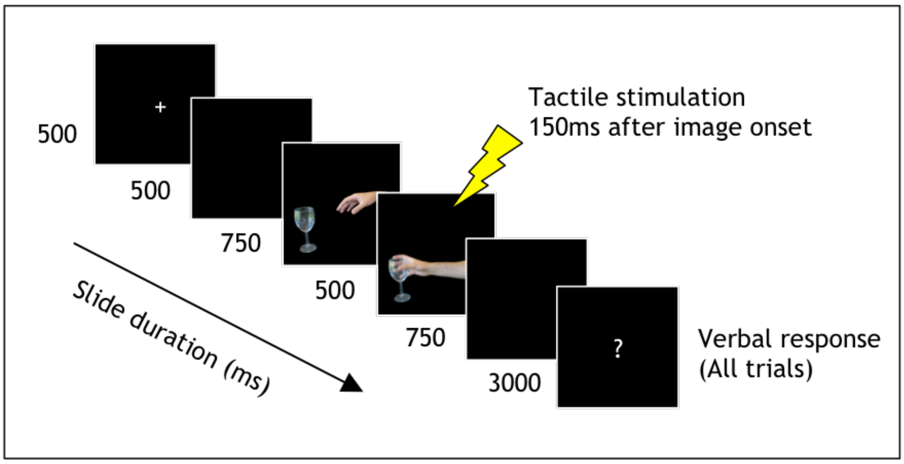

Figure 3.5. Schematic of a trial (6000ms total duration). Participants made a spacebar press in response to the detection of a tactile stimulus. Participants made a verbal response at the end of each trial.

The main experiment began with a computer-driven instruction and a short training phase of 32 trials, which was repeated until the experimenter was satisfied that the task was understood. Participants viewed two frame sequences of a hand either approach and grasp, or withdraw from, painful and non-painful objects in a randomised order (see Figure 3.1). Tactile stimulation occurred 150 ms after the onset of the second frame (where the hand performed the action) on 50% of the 320 trials (80 trials per condition). Stimulation was delivered at 90%, 88%, 86%, 84% and 82% of the stimulation threshold established in the first calibration session. Participants were instructed to press the spacebar with their left hand when they detected tactile stimulation. No error feedback was given, but the instruction emphasised accuracy over response speed. At the end of each trial, regardless of whether there was stimulation or not, participants judged the appropriateness of the seen action when a question mark appeared on the screen by making a verbal response (see Figure 3.1). The experiment lasted for about 45 minutes. During this time the experimenter remained in the room, and paused the experiment upon the participant's request.

3.3.3 Results

We removed pre-emptive reaction times (< 100ms) and reaction times slower than 2500 ms (< 1%) from the analysis. One participant's data was excluded due to failure to feel the stimulation device during the main experiment.

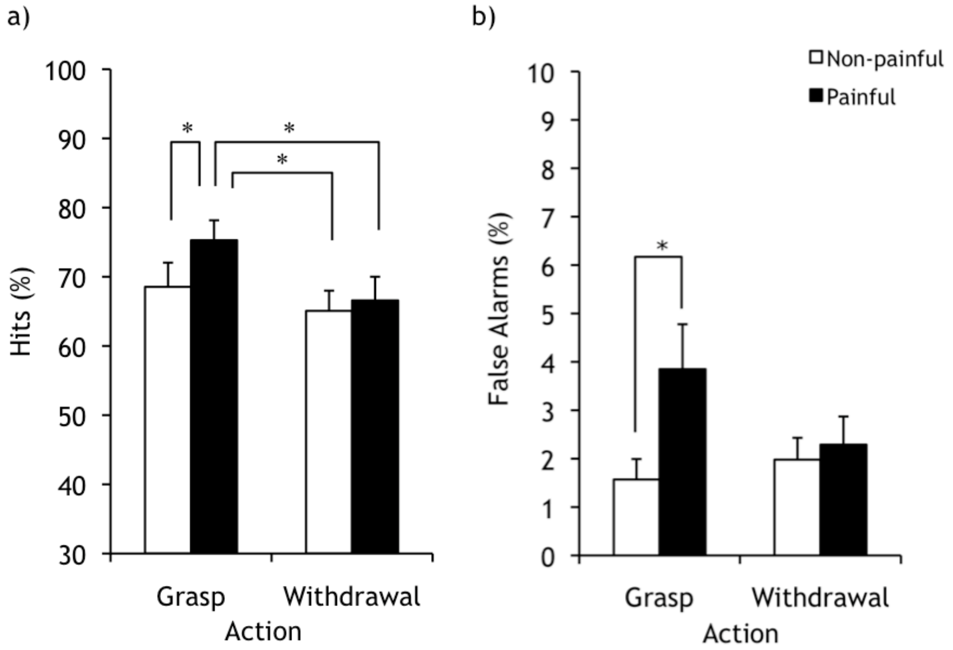

Figure 3.6. a) Mean correct tactile detections (hits). b) Incorrect tactile detections (false alarms). *Significant difference between means ($p \leq .01$). Error bars represent +1 SEM.

Detection rates. The percentages of correct detections (hits)[3.5] were entered into a repeated measures analysis of variance (ANOVA) with the factors action (grasp/ withdrawal) and object (painful/ non-painful). There were main effects of action, $F(1,23) = 31.42$, $p < .001$, $\eta^2_p = .58$, and object, $F(1,23) = 15.37$, $p = .001$, $\eta^2_p = .40$, and a significant interaction between both factors, $F(1,23) = 5.61$, $p = .027$, $\eta^2_p = .20$ (see Figure 3.6a). Post-hoc t-tests showed that participants responded more often to tactile stimuli when the model grasped a painful object compared to a neutral object ($p < .001$); for withdrawals there was no

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[3.5] To reduce the effects of VET in the main experiment, participants were asked to view their own hand during the calibration procedure. Despite this, hit rates were greater than threshold level detection in the main experiment. This is most likely due to the temporal congruency effect of the presentation and delivery of visual and tactile stimuli, which did not occur in the thresholding procedure.

difference between the two object types (*p* = .370). The analysis of the false alarms revealed a similar pattern (see Figure 3.6b). There was no main effect of action, $F < 1$, but a main effect of object, $F(1,23) = 6.30$, $p = .020$, $\eta^2_p = .22$ and a significant interaction between object and action, $F(1,23) = 5.25$, $p = .031$, $\eta^2_p = .19$. Participants more often erroneously reported stimulation when they saw a hand grasp a painful object than when the hand grasped a neutral object (*p* = .010), but there was no difference between the two object types for withdrawals (*p* = .480).

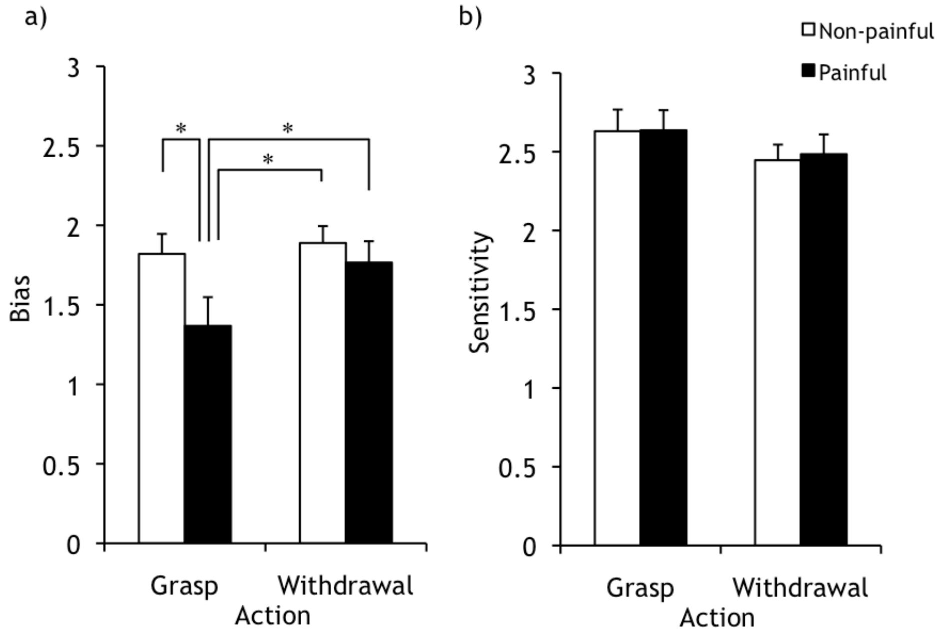

Figure 3.7. a) Mean tactile bias. b) Mean tactile sensitivity. *Significant difference between means (*p* ≤ .01). Error bars represent +1 SEM.

Signal Detection Analysis. [3.6] The analysis of hits and the false alarms suggest that observing painful grasps has a direct effect on the observers' own tactile detection. This effect does not appear to reflect a better differentiation between stimulation and no stimulation, but suggests an increased likelihood to report stimulation, even when there was none. To confirm this effect on bias rather than tactile sensitivity, we performed a signal detection analysis (see Figure 3.7). For the d-prime measure, there was a trend towards a main effect of action, $F(1,23) = 3.62$, $p = .070$, $\eta^2_p = .14$, but no main effect of object and no interaction, $F < 1$, for both. Planned comparisons failed to reveal differences in tactile acuity between the painful grasp condition and any of the other conditions. Effects were, however, found on the bias measure and mirrored the data from the false alarms and hits. There were main effects of

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[3.6] If a participant made no false alarms, false alarms were denoted by 0.5/total number of trials in the experiment to enable a bias and sensitivity measure to be obtained (Stanislow & Todorov, 1999).

action, $F(1,23) = 4.79$, $p = .039$, $\eta^2_p = .17$, and object, $F(1,23) = 7.54$, $p = .012$, $\eta^2_p = .25$, that were qualified by a significant interaction, $F(1,23) = 5.21$, $p = .032$, $\eta^2_p = .19$. Post-hoc t-tests showed that participants had a greater propensity to report tactile stimulation whilst viewing painful grasps, compared to all other conditions ($p < .01$, for all). There were no significant differences between any of the other conditions.

3.3.4 Conclusions

Participants accurately detected more tactile stimuli when viewing touch, compared to no touch conditions, replicating the effects of VET reported by Serino et al. (2008). More importantly, there was an interaction between action and object painfulness in the hits and FA data. Participants detected most tactile stimuli during the observation of others in pain, but also made more erroneous detections in this condition. The relationship between hits and false alarms was explored further with the application of SDT. Similar to findings of Johnson et al. (2006), the "painful grasp effect" was evident in the bias measure: rather than being better able to detect touch, participants were more biased to report touch during the observation of others in pain. These findings, combined with the selective activation of somatosensory cortex during viewing of the same visual stimuli (Morrison et al., 2012), support the notion that viewing others in pain specifically affects tactile processing in the observer. However, it may be the case that viewing others in pain has a more general effect, such that participants' bias to detect a stimulus from any modality may be similarly affected.

3.4 Experiment 3. The effects of viewing others in pain on the detection of threshold level auditory stimulation

Experiment 2 demonstrated that visual stimuli displaying others in pain influence the detection of touch. However, vision can also influence other sensory modalities (Driver & Spence, 2000), such as audition. Experiment 2 alone, therefore, cannot determine whether the effects of viewing others in pain are specific to tactile perception or generalise to other modalities. In a study related to this issue, Van Damme et al. (2009) aimed to investigate the sensory specificity of viewing physical and generally threatening images on the detection of touch and sound. As previously cited, the authors suggest the effects of vision are sensory specific: physically threatening images bias tactile processing, whereas viewing general threat images biases auditory processing. However, the visual stimuli used to test the effects of viewing threat on other modalities contained a potential confound. Not only did the threatening stimuli pertain to general and physical threat, but also to loud noises and no noise respectively. For example, the physically threatening stimuli included a knife and a meat slice near a hand, whereas the general threatening stimuli included a jet exploding and guns. Therefore, reported differences between the effects of vision on auditory and tactile perception may be due to the presence and absence of sound, rather than physical or general threat. As such, the question of whether the effects of viewing threat, or indeed others in pain, are specific to a sensory modality remains unclear.

With consideration of the evidence supporting SI and SII activation during the observation of others in pain (Bufalari et al., 2007; Morrison et al., 2012), and research reporting a causal role for SI activation in touch perception (Fiorio & Haggard, 2005), we suggest that the effects of viewing others in pain are specific to the tactile modality. To test this assertion directly, participants completed a modified version of Experiment 2, by detecting threshold level auditory stimulation, rather than tactile stimulation. If the effects of viewing others in pain are specific to the tactile modality, the “painful grasp effect” reported in Experiment 2 should not be replicated during the detection of auditory stimuli. However, if the effects of viewing others in pain are more general, then the distribution of auditory detections should mirror those recorded during the detection of touch.

3.4.1 Methods

Participants

Participants ($n = 24$, female = 12) were aged 18 years or over ($M = 22.5$), all were right handed, and had normal or corrected-to-normal vision.

Stimuli

The stimuli were identical to Experiment 2.

Design and Procedure

The procedure was the same as Experiment 2, with the exception that participants had to detect the sound created by the tactile stimulator, rather than the somatosensory input. Consequently, earplugs were not used and the tactile stimulation device was not attached to the participant’s right index finger. The tactile stimulator was placed in the same environmental location as the previous experiment, and the participants’ right hand rested in their lap (see Figure 3.8). Participants were instructed to report auditory stimulation by making a spacebar response. There were 80 trials per condition, 50% of which were stimulation trials.

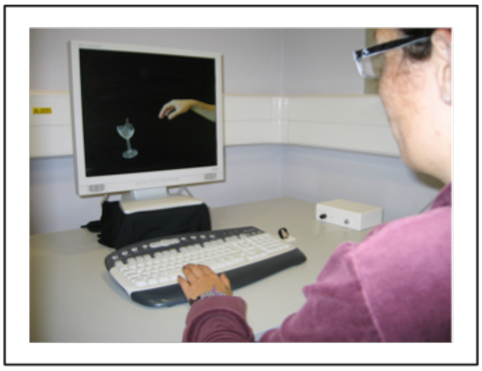

Figure 3.8. Experimental set-up for the auditory control task. Note the stimulation device remained in the same spatial location for both the tactile and auditory detection task.

3.4.2 Results

We removed pre-emptive reaction times (< 100ms) and reaction times slower than 2500 ms (< 1%) from the analysis.

Detection rates. The analysis of accurate auditory detections (hits) revealed a main effect of action, $F(1,23) = 13.97$, $p = .002$, $\eta^2_p = .36$, but no main effect of object and no interaction ($F < 1$, for both). Irrespective of object painfulness, participants detected more auditory stimulation when they observed hands grasping objects, in comparison to hands withdrawing from objects (see Figure 3.9a). The analysis of reported auditory stimulation during null trials where there was no stimulation (false alarms) displayed a similar pattern to the hit data (see Figure 3.9b). There was a trend towards a main effect of action, $F(1,23) = 3.64, p = .069, \eta^2_p = .14$, but no main effect of object and no interaction ($F < 1$, for both). Thus, unlike the processing of somatosensory information, observing neutral and noxious objects did not differentially affect auditory detection rates.

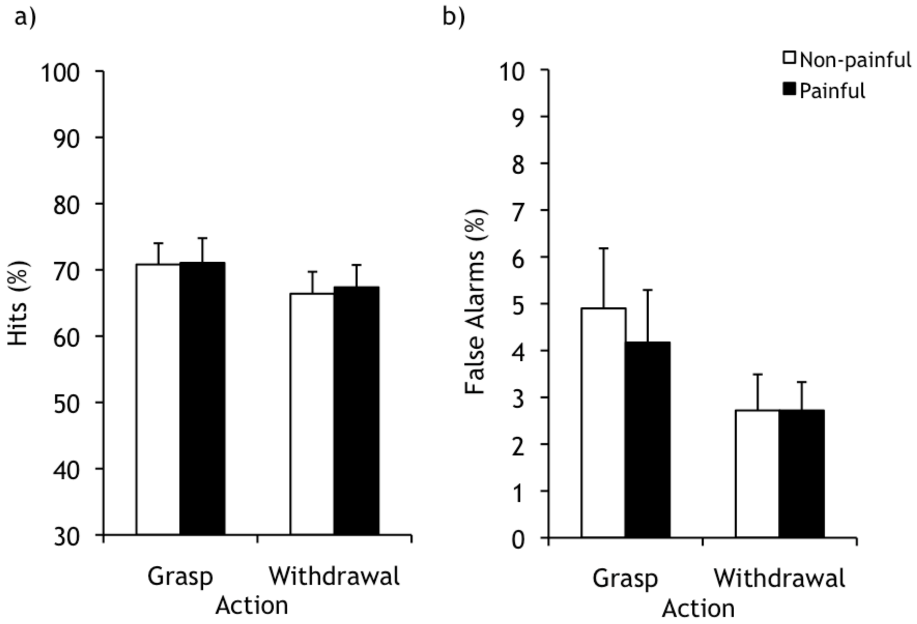

Figure 3.9. a) Mean correct auditory detections (hits). b) Incorrect auditory detections (false alarms). Error bars represent +1 SEM.

Signal Detection Analysis. Further analysis of the hits and false alarms revealed a main effect of action $F(1,23) = 7.90, p = .010, \eta^2_p = .26$, but no main effect of object and no interaction ($F < 1$, for both) for the bias measure (see Figure 3.10a). Participants were more likely to report auditory stimulation when they observed hands grasping objects, rather than withdrawing from objects. Participants' sensitivity to detecting sound was not affected by observing the hand-object interactions ($F < 1$, for action, object, and the interaction between action and object; see Figure 3.10b).

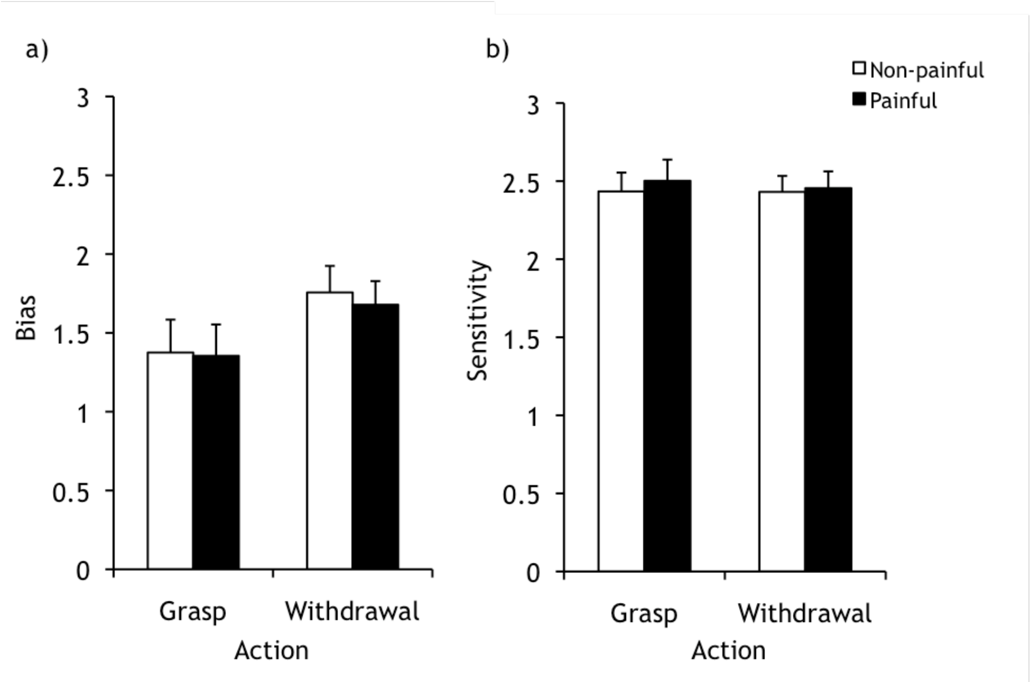

Figure 3.10. a) Mean auditory bias. b) Mean auditory sensitivity. Error bars represent +1 SEM.

3.4.3 Conclusions

In contrast to the detection of tactile stimulation, there were no effects of viewing others in pain on auditory detection. The detection of sound was only affected by viewing the action the hand performed: participants were more biased to report sound during the observation of grasping actions compared to withdrawals. Auditory processing may be influenced by the common association between two objects making contact with each other and the occurrence of sound. The absence of any effects of viewing painful objects or painful actions during the auditory task suggests that the previously reported findings in Experiment 2 are sensory specific.

A recent study by Valentini, Liang, Aglioti, and Iannetti (2012) supports the modality specific effects of viewing others in pain. Participants experienced a painful pricking sensation (delivered by a laser), or an aversive tone (delivered through speakers) whilst viewing a hand being penetrated by a needle or touched by a cotton wool bud. Results from EEG recordings revealed that event-related desynchronisation (implicated in the preparation of action) only occurred when participants received painful cutaneous stimulation, and not aversive auditory stimulation, during the observation of others in pain. Interestingly, source analysis localised the region of the desynchronisation to primary somatosensory cortex, providing further evidence that SI plays a role in processing the direct experience of touch and pain, and viewing the pain of others.

Although Experiment 2 and 3 establish the modality specificity of the “painful grasp effect” it is not clear from these studies how general the effects on touch may be. Experiment 2 utilised a sensitive measure to investigate tactile processing with the use of threshold level tactile stimuli. However, it is important to investigate if the effects of viewing others in pain are only revealed during the detection of an ambiguous stimulus, as suggested by Press et al. (2004), or whether the effects can be generalised to situations where the tactile stimulation is easily detectable.

3.5 Experiment 4. The effects of viewing others in pain on the detection of above threshold tactile stimulation

Press et al. (2004) suggest that the effects of vision on touch only occur during the detection of ambiguous stimuli or difficult tasks. In contrast, Tipper et al. (1998) reported speeded reaction times to above threshold tactile targets when participants viewed their stimulated body part. To differentiate between these two alternative accounts of the effects of vision on touch perception, Experiment 3 required participants to make a speeded response to above-threshold tactile stimuli during the observation of others in pain. Due to the increased saliency of viewing others in pain, we anticipated that we would replicate the “painful grasp effect” reported in Experiment 2, with faster reaction times to the detection of touch during the observation of others in pain.

Experiment 4 was also designed to address a potential attentional confound in Experiments 2 and 3. During the observation of grasp trials, a participant’s attention is drawn towards the object, whereas in withdrawal trials, a participant’s attention is drawn away from the object, to the opposite visual field. Previous research has demonstrated that threatening objects alone can affect tactile processing, without a hand interacting with the object (Poliakoff et al., 2007; Van Damme et al., 2009). Therefore, it is important to distinguish whether our findings are best explained by attention being drawn to the painful object, or, as we assert, the encoding of the sensory consequences when viewing a hand grasp a painful object. To begin to address this issue, the withdrawal action made by the hand was modified to a miss action. During miss trials the hand still avoided contact with the object, but did so by reaching towards and above the object, rather than away from the object (see Figure 3.11a). In this way, during both grasp and miss trials, attention was now drawn to the same side of the screen as the object.

In a modified version of Experiment 2, participants made a speeded response to an above threshold stimulus whilst viewing hands either approach and grasp, or miss, painful and non-painful objects. Due to the change in hand actions, two objects were removed from the visual stimulus set because, even in the miss condition, the hand would still be able to experience pain: heat from a lit match, and direct contact with a tall stinging nettle (see Figure 3.11b).

3.5.1 Methods

Participants

Participants (*n* = 24, female = 18) were aged 18 years or over (*M* = 20.2, *SD* = 4.0), 4 participants were left-handed, and all had normal or corrected-to-normal vision.

Stimuli

Participants' viewed a hand approach and grasp, or miss, six potentially painful and six non-painful objects (see Figure 3.11).

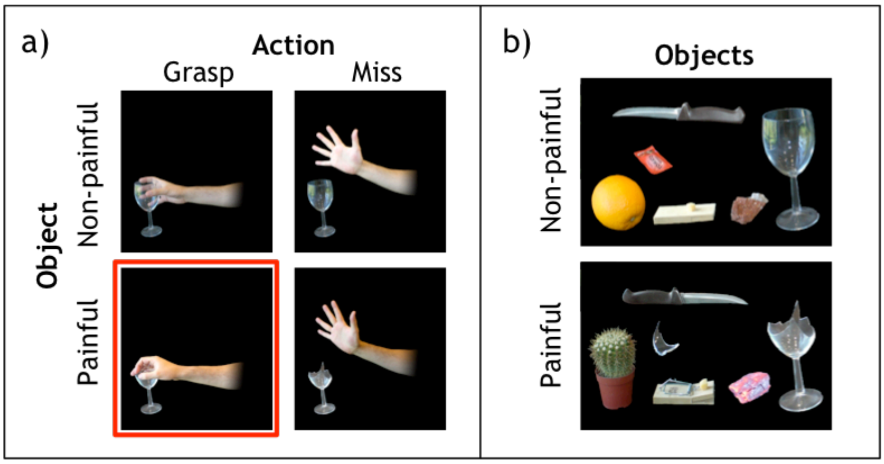

Figure 3.11. a) Example of the four experimental conditions. From top left to bottom right: grasping a non-painful object, missing a non-painful object, grasping a painful object, and missing a painful object. The red square highlights the only condition that would result in pain for the actor. b) Experimental Stimuli. Non-painful objects: knife (handle facing the actor), tomato sauce sachet, orange, wooden board with cheese on, a stone and an intact wine glass. Painful objects: knife (serrated blade facing the actor), shard of glass, cactus, loaded mousetrap, a hot coal, and a broken wine glass.

Design and Procedure

The procedure was similar to Experiment 2. However, no calibration was performed because the tactile target was an above-threshold stimulation, similar to a small vibration. The stimulation device was switched on to familiarise the participant with the tactile sensation and the tactile detection task. Participants were requested to press the spacebar on the keyboard with their left hand as quickly as possible whenever they felt the tactile stimulation. When the experimenter was confident the participant could perform the task correctly, the practise trials for the main experiment began.

The practice trials and main experiment were similar to Experiment 2. However, on stimulation trials, tactile stimulation was always delivered at 90%. Stimulation occurred on 50% of the 240 trials (60 trials per condition).

3.5.2 Results

The hits, reaction times and false alarms data were analysed with three separate 2 x 2 ANOVAs. Pre-emptive detection (< 100 ms) and reaction times slower than 1500 ms were removed from the analysis (<1%). An additional participant was excluded from data analysis due to failure to respond appropriately to the tactile stimulus. As expected, because the stimulation level was above threshold, the analysis of hits data revealed no differences between conditions (*p* > .05, for all).

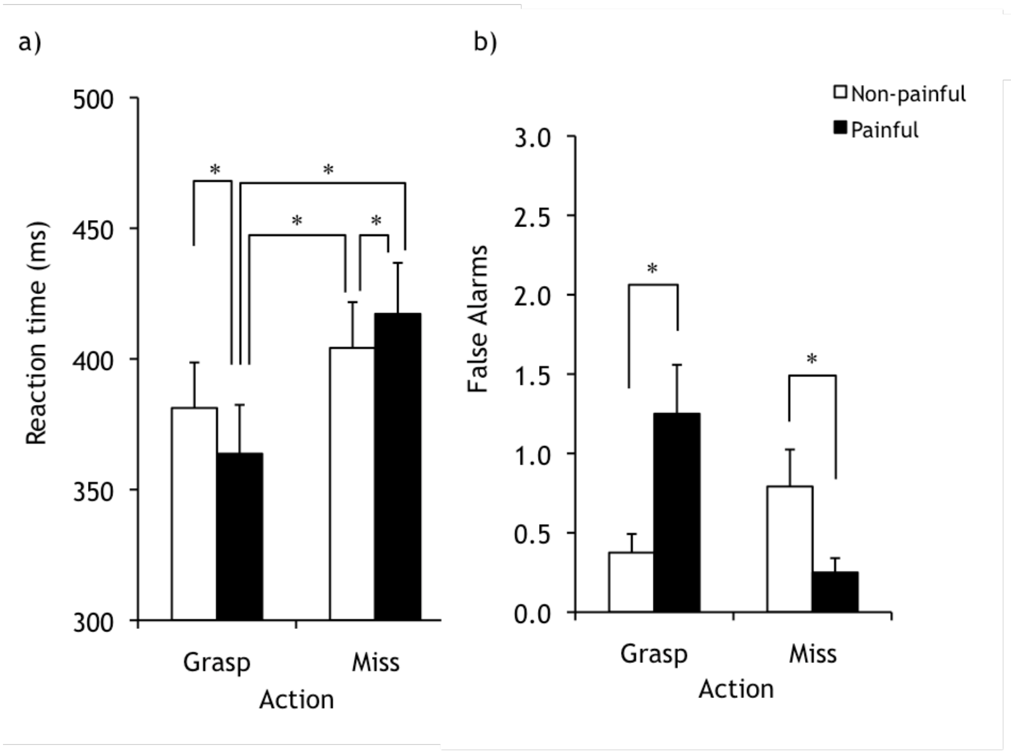

Figure 3.12. a) Mean reaction time for Hits b) Incorrect tactile detections (false alarms). *Significant difference between means (*p* < .04). Error bars represent +1 SEM

Reaction times Unlike Experiment 2, analysis of the reaction times to the speeded detection of the tactile stimulus did not reveal a main effect of object. However, there was a main effect of action on reaction times, $F(1,23) = 22.77$, $p < .001$, $\eta^2_p = .50$, and an interaction between action and object, $F(1,23) = 8.89$, $p = .007$, $\eta^2_p = .28$. Participants were faster to respond to the tactile stimulus when they saw a hand grasping an object ($M = 372.28$ ms), compared to missing the object ($M = 410.72$ ms), regardless of object painfulness. Planned pairwise comparisons were carried out to investigate the interaction between action and object. Participants were fastest to detect touch on their own body when they viewed a painful grasp ($M = 363.74$ ms), compared to all other conditions (p < .035, for all; see Figure 3.12a). In contrast to reaction times during the observation of grasps, participants were actually faster to respond to touch during the observation of neutral misses ($M = 404.21$ ms), compared to painful misses ($M = 417.23$ ms), $p = .032$.

False Alarms The analysis of erroneous detections did not reveal a main effect of action, $F(1,23) = 2.19$, $p = .153$, $\eta^2_p = .09$, or object, $F < 1$. However, importantly, there was a significant interaction between action and object, $F(1,23) = 16.83$, $p < .001$, $\eta^2_p = .42$. Planned comparisons revealed this was driven by more false alarms during the observation of painful grasps, compared to non-painful grasps, $p = .004$, and less false alarms being made during the observation of painful misses, compared to non-painful misses, $p = .025$ (see Figure 3.12b).

3.5.3 Conclusions

Experiment 4 replicated the “painful grasp effect”: participants were fastest to report touch during the observation of painful grasps. As such, the effects of viewing others in pain can be extended from the detection of an ambiguous, to an above threshold tactile stimulus. Interestingly, the false alarm data suggest the speeded response during the observation of others in pain may also be due to a response bias, as most false alarms were made in this condition. Indeed, preactivation of somatosensory cortices during the observation of others in pain may underlie an increased readiness to report touch during the “painful grasp” condition (as evidenced by both speeded reaction times and an increased number of erroneous reports of touch), by ostensibly reducing the sensory threshold necessary to perceive tactile stimulation.

Unlike Experiment 2, the interaction between action and object on reaction times was driven by a difference between object painfulness in both the grasp and miss conditions. Reaction times were fastest for painful compared to non-painful grasps, but slowest for painful compared to non-painful misses. In an experiment exploring the effects of viewing others in pain on motor responses, Morrison, Peelen et al. (2007) also report slower reaction times when participants viewed a painful implement, compared to a non-painful implement, missing a hand. The authors suggest the slowing of responses in painful miss trials may be due to a need for increased inhibitory control in this condition. In the current task, for example, the sensory consequences of an observed action are computed on a trial-by-trial basis. Thus, the observation of a painful object alone is predictive of a potentially painful hand-object interaction. However, in the second frame, when the hand then misses the potentially painful object, any anticipatory response to the perception of pain would be erroneous and consequently inhibited, leading to a comparative slowing of reaction times in this condition.

The replication of the interaction between action and object, and slowed responses during the observation of painful miss trials, argues against an attentional account of the "painful grasp effect". If viewing a threatening or pain-inducing object modulated tactile detection one might expect that, even during the miss trials, an effect of object, albeit a weaker one, would be observed. Importantly, there was no main effect of object in the critical analysis of reaction times; indeed, as previously described, reaction times to painful objects during miss trials are actually slower than reaction times to non-painful actions. Although the findings of Experiment 4 begin to address the possible influence of attention on the tactile effects of viewing painful objects, it may still be the case that viewing a hand touch an object merely draws attention to that object, rather than the participants encoding the sensory consequences of the observed action.

3.6 Experiment 5. The effects of viewing bare and gloved hand actions on the detection of above threshold tactile stimulation

Experiment 5 was designed specifically to differentiate between the two alternate accounts of the "painful grasp effect": i) viewing a hand move toward a painful object draws attention to the painful object which, in turn, affects tactile processing and ii) encoding the sensory consequences of a bare hand grasping a painful object affects tactile processing.

A gloved hand, protected from pain, was added to the paradigm used in Experiment 4. The glove was similar to a gardening glove, but contained Kevlar, a material used in body armour, such as bullet-proof vests. In Experiment 5, participants viewed both bare hands and gloved hands, grasp and miss the painful and non-painful objects whilst detecting above threshold tactile stimulation. If the effects on tactile processing were due to the allocation of attention during grasping trials, the “painful grasp effect” should be revealed during both bare hand trials and gloved hand trials. In contrast, if the effects of viewing others in pain were due to understanding the sensory consequences of an observed action, then the “painful grasp effect” should only be revealed when participants view the bare hand grasp painful objects, as this is the only condition where pain could be experienced.

3.6.1 Methods

Participants

Participants ($n = 36$, female = 26) were aged 18 years or over ($M = 20.8$, $SD = 2.8$), two were left-handed, and all had normal or corrected-to-normal vision.

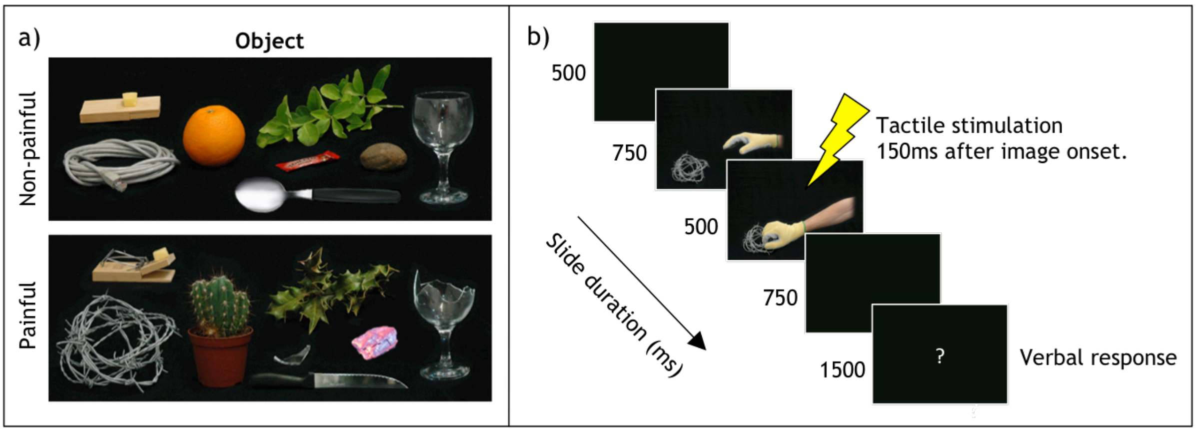

Figure 3.13. a) Experimental stimuli. Non-painful objects: cheese on board, cable, orange, plant, ketchup packet, pebble, spoon and intact glass. Painful objects: mousetrap, barbed wire, cactus, holly, shard of glass, hot coal, knife (serrated blade facing the actor) and broken glass. b) Trial diagram.

Stimuli

Each participant viewed a bare hand and a gloved hand approach and grasp, or miss, eight potentially painful and eight non-painful objects (see Figure 3.13 & 3.14). The photographed objects changed in this experiment for two reasons. Firstly, for practical reasons, some of the originally photographed objects were no longer available to include in this new stimulus set incorporating a gloved hand. Secondly, for experimental control, the stone was changed to a smooth pebble because the fragment of house brick had potentially dangerous sharp edges. Similarly, the knife in the neutral condition was replaced with a spoon to make the distinction between the potential threat of the knife and safety of the spoon explicit. The barbed wire and cable were added to replace the objects that had been removed in Experiment 4.

Design and Procedure

Prior to rating how painful the objects would be to grasp, participants were asked to try on the protective glove that they would see during the experiment. Participants were informed the glove was made of Kevlar (a bullet proof material found in body armour) with the palm covered in leather. Participants were invited to touch the cable in order to experience the glove, but were not allowed to interact with the painful objects due to ethical considerations. However, the experimenter assured the participant that wearing the glove meant grasping the potentially painful objects was a non-painful experience.

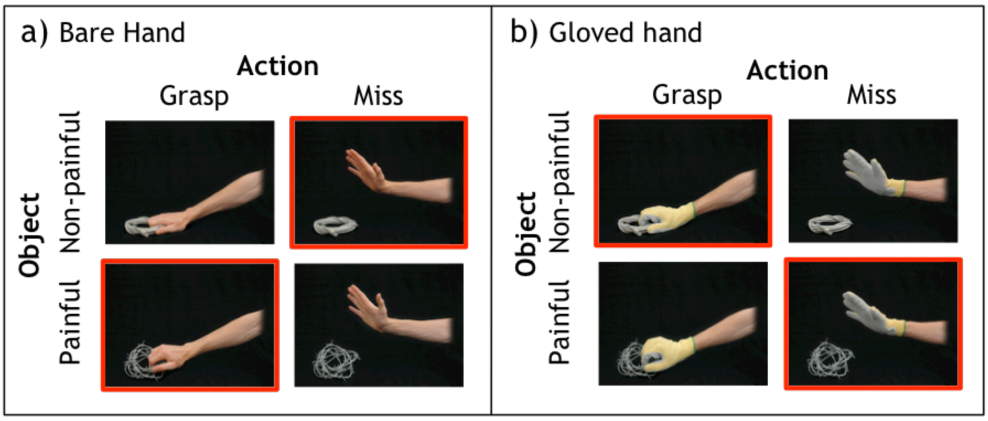

Figure 3.14. The 8 experimental conditions. Red squares highlight the conditions requiring the verbal response "inappropriate" for a) bare hands, and b) gloved hands.

The procedures for attaching the stimulation device were the same as Experiment 4. Participants performed 32 practice trials viewing the bare hand, and 32 practice trials viewing the gloved hand. The order in which glove and hand blocks were presented was counterbalanced between participants. The proportion of stimulation to no stimulation trials was modified to account for the extra conditions created by the addition of the gloved hand stimuli. Stimulation was delivered on 24 of out 32 trials (75%) per condition. As in Experiment 4, participants made a speeded response to the detection of an above threshold tactile stimulation. Participants completed two blocks of hand trials and two blocks of glove trials in an ABAB design[3.7].

Participants made the same appropriateness judgement as in previous experiments for the bare hand, however the contingencies for an appropriate action were reversed for the

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[3.7] A blocked design was chosen because pilot data showed that the gloved hand condition, in a trial-by-trial randomisation, influenced the bare hand condition, leading to a failure to replicate the previously reported "painful grasp effect". Chapter 4 addresses directly the issue of influential companions.

protected gloved hand (see Figure 3.14). When the gloved hand grasped a non-painful object or when it missed a painful object, the correct response was "inappropriate", whereas grasping a painful object or missing a neutral required the response "appropriate". The rationale for these responses was that wearing the protective glove was specifically for removing painful objects from the environment, and not appropriate for non-painful objects. In contrast, a bare hand would be vulnerable to painful objects and therefore should avoid these. The verbal response task was therefore more difficult in this experiment than previous experiments. To control for this and potential carry-over effects from one block to the next, an additional 8 trials at the beginning of each block were included, but later discarded from the analysis.

3.6.2 Results

Pre-emptive detection (< 100 ms) and reaction times slower than 1500 ms were removed from the analysis (<1%). An additional four participants were excluded from data analysis due to failure to respond appropriately to the tactile stimulus. The hits, reaction times and false alarms data were analysed with three separate 2 x 2 x 2 ANOVAs, with the factors of hand (bare/ gloved), action (grasp/ miss) and object (painful/ non-painful).

Hits The analysis of correct detections revealed a main effect of hand, $F(1,35) = 5.49$, $p = .025$, $\eta^2_p = .14$. Participants detected more tactile stimuli when they viewed a bare hand interact with the objects ($M = 23.34$) compared to the gloved hand ($M = 23.62$). All other main effects and interactions were non-significant ($F < 1$, for all).

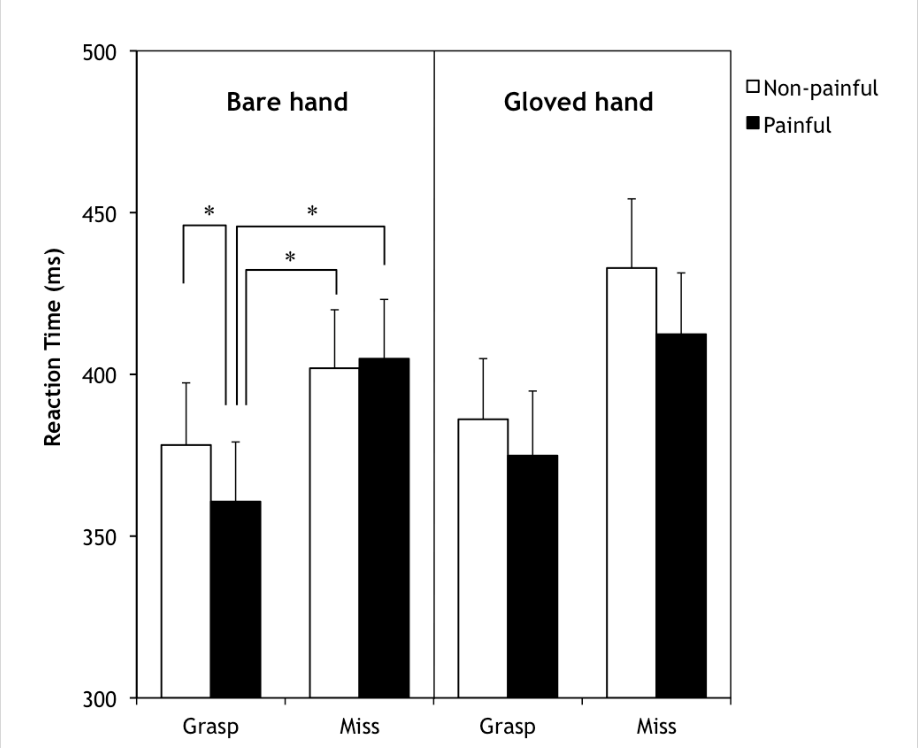

Figure 3.15. Mean reaction times to the detection of touch when participants viewed the bare hand and the gloved hand interact with the objects. *Significant difference between means ($p < .03$). Error bars represent +1 SEM

Reaction times Participants were faster to respond to the detection of touch when they viewed a bare hand grasp objects ($M = 386.40$ ms) compared to the gloved hand ($M = 401.57$ ms), $F(1,35) = 4.79, p = .035, \eta^2_p = .12$. Participants were also faster to report touch during the observation of grasps ($M = 374.96$ ms) compared to misses ($M = 413.01$ ms), replicating the main effect of action reported in previous experiments, $F(1,35) = 38.55, p < .001, \eta^2_p = .52$. The painfulness of the object affected participants' reaction times, $F(1,35) = 4.47, p = .042, \eta^2_p = .11$. Reactions times to the detection of touch were faster when participants viewed painful objects ($M = 388.21$ ms) compared to non-painful objects ($M = 399.76$ ms). There was no interaction between hand and action, or hand and object ($F < 1.5$, for both). Interestingly, the interaction between action and object, indicative of the "painful grasp effect", was not significant ($F < 1$). However, the interaction between hand, action and object, $F(1,35) = 4.96, p = .032, \eta^2_p = .12$, suggested that the effects of observing painful and non-painful actions may be mediated by the viewed hand (bare/ gloved; see Figure 3.15). Indeed, when we performed separate 2 x 2 ANOVAs with the factors of action (grasp/ miss) and object (painful/ non-painful) the results differed between the two hand conditions.

The analysis of the reactions times to the detection of touch when viewing only bare hands replicated the effects reported in Experiment 4. There was a main effect of action, $F(1,35) = 19.39, p < .001, \eta^2_p = .11$, and no main effect of object ($F < 1.5$). Crucially, the interaction between action and object was significant, $F(1,35) = 5.74, p = .022, \eta^2_p = .14$. Pairwise comparisons revealed that the painful grasp condition was significantly different to all others ($p < .023$, for all). There was no difference in reaction times between painful and non-painful misses ($p = .685$). In contrast, when participants viewed a gloved hand interact with the objects, only a main effect of action, $F(1,35) = 37.13, p < .001, \eta^2_p = .52$, and a main effect of object , $F(1,35) = 5.09, p = .030, \eta^2_p = .13$, similar to those reported in the main analysis, were revealed. Importantly, the interaction between action and object was not significant, $F < 1$. Thus, the "painful grasp effect" was only replicated during the observation of bare hands grasping painful objects, and not gloved hands which were protected from pain.

False alarms There was no difference in the number of erroneous detections when participants viewed the bare hand or the gloved hand, $F < 1$. However, participants did make more false alarms when viewing grasping actions ($M = 0.93$) compared to miss actions ($M = 0.49$), $F(1,35) = 11.64, p = .002, \eta^2_p = .25$. Participants also reported detecting touch when there was none, more often when they viewed a painful object ($M = 0.83$) compared to a non-painful object ($M = 0.58$), $F(1,35) = 4.85, p = .034, \eta^2_p = .12$. Similar to the reaction time data, there was no interaction between action and object, *F*(1,35) = 1.86, *p* = .181, $\eta^2_p = .05$. There was a trend towards an interaction between hand, action, and object, *F*(1,35) = 3.13, *p* = .086, $\eta^2_p = .08$ (see Figure 3.16).

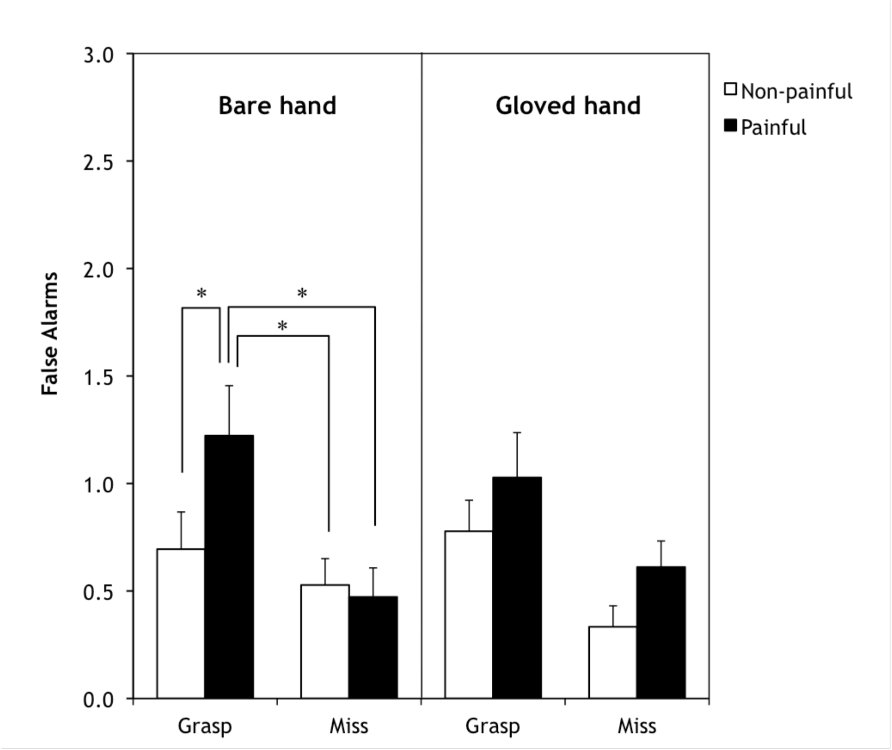

Figure 3.16. Mean number of false alarms (erroneous detections of touch) when participants viewed the bare hand and the gloved hand interact with the objects. *Significant difference between means (*p* < .02) based on exploratory analyses. Error bars represent +1 SEM

We explored the interaction between hand, action, and object further because we predicted that viewing the bare hand and the gloved hand might have differential effects on behaviour. Indeed, the results of two separate 2 x 2 ANOVAs of the false alarm data revealed similar results to those reported for the reaction times. When viewing bare hands, participants made more false alarms during grasp trials, *F*(1,35) = 6.93, *p* = .013, $\eta^2_p = .17$, but were not significantly affected by the observation of painful objects per se, *F*(1,35) = 3.09, *p* = .088, $\eta^2_p = .08$. However, the interaction between action and object was significant, *F*(1,35) = 5.44, *p* = .026, $\eta^2_p = .14$. Participants made more false alarms when they viewed a bare hand grasp a painful object, compared to all other conditions (*p* < .014, for all). There was no difference between the number of false alarms made when participants viewed the bare hand miss painful and non-painful objects (*p* = .729). In contrast, when participants viewed a gloved hand interact with the objects, only a main effect of action, *F*(1,35) = 9.91, *p* = .003, $\eta^2_p = .22$ and object was revealed, *F*(1,35) = 4.44, *p* = .042, $\eta^2_p = .11$. The interaction between action and object was non-significant, *F* < 1.

3.6.3 Conclusions

The results of this study demonstrate that participants' reaction times to the detection of touch are differentially affected by viewing a bare hand and a gloved hand interact with objects. Importantly, the "painful grasp effect" was only revealed when participants viewed the bare hand perform actions. Exploratory analyses of the false alarm data support this interpretation of the data. Participants made most false alarms when they viewed a bare hand grasping painful objects. As such, the "painful grasp effect" does not appear to be caused by the hand drawing attention to the painful object, but rather, the encoding of the sensory consequences of an observed action.

3.7 Discussion

The studies in this chapter demonstrate, for the first time, that viewing others in pain affects an observer's own behaviour. Interestingly these effects are sensory specific, mediating tactile, but not auditory perception; participants were more biased to report a threshold level tactile stimulus, and were faster to report an above threshold tactile stimulus, when viewing others in pain. Importantly, the "painful grasp effect" cannot merely be attributed to attention being drawn to the painful objects during the grasping trials. Rather, the sensory consequences of viewing a hand interacting with a painful object are encoded by the observer.

Johnson et al. (2006) suggest that the effects on tactile detection during the observation of visual information are due to learnt associations between vision and touch. McKenzie, Lloyd, Brown, Plummer, and Poliakoff (2012) provide evidence for the tactile biasing effects of learnt associations between vision and touch. McKenzie et al. (2012) demonstrated that even when participants had no prior experience (within an experiment) of touch and light occurring in synchrony, participants were more likely to report touch in light present, than light absent trials, suggesting a predisposition to anticipate the two stimuli occurring together. Indeed, parts of the body that are viewed more frequently, such as the face, exhibit greater facilitation effects of vision on tactile detection, than those body parts that are not seen, such as the back of the neck (Tipper et al., 2001). This difference in facilitation of touch is presumably because touch of the face (such as removing an eyelash from one's eye, or adjusting one's hair) is more often combined with vision of the face through a reflection in a mirror, or viewing others make a similar gesture. In comparison, touch of the neck is rarely, if ever, combined with vision of the back of the neck. Important to note is that the visual stimuli in our experiment do not provide information about the occurrence of the tactile stimulus, beyond the temporal window in which a tactile stimulus could occur. Therefore any associations between viewing others in pain and the expectation of touch were not beneficial to the detection of touch, but merely biased the observer to report touch during painful grasp trials.

A bias to report touch during the observation of others in pain is indexed by an increased number of erroneous tactile detections in this condition. The increased number of false alarms may reflect an anticipation of touch based on prior experience. Heyes (2010) suggests that when associations between vision and actions are strong, prediction of the action outcome may occur. In such a situation, given the available visual information, an observer can utilise their own motor experience to best guess the outcome of an observed action. This idea is in line with motor control mechanisms which incorporate internal forward models, enabling the consequences of an action to be predicted (Wolpert & Flanagan, 2001; see Chapter 6). Indeed, participants made most false alarms when they viewed hands grasping painful objects – the condition in which the expectation of a tactile stimulus would be most salient.

Alongside forward models of action understanding, viewing others in pain may have primed participants to make a response, in a similar manner to visuomotor priming. For example, when participants were instructed to reach forward and grasp a bar in a particular orientation, reaction times to initiate the movement were faster when a visual cue and the actual bar were in the same orientation (Craighero, Fadiga, Umiltà, & Rizzolatti, 1996). Similarly, Kirwilliam, and Derbyshire (2008) report that participants were more biased to report heat and pain on their own forearm following priming with emotional images inferring pain (for example, a bruised face). In the current study, participants may have been primed to respond to touch when viewing grasping actions compared to misses, and more so during the observation of a painful grasp. Indeed, faster reaction times may be indicative of a facilitation to report touch due to priming. However, the increased number of false alarms during the observation of others in pain may favour the predictive coding account of shared representations of pain.

Although some studies posit that a prediction of touch should lead to an attenuation of touch (Blakemore, Wolpert, & Frith, 1998), possibly reducing in the number of false alarms, Wolpert and Flanagan (2001) note that “prediction allows us to filter sensory information, attenuating unwanted information or highlighting information critical for control” (p.R730). In the context of observing others in pain, highlighting information relevant to somatosensation would appear to be adaptive (Avenanti et al., 2009). Similarly, Johnson et al. (2006) suggest that a bias arises from "strategic sensory encoding processes" (p. 398) promoting the feeling of touch when receiving ambiguous stimuli. However, it is unclear how the feeling of touch is "promoted": this bias could occur at the decision making level, or result in a "hallucination" of touch. By combining fMRI with a behavioural paradigm that promotes the occurrence of erroneous tactile detections, Lloyd, McKenzie, Brown, and Poliakoff (2011) provide evidence in support of the former explanation. Cortical activity in higher level processing regions, including the posterior cingulate cortex, but not primary somatosensory cortex, was associated with participants making false alarms. However, the authors do suggest that the lack of predicted SI activation may be due to the limited number of false alarms made by the participants in their study.

Although the underlying mechanisms that promote speeded reaction times and a bias to report touch remain unclear, the behavioural responses appear to be adaptive. For example, hypervigilance to touch in a threat prone environment may speed avoidance behaviours, protecting the observer from harm. If shared representations of touch are truly adaptive for self, one might expect these to occur automatically. Indeed, proponents of the direct matching hypothesis focus on the importance of relatively automatic, bottom-up processing (Rizzolatti & Gallese, 2001). However, the experiments in this chapter cannot provide evidence in support of automatic encoding: on a trial-by-trial basis participants had to attend to the action and object properties in the visual stimulus in order to accurately judge whether the action they had just seen was appropriate or not appropriate.

Interestingly, the results of Experiment 5 suggest that there may be a role for top-down modulation of the "painful grasp" effect. Reaction times to the detection of a tactile stimulus were differentially affected by viewing a hand protected from pain and a bare hand interact with painful and non-painful objects, despite the action and object information remaining the same in both conditions. Lamm et al. (2007) provide more striking evidence for the role of top down modulation in shared representations of pain. Participants viewed a hand being penetrated by a needle and an anaesthetised hand penetrated by a needle, whilst they were scanned. The syringe attached to the needle varied between the hand experiencing pain and the numbed hand condition to enable participants to discriminate between the two stimuli. Activity in cortical areas associated with pain processing differed even though the image of the needle penetrating the hand was identical in the pain and no pain condition. Region of interest analysis revealed increased activity in the anterior insula and midcingulate cortex whilst observing the pain condition, with a trend for decreased activity in primary somatosensory cortex when viewing the anaesthetised hand. Although top-down modulations may be accounted for by evolved theories of mirror neuron development and associative learning accounts, different cortical responses to visually identical stimuli pose a problem to the automaticity of mirroring suggested by the direct-matching hypothesis.

Although the research carried out by Lamm et al. (2007) highlights the role of higher level processing during the observation of others in pain, the results do not pertain to the automaticity of such effects. Participants were asked to judge the intensity or unpleasantness of the visual stimuli at the end of every trial, drawing attention to the painful aspect of the images on a trial-by-trial basis, similar to the studies in the current chapter. Therefore, it is not possible to discount the notion that mirroring does occur automatically, but is mediated by top-down factors. These issues are addressed directly in Chapter 4.

Chapter 4

Do task demands mediate the behavioural effects of viewing others in pain?

4.1 Summary

The experiments in Chapter 3 demonstrated that viewing others in pain affects an observer's tactile processing, speeding the detection of touch and biasing an observer to report touch on their own body. However, the automaticity of the "painful grasp effect" is not known, as participants were required to judge the appropriateness of the observed action at the end of every trial. In Experiment 6, participants passively viewed the hand-object interactions, responding to occasional catch trials and the detection of touch with a button press response. No effects of viewing painful actions on tactile detection were observed, suggesting that mere observation of others in pain is not sufficient to evoke the "painful grasp effect". However, participants were faster to respond to the tactile stimulus when they viewed hands grasping objects, compared to miss actions.

The role of the appropriateness judgement task in mediating the "painful grasp effect" was investigated further in Experiment 7. Participants made one of four verbal judgements at the end of every trial to assess the individual contribution of action understanding and object knowledge on reaction times to the detection of touch. In a within-subjects design, participants judged the appropriateness of the action (appropriate/ not appropriate), the object (painful/ not painful), the action performed by the hand (contact/ no contact), or passively viewed the stimuli. Surprisingly, unlike the apparent differences in behaviour reported in Experiments 5 and 6, there was no effect of task on reaction times in Experiment 8. Further, the "painful grasp effect" typically revealed during the appropriateness judgement task failed to replicate. However, exploratory analyses demonstrated that the experiment had been affected by the influence of every task on each other – the influential companions problem highlighted by Poulton (1982).

Experiment 8 was designed to directly investigate the effects of making an action judgement or object judgement on reactions times to the detection of touch. Participants who made an action judgement showed more of an action effect than those judging the painfulness of the objects, but in neither task was the "painful grasp effect" revealed. The results of Experiment 8 were compared against the same judgement tasks in Experiment 7 to assess the role of influential companions on reaction times.

4.2 Introduction

The experiments in Chapter 3 demonstrated that viewing others in pain biases an observer to report touch on their own body, speeding reaction times to the detection of touch. These novel findings extend the possible functional role of shared representations of pain from understanding others, to adaptive behaviour change for self. However, the data do not enable a distinction to be made between mirror neuron theories and associative learning accounts of such processes. Further research examining the automaticity of the "painful grasp effect" may help to tease the two accounts apart.

Theories that posit a primary role for mirror neurons in understanding others' actions suggest that "…every time we are looking at someone performing an action, the same motor circuits that are recruited when we ourselves perform that action are concurrently activated" (Gallese & Goldman, 1998, p.495), implying that shared action representations occur automatically [4.1]. Indeed, an elegant study by Hasson, Nir, Levy, Fuhrmann, and Malach (2004) is suggestive that mere observation of actions does activate cortical regions involved in the performance of actions. The authors utilised a novel paradigm whereby participants passively viewed a half hour segment of the film "The Good, the Bad, and the Ugly", and were instructed to recall the overall storyline. In contrast to standard fMRI analyses which correlate experimental events with cortical activity, Hasson et al. (2004) used a reverse correlation method to enable cortical activity to drive the association with the stimuli in the movie. The time point in the movie that was associated with significant cortical activity in a particular brain region was extracted and the content of the clip examined. For example, significant cortical activations in the post-central gyrus coincided with a set of scenes which all contained hands performing actions, such as a person lighting a cigarette. Further, the spatial specificity and generalisability of such effects were investigated by correlating the cortical activity between subjects, at the voxel level. Even with this fine-grained analysis, somatosensory and inferior frontal gyrus (IFG; a region suggested to contain action related mirror neurons; Kilner et al, 2009), were significantly activated across participants by the same visual stimuli.

The findings of Hasson et al. (2004) provide some evidence supporting the automatic encoding of others' actions, however, the reported cortical activations were not compared to

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[4.1] Although the basis of mirror neurons is in action understanding, these processes have been extended to emotions, touch and pain. If this extension is a valid one, then similar assumptions about the automaticity of shared representations should remain.

activity associated with the actual performance of actions. Focusing on shared representations of touch, Keysers et al. (2004) scanned participants whilst they passively viewed videos of other peoples' lower legs being touched. Importantly, Keysers et al. (2004) also recorded cortical activity evoked by the participant's own leg being stroked. Univariate imaging analyses revealed secondary somatosensory regions activated by the direct experience of touch were also activate during the observation of touch. In a further study, these clusters of bimodal activity were extended beyond SII, incorporating more diffuse somatosensory and motor processing regions at the single voxel level (Gazzola & Keysers, 2009).

The apparent automaticity of shared representations of actions and touch were investigated directly by Iacoboni et al. (2005). Participants viewed clips pertaining to different contexts, actions and intentions, whilst either passively viewing the clips, or attending to the objects, grip type and intentions in each trial. The authors highlighted the role of IFG in representing the intentions of others, but also concluded that this activity was not mediated by task instructions. Further, that the "… lack of top down influences is a feature typical of automatic processing" (Iacoboni et al., 2005, p. e79), providing further evidence to support the automaticity of mirror neuron function. Interestingly, and in contrast to the authors' conclusions, overall cortical activity related to viewing the clips was greater when participants were given explicit instructions compared to passively viewing the stimuli, suggesting that the task instructions did have some effect on cortical activity (yet the authors attribute this to increased attention paid towards the clips). More importantly, IFG and a region encompassing both pre-supplementary motor area and anterior cingulate cortex, were significantly more active when participants were given explicit task instructions during the observation of trials containing the contextual and intentional information respectively. Although baseline activity was subtracted from the comparison between cortical activity associated with passive viewing and the explicit instruction task (indicating that these regions were active during both tasks) the difference in cortical activity between the two suggests there is a role for top down modulation when mirroring others' actions.

In contrast to the apparent automaticity of vicarious activity evoked by viewing actions and touch, studies investigating shared representations of pain highlight the role of tasks instructions on the extent of the cortical overlap between felt and observed pain. For example, only cortical activity associated with the affective aspects of pain is evoked when participants simultaneously view others in pain whilst making relatively arbitrary decisions of whether an object touched a hand (Morrison, Peelen et al., 2007) or whether the hand was a left or right hand (Corradi-Dell'Acqua et al., 2011). In contrast, somatosensory processing regions, but not necessarily affective processing regions, are activated when participants more actively engage with the visual stimuli by rating the intensity and unpleasantness of the painful event they observe (Bufalari et al., 2007; Lamm et al., 2007).

The notion that shared representations of pain are not automatic, but rather mediated by task demands may seem counter intuitive given the evolutionary advantage of detecting threat (Öhman, Flykt, & Esteves, 2001). Yet, Vogt, De Houwer, Crombez, and Van Damme (2012) demonstrate that even task-irrelevant goals are effective at diminishing the perception of threat. Participants performed a dot probe task whereby threatening and neutral pictures were displayed on screen, followed by a shaded target in one of the previously displayed picture locations. Participants were required to respond to the location of the shaded target as quickly as possible. Typically, the probe is detected more quickly if it appears in a location that was previously occupied by a threatening image compared to a non-threatening image. However, in this experiment, following each dot probe trial, participants completed a goal task where they were awarded points for detecting a goal stimulus. The goal stimulus was either a threatening image (such as an attacking snake) or non-threatening image (such as a mug) selected from the stimuli in the dot-probe task. In contrast to the usual findings of the dot probe task, when the participant's target was a neutral stimulus, probes were detected faster when presented at the same location as all neutral stimuli, reversing the usual effects reported in this task. These results demonstrate that, similar to the cortical processing of threat related stimuli, task demands can mediate behavioural responses to threat.

The striking difference in cortical activity and behaviour elicited by task instructions not only highlights the role of top down modulation in the perception of threat and pain, but also suggests that vicarious representations of pain may not be automatic. In contrast to the consistent activation of somatosensory cortex during the observation of others being touched (Keysers et al., 2004), only when task instructions draw attention to the physical aspects of pain are these encoded by the observer (see however, Avenanti, Paluello, Bufalari, & Aglioti, 2006). This may be because touch is visually salient, whereas the physical experience of pain must be inferred. In order for a participant to recognise a hand-object interaction is pain evoking, they must access their own understanding of the sensory consequences of interacting with the particular object. Indeed, the "painful grasp effect" reported in Chapter 3 occurs when participants make an appropriateness judgement on a trial-by-trial basis; requiring participants to combine their knowledge of the action being performed, the painfulness of the object and the consequence of the interaction between the two. Therefore, the facilitation and bias to report touch whilst viewing others in pain may be a consequence of top-down modulation, rather than the automatic perception and resonance of pain per se.

The experiments in this chapter aimed to investigate the role of task demands on the behavioural effects of viewing others in pain. In three experiments, we utilised an above threshold tactile detection task to examine changes in reaction times when participants passively viewed the stimuli, reported the action that was performed, the painfulness of the object, or the appropriateness of the hand-object interactions. If the effects of viewing others in pain are automatic, the "painful grasp effect" should be replicated whilst passively viewing the stimuli. In contrast, different instructions may affect reaction times to the detection of touch if shared representations of pain are mediated by task relevance and engagement with the sensory aspects of pain.

4.3 Experiment 6. The effects of performing a catch trial procedure on the detection of touch

Experiments 4 and 5 demonstrated that when participants judged the appropriateness of hand-object interactions on every trial, reaction times to the detection of touch were facilitated during the observation of others in pain. However, it is not known whether, in tasks that only require the detection of occasional catch trials, viewing others in pain also facilitates tactile processing. Therefore in Experiment 6, participants no longer performed the verbal response task on every trial, instead, they were instructed to respond to occasional catch trials. Catch trials were defined by a change in object painfulness from frame one to frame two of the action sequence (see Figure 4.1b). If, as mirror neuron theories suggest (Rizzolatti & Craighero, 2004), observed actions are encoded automatically, the "painful grasp effect" should be replicated during this more passive viewing task. However, given the evidence supporting the role of task demands on vicarious cortical activity during the observation of others in pain (Bufalari et al., 2007; Corradi-Dell'Acqua et al., 2011; Lamm et al., 2007; Morrison, Peelen et al., 2007), it is feasible to suggest that tactile processing, in response to viewing painful grasps, may not be affected in Experiment 6.

4.3.1 Methods

Participants

All participants (n = 24) were aged 18 years or over (*M* = 20.2, *SD* = 2.2), one participant was left handed, and all participants had normal or corrected-to-normal vision. There were 8 male participants.

Stimuli

The stimuli were identical to those used in Experiment 4.

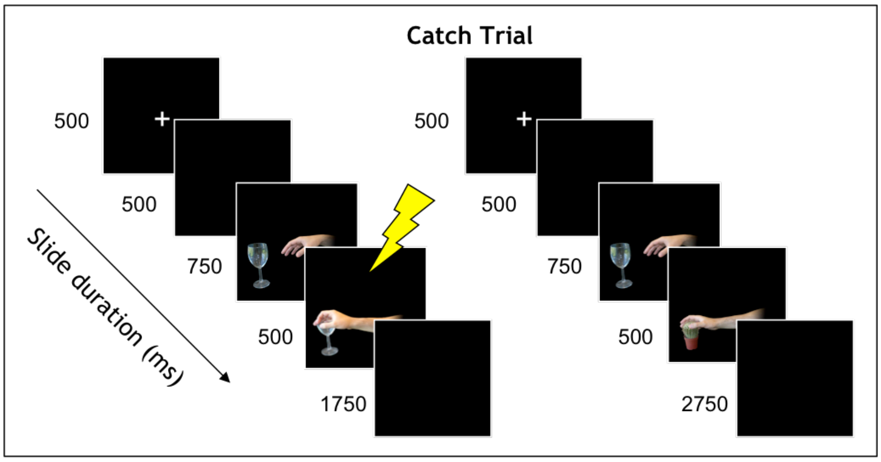


Figure 4.1. Trial diagrams. a) Main experimental trials: Participants responded to the tactile stimulation which occurred 150ms after the onset of the action frame and b) Catch Trials: Participants responded to a change in object.

Design and Procedure

The design and procedures were a modified version of Experiment 4. Participants detected above threshold level tactile stimulation, delivered on 50% of the 60 trials per condition (240 trials total). Importantly, participants did not make an appropriateness judgement at the end of every trial. Instead, participants passively viewed the visual stimuli whilst making speeded responses to tactile stimulation. Catch trials ensured that the participant was attending to the visual stimuli. During a catch trial, the object painfulness changed between the first and second frame, from a painful object to a non-painful object (12 trials) or from a non-painful object to a painful object (12 trials). For example, an orange might change to a cactus, or a shard of glass might change to a tomato sauce sachet between the neutral and action slide (see Figure 4.1b). When participants detected the object change, they were instructed to press the “B” key on the keyboard, which was made easily identifiable with the addition of a red sticker. On catch trials, there were an additional 1000 ms between trials to allow participants to reposition their hand over the spacebar key. No tactile stimulation was delivered during catch trials.

4.3.2 Results

Four additional participants were excluded from the analysis for not responding on 25% or more of the catch trials (leaving n = 24). The hits, reaction times and false alarms data were analysed with three separate 2 x 2 ANOVAs. Preemptive detections (< 100 ms) and reaction times slower than 1500 ms were removed from the analysis (< 1%). As expected, because the stimulation level was above threshold, the analysis of hits data revealed no differences between conditions (*p* > .05, for all).

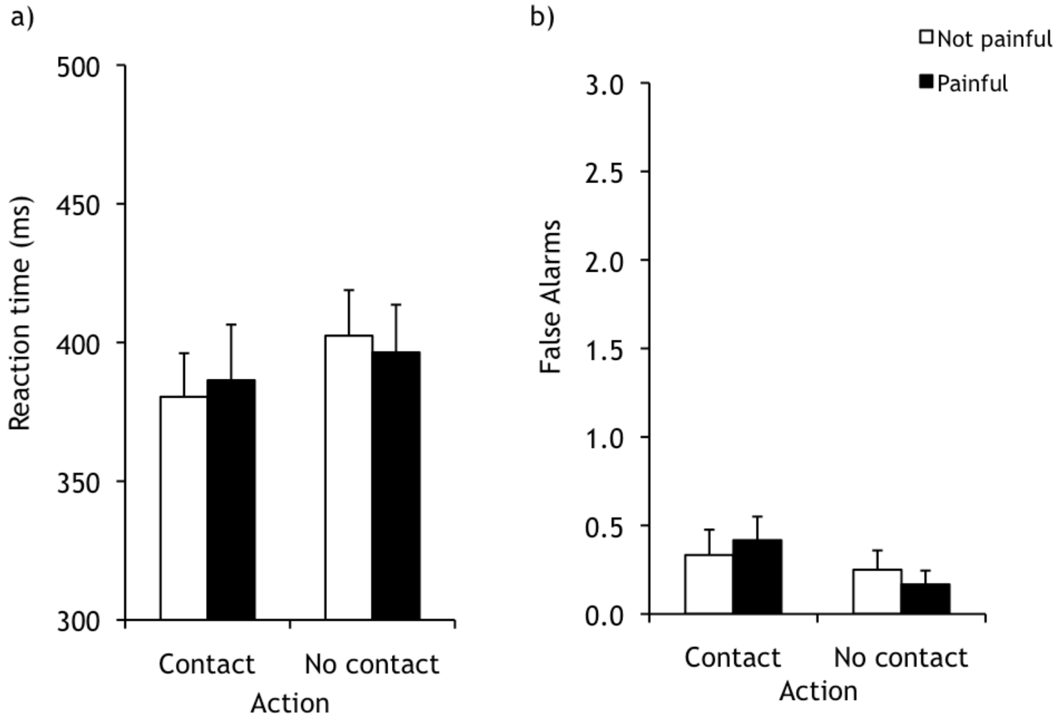


Figure 4.2. a) Mean reaction time for correct detections b) Incorrect tactile detections (false alarms). Error bars represent +1 SEM

Reaction times The analysis of reaction times revealed a main effect of action, *F*(1,23) = 8.86, *p* = .007, η^2_p = .28. Participants were faster to respond to touch on their finger when they viewed a grasping action (*M* = 383.41 ms) compared to a hand missing an object (*M* =

39.43 ms; see Figure 4.2a[4.2]). There was no main effect of object ($F < 1$) and no interaction between action and object, $F(1,23) = 2.15$, $p = .156$, $\eta^2_p = .09$.

False Alarms The number of false alarms was not significantly affected by viewing the hand-object interactions (see Figure 4.2b). There was no main effect of action, $F(1,23) = 2.09$, $p = .162$, $\eta^2_p = .08$, no main effect of object, and no interaction between action and object ($F < 1$, for both).

4.3.3 Conclusions

In contrast to previous studies reporting the "painful grasp effect", passively viewing others in pain did not affect tactile processing. Participants were neither faster to detect touch, nor made more erroneous detections of touch during the observation of painful grasps. The difference in reaction times between the appropriateness judgement task and the current catch trial task was qualified by a significant interaction between experiment (Experiment 4/ Experiment 6), action (grasp/ miss) and object (painful/ not painful), $F(1,46) = 10.51$, $p = .002$, $\eta^2_p = .17$.

Interestingly, no main effects of pain were revealed despite the catch trials drawing attention to object painfulness. However, participants were faster to report touch on their own body when they viewed contact between the hand and the object, regardless of object painfulness. The automatic effects of viewing touch on tactile perception replicate the previously reported somatosensory cortical activity evoked when passively viewing touch (Keysers et al., 2004). In contrast, the absence of the "painful grasp effect" in this task suggests shared representations of pain are dependent upon top-down modulation. Important to note however is that the current task differed from previous experiments in that the participant was not required to make a response on every trial. Therefore, the difference in findings may be due to differences in how attentive participants were to the visual stimuli. Indeed, the number of false alarms across all conditions, not just during the observation of painful grasps, was lower in this task than any previous experiment. It is plausible that a baseline number of false alarms would be expected due to the temporal congruency of the onset of the visual and tactile stimulation, thus encouraging preparatory responses. Yet this potent cue to the possible onset of the tactile stimulus did not appear to promote false alarms in the current task, suggesting participants engaged less with the visual stimuli.

[4.2] Note that the axis labels have been altered. This is to allow the results of all experiments in this chapter to be more easily compared. The action conditions, grasp and miss, have been modified to contact and no contact. However, the visual stimuli remained identical.

4.4 Experiment 7. The effects of alternating task demands on the detection of touch: A within-subjects design

Although passively viewing others in pain did not speed reaction times to the detection of touch, it was not known whether the appropriateness judgement task was the only verbal task to elicit the "painful grasp effect". Therefore, Experiment 7 aimed to extend our understanding of the role of the verbal task on reaction times to the detection of touch by assessing the individual contribution of action and object knowledge. Experiment 7 also aimed to replicate the findings of Experiment 6 with a more controlled task, removing the emphasis on the painfulness of the object, and adding a verbal response on every trial. In a within-subjects mini-block designed task, participants judged the appropriateness of the actions (appropriate/ inappropriate), the action performed (contact/ no contact), the painfulness of the object (painful/ not painful), or passively viewed the stimuli (instead, making a verbal response regarding the content of unrelated stimuli during the response phase of the trial, identified by a prompt slide; see Figure 4.3).

4.4.1 Methods

Participants

All participants (n=24) were aged 18 years or over (*M* = 19.5, *SD* = 1.6), one participant was left handed, and all participants had normal or corrected-to-normal vision. There were seven male participants.

Stimuli

The stimuli were similar to Experiment 4. However, because there were now four possible verbal responses, the two-frame sequences of the hand-object interactions were preceeded by a cue slide and followed by a prompt slide to instruct the participants which judgement task they should perform (see Figure 4.3).

Design and Procedure

The procedure was similar to Experiment 4, except now participants made four different verbal judgements in separate mini-blocks. Participants were instructed to Judge Action (contact or no-contact), Judge Object (painful or not painful), Judge Appropriateness (appropriate or inappropriate), or passively view the stimuli. To match the verbal responses made across conditions, in the passive viewing task participants were asked to state the colour of a word in uppercase letters that appeared at the end of the trial (Judge Colour; see Figure 4.3). Participants were informed of the judgement task at the beginning of each mini-block. Participants completed six blocks, each containing 24 mini-blocks. The order of mini-blocks was counterbalanced, such that each judgement task preceded and followed every other judgement task equally often. Each mini-block contained four trials, including each of the action-object combinations in a counterbalanced order. Participants completed a total of 576 trials, 50% with stimulation, with 36 trials per condition. For example, there were 36 trials where the participant judged the painfulness of the object when viewing a hand grasp a painful object. The experiment lasted 90 minutes.

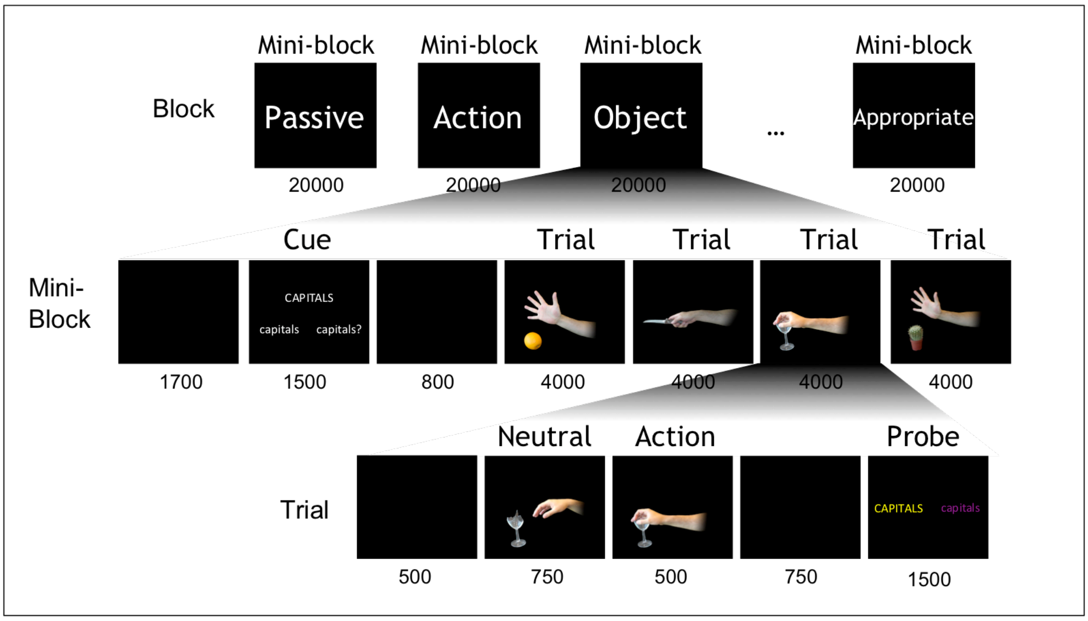


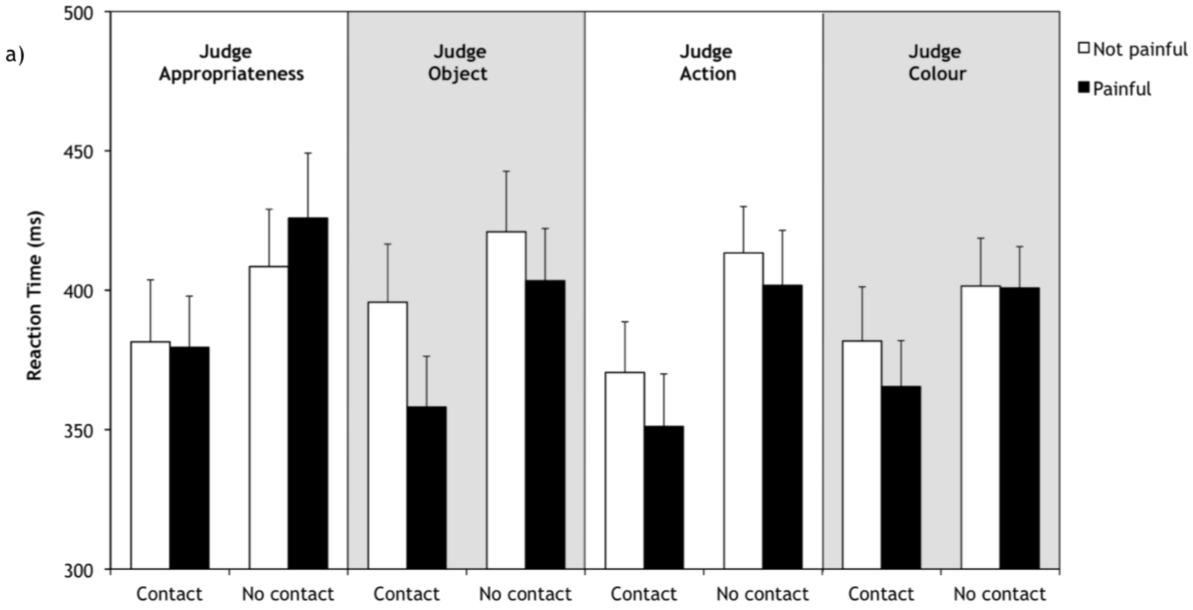
Figure 4.3. Experimental paradigm. In separate blocks, participants passively viewed the hand-object interactions, judged the action, the object and the appropriateness of the action. In each mini-block, participants saw each of the four action-object conditions (a non-painful miss, a non-painful grasp, a painful grasp and a painful miss). In each trial, participants observed the hand perform an action. Participants responded to the tactile stimulus that occurred 150ms after the onset of the action frame. Participants also gave a verbal response at the end of the trial during the prompt slide, dependent on the mini-block the trials were in. Above is an example of a passive viewing trial. Participants had to state the colour of the word in uppercase letters, in this trial the correct response would be “yellow”.

4.4.2 Results

The hits, reaction times and false alarms data were analysed with a 4 x 2 x 2 repeated measures ANOVA with the factors of task (Judge Appropriateness/ Judge Object/ Judge Action/ Judge colour), action (contact/ no contact) and object (painful/ not painful). Preemptive detection (< 100 ms) and reaction times slower than 1500 ms were removed from the analysis (< 1%).

As anticipated, there were no effects of viewing condition on the number of accurately reported detections (hits), $p > .05$ for all. There was a trend for more hits to be made when participants viewed contact made between the hand and object, than no contact trials, $F(1,23) = 3.43, p = .077, \eta^2_p = .13$.

a)



b)

*** $p \leq .001$
** $p \leq .05$
* $p \leq .10$

Effect	Appropriateness	Object	Action	Colour
Action	***	***	***	***
Object	-	***	**	-
Interaction	-	-	-	-

Figure 4.4. a) Mean reaction times to the accurate detection of touch whilst judging the appropriateness of the observed action, the painfulness of the object, whether there was contact or no contact between the hand and object, or the colour of the word in uppercase letters displayed during the prompt slide. Error bars represent +1SEM. b) Exploratory 2 x 2 ANOVA results within each task.

Reaction times. The analysis of reaction times (see Figure 4.4a) did not reveal a main effect of task, $F(3,69) = 1.79, p = .158, \eta^2_p = .07$. However, there was a main effect of action, $F(1,23) = 31.75, p < .001, \eta^2_p = .58$, with faster reaction times to the detection of touch when participants viewed the hand grasp an object ($M = 372.94$), compared to the hand missing an object ($M = 409.50$). Participants were also influenced by the painfulness of the object, $F(1,23) = 7.17, p = .013, \eta^2_p = .24$, responding faster to touch when they observed painful objects ($M = 385.73$), compared to non-painful objects ($M = 396.71$). The interaction between task and object was also significant, $F(3, 69) = 5.75, p = .001, \eta^2_p = .20$. Surprisingly, pairwise comparisons demonstrated that when viewing painful objects only, reaction times were significantly slower during the Judge Appropriateness task compared to the Judge Action ($p = .002$) and Judge Object ($p = .010$) tasks. There was a trend towards an interaction between action and object, *F*(1,23) = 3.56, $p = .072$, $\eta^2_p = .13$, with fastest reactions times to the detection of touch during the observation of others in pain. No other interactions were significant ($p \geq .265$ for all).

Because the aim of this study was to examine whether the "painful grasp effect" was revealed during different judgement tasks, further exploratory analyses were carried out on the reaction times in each of the four task manipulations. A 2 x 2 ANOVA with the factors of action (contact/ no contact) and object (painful/ not painful) was performed for each of the judgement tasks. (see Figure 4.4b). There was no significant interaction between action and object in any of the four judgement tasks. Most surprisingly, the previously reported "painful grasp effect", when participants performed the Judge Appropriateness task, failed to replicate (see Figure 4.4) despite the visual stimuli and judgement being identical. The absence of the "painful grasp effect" in the Judge Appropriateness task supports the idea that the other conditions experienced by participants were interfering with the appropriateness task. That is, each judgement may have influenced every other judgement; an issue known as the influential companions problem (Poulton, 1982; see section 4.6 Discussion). The possibility of influential companion effects prompted further exploration of the data where it might be expected that effects differed with levels of experience in the task between the first and second halves of the experiment.

The analysis of block (1st half/ 2nd half) by task by action by object was not significant ($p = .149$), therefore the following analyses are exploratory. Analysis of the first half of the experiment (see Table 4.1 & Figure 4.5a) revealed the main effect of action *F*(1, 23) = 35.62, $p < .001$, $\eta^2_p = .61$ and the interaction between task and object, *F*(3, 69) = 4.06, $p = .010$, $\eta^2_p = .15$ that was found in the analysis of the experiment as a whole. Importantly, the interaction between action and object was not significant, *F*(1, 23) = 0.46, $p = .507$, $\eta^2_p = .02$, suggesting the consequences of viewing a hand grasp a painful object were either not being encoded, or not affecting behaviour at this stage in the experiment.

In contrast, the analysis of the second half of the experiment (see Table 4.1 & Figure 4.5b) replicated the main effect of action, *F*(1, 23) = 30.27, $p < .001$, $\eta^2_p = .57$, but also revealed a main effect of object, *F*(1, 23) = 13.81, $p = .001$, $\eta^2_p = .38$ and an interaction between action and object, *F*(1, 23) = 4.59, $p = .043$, $\eta^2_p = .17$, with faster reaction times during the observation of hands grasping painful objects (332.08 ms). There was also a trend for a main effect of task, *F*(1, 23) = 2.68, $p = .054$, $\eta^2_p = .10$, reflecting faster reaction times when participants performed the Judge Action task (353.13 ms) compared to the Judge Appropriateness task (373.21 ms).

Table 4.1.

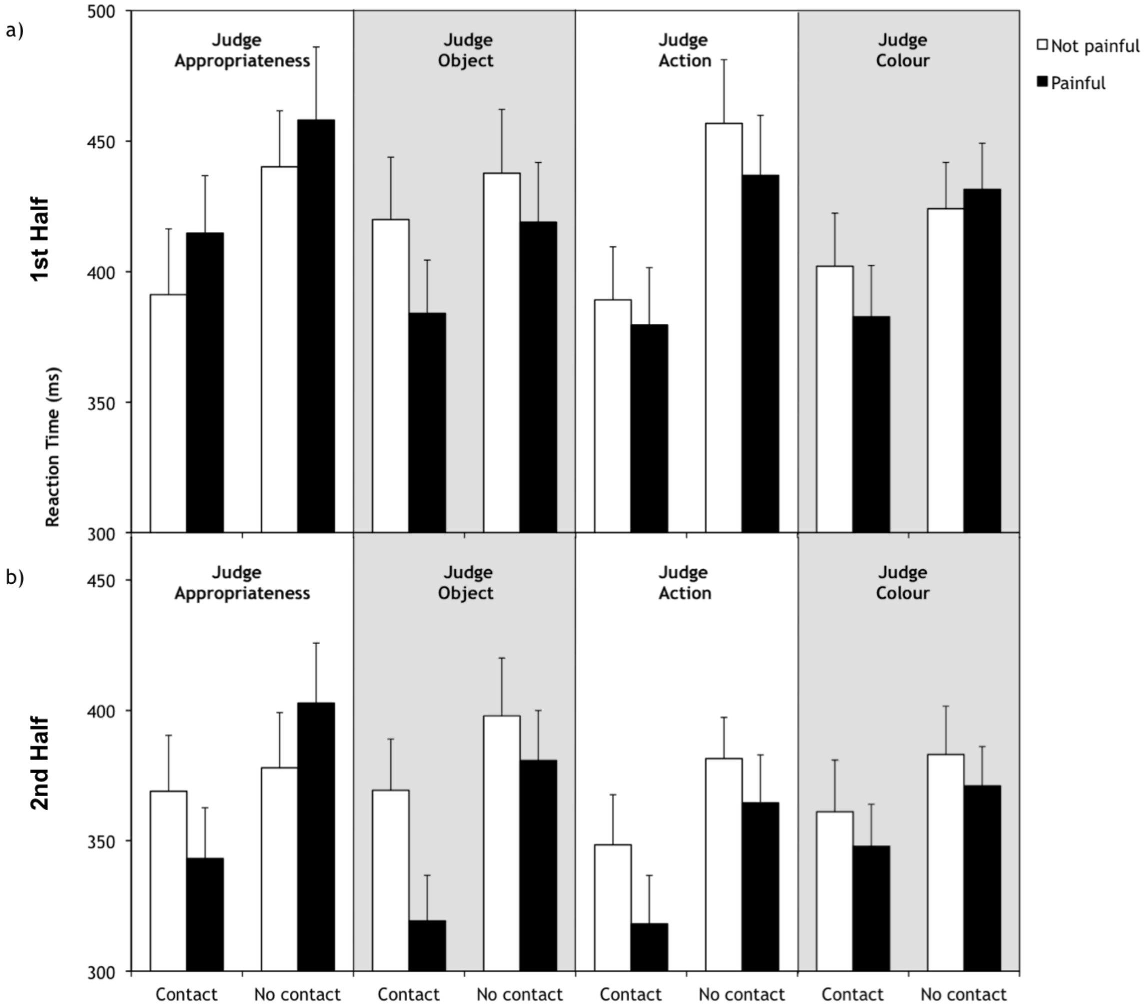
Summary of exploratory split-half analyses. 3-way ANOVA task x action x object (4x2x2).

	1st Half			**2nd Half**		
Effects	**F**	***p***	**η^2_p**	**F**	***p***	**η^2_p**
task	1.00	.397	.04	2.68	.054*	.10
action	35.62	**.000*****	.61	30.27	**.000*****	.57
object	0.86	.364	.04	13.81	**.001*****	.38
task x action	2.04	.117	.08	1.57	.204	.06
task x object	4.06	**.010****	.15	2.44	.072*	.10
action x object	0.46	.507	.02	4.59	**.043****	.17
task x action x object	0.85	.473	.04	1.39	.262	.06

*** $p \leq .001$
** $p \leq .05$
* $p \leq .10$

We examined the results further within each judgement task by exploring the main effects of action and object, and the interaction between action and object in the first and second half of the experiment. As predicted, the judgement tasks did appear to mediate reaction times independently of each other in the first half of the experiment (see Figure 4.5a & 4.5c). For example, the main effect of action was present in all tasks. This is a robust effect, which is found during passive viewing (see Experiment 6) and auditory detection tasks (see Experiment 3). In contrast to the main effect of action, there was only an effect of object when participants were specifically instructed to attend to the painfulness of the object, in the Judge Object task. Interestingly, the "painful grasp effect" was not revealed during the Judge Appropriateness task in the first half of the experiment, perhaps because of the comparative difficulty of this task, compared to all other conditions.

Crucially, analysis of the second half of the experiment (see Figure 4.5b & 4.5c) revealed the expected "painful grasp effect" during the Judge Appropriateness task, and the role of influential companion effects in the latter part of the experiment. For example, in trials where participants Judged Action (contact/no contact), both a main effect of action, and a main effect of object were now observed. Similarly, when participants only Judged Object (painful/ not painful) a main effect of object, but also an interaction between action and object, was now revealed in the second half of the experiment. These findings suggest that previously ignored task-irrelevant aspects of the scene were encoded after repeated exposure to trials where these aspects were task-relevant.



c)

	Effect	Appropriateness	Object	Action	Colour
1st Half	Action	***	***	***	***
	Object	*	**	-	-
	Interaction	-	-	-	-
2nd Half	Action	***	***	***	**
	Object	-	***	**	-
	Interaction	**	**		

*** $p \leq .001$
** $p \leq .05$
* $p \leq .10$

Figure 4.5. Split-half mean reaction times to the accurate detection of tactile stimulation. a) first half. b) second half. Note the difference in scale for the reaction times in the 1st half (300ms – 500ms) and 2nd half (300ms – 450ms). Error bars represent +1SEM. c) Summary of exploratory analyses within each task for 1st and 2nd half: 2 x 2 ANOVA, action (contact/ no contact) by object (painful/ not painful).

False Alarms. Although the main aim of the verbal response task manipulation was to mediate reaction time, we also examined the number of false alarms that were made in each condition (see Figure 4.6). Where necessary Greenhouse-Giesser corrections were implemented.

There was a main effect of action, $F(1, 23) = 25.81, p < .001, \eta^2_p = .53$ and a main effect of object, $F(1, 23) = 6.51, p = .018, \eta^2_p = .22$. Participants made more false alarms when they viewed grasping actions ($M = 0.54$) compared to missing actions ($M = 0.10$). Participants also erroneously detected touch more often when they viewed painful objects ($M = 0.39$) compared to non-painful objects ($M = 0.25$). There was a trend for a main effect of task, $F(1.67, 38.40) = 3.37, p = .053, \eta^2_p = .13$, with most false alarms made during the Judge Action (contact/ no contact) task. There was a trend towards an interaction between task and action, $F(2.29, 52.76) = 2.86, p = .059, \eta^2_p = .11$, as participants made less false alarms when the task was Judge Colour, compared to all other tasks, during the observation of grasps (no difference between false alarms during miss trials was observed). The interaction between action and object was not significant, $F(1, 23) = 2.90, p = .102, \eta^2_p = .11$, although most false alarms were made during the observation of painful grasps ($M = 0.57$). No other interactions were significant, $F < 1$, for all.

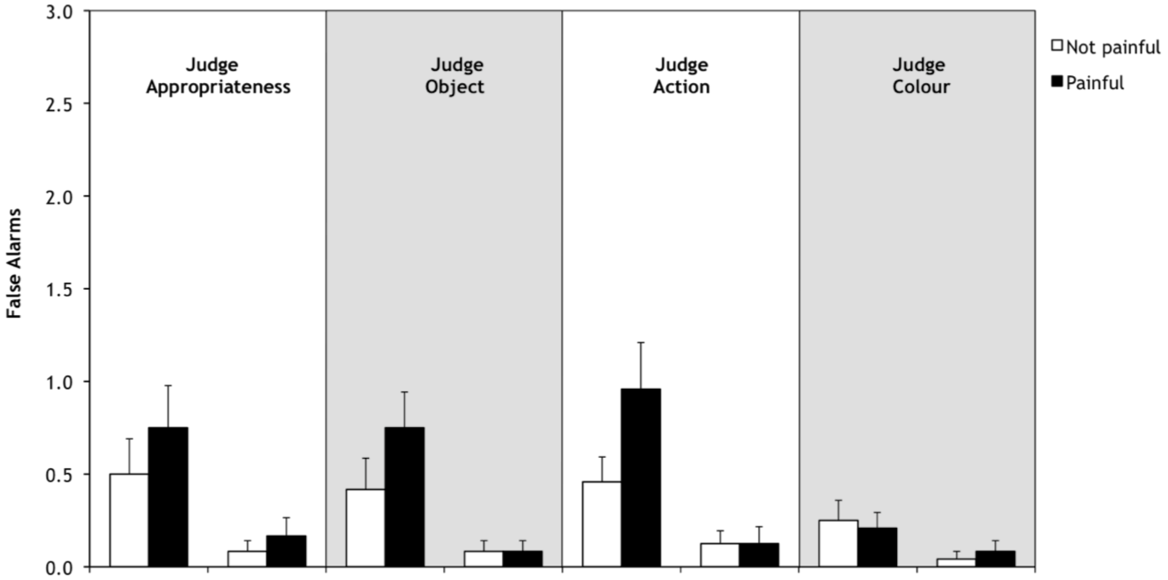


Figure 4.6. Mean false alarms (erroneous detections of touch) whilst judging the appropriateness of the observed action, the painfulness of the object, the action that had been performed, or the colour of the word in uppercase letters displayed during the prompt slide. Error bars represent +1SEM.

4.4.3 Conclusions

The main analysis of reaction times suggested that the individual contribution of action and object knowledge was not dissimilar to the reaction times reported during the appropriateness judgement task, or indeed passive viewing. Importantly, the lack of predicted effects cannot be attributed to participants not knowing which task they were performing in each mini-block, as their verbal responses were 97% accurate across all conditions. Rather, further exploratory analyses of the data revealed that the within-subject mini-block design may have suffered from the effects of influential companions (Poulton, 1982). In the first half of the study the established "painful grasp effect" was not observed in the Judge Appropriateness task, suggesting that the presence of the other conditions (Judge Action, Judge Object and Judge Colour) interfered with the effect. In sharp contrast, in the second half of the experiment, after further experience of the various conditions, the opposite trend appeared. That is, the "painful grasp effect" interaction was now replicated in the Judge Appropriateness task, and there were influential effects in the Judge Action task, where object effects appeared, and in the Judge Object task, where the interaction between contact and object, the marker for the "painful grasp effect", was now obtained.

4.5 Experiment 8. The effects of judging objects and actions on the detection of touch: A between-subjects design

Experiment 8 was designed to overcome the influential companions problem (Poulton, 1982) revealed in Experiment 7. In a between-subjects task, participants only performed the Judge Action (contact/ no contact) or the Judge Object (painful/ not painful) task, in each hand-object interaction, to assess the individual contribution of these tasks to the speed of tactile detection.

4.5.1 Methods

Participants

All participants (n = 48) were aged 18 years or over (*M* = 20.4, *SD* = 3.2), all participants were right-handed, and had normal or corrected-to-normal vision. There were 16 male participants.

Stimuli

The stimuli were similar to Experiment 7. Participants performed the same verbal response throughout the experiment, and therefore participants were only cued as to the verbal response to make at the beginning of each block, rather than every four trials.

Design and Procedure

The procedures were similar to Experiment 7. In a between-subjects design, participants either completed 144 trials/ 36 trials per condition (50% stimulation) of the Judge Action task (contact/ no contact) or the Judge Object task (painful/ non-painful), whilst detecting above threshold tactile stimulation. Participants only received instructions for the task they were to perform. Participants completed two blocks of 72 trials, which lasted approximately 10 minutes.

4.5.2 Results

The hits, reaction times and false alarms data were analysed with three separate 2 x 2 repeated measures ANOVAs with the between subjects factor of task. The data were also directly compared with the equivalent task manipulation in Experiment 7 to assess the possible effects of influential companions on reaction times and false alarms. Preemptive detection (< 100 ms) and reaction times slower than 1500 ms were removed from the analysis (< 1.5%).

Hits On average, across both tasks, participants detected 17.59 out of 18 tactile stimuli. However, there was a significant interaction between action, object, and the between subjects factor of task, $F(1, 46) = 4.50$, $p = .039$, $\eta^2_p = .09$. Participants detected significantly less tactile stimuli during the observation of non-painful grasps when performing the Judge Object task ($M = 17.29$) compared to the Judge Action task ($M = 17.83$; $p < .030$). There were no differences between the number of hits between the two judgement tasks when participants viewed painful grasps, or painful and non-painful misses ($p > .05$, for all). All other effects were non-significant, $F < 1.6$.

Reaction times Analysis of reaction times revealed a main effect of action, $F(1, 46) = 67.18$, $p < .001$, $\eta^2_p = .59$, and object, $F(1, 46) = 13.46$, $p = .001$, $\eta^2_p = .23$, across both tasks, with faster reaction times to the detection of touch when viewing grasps compared to misses, and painful objects compared to non-painful objects (see Figure 4.7a). Interestingly, there was also an interaction between action and task, $F(1, 46) = 10.33$, $p = .002$, $\eta^2_p = .18$. Participants who Judged Action, where contact between the hand and object was task relevant, were faster to respond to touch on their own finger when viewing grasps (*M* = 390.92 ms) in comparison to participants who Judged Object (*M* = 461.19 ms; *p* = .019). In contrast, there was no difference in reaction times between those participants who were required to Judge Object, and those who Judged Action, when misses were viewed (*p* = .286). There was no interaction between object and task and, more importantly, no interaction between action and object ($F < 1$ for both). There was a trend towards an interaction between action, object and task, $F(1, 46) = 3.52$, $p = .067$, $\eta^2_p = .07$. However, further scrutiny of the data did not reveal any significant findings. There was also a trend for a main effect of task, $F(1, 46) = 3.10$, $p = .085$, partial $\eta^2 = .06$, with slower reaction times during the Judge Object task (*M* = 475.38 ms) compared to the Judge Action task (*M* = 423.41 ms).

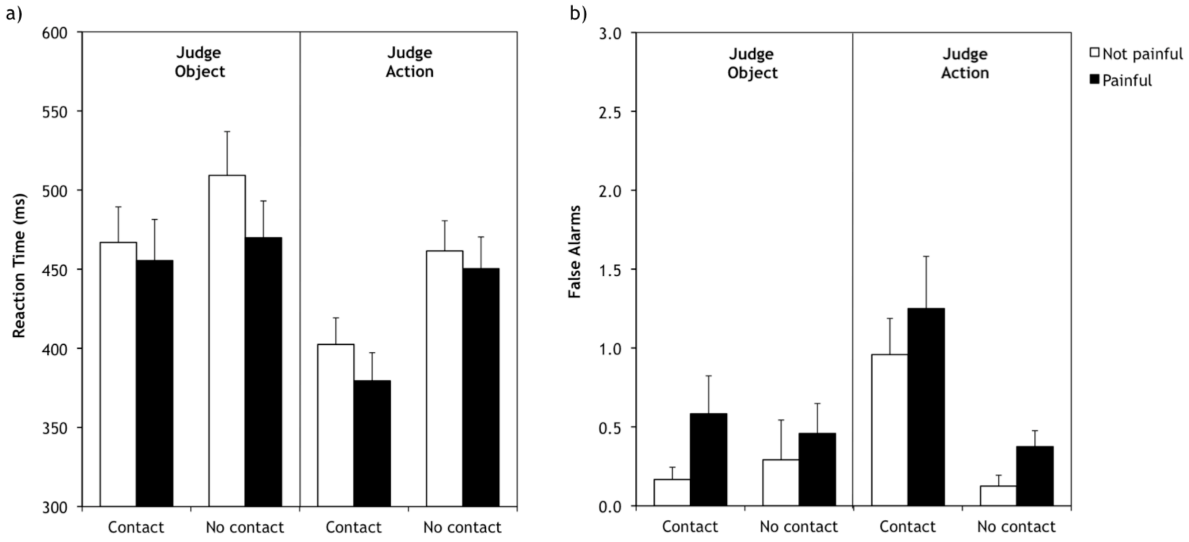


Figure 4.7. Experiment 8. Between groups factor of task: Judge Action and Judge Object. a) Mean reactions times for the detection of touch b) Mean false alarms (erroneous detections of touch). Error bars represent +1SEM.

False Alarms The analysis of false alarms revealed a similar pattern to the reaction time data (see Figure 4.8). Participants were more likely to erroneously report touch during the observation of grasps compared to misses, $F(1, 46) = 7.49$, $p = .009$, $\eta^2_p = .14$, and during the observation of painful compared to non-painful objects, $F(1, 46) = 5.07$, $p = .029$, $\eta^2_p = .10$. Participants performing the Judge Action task also made more false alarms during the observation of grasp trials (*M* = 1.10), than those who Judged Object (*M* = 0.38; *p* = .010), as revealed by the interaction between action and task, $F(1, 46) = 7.49$, $p = .009$, $\eta^2_p = .14$. No difference in the number of false alarms during observation of miss trials was revealed between the Judge Action and Judge Object tasks (*p* = .564).

These reaction time and false alarm data demonstrate that the "painful grasp effect" does not occur when participants only judge the action or the object being viewed. In contrast, in Experiment 7, when participants performed the action and object judgements alongside each other and the appropriateness judgement task, there a trend towards faster reaction times during the observation of painful grasps across all task instructions. Further analyses suggested that this effect may be due to the consequence of performing each judgement task alongside each other, over the course of an experiment. To explore this hypothesis further, we compared reaction times and false alarms between Experiment 7 and

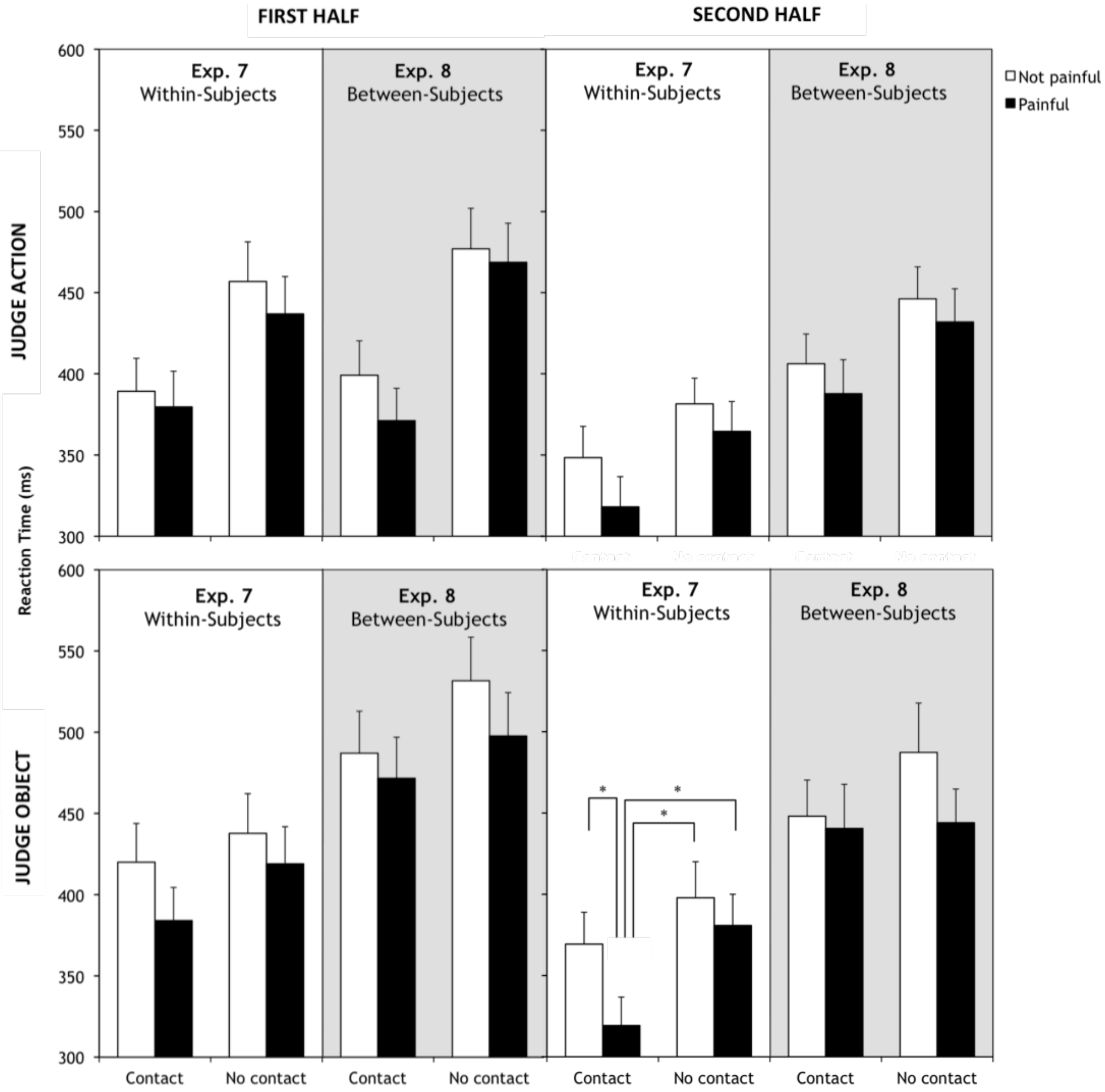


Figure 4.8. Comparison of Experiment 7 and Experiment 8 reaction times. Upper panel: Judge Action, 1st and 2nd half. Lower panel: Judge Object, 1st and 2nd half. Error bars represent +1SEM. *Significant difference between means ($p < .01$).

Experiment 8 for the Judge Action and Judge Object tasks. Reaction times were analysed by comparing data from the first half of Experiment 7 with the first half of Experiment 8 for the two tasks, and again for the second half of the data. Due to the low number of false alarms, these data were analysed between experiments, but not by block.

Judge Action: Reaction Times The analysis of reaction times when participants Judged Action did not differ between Experiment 7 and Experiment 8 (see Figure 4.8, Upper panel). There was a main effect of action in both the first, $F(1, 46) = 52.01, p < .001, \eta^2_p = .53$ and the second half of the task, $F(1, 46) = 32.33, p < .001, \eta^2_p = .41$. Regardless of whether the Judge Action task was performed alone or alongside other judgement tasks, reaction times were faster during the observation of grasps compared to misses. Similarly, participants were faster to respond to touch when viewing painful objects compared to non-painful objects in both the first, $F(1, 46) = 5.59, p = .022, \eta^2_p = .11$, and second halves of both experiments, $F(1, 46) = 8.08, p = .007, \eta^2_p = .15$. No other interactions were revealed ($F < 1.5$ for all). There was a main effect of experiment in the second half of the trials. Participants who performed the Judge Action task alone in Experiment 8 were slower ($M = 418.00$ ms) than participants who performed the Judge Action task alongside other tasks in Experiment 7 ($M = 353.13$ ms).

Judge Action: False Alarms The analysis of false alarms, similar to the analysis of reaction times, also failed to reveal any differences between the number of erroneous detections reported in Experiment 7 and Experiment 8, when participants performed the Judge Action task ($F < 1.7$ for all). Comparing the two experiments only revealed the main effects of action, $F(1, 46) = 32.52, p < .001, \eta^2_p = .41$ and object, $F(1, 46) = 6.11, p = .017$,

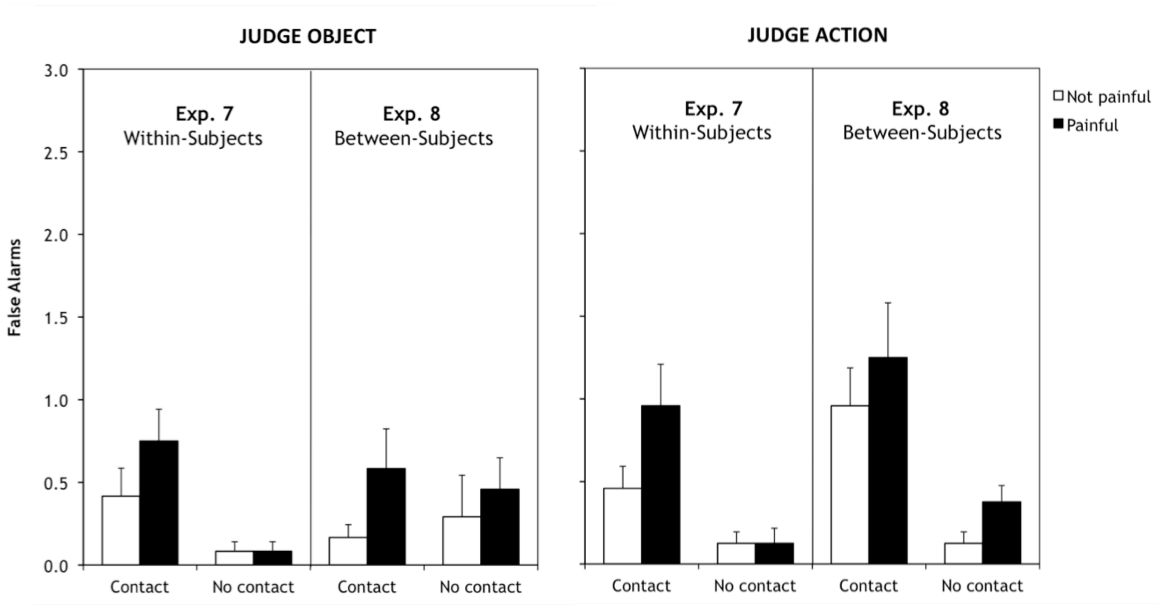


Figure 4.9. Comparison of Experiment 7 and Experiment 8 false alarms. Left panel: Judge Object. Right panel: Judge Action. Error bars represent +1SEM.

$\eta^2_p = .12$ when making an action judgement (see Figure 4.9, right panel).

Judge Object: Reaction Times Participants were faster in Experiment 7 than Experiment 8 in both the first $F(1, 46) = 6.22$, $p = .016$, $\eta^2_p = 12$, and second half of the task, $F(1, 46) = 8.35$, $p = .006$, $\eta^2_p = .15$. Reaction times to the detection of touch revealed a main effect of action in both the first, $F(1, 46) = 16.819$, $p < .001$, $\eta^2_p = .27$ and second half of the experiments, $F(1, 46) = 22.28$, $p < .001$, $\eta^2_p = .33$. Participants were also faster to respond to touch when viewing painful objects compared to non-painful objects in the first, $F(1, 46) = 8.74$, $p = .005$, $\eta^2_p = .16$ and the second half of the experiments, $F(1, 46) = 11.25$, $p = .002$, $\eta^2_p = .20$. Importantly, although no interactions were revealed between the experiments in the first half of the experiment ($F < 1.7$, for all), the reaction times in the second half of the trials differed between Experiment 7 and 8 (see Figure 4.8, Lower panel). When participants performed the Judge Object task alongside the Judge Action and Judge Appropriateness tasks (Experiment 7), participants were faster to respond when viewing grasping actions than when the Judge Object task was performed alone (Experiment 8), $F(1, 46) = 2.84$, $p = .099$, $\eta^2_p = .06$. Further, there was a trend towards an interaction between action, object, and the experiment, $F(1, 46) = 3.47$, $p = .069$, $\eta^2_p = .07$. In Experiment 7, when participants performed the Judge Object task, the "painful grasp effect" was revealed. Participants were faster to respond to touch on their own finger when viewing others in pain, compared to all other conditions ($p < .001$, for all). Crucially, this effect was not revealed in Experiment 8. Hence the influential companion conditions in Experiment 7 did affect reaction times to touch in the different tasks.

Judge Object: False Alarms The analysis of false alarms revealed a main effect of object, $F(1, 46) = 4.50$, $p = .039$, partial $\eta^2 = .09$, with more false alarms being made whilst participants viewed painful objects compared to non-painful objects (see Figure 4.9, left panel). Unlike previous tasks, there was only a trend towards a main effect of action, $F(1, 46) = 3.49$, $p = .068$, $\eta^2_p = .07$. This is possibly due to the difference in false alarms made in grasp trials and miss trials between the two experiments. In Experiment 7, when the object task was intermingled with other judgement tasks, there were more false alarms during grasp trials compared to miss trials ($p = .003$), whereas in Experiment 8, when participants only ever made an object judgement, there was not difference between the two action conditions ($p = 1$). However the interaction between action and experiment did not reach significance, $F(1, 46) = 3.49$, $p = .068$, $\eta^2_p = .07$. In contrast, there was an interaction between action and object; erroneous detections of touch were reported more frequently when participants viewed a hand grasp a painful object compared to all other conditions ($p < .027$ for all).

4.5.3 Conclusions

No effects of viewing others in pain on reaction times or false alarms were revealed when participants performed the Judged Action or Judge Object task in isolation. However, when action was task-relevant (in the Judge Action task), participants were faster to respond to touch, and made more erroneous detections of touch during grasp trials, compared to those participants who performed the Judged Object task. No differences in reaction times or false alarms were revealed during the observation of miss trials between the judgement tasks (Judge Action/ Judge Object). These results demonstrate that although neither the Judge Object task or the Judge Action task replicate the “painful grasp effect”, task relevance does mediate reaction times during the observation of grasping actions.

To assess the possible role of influential companions on reaction times to touch, further analyses compared the Judge Object and Judge Action tasks in Experiment 7 with those in Experiment 8. Recall that in Experiment 7 participants performed four judgement tasks (Judge Action, Judge Object, Judge Appropriateness, and Judge Colour), whereas in Experiment 8 participants only responded to the action or object properties in the scene. The comparison of reaction times and false alarms when participants performed the Judge Action task did not differ between the two experiments. In contrast, the effects of the Judge Object task were mediated by the context of the task. In the first half of the experiments the behavioural data for Judge Object did not differ between Experiment 7 and 8. However, in the second half of the trials, there was a trend towards an interaction between action, object and experiment in the reaction time data. Exploratory analyses revealed that when participants performed the Judged Object task, the “painful grasp effect” was present in the second half of Experiment 7, but not in Experiment 8.

4.6 Discussion

The experiments in this chapter aimed to explore the automaticity of the “painful grasp effect”. In Experiment 6 reaction times to the detection of touch were not speeded when participants passively viewed others in pain. However, the robust facilitatory effects of viewing grasping actions on reaction times to touch were replicated. Participants responded more quickly to touch when there was contact between the hand and object, compared to no contact trials. Experiment 7 investigated the role of task instructions on shared representations of pain by contrasting action, object, appropriateness judgements, and passive viewing within participants. Rather than revealing the independent contribution of each of these judgements on reaction times to the detection of touch, the results highlighted the problem of influential companions (Poulton, 1982).

The influential companions problem occurs in within-subjects designs when the results of the study may be due to the influential effects of each condition on every other condition, rather than the desired experimental manipulation (Poulton, 1982). Although most researchers are aware of possible carry-over effects, and compute optimal counterbalancing of trial orders in an attempt to overcome these, the only way to account for or exclude the possibility of influential companions is to run reduced condition or between subjects control tasks (Poulton, 1982).

Poulton (1982) suggests the influential companions problem may arise because participants "…learn a strategy in one condition and [continue] to use the strategy in a subsequent condition where it is not necessary or appropriate..." (p. 674). In the context of Experiment 7, this could mean participants encoded the appropriateness of an action on trials when they only needed to state the painfulness of the object. Indeed, by comparing the action and object tasks in Experiment 7 with those in Experiment 8, we provide tentative evidence in support of such influential companions effects. Only when participants performed the object judgement task alongside the action and appropriateness judgement task were reaction times to the detection of touch faster when participants viewed others in pain.

Bekkering, Wohlschlager, and Gattis (2000) provide a striking example of the effect of influential companions whilst investigating action imitation in children. In Experiment 1, an actor performed six different actions that the child was instructed to imitate. These actions consisted of the actor touching their left or right ear, with either their left or right hand, or both hands creating the combinations: left hand to left ear, right hand to right ear, right hand to left ear, left hand to right ear, left and right hand to left and right ears and finally, left hand to right ear and right hand to left ear. Children made a mistake on 40% of trials when they saw an actor make a contralateral movement (for example, left hand to right ear). Instead of imitating the same action, children produced an ipsilateral movement (for example, right hand to right ear), known as a contra-ipsi error (Bekkering et al., 2000). Consequently, based on these findings, it would seem plausible to suggest that children struggle to perform contralateral movements. However, in Experiment 2, the children only observed two of the six actions (left hand to right ear/ right hand to right ear, or right hand to left ear/ left hand to left ear). Importantly in this experiment children only made contra-ipsi errors on 1.9% of the trials. In contrast to the results of Experiment 1, Experiment 2 suggests children are adept at making contralateral movements but were affected by the context of these trials in Experiment 1.

More similar to the experiments presented in this chapter, Taylor-Clarke et al. (2002) investigated the role of task demands on mediating somatosensory processing during vision of the body. Participants received tactile stimulation delivered to their forearm and then heard a tone whilst ERPs were recorded. In separate blocks, participants either judged whether there had been one or two tactile stimuli delivered to their forearm, or judged whether the tone was mono or stereo. The authors found increased amplitude in the N80 (analogous to SI) during the tactile task, compared to the judge tone task. However, the amplitude of the N140 (analogous to SII) was equal in both the judge touch and judge sound task. When the authors analysed their data taking into account which block was performed first (although both judge tone first and judge tone second revealed significant N140 amplitude change) there was a trend towards larger amplitude change in the judge tone condition when it occurred after the judge touch condition. Again, highlighting the effects of influential companions, similar to those reported in Experiment 7.

Although the potential effects of influential companions are always important to consider, they are critical in experiments investigating mirror neuron activity. For example, overlapping cortical activation between two conditions attributed to shared representations, but might actually be due to the different experimental conditions blending into each other during the task. Although some authors have explicitly controlled for the effects of influential companions, many others have not. Oosterhof, Tipper, and Downing (2012) investigated the role of viewing perspective on shared action representations by asking participants to observe or perform hands actions. Crucially, viewpoint was a between-subjects factor, such that those participants viewing actions from the first person perspective never viewed actions from the third person perspective, and vice versa. Consequently, any similarities in cortical activity between the two viewing perspectives could not be attributed to the influence of one perspective on the other.

In contrast, Ebisch et al. (2008) randomised trials within-subjects in a task designed to assess whether shared representations of touch occur during observation of animate and inanimate touch. Participants were instructed to “attentively” watch video clips of a person touch another person or a chair, and a plant brush against a person or a chair (Ebisch et al., 2008). The results demonstrated that somatosensory regions were similarly active during all conditions. This finding suggests that shared representations of touch are not limited to human contact, but rather, generalise to contact between a plant and a chair. Although this may be the case, it is also possible that by using a within-subjects design, the typical strategies for understanding observed actions (feasibly resonance with other) were applied inappropriately during the inanimate touch trials. Indeed, Poulton (1982) suggests that randomising trials, as was the case in this study, maximises the effects of influential companions. However, Keysers et al. (2004) demonstrated similar findings to Ebisch et al. (2008) using a within-subjects blocked design. The authors accounted for the possible influence of carryover effects by fixing the order of experimental blocks, starting with the most abstract observation of touch (an aeroplane wing over a land mass), followed by a kitchen roll and lever-arch file being touched, and finally, viewing other peoples' legs being touched. However, it is not clear from the methodology section whether the participants knew ahead of time what each block in the experiment contained.

As noted previously, all within-subjects tasks carry the possibility of influential companions accounting for some or all of the data, but some studies actually increase the likelihood of such effects. In hindsight, the within-subjects design utilised in Experiment 7, where trials were randomised and task demands varied, the possible influence of every condition on every other condition was strengthened (Poulton, 1982). Fortunately, we were made aware of this issue by the failure of the "painful grasp effect" to replicate in Experiment 7, leading us to explore our data further. We continued to address the possible role of task demands on shared representations of pain by utilising a between-subjects task in Experiment 8.

Although the role of task demands had previously been investigated in imaging studies, the results were conflicting. For example, Gu and Han (2007) demonstrated that when participants viewed still frame images of hands in painful situations, activation of pain processing regions was greater when participants rated the intensity of the observed pain, in comparison to counting the number of hands in each image. In contrast, Avenanti et al. (2006) explored the effects of passively viewing or imagining the pain felt by the actor when participants observed hands penetrated by needles. No difference in the amplitude of motor evoked potentials was revealed between the task instructions. However, an important difference between the experiment of Gu and Han (2007), and Avenanti et al. (2006) was that static stimuli were used in the former, and video stimuli in the latter. Thus, the potency of the viewed pain stimulus may also have a role in mediating the effects of task demands on shared representations of pain.

We have shown that when participants make appropriateness judgements whilst viewing two-frame sequences of hands interacting with painful and non-painful objects, participants were faster to respond to a tactile stimulus, and more biased to report touch during the observation of others in pain. However, when participants passively view the stimuli, reaction times were only speeded during the observation of grasp trials. Similarly, in Experiment 8 where participants judged whether there was contact made between the hand and the object, or judged the painfulness of the object, participants were faster to respond to touch when they observed grasping actions or painful objects, but in neither task were participants faster to detect touch whilst viewing painful grasps. These data suggest that although the shared representation of touch is automatic (Keysers et al., 2004), the effects of viewing others in pain on behaviour are not.

The failure of identical visual stimuli to evoke similar vicarious representations (Gu & Han, 2007) or behaviour change in the observer, challenges the automatic account of mirror neuron function (Rizzolatti & Craighero, 2001), and the direct-matching of viewed actions (Gallese & Goldman, 1998). Further, these findings suggest that only when the viewed stimulus is sufficiently salient to the observer (Avenanti et al., 2006), or when participants engage with the painful consequences of an observed action are the somatosensory aspects of observed pain encoded. Interestingly, the appropriateness judgement task, which reveals the “painful grasp effect”, is reliant on an observer accessing their own understanding of the sensory consequences of grasping an object. The importance of self-reference is explored further in Chapter 5.

Chapter 5

Is the "painful grasp effect" mediated by viewpoint?

5.1 Summary

The evidence presented so far in this thesis suggests that viewing others in pain affects an observer's tactile processing. However, the ambiguous viewpoint of the visual stimulus means the hand interacting with the objects may be interpreted as self, rather than other. It is important to ascertain the perceived viewpoint in order to understand the boundary conditions and underlying mechanisms of shared representations. Critically, evolved mirror neuron theories propose that vicarious cortical activity enables understanding of others. In contrast, associative learning accounts suggest that the development of these bimodal neurons are a consequence of our own learning history, performing and observing predominantly our own, but also other peoples' actions.

Experiment 9 aimed to directly test whether the "painful grasp effect" was mediated by viewpoint. Participants viewed two frame sequences of a hand approaching and grasping, or missing objects in a first person perspective and a third person perspective. Similar to Experiment 8, participants made a speeded response whenever they perceived a tactile stimulus delivered to their right index finger. The previously reported "painful grasp effect" was only replicated when participants viewed the hand-object interactions from the first person perspective (1PP), and not the third person perspective (3PP). These data suggest that the effects of viewing painful actions are mediated by relevance to self, rather than understanding of others.

5.2 Introduction

Evidence from the preceding chapters has shown that observers are able to infer the sensory consequences of hands grasping painful objects. These shared representations of touch and pain are often discussed in relation to understanding others (Iacoboni & Dapretto, 2006). However, these vicarious representations also have specific, and potentially adaptive, effects on observers' own tactile processing. Therefore, the primary role of such processes may not be action understanding per se, but rather a means of encoding potential threat to the self by observing another person's body-object interactions. If shared representations of touch do provide crucial information for self, it is important to know whether these effects are dependent on the viewing perspective of the observer. The visual stimuli used in all previous experiments in this thesis were captured from an ambiguous viewpoint, namely they could be interpreted as self or other. Therefore, in the current chapter, we examined the effects of observed pain from both an egocentric first person perspective (1PP) and the other, third person perspective (3PP). If vicarious activations are primarily concerned with simply representing the experience of another person, perspective may make little difference. In contrast, if the role of these action-observation processes is to predict future consequences for self, the "painful grasp effect" may only be revealed in the 1PP.

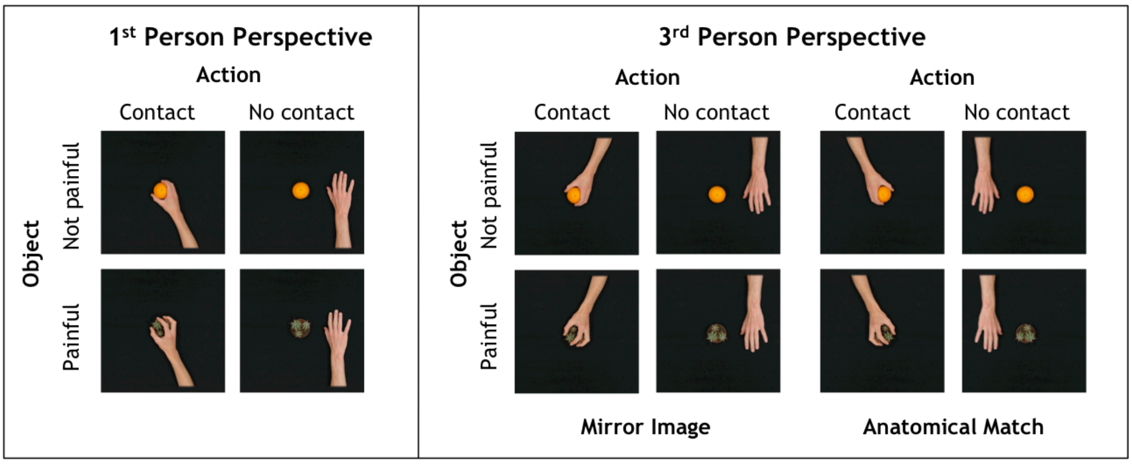


Figure 5.1. Example of experimental conditions. *Within participants*: viewpoint (first person perspective/ third person perspective), action (contact/ no contact) and object (painful/ not painful). *Between participants:* third person perspective (mirror image/ anatomical match).

By comparing viewpoint, we mean the visual properties of the experimental stimuli (see Figure 5.1), not task instructions associated with perspective taking. For example, Ruby and Decety (2001) asked participants to imagine themselves or the experimenter performing an action, based on a verbal description of an action, or a picture of an object. Similarly Jackson, Brunet, Meltzoff, and Decety (2006) investigated the effects of viewing others in pain by perspective taking through task instruction: imagining self or imagining other. Briefly, the authors revealed that, although both perspective taking tasks activated pain processing regions, imagining self pain elicited greater activation in the ACC, bilateral insula and SII. However, these instructions required participants to engage in effortful motor imagery and motor simulation, rather than more passive action observation (Grèzes & Decety, 2001).

The experiment is this chapter specifically aimed to manipulate viewpoint by way of visual stimuli, therefore, we will focus on the available evidence from imaging and behavioural studies using a visual manipulation task, albeit with non-painful stimuli. These studies also suggest that a difference may exist between 1PP and 3PP. Of importance is the finding that activation of somatosensory processing regions is mediated by viewpoint (Schaefer, Xu, Flor, & Cohen, 2009). Viewing hands being stroked by a paintbrush activated left SI and bilateral SII/parietal ventral (PV) in both 1PP and 3PP. However, the 1PP activated anterior SI and right PV, whereas 3PP revealed activation in more posterior regions of S1 and greater activation in a sub-region of left SII/PV. In contrast, Keysers et al. (2004) do not report differences in somatosensory activations during the observation of 1PP and 3PP touch. However, the stimuli in this experiment were legs being touched, rather than hands being touched. As legs have a smaller cortical representation than hands, this may explain why no difference between viewpoints was observed in this study (Schaefer et al., 2009).

In a more sensitive analysis of fMRI data utilising MVPA, patterns of activation have been shown to differ between 1PP and 3PP during the cross-modal coding of executed and observed slapping and lifting hand actions (Oosterhof, Tipper, & Downing, 2012). Although cross-modal coding was accurate for both perspectives in regions implicated in processing the visual features of a scene (bilateral occipital temporal cortex) and more abstract goal representation (anterior parietal cortex), only 1PP executed and observed actions were coded accurately in the ventral premotor cortex, a region involved in processing the motor components of actions.

Motor evoked potentials (MEPs) at the hand, generated by TMS over motor cortex, are also mediated by viewpoint (Maeda, Kleiner-Frisman, & Pascuel-Leone, 2002). Participants viewed a hand in the 1PP or 3PP performing finger movements with the thumb or index finger. MEPs from baseline were greater when participants viewed hand actions from the 1PP compared to 3PP and, interestingly, MEPs recorded from specific muscle sites, analogous to the index finger and thumb, only differentiated between actions during the 1PP and not 3PP. Importantly, differences caused by viewpoint are not isolated to experiments using imaging or TMS, but have also been reported in behavioural experiments (Vogt, Taylor, & Hopkins, 2003). In a visuomotor priming task, participants received an auditory cue informing them of the action they had to perform: grasping either a horizontal or vertical bar. This cue was followed by a hand prime and a go signal. The hand prime stimulus was either in the 1PP or 3PP, and in a congruent or incongruent configuration to the previously cued to-be-performed action. Participants were faster to respond to the go signal in congruent trials (ie. auditory cue and hand prime configuration were matched), but only in the 1PP (Vogt et al., 2003).

Although we have summarised a selection of articles that provide evidence in support of differences between 1PP and 3PP, a comprehensive review of the literature is difficult to perform as the stimuli in viewing perspective tasks differ between studies, sometimes substantially. For example, the limb, either right or left, that the participant views varies between experiments. Some studies use a mirror image (see Jackson, Meltzoff, et al., 2006; Vogt et al., 2003) to represent the 3PP, whereas others use an anatomical match (see Figure 5.1; Anquetil & Jeannerod, 2007; Maeda et al., 2002; Scheafer et al., 2009), but few directly compare right and left hands or feet in the 3PP. Indeed, it is not clear whether similarities and differences between findings are due to the 1PP and 3PP manipulation, or an intervening variable. For example, differences in luminance levels of the stimuli in 1PP and 3PP may alter cortical activity between perspectives (see Schaefer et al., 2009). Visual information gained from seeing the object and hand can also vary between viewpoint; the object may be occluded more in the 3PP than the 1PP (see Ogawa & Inui, 2011; Oosterhof et al., 2012) potentially making object identification more difficult in the occluded 3PP condition; or visibility of the hand and fingers differs between viewpoints (see Vogt at al., 2003) which may impede motoric and kinematics information from being extracted in either perspective. Finally, objects or limbs may be rotated between viewpoints (see Saxe, Jamal, & Powell, 2006) potentially altering the speed and accuracy of object recognition when the items are viewed from an atypical perspective (see Jolicouer 1985).

Campanella, Sandini and Morrone (2010) provide a striking example of the difficulties in producing balanced 1PP and 3PP stimuli. The authors created point light movies of hands interacting with objects, differing in size and shape, from a 1PP and 3PP, and participants were required to judge which object the hand had grasped. Participants were better able to discriminate between large and small object sizes when viewing the point light movies from a 1PP perspective. However, of fundamental importance is that, when collapsing the three dimensional point light information onto a two dimensional space, kinematic information relevant to size discrimination, including maximum grip aperture and maximum velocity was lost, but critically, only in the 3PP. Disparity such as this and others such as luminance levels, object occlusion, and hand details, could potentially account for the difference between 1PP and 3PP in a range of previous studies.

In the current study we aimed to overcome some of the difficulties associated with investigating 1PP and 3PP by photographing hand-object interactions from a bird's eye perspective (see Figure 5.1; for other studies using bird's eye view see Jackson, Meltzoff, et al., 2006; Maeda et al., 2002). The images of hand actions were then flipped and rotated to ensure matching visual information across conditions. Between groups, in the 3PP, participants viewed either an anatomical match or mirror image of the hand viewed in the 1PP to enable the comparison between these differing 3PPs (see Figure 5.1). In order to test whether viewing perspective affects the tactile processing of the observer, the current study adapted the behavioural methodology used in Chapter 4 to incorporate both 1PP and 3PP hand-object interactions. Participants viewed hands either approach and grasp, or miss, potentially painful and non-painful objects whilst detecting an above threshold stimulation delivered to their right index finger.

Therefore we examine the effects of observed pain from both an egocentric 1st Person Perspective (1PP) and the other 3rd Person Perspective (3PP). If the process is primarily concerned with simply representing the experience of another person, as the direct-matching hypothesis suggests (Rizzolatti et al., 2001), the "painful grasp effect" should be observed in both perspectives. In contrast, if the role of these action-observation processes is for predicting future consequences for self, effects may be more prominent from a 1PP. Indeed, a life history of associating vision and touch from an egocentric perspective (Heyes, 2010) would suggest such associations between vision, grasping and pain would be most profound in the 1PP condition.

5.3 Experiment 9. The effect of viewpoint on the "painful grasp effect"

5.3.1 Method

Participants

All participants (*n* = 48, male = 14, left-handed = 3) were aged 18 years or over (*M* = 20.23, *SD* = 3.14), and had normal or corrected-to-normal vision.

Measures

Participants completed a 28-item rating scale questionnaire to engage them with the painfulness of the stimuli. To familiarise participants with each of the objects, a side view of the object (see Figure 5.2a) was displayed for 2000 ms prior to the rating slide where the object was viewed from above (see Figure 5.2b). The more familiar side views were initially presented to facilitate recognition of the somewhat unusual bird's eye view used throughout the rest of the study.

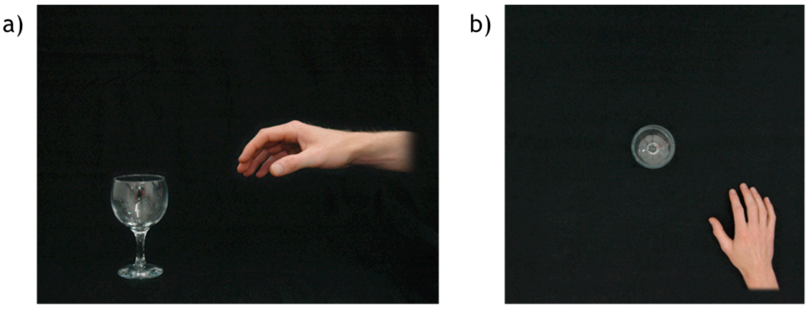


Figure 5.2. Example images from the 28-item rating scale questionnaire. a) Participants first saw the image of the object from a typical viewing perspective. b) The rating was made during the second frame, where the object was shown from a bird's eye perspective.

Stimuli

Each participant viewed hands interacting with 7 painful and 7 non-painful objects (see Figure 5.1 & 5.3a). Participants viewed a right hand from a 1PP and a hand viewed from the 3PP, grasp or miss the objects (see Figure 5.1). In the 3PP (see Figure 5.1), as a between-groups factor, participants either viewed an anatomical match of the 1PP hand (ie. a right hand in the 1PP and a right hand in the 3PP) or a mirror image of the 1PP hand (ie. a right hand in the 1PP and a left hand in the 3PP). The same photographs of hands and objects were used in each viewing perspective by flipping and rotating the images.

Design and Procedure

Initial procedures were similar to the other above threshold tactile detection tasks presented in this thesis (see Experiment 4). Participants completed 16 practise trials that were randomly selected from the main experimental trials. Participants viewed two frame sequences of a hand either approach and grasp, or miss, painful and non-painful objects, from a 1PP and 3PP (see Figure 5.1 & 5.3). Tactile stimulation occurred 150 ms after the onset of the second frame (where the hand performed the action) on 80% of the trials[5.1]. At the end of each trial, regardless of whether there was stimulation or not, participants had to make a verbal response about whether the action involved “contact” or “no contact”.

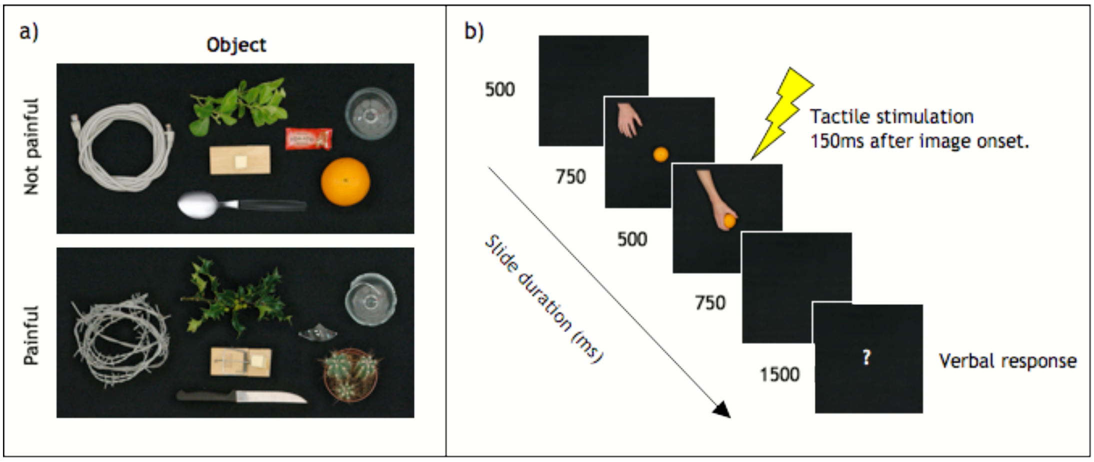


Figure 5.3. a) Examples of object stimuli. Non-painful objects: cable, plant, cheese on a wooden board, spoon, tomato sauce sachet, wine glass and an orange. Painful objects: barbed wire, holly, loaded mousetrap, serrated sharp knife, shard of glass, broken wine glass and cactus. b) Schematic of tactile detection trial (4000 ms total duration). Tactile stimulation (50ms duration) occurred 150ms after the onset of the frame where the hand interacted with the object. The delayed verbal response occurred during the final frame of the trial sequence, when the question mark was on screen. Example trial: 3PP, non-painful grasp.

The experiment proper consisted of 280 trials (28 stimulation trials out of 35 trials per condition) and was subdivided into four blocks. The trials in each block were identical to the training trials, and equally distributed over the eight different conditions (1PP/3PP by painful/not-painful by contact/no contact; see Figure 5.1). Each of these four blocks was preceded by a shorter block of 16 trials that served to remind participants about the painfulness of the objects. In these blocks, participants saw the same actions but were simply asked to state whether the object they had seen was potentially “painful” or “not painful” [5.2].

5.3.2 Results

Three additional participants were excluded for not performing the task correctly. Preemptive detections (<100ms) and reaction times greater than 1500ms were removed from the data (0.49%). The data for hits, reaction times (see Figure 5.4), and false alarms (see

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[5.1] The proportion of stimulation to no stimulation trials was modified from 50% to account for the extra conditions created by the two viewing perspectives, and to represent the above threshold reaction time, rather than SDT nature, of the task.

[5.2] The change of verbal task was motivated by the findings in Chapter 4. In order to allow possible differences between the 1PP and 3PP to be revealed, the Judge Action task was used alongside the Judge Object task to ensure participants engaged with the physical aspects of the stimuli.

Figure 5.5) were entered into three separate 2 x 2 x 2 repeated measures ANOVAs with the factors viewpoint (1PP/ 3PP), action (contact/ no contact) and object (painful/ not painful) and the between groups factor of 3PP (anatomical match/ mirror image).

Hits Participants detected a mean of 27.43 stimulation trials out of 28. There was no between group effect of 3PP (anatomical match/mirror image), $F < 1$, $p = .642$, $\eta^2_p < .01$. The three-way ANOVA revealed a significant interaction between action and the between group effect of 3PP, $F(1,47) = 6.98$, $p = .01$, $\eta^2_p = .13$, whereby participants in the anatomical match group detected more stimulation during grasping trials than miss trials ($p = .019$). There was no difference in the number of hits between the grasp and miss trials when participants viewed the mirror image ($p = .337$). However, this effect did not interact with the key research question.

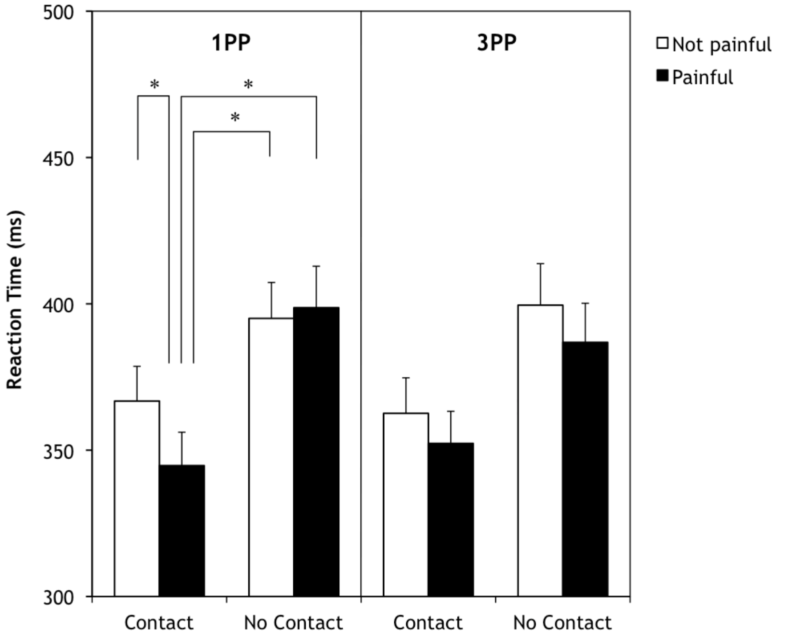

Figure 5.4. Mean reaction time (ms) to the detection of a tactile stimulus, whilst observing hands from 1PP and 3PP interact with painful and non-painful objects. *Significant difference between means ($p < .01$). Error bars represent +1SEM.

Reaction Times There was no between group effect of 3PP (anatomical match/ mirror image), $F < 1$, and there were no interactions between 3PP, viewpoint, action or object. Reaction times did not differ between 1PP and 3PP, and viewpoint did not interact with action or object ($F < 1.2$, for all). However, there was a main effect of action, $F(1,47) = 58.37$, $p < .001$, $\eta^2_p = .56$ such that reaction times to the detection of touch were faster when participants viewed contact ($M = 356.61$ ms), compared to no contact trials ($M = 395.03$ ms).

There was also a main effect of object, *F*(1,47) = 10.61, $p = .002$, $\eta^2_p = .19$; reaction times to the detection of touch during the observation of painful objects (*M* = 370.65 ms) were faster than non-painful objects (*M* = 380.99 ms). There was a trend towards an action by object interaction *F*(1,46) = 3.64, $p = .063$, $\eta^2_p = .07$, but more importantly, there was a significant three-way interaction between viewpoint, action and object, *F*(1,46) = 6.14, $p = .017$, $\eta^2_p = .12$.

To better understand the critical three-way interaction, 1PP and 3PP reaction times were analysed in two separate 2 x 2 ANOVAs, with the factors of action (contact/ no contact) and object (painful/ not painful). As no between groups effects were found in the initial ANOVA, subsequent analyses were collapsed across 3PP (anatomical match/ mirror image) conditions. As revealed in the initial three-way ANOVA, there was a main effect of action in both the1PP, *F*(1,47) = 52.67, $p < .001$, $\eta^2_p = .53$, and the 3PP, *F*(1,47) = 41.31, $p < .001$, $\eta^2_p = .47$, with faster reaction times during the observation of contact trials. The main effect of object was also apparent in the 2 x 2 analysis for both the 1PP *F*(1,47) = 4.75, $p = .034$, partial $\eta^2 = .09$, and the 3PP *F*(1,47) = 9.72, $p = .003$, $\eta^2_p = .17$, with faster reaction times recorded during the observation of painful, compared to non painful objects. Notably, a significant interaction between action and object was only observed in the 1PP, *F*(1,47) = 7.65, p = .008, $\eta^2_p = .14$, and not the 3PP, *F*(1,47) = 0.11, $p = .737$, $\eta^2_p < .01$.

Planned comparisons demonstrated the action by object interaction, unique to the 1PP, was driven by the painful grasp condition. Reaction times were faster during observation of others in pain from the 1PP, compared to all other 1PP non-painful actions ($p < .002$ for all; see Figure 5.4). There was no difference in reaction time between 1PP painful and non-painful actions where no contact occurred ($p = .579$). These data suggest that only when actions are viwed in the 1PP are action and object properties combined to create a sensory expectation. In contrast, during 3PP trials, reaction times to touch are only influenced by the action and object properties of the stimuli and not the combination of the two.

False Alarms There was no between group effect of 3PP (anatomical match/ mirror image), *F*(1, 46) = 1.59, $p = .213$, $\eta^2_p < .03$, and no interactions with the within subjects conditions. Although participants made most false alarms whilst observing hands grasp painful objects in the 1PP (*M* = 1.08, see Figure 5.5), there was no three-way interaction between viewpoint, action and object, *F*(1,46) = 1.04, $p = .312$, $\eta^2_p = .02$. The number of false alarms did not differ between viewpoint (*F* < 2) or object painfulness (*F* < 1), and no interaction between viewpoint and action (*F* < 1) was observed. However, the ANOVA did reveal a main effect of action, *F*(1,46) = 17.34, $p < .001$, $\eta^2_p = .27$, such that more false alarms were made when participants viewed hands making contact with objects (*M* = 0.85) than when the hands missed the objects (*M* = 0.42). Interestingly, the ANOVA also revealed an interaction between viewpoint and object, *F*(1,46) = 4.08, $p = .049$, $\eta^2_p = .08$. Planned comparisons demonstrated that during the observation of non-painful objects (regardless of the action made) there was no difference, $p = .908$, in the false alarms made between 1PP and 3PP. However, during the observation of painful objects, participants made more false alarms in the 1PP (*M* = 0.76), than the 3PP (*M* = 0.54), $p = .044$.

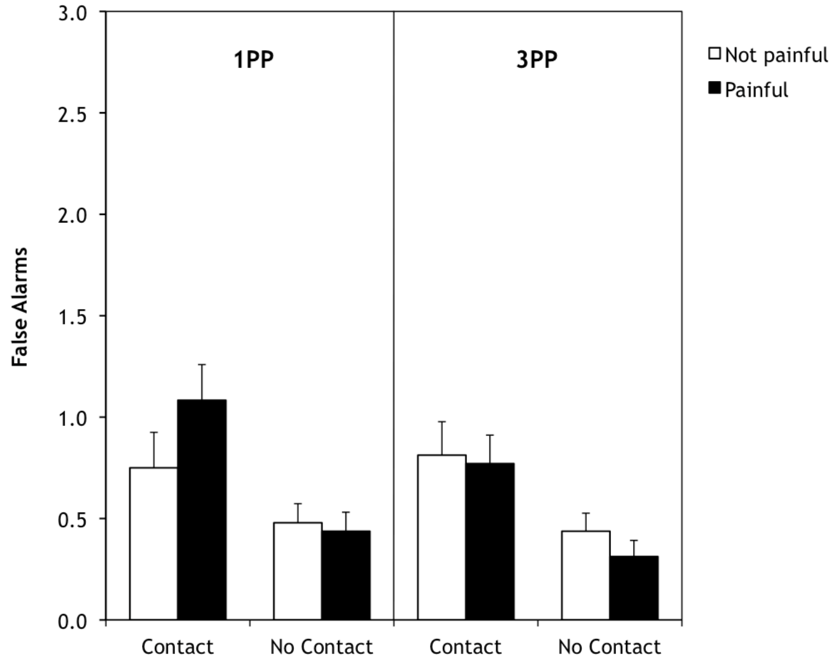

Figure 5.5. Mean number of FAs (erroneous detections) during the observation of hands interacting with painful and non-painful objects from 1PP and 3PP. Error bars represents +1SEM.

5.4 Discussion

For the first time, the behavioural effects of viewing someone else grasping a painful object from either a 1PP or 3PP have been investigated. Only when viewed from a 1PP does observing someone else in pain facilitate the reaction time to detect a tactile stimulus on the observer's own hand. This finding suggests that during 1PP viewing, the object information, action information, and the interaction between action and object are encoded to infer the sensory outcome of the action. In contrast, viewing someone in pain from a 3PP does not selectively affect tactile processing. Instead, reaction times to tactile detection are mediated independently by action and object information.

Morrison et al. (2012) report activation in somatosensory processing regions that encode the action, the object, and the painful consequences of an observed hand interacting with different objects. In this context it would appear that actions viewed from the 3PP may activate these separate components of object (painful/ non-painful) and action (contact/ no contact), as these main effects were highly significant in our behavioural data. In contrast, only from the 1PP is the separate encoding of object and action combined to represent the sensory consequences of painful actions. Shared cortical activations may serve to prime the detection of touch, facilitating reaction times when viewing contact trials, painful objects, and, specifically in the 1PP, observing painful grasps. If somatosensory activation does underlie facilitated reaction times, one might predict that the somatosensory region preferentially active during painful grasps (combined object and action representations) reported by Morrison et al. (2012) would be more active in the 1PP than the 3PP. If this were true, it would have ramifications for imaging studies that use images in the 1PP and 3PP, but do not analyse these conditions separately. For example, both Corradi-Dell'Acqua et al. (2011) and Morrison, Peelen et al. (2007) collapsed across 1PP and 3PP viewpoints when analysing their data, and failed to reveal shared representations of pain in somatosensory processing regions. This lack of activation may be due to combining activation from the 1PP, where the painful consequences of an action are encoded, and the 3PP, where action and object information may be represented separately.

Similar to the reaction times results, false alarms also differed between 1PP and 3PP during the observation of painful objects: participants reported tactile stimulation when there was none, more often during the observation of painful objects in the 1PP regardless of the action that was being performed. Although the interaction between viewpoint, action and object was not significant, the distribution of false alarms was similar to those reported in previous studies in this thesis, with most false alarms made during the observation of painful grasps in the 1PP.

The between group factor of 3PP (mirror image/ anatomical match) did not mediate reaction times or false alarms, suggesting that the limb (right or left) being viewed does not affect action understanding in this task. These findings are in line with Campanella et al. (2010) who did not observe size discrimination accuracy differences when participants observed left or right hands in the 1PP or 3PP.

So why was action and object information not combined to create a sensory expectation of pain from the 3PP? Evidence suggests that understanding the 3PP may involve a mental rotation from the observer's perspective into the 3PP; a computation which is cognitively demanding and time consuming (Zacks, 2008; Reed & McGoldrick, 2007). The additional processing time may mean that when tactile stimulation occurs only 150ms after the hand-object interaction slide, only action and object information have been understood in the 3PP, and not the interaction between the two. However, Vogt et al. (2003) provide evidence against this explanation. The authors varied the length of time their hand prime stimulus was displayed for: 0 ms, 200 ms, 400ms, or 600ms. Even at longer stimulus onset asynchronies, the 3PP still did not gain a reaction time advantage for congruent versus incongruent trials. The additional cognitive demands required to interpret the 3PP may also affect the depth of action understanding in this condition. However, in the current task, the contents of the visual stimuli were identical between 1PP and 3PP, and RTs between 1PP and 3PP were not significantly different.

We argue that in order to combine action and object information, to infer the sensory consequences of an observed action, participants must engage a self referential perspective. Indeed, brain regions active during tasks involved in understanding others, are also activate in self referential tasks (Northoff et al., 2006). What is critically important is not viewing perspective per se, but the relevance of the visual stimuli and task to the observer, or the similarity of the person being observed to self. As Northoff et al. eloquently put it: “When objects and events are viewed through the ‘eyes’ of the self, stimuli are no longer simply objective aspects of the world, but they typically become emotionally colored, and thereby more intimately related to one’s sense of self.” (Northoff et al., 2006, p.441).

Interestingly, the reaction time data pattern (interaction between object and contact) for the 1PP, and not 3PP, are similar to those we report in Chapter 3. The congruency in the reaction times between the experiments suggests that the ambiguous viewpoint during Experiments 2, 4 and 5, were interpreted from the 1PP. This may be due to the high level of encoding that was required by the participants on a trial-by-trial basis; recall that participants had to report whether the action they had seen was appropriate or not. To answer this question, they must access their own action understanding to predict the consequences of the observed action: “Would grasping that object hurt?” or rather, “If I grasped that object, would it hurt me?”.

Griffiths and Tipper (2009; 2012) provide other examples of how the relevance of the task to self can mediate shared action representations. Griffiths and Tipper (2009) demonstrated that when a participant observed another person reach over an obstacle, their own reach in the subsequent trial was more curved, suggesting that the observed reach path was activated in the observer. Importantly however, such reach trajectory priming effects were only detected when the observed action was within the peripersonal action space of the observer in this task. Hence this result supports our proposal of the importance of the relevance to self, in this instance, within the actor's action space. Furthermore, when the acted upon objects were explicitly shared between two people, even when the observed action was in far extrapersonal space, the reach trajectory priming effect re-appeared (Griffiths & Tipper, 2012). Thus, object relevance to the participant, either in terms of being within peripersonal action space or shared ownership when in far extrapersonal space, was critical for activating shared action representations.

The perceived similarity (or dissimilarity) between the observer and the person being observed also mediates the extent of shared representations. A potent example of this relation to self is evidenced in the following pain observation study. Avenanti et al. (2005) showed participants videos of a needle penetrating a hand, or cotton wool bud pressing against a hand from the 1PP. During the observation of the painful needle condition, MEPs, recorded at the participant's own hand were reduced. However, in a later study, the authors found that the reduction in corticospinal excitability, associated with withdrawal or escaping actions, did not occur when the hand being viewed was from an out-group race (a white-Caucasian participant viewing a black-African hand, or a black-African participant viewing a white-Caucasian hand) even though the stimuli remained in a 1PP (Avenanti, Sirigu, & Aglioti, 2010).

The examples above and the findings from the current experiment begin to map the boundary conditions that exist when observing others' actions. More specifically, the behavioural effects of viewing others in pain are not automatic, but rather, are mediated by similarity to self. Combining action and object information to create a sensory expectation during the painful grasp only occurred in the 1PP. Unlike many experiments investigating the role of viewing perspective on action understanding, the difference in encoding between 3PP and 1PP cannot be attributed to differences in visual stimuli. Instead, we argue that the selective effects on behaviour are consistent with participants taking a self-referential, rather than viewpoint specific, perspective in the 1PP.

Chapter 6

From vision to touch: The cortical and behavioural effects of viewing others in pain

6.1 Summary

The experiments in this thesis have explored the cortical and behavioural effects of viewing others in pain. The specificity of this vicarious cortical activity was addressed in Chapter 2, utilising MVPA to investigate whether an observer represents different types of pain at a somatosensory level. Chapter 3 focused on the possible behavioural effects viewing others in pain may have on an observer, including their ability to detect tactile and auditory stimuli. The effects of viewing hands grasping painful objects were examined further in Chapter 4 by assessing the contribution of task demands on reaction times to the detection of touch. In the final experimental chapter, Chapter 5, viewing perspective was directly manipulated to test whether shared representations of pain were mediated by viewing painful actions from a first or a third person perspective.

The experimental findings are summarised in this chapter, and related to current theories of action understanding. The notion that shared representations of pain developed to allow us to understand the actions of others is challenged. Instead, we propose that vicarious activations are a consequence of misattributing observed actions onto one's own action system. As such, our results are explained in line with associative learning accounts of bimodal neuron development, rather than evolved mirror neuron accounts. Further, we outline the possible mechanisms which may give rise to speeded reaction times, and an increased bias to report touch, during the observation of others in pain. The implications of our findings are briefly reviewed in relation to theoretical and practical applications.

6.2 The cortical and behavioural effects of viewing others in pain

The experiments in this thesis aimed to extend our understanding of shared representations of pain by focusing on fine-grained analyses of cortical activity evoked by viewing painful grasping actions. We also explored the possible consequences this vicarious activity might have on behaviour and the boundary conditions surrounding such effects. In Chapter 2, we investigated whether an observer represents the type of pain that they view, for example, a pricking pain in comparison to a stinging pain. In our fMRI study, participants viewed hands grasping stinging nettles or holly, or two neutral plants (ivy and balsam), whilst occasionally responding to the appropriateness of the viewed action. Traditional univariate analyses revealed greater cortical activation in regions previously associated with the encoding of others pain, including the anterior insula, when participants viewed the hand grasp the nettle or holly. However, no difference in cortical activity evoked by viewing stinging versus pricking pain was revealed outside visual cortex. Critically, MVPA extended these findings, demonstrating that, despite not being significantly active in the univariate analysis, secondary somatosensory cortex accurately represented the painfulness of the stimulus, whereas visual regions accurately discriminated between the types of pain-evoking stimuli. These findings suggest that although an observer encodes the painful consequence of an observed action, the precise sensory details are not represented. Further research utilising MVPA and experiments directly comparing the experience with the observation of pain will help to assess the efficacy of our preliminary findings.

Activation of somatosensory regions during the observation of others in pain raised the possibility that an observer's own ability to detect touch might be mediated by viewing painful actions. Indeed, our experimental findings extend evidence of shared cortical representations to behaviour change in the observer. In Chapter 3, we revealed that participants were more biased, as well as faster to report touch on their own body, when they viewed hands grasp painful objects. Importantly, the "painful grasp effect" was not revealed when participants detected auditory stimulation, suggesting the effects of viewing others in pain are sensory specific. Further, the speeded reactions times to the detection of touch cannot be explained by attention being drawn to the painful object during grasping trials as a gloved hand, protected from pain, did not result in the "painful grasp effect".

Although the specificity of the "painful grasp effect" has been bound to somatosensation, it is not known from the experiments presented in this thesis whether the effects are limb specific. For example, we did not investigate whether observation of a hand in pain mediates tactile processing at the foot, or whether observation of feet in pain changes tactile detection on an observer's feet. Indeed, many studies investigating shared representations of pain have only used hand stimuli (Bufalari et al., 2007; Corradi-Dell'Acqua et al., 2011; Morrison et al., 2012) or have combined the results of viewing hands and feet in pain (Jackson et al., 2005). However, Avenanti et al. (2005) have shown that viewing others in pain only affects motor evoked potentials recorded from a similar muscle site to that of the viewed hand penetrated by a needle. Furthermore, that the reduction in MEPs recorded at the hand is not revealed when participants view a foot being penetrated by a needle; an effect which has been extended from motor to somatosensory processing regions using EEG (Voisin, Marcoux, Canizales, Mercier, & Jackson, 2011). Together, these findings suggest that the behavioural effects of viewing others in pain may well be limb specific.

The "painful grasp effect" revealed in Chapter 3 appeared robust, replicating across three separate studies, utilising both above and below threshold tactile stimulation. However, in each task participants were asked to judge the appropriateness of the observed action on a trial-by-trial basis. In order to make this judgement, participants had to combine both action and object knowledge to infer the outcome of an observed action. Therefore, the contribution of action or object knowledge, or the inference of painful consequences in causing the "painful grasp effect" was not known. Indeed, it was possible that the effects on tactile detection would occur when participants passively viewed the stimuli. However, when participants only responded to occasional catch trials, the "painful grasp effect" failed to replicate. To further our understanding of the role of the verbal task on evoking speeded reactions times to the detection of touch, participants judged the appropriateness of actions, object painfulness, the action performed, or passively viewed the hand-object interactions. Interestingly, rather than enabling the individual contribution of each verbal response task on reaction times to be assessed, the experimental findings highlighted the problem of influential companions (Poulton, 1982). Consequently, in a further set of experiments designed to record potential differences in reaction times solely due to judging the painfulness of objects or the actions performed, participants only completed one verbal task. In both the action and object tasks participants were faster to respond to touch during the observation of grasping actions and painful objects, but not the interaction between the two. Rather than automatically encoding the painful consequences of an observed grasp, the "painful grasp effect" appears dependent on a task demanding the combination of action and object knowledge.

In Chapters 2 to 4, the hand interacting with the objects was oriented in an ambiguous viewpoint, such that it could be perceived as self or other. In the final experimental chapter, we directly manipulated the hand orientation to investigate the possible role of viewing perspective on shared representations of pain. Participants viewed a hand from a first person perspective and a third person perspective, grasping or missing the painful and non-painful objects. Only during first person perspective viewing were participants faster to respond to a tactile stimulus on their own hand during the observation of a painful grasping action. Importantly, unlike previous studies in the field, the differences in reaction times between the viewing perspectives could not be attributed to variation in the visual stimuli.

Overall, the experiments presented in this thesis further our understanding of shared representations of pain, including the behavioural consequences of such vicarious cortical activity. The boundary conditions surrounding the "painful grasp effect" also provide some insight into the underlying mechanisms mediating speeded reaction times to touch and a bias to report touch during the observation of others in pain.

6.3 Potential mechanisms underlying the "painful grasp effect"

6.3.1 Mirror neuron theories versus associative learning accounts

Overlapping cortical activity during the observation and experience of pain has frequently been attributed to mirror neuron activity (Keysers et al., 2010). Evolved accounts of mirror systems suggest "…these mechanisms were selected because they offer the adaptive advantage of enabling the understanding of the feelings and mental states of others, a cornerstone of social behavior." (Iacoboni, 2009, p. 654). In contrast, we focused on the possibility that activation of core somatosensory processing regions, when viewing others in pain, might result in adaptive behaviour change for the observer. Using experimental stimuli known to evoke such shared cortical representations of pain (Morrison et al., 2012), we demonstrated that this activity is associated with changes in tactile processing. Participants were faster to report touch on their own hand, but also more likely to report touch, when they viewed a hand grasp painful objects. Although these findings alone do not challenge the notion of mirror neuron activity enabling the understanding of others action - for example, the behavioural effects may be a by-product of such activity - the mediation of the "painful grasp effect" by task demands and viewing perspective are suggestive that alternative accounts need to be considered.

Rather than a system evolved to understand others, we believe vicarious activations during the observation of others in pain, and the boundary conditions surrounding such effects, may be more parsimoniously explained by a mechanism evolved for action production which is also attributed to observed actions (see also Hickok, 2009; Hickok & Hauser, 2010). This theory aligns with the associative learning account of mirror neurons proposed by Heyes (2001, 2010), whereby a lifetime of associations between vision and action, predominantly of one's own actions, leads to the development of bimodal neurons. In contrast to the supposed automaticity of the mirror system specialised for understanding others (Rizzolatti & Craighero, 2004), the activation of these bimodal neurons appears dependent on the similarity or relevance of the observed actions to self.

Single unit recordings in monkeys support the notion that relevance of an observed action to self mediates vicarious activity. For example, mirror neurons respond far less consistently when the animal views goal-directed actions that do not contain food (Fogassi et al., 2005; Gallese et al., 1996). Similarly, in humans, only when objects are shared between two actors (Griffiths & Tipper, 2012), or are in peripersonal space (Griffiths & Tipper, 2009), is an observer's own reach trajectory affected by observing others' actions. Further evidence that shared representations of pain may not be driven by a mechanism created to understand others is that, even in a first person perspective, recorded MEPs are not affected by viewing a hand penetrated with a needle from an out-group race (Avenanti et al., 2010). Further, Lorey et al. (2009) demonstrated that when participants adopt a hand posture incompatible with an observed action, such as an open palm, cortical activity is reduced in precentral gyrus and secondary somatosensory cortex, in comparison to when the participants adopt an congruent hand posture. Rather than an automatic resonance system (Rizzolatti & Craighero, 2004), these findings suggest similarity with the self determines the extent of shared cortical activations.

The proposal that the similarity of an observed action to self modulates shared representations provides an opportunity to distinguish between evolved mirror neuron and associative learning accounts of such activity. Crucially, the two accounts would likely make different predictions about the consequences of viewing actions from a first person and third person perspective. It seems plausible that a system created to understand others' actions would function equally efficiently, or more so, when actions were viewed from the typical, third person perspective. In contrast, a system evolved for action production would be preferentially active in the first person perspective. Experiment 9 provided evidence in support of the latter hypothesis: only when participants viewed painful actions from the first person perspective, and not the third person perspective, were they faster to respond to touch on their own body.

Further evidence that shared representations of pain may be mediated by relevance to self, rather than understanding others, is that the "painful grasp effect" does not occur when participants passively view painful actions from an ambiguous viewpoint. Only when participants are required to engage with the sensory consequences of an observed action, on a trial-by-trial basis, are the behavioural effects during the observation of others in pain revealed. Interestingly, the verbal judgement task in Experiment 9, where viewpoint was directly manipulated, required participants to respond to whether there was contact made between the hand and the object. Even though this judgement did not pertain to the painful consequence of an action, speeded detection of touch was reported during the observation of painful actions in the first person perspective. It is therefore possible that the painful consequences of an observed action viewed from the 1PP are more readily attributed to self, due to the similarity between one's own actions and those being observed.

6.3.2 Predicting the consequences of an observed action

An important aspect of the experimental tasks presented in this thesis is that no evidence of pain, such as skin damage or facial expressions of pain, were displayed in the visual stimuli. Therefore, the consequences of the grasping actions had to be inferred by the observer. Indeed, during the condition that required participants to understand the sensory consequences of a hand grasping a painful object, reaction times to the detection of touch were speeded, and participants were more biased to report touch. The possibility of prediction in vicarious representations of pain is not easily explained by initial accounts of mirror neuron function, such as the "direct-matching hypothesis" (Rizzolatti et al., 2001). However, Heyes (2010) includes a predictive element in the associative learning account of mirror neuron development: when a sequence of learnt associations between vision and action are strong, the outcome can be inferred based on prior experience.

Importantly, the ability to predict the consequences of ones own actions is fundamental to current action control theories incorporating both internal forward and inverse models (Miall & Wolpert, 1996; Wolpert & Kawato, 1998). Forward models are essentially predictive, where the current state information, for example joint angles and position of the hand, is used to infer the most likely consequent state (Wolpert & Ghahramani, 2000). This prediction is then compared against sensory feedback, and discrepancies between predicted and actual sensory information update the current state estimate. In contrast, inverse models provide commands for what needs to happen next to complete a desired goal, and hence are often referred to as the “controller” (Wolpert & Kawato, 1998).

The computations made by forward and inverse models can be explained by Bayesian statistics (Wolpert & Ghahramani, 2000). Briefly, Bayes’ rule enables current information and previous experience to be combined to calculate the probability of a given situation or context (Westbury, 2010). Bayes’ rule can be used to compute more general phenomena, such as the probability of a person suffering from a particular illness given their current symptoms, the results of their blood test, and the prevalence of a condition (Westbury, 2010). Equally, Bayes’ rule can be applied to more low-level phenomena, such as the estimate of distance from an object, given prior knowledge of object size and current depth cues. The probability of a given context based on current information or sensory cues is known as the likelihood estimate, whereas the probability of a given context based on previous knowledge and experience is known as the prior probability, or prior (Wolpert & Ghahramani, 2000).

In action control, the forward model is guided by the likelihood estimate, whereas the inverse model is guided by priors (Wolpert & Ghahramani, 2000). We will expand on these concepts using the example of a person weeding the lawn with bare hands, deciding whether to perform a withdrawal action or grasping action, given the painfulness of a perceived plant. The likelihood estimate is calculated by combining available sensory cues, such as the texture and colour of the leaves, and the tactile information on first contact with the plant, to obtain an estimate of the potential painfulness of the plant (Ernst & Banks, 2002). This cue combination has been shown to be optimal, such that more reliable cues are weighted more heavily, compared to less reliable cues (Ernst & Banks, 2002). The rationale for integrating cues, rather than relying on the most reliable cue, is that even the least reliable cue contributes to a more precise estimate of the environment (Ernst & Banks, 2002; Ernst & Bülthoff, 2004).

In contrast to the likelihood estimate, as previously mentioned, priors are based on the life experience of an organism (Wolpert & Ghahramani, 2000). In the current circumstance, the gardener had previously removed hundreds of dandelions from the lawn, as such, the probability that the plant is painful, based on priors, is low. Importantly, more weight is given to these priors when the information provided by the current cues in the environment become ambiguous or unreliable, for example, if the gardener was not wearing their glasses (Körding & Wolpert, 2004). Fundamentally, priors do not necessarily reflect the true probability of a given situation, but instead may be biased by current demands or previous salient experiences (De Ridder, Vanneste, & Freeman, 2012; Friston, 2005; Trommershäuser, Maloney, & Landy, 2003). For example, if the person gardening had previously been prickled by a thistle in the lawn, current predictions, driven by previous costs associated with grasping a painful plant, may be biased to assume the plant was a thistle, despite the true probability, based on both the likelihood estimate and alternative prior, that it was most likely a dandelion.

6.3.3 Attributing observed actions to self

Bayesian models are important for the efficacy of an action production system, which can be attributed to others, for two core reasons. Firstly, the model can account for the predictions made of the sensory consequences of an observed action, and secondly, optimal cue combination may offer a crucial explanation for how an observed action can be misattributed to self. Although the term “misattribution” sounds like an error - indeed Jeannerod (2003) suggests blurred distinctions between self and other are symptomatic of dysfunction - this ostensible illusion of self merely highlights how our brain normally functions. For example, Botvinick & Cohen (1998) demonstrated that participants experience a rubber hand as their own when they view the prosthetic being stroked in synchrony with their own hand (obscured from view). This so-called “rubber hand illusion” (RHI) is attributed to the conflict between visual, tactile and proprioceptive information created in the task, providing insight into how these cues are normally combined (Botvinick & Cohen, 1998**).**

Although the RHI is not typically related to mirror neuron theory, observing a rubber hand threatened by a needle, following synchronous stroking, elicits similar cortical responses as viewing another person’s hand or indeed one’s own hand being threatened, including increased cortical activity in the anterior insula and anterior cingulate cortex (Ehrsson, Wiech, Weiskopf, Dolan, & Passingham, 2007). The apparent similarity of such cortical representations is suggestive that similar processes may mediate each effect. Indeed, the cues from vision, touch and proprioception provide apparently conflicting information about the current context in both the RHI and the behavioural tasks presented in this thesis.

In relation to Bayesian models, calculating a likelihood estimate of the situation from available cues, in both the RHI and the tasks in this thesis, means that optimal cue combination may result in vision being weighted more heavily due to the greater reliability that the visual cue affords (Ernst & Banks, 2002). However, the effect may also be influenced by the degradation of proprioceptive information available to the participant (Wann & Ibrahim, 1992). In both tasks, the participant is required to remain still, and during this period of stillness, proprioceptive cues providing information about the participant's limb location are not updated and, consequently, become more unreliable (Wann & Ibrahim, 1992). Again, given the combination of available cues, taking into account the reliability of each, the most likely estimate converges on the assumption that the viewed hand is one's own.

6.3.4 The "painful grasp effect"

We propose that the behavioural effects of viewing others in pain are most parsimoniously explained by activation of one's own action production system. In contrast, the consistent action effect, typified by faster reaction times to touch during contact trials, compared to no contact trials, is not dependent on activation of one's own motor system. It is important to make this distinction between the two effects because we believe the main effect of action does not speak to the efficacy of mirror neuron theories. Firstly, the action effect is also revealed when participants detect auditory stimuli whilst observing hand-object interactions, suggesting that the effect is not based on sensory specific shared representations. Secondly, pilot data from our laboratory shows that a main effect of action is also observed when participants view two inanimate objects make contact. Further, the action effect may, in part, be mediated by a response compatibility effect: the spacebar press response was more similar to the observed action of the hand grasping an object, than the hand missing or withdrawing from the object.

Returning specifically to the behavioural effects of viewing others in pain, if we assume that our actions are guided by Bayesian models, the sensory outcomes of both observed and performed actions can be predicted. Similarly, a mechanism which optimally combines multisensory cues provides a plausible explanation for the integration of viewed actions into one's own body schema. How though does such a system account for speeded reaction times to the detection of touch and an increased biased to report touch during the observation of painful grasping actions?

A lifetime of performing grasping actions means that the association between contact with an object and somatosensation is strong – creating a prior whereby the probability of experiencing touch when viewing grasps is high. Consequently, the observation of contact between a hand and object may lead to the expectation of a tactile stimulus, pre-activating tactile and pain processing regions (Sawamoto et al., 2000). Indeed, vision of objects alone activates somatosensory and action encoding regions (Grèzes & Decety, 2002). Increased activation of somatosensory processing regions may serve to prime the sensation of touch, speeding reaction times to the detection of touch during grasping actions - an effect which is observed across all reaction time studies in this thesis. Further, the expectation of a more intense tactile sensation during a painful grasp may account for the greater facilitation to report touch in this condition.

Facilitated reaction times and an increased likelihood to report touch may also be mediated by priors, which are influenced by the current task (Trommershäuser et al., 2003). For example, perceptual judgements are biased by the costs associated with making a particular judgment (Fleming, Whitely, Hulme, Sahani, & Dolan, 2010; Friston, 2010). In the potentially pain evoking situation depicted in our experiment, the failure to report a tactile stimulus could be interpreted as a cost, thus participants are actually biased to report touch. For example, imagine there was a wasp in the room, which you then lose sight of. If you thought you felt something on your skin, your reaction would most likely be to assume it was the wasp, in an attempt to protect yourself from potential harm. Crucially, one does not wait for the pain (the sting) to respond to the threat in the environment, hence this bias occurs even when the detected stimulus is neutral, such as the tactile targets in our experiments. Biased priors may therefore also contribute to the "painful grasp effect" reported in this thesis.

Although, the preactivation of tactile and pain processing regions based on priors may help to explain the speeded reaction times to the detection of touch, the model fails to account for the proportion of erroneous detections of touch in our tasks. If pre-activation of somatosensory regions alone caused false alarms to be made, participants would report the detection of touch on every grasp trial. In contrast, the number of false alarms made throughout the experiments is low [6.2]. However if pre-activation of tactile processing regions is combined with baseline fluctuations in cortical activity, the occurrence, yet scarcity of false alarms may be accounted for. For example, baseline fluctuations in inferior frontal gyrus and anterior cingulate cortex predict whether subsequent laser evoked stimulations are perceived, and increased activity in the insula and posterior ACC, prior to stimulus onset correlate with increased ratings of pain (Boly et al., 2007). Interestingly this activity does not include somatosensory cortex, suggesting that false alarms may be a consequence of a change in decision-making criteria, rather than tactile perception. Indeed, both Lloyd et al. (2011) and Wiech et al. (2010) provide further evidence that suggests erroneous reports of touch and the

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[6.2] Recall however, that we used an above threshold level of stimulation in many of the tasks. Yet, even in the threshold level task, the proportion of false alarms remained low.

perception of pain respectively are mediated by cortical activity outside sensory processing regions.

The neurological basis of phantom pain also provides some insight into the occurrence of false alarms in our behavioural tasks (De Ridder et al., 2012). Phantom pain is characterised by the perception of pain and a hyperactive sensory cortex, despite the deaffernation of neurons carrying painful, or indeed non-painful, information (Flor, 2002). Interestingly, phantom pain is more likely to occur in patients who experienced chronic pain before the limb was amputated (Flor, 2002); an intriguing observation which may be linked to the role priors play in current perception. Indeed, De Ridder et al. (2012) suggest phantom pain highlights how the brain normally functions, minimising the ambiguity in the system by "filling in the gaps" of information – a process which is proposed to be reliant on prior experiences. However, in the case of phantom pain, reducing the ambiguity that arises from sensory cortex hyperactivity inadvertently leads to "topographically restricted prediction errors" and hence the percept of pain (De Ridder et al., 2012, p. 9). If, as we propose, viewed actions can be perceived as one's own, the lack of sensory feedback during a painful grasp is analogous to deaffernation – activation of sensory regions without sensory input – resulting in erroneous reports of tactile stimulation.

The occurrence of false alarms revealed in our behavioural tasks combining visual and tactile stimuli has intriguingly been reported in research investigating the causes of medically unexplained symptoms (MUS; Lloyd, Mason, Brown, & Poliakoff, 2008; McKenzie et al., 2012). Medically unexplained symptoms differ from phantom pain because there is seemingly no explanation for their cause (Brown, 2004). However, similar to phantom pain, individuals are more likely to have MUS if they have directly experienced illness or trauma, but also if they have observed illness or trauma in others (Brown, 2004). As such, Brown (2004) emphasises the importance of memory, as well as attention to bodily sensations, in the formation of MUS.

Lloyd et al. (2008) designed a task known as the somatic signal detection task (SSDT) to investigate MUS experimentally in both clinical and normal populations displaying somatoform dissociation-like traits. Participants detected threshold-level tactile stimuli delivered to their finger either concurrently with a light stimulus delivered at their fingertip, or in the absence of the light. Despite the light being task-irrelevant, participants were more biased to report touch during light present trials, than the light absent trials (Lloyd et al., 2008). The authors suggest that "these illusory sensations of touch may arise from the activation of memory by the light" (Lloyd et al., 2008, p. 22). Further, participants scoring more highly on the somatoform dissociation questionnaire make more false alarms and are more biased to report touch (Brown, Brunt, Poliakoff, & Lloyd, 2010). The suggestion that the normal population also experience "illusory sensations of touch" and are more inclined to do so if they report traits associated with MUS, suggests that a similar mechanism may explain the behaviour displayed in the SSDT task, clinical populations with MUS, and the "painful grasp effect". Indeed, although Lloyd et al. (2008) use the phrase "activation of memory" and Brown (2004) discusses "memory traces", whereas we have utilised terminology from Bayesian models, such as priors, the explanation for the behavioural effects in both tasks are similar. Further, false alarms are suggested to be the product of "rogue representations" or salient memories by Brown (2004), whereas we attribute these to biased priors, where the true probability of an event occurring is actually skewed, yet the semantics of both our explanations are inherently the same. Interestingly, in a recent account of MUS incorporating many of Brown's ideas, Edwards, Adams, Brown, Pareés, and Friston (2012) do apply Bayesian models to explain the symptoms of the condition. Furthermore, the authors conclude that "the overweighting of prior beliefs over sensory data" (p. 14) is responsible for both MUS and perceptual illusions in the normal population, corroborating our proposal that the behaviour reported in the SSDT task and the "painful grasp effect", may indeed be explained by a similar model.

6.4 Alternative accounts

Although we have outlined an alternative explanation for the underlying mechanisms supporting shared representations of touch, further research will need to be carried out to assess the efficacy of our proposal. For example, different interpretations of the role of sensory expectation may account for the "painful grasp effect". It is possible that although the tactile sensation is predicted during the observation of grasps, the effects on reaction times are caused by a mismatch error between the primed tactile input and the actual tactile stimulus. Recall that the tactile stimulus in the current task is a small vibration, dissimilar to the expected sensation of interacting with the non-painful stimuli and very different to the pain evoking objects. Consequently, the salience of the unexpected stimulus may cause speeded reaction times to touch, whereas an absence of stimulation is also surprising and may lead to false alarms. The degree of mismatch is greater in the painful grasp condition than the non-painful grasp condition, which may account for the difference in responses between these two conditions. Further studies utilising tactile stimuli both congruent and incongruent with the observed consequences of the hand-object interaction will need to be employed to confirm the possibility of this interference effect.

The “painful grasp effect” is typified by speeded reaction times to the detection of touch, and an increased bias to report touch during the observation of painful grasps. However, these seemingly facilitatory effects are in conflict with the apparent attenuation afforded by a system that predicts the sensory consequences of an action (Blakemore et al., 1998). Indeed, Blakemore et al. (1998) demonstrated that when participants touch their own hand with a soft foam stimulator, activation of secondary somatosensory regions, anterior cingulate cortex, and the cerebellum was reduced in comparison to an identical stimulus delivered by the experimenter. The attenuation of somatosensory information due to self-touch was attributed to the similarity between the predicted and experienced sensory information. Indeed, Wolpert and Flanagan (2001) state that “it is possible to cancel out the effects of sensory changes induced by self-motion, thereby enhancing more relevant sensory information” (p. R730). What is crucial, and is absent in this explanation, is the ability to enhance relevant information to guide overt action. In the context of expectation of pain for example, attenuation of such a stimulus might negate adaptive avoidance behaviours being initiated. Interestingly, Kok, Rahnev, Jehee, Lau, and de Lange (2012) have recently demonstrated that, within the visual modality, attention reverses the sensory attenuation of predicted signals. These results are in line with the role of task demands observed in our behavioural experiments: only when participants actively attend to both the action and object properties of the scene is the “painful grasp effect” revealed. To our knowledge, there are no studies directly investigating the role of salience on mediating subsequent attenuation of touch, and this would be an interesting extension to the current literature.

6.5 Conclusions

The research presented in this thesis was motivated by studies demonstrating that observing others in pain activates pain processing regions involved in encoding the direct experience of pain (Lamm et al., 2011). Although shared representations of pain had previously been attributed to a mirror mechanism evolved to understand the actions of others (Iacoboni & Dapretto, 2006), we hypothesised that activation of core somatosensory regions during the observation of painful grasps might mediate tactile processing in the observer. Indeed, participants were faster to report touch and more biased to report touch when viewing a hand grasp a painful object. Further, the boundary conditions surrounding the “painful grasp effect" were incongruent with mirror neuron theories of action understanding. Critically, the behavioural effects of viewing others in pain were replicated when participants viewed painful grasps in a first person perspective, and not in the more typical third person perspective. We believe these data cannot easily be accounted for by mirror neuron theories and have outlined an alternative explanation for our findings.

Interestingly, the hypothesis that one's own action production system may be involved in representing observed hand-object interactions is not so far removed from more recent interpretations of the mechanisms underlying vicarious cortical activity. For example, Kilner, Friston, and Frith (2007) proposed a Bayesian model to explain the function of the mirror neuron system, but maintained that this mechanism was specialised for understanding the actions and intentions of others. However, the authors have incorporated the associative learning account, rather than the evolved account, of mirror neuron development in a more recent formulation of their ideas (Press, Heyes, & Kilner, 2011). Consequently, our proposal that it is one's own action system, and not a "mirror system", that mediates shared cortical activity may appear only subtly different to other available interpretations. However, we argue that this difference is fundamental to the interpretation of data within the field of vicarious representations, particularly when findings guide clinical research and therapeutic interventions.

Currently, the clinical relevance of mirror neurons focuses on people who have autism (Iacoboni & Dapretto, 2006; Ramachandran & Oberman, 2006; Rizzolatti, Destro, & Cattaneo, 2009). Autism is a heterogeneous disorder, typified by difficulties in functioning in social interactions (Ramachandran & Oberman, 2006). Consequently, for those people who believe mirror neurons imbue the ability to empathise with others, a logical next step is that "…people with autism have a dysfunctional mirror neuron system…" (Ramachandran & Oberman, p. 67). Indeed, therapeutic interventions have been suggested to overcome autism based on this interpretation of the disorder (Altschuler, 2008; Ramachandran & Seckel, 2011). However, the same authors that propose a deficit in mirror neuron function in people with autism also provide evidence that when a child with autism views themselves, a caregiver, or sibling perform an action, their mirror neuron system performs as well as aged-matched controls (Oberman, Ramachandran, & Pineda, 2008). Indeed, Southgate and Hamilton (2008) suggest the evidence for "broken mirrors" is not only inconclusive, but that the proposal fails to account for the complexity of the disorder.

In contrast to an evolved system designed to understand the actions of others, we believe variability in a person's ability or likelihood to perceive observed actions as their own might have more clinical relevance. Recall that, key to our proposal is that shared cortical representations are a consequence of misattributing one’s own action production system to observed actions. Further, although this misattribution may appear like a computational error, it actually highlights what the brain normally does – optimally integrate both current information and prior knowledge. Thus, variation in cortical shared representations may reflect variation in cue integration strategies, and not an ability to understand others’ actions or empathise with conspecifics. Indeed, Gowen and Hamilton (2012) have recently highlighted the possibility that multisensory integration and the reliability of cues perceived by people with autism may be atypical. Similarly, medically unexplained symptoms (Edwards et al., 2012), phantom pain (De Ridder et al., 2012) and so-called “positive” symptoms in schizophrenia (Fletcher & Frith, 2009; Synofzik, Their, Leube, Schlotterbeck, & Lindner, 2010) have also all been attributed to dysfunctional cue integration.

We acknowledge that further research is necessary to assess the efficacy and generalisability of our proposal that one’s own action production system can be misattributed to observed actions. However, we believe that an alternative explanation of shared cortical representations beyond mirror neuron theory needs to be considered to account for the extent and diversity of such effects. Although the research in this thesis has focused on the cortical and behavioural effects of viewing others in pain, we believe the interpretation of our findings may provide a promising line of enquiry for future research.

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