THE PHYSIOLOGY AND PSYCHOLOGY OF SELECTIVE ATTENTION TO TOUCH

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1. ABSTRACT

In this chapter we review psychological and physiological experiments on selective attention to touch stimuli. We explore the role of selective attention in tactile target detection and search, determining those tasks that benefit from attention and those which can be effectively performed pre-attentively. We also try to determine the stage at which attentional selection occurs. We review electrophysiological and human brain imaging (PET, fMRI, MEG, SEP) studies to assess how early in the somatosensory processing pathway attentional modulation occurs. There is some evidence that the primary somatosensory cortex (S1) can show attentional effects. However, a number of studies have suggested that there is a hierarchy to attentional modulation in the somatosensory system, with the greatest effects being observed in secondary and association areas.

2. INTRODUCTION

After decades of research on selective attention, one of the clearest definitions of attention is still to be found in William James' Principles of Psychology, written in 1890.

"Everyone knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others" (1).

It is this ability which allows us to attend to one conversation in a crowded room, blocking out all other noise – the so called 'cocktail party effect'. This voluntary or 'top-down' focussing of attention is distinct from the reflexive or 'bottom up' shifting of attention that occurs when we hear our name in another, unattended conversation. The cocktail party scenario illustrates some of the main issues in attentional research. For example – does selective attention to one input lead to increased sensitivity to the attended input? Does the presence of competing conversations affect processing of the attended input? To what level are unattended stimuli processed? This last question is of interest both from the psychological point of view (eg is an unattended word processed to the level of phonology/semantics? (2)) and from the physiological point of view (eg does attention operate at the level of the peripheral receptors, primary sensory cortex or secondary sensory cortices?). This review will attempt to address some of these issues using psychological and physiological evidence from studies of attention and touch.

Section 3 provides a brief overview of the anatomy of touch. Particular attention is paid to the question of whether touch processing occurs in series. This is important if we are to relate psychological models of attention (often serial box and arrow models – eg ref 3) to neuroscientific findings.

Many studies of selective attention have focussed on the visual system (eg 4-6). It is known that selectively attending to a location in space enhances our perception of visual stimuli appearing at that location (4). However, it is only recently that studies have explored the role of selective attention in touch (5-14). Section 4.1 will explore these basic phenomena of selective attention to touch stimuli to determine whether selective attention facilitates detection of a tactile target.

Studies of visual attention have also made much use of the visual search paradigm where subjects have to search for a target stimulus in an array of distractor stimuli (15). One of the functions of attention is to enable us to search efficiently. Section 4.2 outlines some of the ways in which tactile attention enables efficient search through time and space (16-27).

Many psychological models of selective attention assume that attention acts to filter out irrelevant information in order to protect our limited-capacity processing systems from information overload (4). However, such models vary as to whether they place the attentional filter early or late in a processing stream. Section 5 explores this question with evidence from behavioural and neuronal studies. Behavioural studies enable us to determine whether competition between attended and unattended stimuli occurs at the perceptual stage or at the response stage (28). Electrophysiological and human imaging studies can help determine how early in the somatosensory system attentional modulation occurs (29-39).

Neuronal studies can also help elucidate the mechanisms of attentional modulation. It is often assumed that directing attention to a stimulus produces a gain in perceptual sensitivity that is reflected by an increase in the neuronal signal evoked by the attended stimulus. However, effective attentional selection might also depend on damping down signals from distractor stimuli –such as non-relevant sensory modalities, or distractor stimuli of the same modality (36). Section 6 explores this and related issues in considering possible mechanisms of attentional selection.

Finally, section 7 considers the ways in which perception of touch stimuli can be influenced by information from other sensory modalities (40-45).

3. ANATOMY OF TOUCH

3.1. Touch pathways - from mechanoreceptors to thalamus

The sense of touch is just one component of somatosensation (or 'somesthesia', see 46 for review). Included in somatosensation are senses such as temperature, pain, pressure and proprioception. All are mediated by physiologically and anatomically distinct pathways and each can be studied to determine the degree to which attention affects processing. Although this review will concentrate mainly on the tactile sensations induced by vibration or mechanical depression of the skin, it is important to emphasise that normal behaviour is very much dependent on all aspects of somatosensation. This is lucidly demonstrated by the experiences of Ian Waterman, a man who lost all touch and position sense after large fibre deafferentation and who must now rely on his other available senses (vision, hearing and temperature) to provide the necessary feedback to guide him through his sensory environment and complete goal-directed movements successfully (47).

The sense of touch is initiated by mechanical stimulation of the body (48). Mechanoreceptors are situated at different depths in the skin and have different response properties. Studies on the glaborous (hairless) skin of the hand support the view that there are, in general, four different types of mechanoreceptive afferents (49, 50). There are afferents that are slowly adapting, with small receptive fields (SAIs); slowly adapting with large receptive fields (SAIIs); rapidly adapting with small receptive fields (RAs – these are also known as fast adapting or FAIs) and rapidly adapting with large receptive fields (the Pacinian corpuscles – PCs or FAIIs). Although many studies investigating touch have looked exclusively at the effects of applying stimulation to a single channel (such as vibration on the pacinian receptor) the four-channel model of mechanoreception maintains that normal tactile experience results from the combined neural activity of all four mechanoreceptive channels (for review see 51).

Peripheral nerves project from mechanoreceptors to the dorsal root ganglia. Fibres from the dorsal root ganglia project along the dorsal columns of the spinal cord to the dorsal column nuclei in the medulla. Fibres from these nuclei project to the ventroposterior thalamus (VP) which projects to somatosensory areas in the parietal cortex (for review see 52).

3.2. Cortical touch pathways – does processing occur in series?

There are thought to be nine cortical areas with primarily somatosensory function: the primary somatosensory cortex (SI – comprising areas 3a, 3b, 1 and 2 – see reference 53), the second somatosensory area (SII) located along the superior bank of the sylvian fissure (54, 55), the granular insula and retroinsular cortex (56), and in the posterior parietal cortex areas 5 and 7b (57).

The debate over whether attention acts early or late in the sensory processing system depends on the assumption that processing occurs in series. This assumption has been tested in a number of different species by anatomical and inactivation studies (58-70).

The investigation of hierarchical processing of touch information in mammals has mainly focussed on the flow of information between SI and SII. VP sends direct reciprocal projections to both S1 and S2 (58-60). This therefore led to the belief that somatosensory information was processed in parallel.

Whether processing occurs in series can also be tested by inactivating proposed early processing regions and seeing whether this silences other areas. Inactivation of S1 does not effect responses in S2 in the cat (61), rabbit (62), tree shrew or prosimian galago (63). These studies lend further support to the idea of parallel processing of somatosensory information.

However, in other primate species a different model is emerging. In macaques it appears that VP sends only sparse projections to S2 (64, 65). By contrast there are dense projections from all four subregions of S1 to S2 (66,67). This is consistent with a serial processing scheme with information passed from VP via S1 to S2. In a study by Pons et al (68) selective lesions were made of the hand representation in the different subunits of S1 and responses to touch stimuli were recorded in S2. S1 lesions caused

highly specific reductions of S2 responses. Responses were reduced only in the hand region of S2 and only to stimulus types corresponding to the processing selectivities of the lesioned S1 region (ie lesions to areas 3b and 1, which process mainly cutaneous information, led to reduced response only to cutaneous stimulation in the hand area of S2). This suggests a highly specific, somatotopically-organised serial processing stream. The notion of serial processing in the primate somatosensory system is further supported by a recent neurophysiological study looking at firing periodicity in S1 and S2 (69)

Evidence from humans also supports the serial processing model. Using MEG, Mima et al (34) found that the earliest responses to electrical stimulation of the median nerve occurred at 20ms and were maximal over the hand area of contralateral S1. Later responses, at 100-200ms, were found over bilateral temporal-parietal areas, thought to correspond to S2.

The evolutionary stage at which the switch from parallel to serial processing occurs is debatable. Garraghty et al (63) showed that lesions of S1 in marmosets rendered S2 unresponsive to peripheral stimulation. However, Zhang et al (70) performed rapidly reversible cooling of S1 in marmosets and recorded from the same S2 cells before, during and after cooling. They found that S1 inactivation had very little effect on S2 responsiveness.

4. THE BEHAVIOURAL CORRELATES OF SELECTIVE ATTENTION TO TOUCH

4.1. Simple target detection

James suggested that selective attention allows us to 'deal effectively' with the attended stimulus (1). In more recent years there have been a number of studies testing the hypothesis that selective attention to touch facilitates processing of the attended stimulus. Many of these studies have made use of paradigms originally developed for investigation of attention primarily in the visual domain. A classic visual attention paradigm is provided by Posner (4). The following paradigm provides a test of covert visual attention (ie not dependent on overt eye movements). Subjects fixate centrally and are required to detect the appearance of a peripheral target stimulus. The target stimulus can be preceded by a cue. 80% of the cues validly predict the location of the subsequent target. 20% of cues are invalid (ie the target appears in the opposite location). A baseline measure of subjects' reaction time (RT) is found by testing the response to uncued targets. Preceding the target with a valid cue speeds RT relative to baseline whilst presentation of an invalid cue slows RT. This suggests that covert visual attention can be directed to a particular location in space, takes time to be shifted in space, and enhances processing of stimuli within the attended location.

This paradigm has been adapted for use with tactile stimuli (71,7,10). Subjects are cued to expect a tactile stimulus to a particular body location. The results from these experiments have not always matched those from the visual cueing experiments. For example, Posner (71) cued subjects to expect a tap to either the left or right index fingertip and found no significant effect of cueing on response time. A similar experiment by Butter et al (7) used both visual and tactile cues. A significant effect of cueing was found for a tactile detection task (for both cue types), although the effect was smaller than for the analogous visual detection task. Bradshaw et al (10) also report significant cueing effects in a tactile detection task.

As cueing can be shown to affect reaction time to tactile targets, it seems that as for visual attention, the focus of tactile attention can be shifted through space, and that the shifting takes time. An experiment by Lakatos and Shepard (72) attempted to demonstrate that the time to shift attention depends on the distance between attended locations, and to establish whether the crucial distance was a direct line through space, or a distance through the subject's body. Subjects heard the name of a body part and attended to that location. Two seconds later a second body part was named, simultaneous with air puffs applied to 4 body parts. The subject had to report whether any of the air puffs had been applied to the second named body part. RT increased with distance between the first and second attended body parts. The crucial distance was the straight line through space, rather than a route through the subject's body.

4.2. Effective search

Another widely used visual attention paradigm is visual search (15). Subjects are required to detect a target stimulus amongst an array of distractor stimuli. When a target is defined by the presence or greater intensity of a feature (eg a long line amongst short lines) subjects are very quick to report the presence of the target, and RT is not affected by the number of distractors in the array. However, when the target is defined by the absence or lesser intensity of a feature, subjects are slower and RT increases linearly with increasing numbers of distractors (74, 74). This suggests that searching for the absence of a feature is a more demanding task and is performed in a serial manner. This paradigm has been adapted to test whether cueing has differential effects on different target types (11). In this experiment, vibrotactile stimuli could appear at four possible body locations - the index and middle fingers of both hands and in one of two possible intervals. Subjects had to report in which interval the target appeared. In one task the target stimulus was an amplitude change amongst distractors of constant amplitude (ie target defined by the presence of a feature). In a second task the target stimulus was a constant amplitude amongst distractors of changing amplitude (ie target defined by the absence of a stimulus). Valid and invalid tactile cues were presented to one of the fingertips before the test stimuli. Consistent with the presence-absence asymmetry in the visual experiments, cueing had a greater effect when the target was defined by the absence of an amplitude change. This suggests that detecting the presence of a tactile feature is not necessarily aided by selective attention. In line with this conclusion, Sathian and Burton (12) report that cueing does not affect detection of an abrupt change in texture. As direction of attention by cueing did not assist target detection, these results suggest that the presence of certain tactile features can be detected pre-attentively.

This conclusion is supported by a study of somatosensory evoked potentials (SEPs). A much studied evoked potential is the P300 which is characteristically evoked by oddball events (75). Bruyant et al (43) detected this potential using a tactile paradigm in which rare electric shocks were presented to an attended or unattended hand whilst frequent distractor stimuli were presented to the other hand. The P300 was present even when the oddball stimulus was presented to the unattended hand. Again, this suggests that much perceptual analysis can take place without the subject orienting attention to the stimulus.

Search in natural environments and in psychology experiments depends both on attending to objects/locations of relevance and on inhibiting attention to irrelevant objects/locations. One way in which a location is marked as irrelevant is if it has previously been searched and found to lack anything of interest. The mechanism which prevents us returning to such a location is known as 'inhibition of return' (IOR - 4). Although this was initially thought to be a purely visual phenomena, elicited by the saccade-generating system of the superior colliculus, it is now appreciated that the superior colliculus controls orienting behavior to auditory and tactile stimuli also (76,78) and tactile versions of the IOR task have demonstrated that a similar mechanism operates in touch (9, 16,17). Indeed, a recent neuroimaging study has shown superior colliculus activation in a tactile IOR task (78). In a pioneering study by Tassinari and Campara, detection of electrocutaneous targets could be delayed following an electrocutaneous cue at the same somatotopic location, suggesting a possible within-modality IOR for touch (15, see 9 and 17 describing similar results using vibrotactile stimuli). Unfortunately, there are criticisms of this study, which make the interpretation of a true IOR effect difficult. The main criticisms are that there may have been a reduction of motor readiness at the cued location (18) or an inhibition of eye-movements to the cued location (19). However, a recent study by Spence et al., (20) has demonstrated that inhibition of return can occur purely within the tactile system when both of these confounding factors have been controlled for. This inhibition of tactile inputs has also been observed within the pain system and between the different somatosensory systems, (21).

A similar inhibitory phenomenon exists to enable effective search in the *temporal* domain. Again, this has been widely studied in the visual domain, using the 'attentional blink' paradigm (22). In this task, subjects are required to find visual targets in streams of rapidly changing, serially presented objects (23,24). Correct identification of one target can produce an 'attentional blink' lasting approximately 100-400ms, during which detection of a second target is impaired (see 25 and 26 for reviews). In a tactile version of this experiment, subjects experienced rapid, serially presented streams of vibrations and responded to specific targets in the streams (27). Targets could differ from distractors in terms of frequency, duration, intensity or location. An attentional blink was found *only* when targets were defined by location. This suggests that spatial processing is crucial in determining allocation of tactile selective attention even within the temporal domain.

5: HOW EARLY DOES THE TACTILE ATTENTIONAL FILTER OPERATE?

5.1 . At what stage does competition occur?

The filtering of irrelevant or unattended stimuli is a crucial feature of many models of selective attention (3). However the models vary in how far an unattended stimulus is processed before being filtered out. One way to address this question is to determine whether competition between target and non-target stimuli occurs early or late in processing. Evans and Craig addressed this with a paradigm that allowed them to distinguish competition at the level of stimulus perception or response (28). Subjects attended to one finger where target stimuli would be presented. Distractor stimuli were presented to an adjacent finger. Subjects had to make one of two responses based on the direction of movement of the stimulus to the target finger. Stimulus movements up or left were associated with finger response 1 and stimulus movements down or right with finger response 2. Thus the similarities between target and distractor stimuli could be systematically varied:

1. *Stimulus and response compatible:* Target and distractor identical
2. *Stimulus incompatible, response compatible:* Target and distractor move in different directions but are associated with the same response
3. *Stimulus and response incompatible:* Target and distractor move in different directions and are associated with different responses

Results showed that competition occurred at the level of **response**: Subjects were faster to respond in the *stimulus incompatible, response compatible* condition then the *stimulus and response incompatible* condition suggesting the unattended distractor stimuli must have been processed up to the stage of response activation. This is consistent with models of attentional selection with late filters (79,80).

However, Evans and Craig (28) also found evidence for competition at the level of the **stimulus**: subjects were faster to respond in the *stimulus and response compatible* condition (condition 1) than in *stimulus incompatible, response compatible* condition. This suggests that attentional selection is also operating at an earlier level of stimulus perception. Similarly, a study by Driver and Grossenbacher (41) demonstrated an interference effect between target and distractor stimuli presented to different hands when the stimuli were the same but not when they were different.

Taken together, these results suggest that attempting to classify attentional selection as either early or late may not be appropriate here. Instead the mechanism of attention selection might be more flexible, allowing different strategies to be used in different contexts (81)

5.2. Does attentional modulation occur in S1?

It was established in section 3.2 that in monkeys and arguably in humans, the neural pathways for touch processing are organised serially, with the main projections going from the ventroposterior thalamus to SI then from SI on to SII and other association areas. The issue of how early the attentional filter operates can be addressed by determining the degree of attentional modulation at different stages along this pathway.

This question has been extensively studied in the visual system. (5,6, 82, 83). It is now widely accepted that attention modulates extrastriate visual areas (3) and that attentional effects can be seen in the primary visual cortex in certain conditions (6,82,83). However, a number of studies have shown that the effects are larger (84) and occur earlier (85) in extrastriate areas than in the primary visual cortex. Attentional effects have also been demonstrated in the auditory system where a recent fMRI study reported greater attentional modulation of primary than secondary auditory cortex (86).

Attentional modulation of somatosensory regions has been demonstrated using single unit recording in monkeys (30-32), SEPs (33,42,43), MEG (34,35), PET (30,36,37,39) and fMRI (38). Although a number of these studies have reported attentional modulation of S1 (29,38,39), some studies have found that S1 is not modulated by attention (34,35) or is modulated to a lesser degree than S2 (37,30). This section shall explore some of the possible reasons for the discrepancies between these studies, including differences in paradigm design, analysis methods and imaging modality.

One practical issue that has emerged from studies of somatosensory attention is that the likelihood of detecting modulatory effects in S1 depends on the choice of control task. One of the earliest studies of the neural correlates of selective attention to touch was an electrophysiological study of S1 responses whilst monkeys were instructed to attend to or ignore vibration to the hand (31). This study found that only 16% of recorded S1 cells showed increased activity levels when attention was directed towards the vibration stimulus. By contrast, a later electrophysiological study by Hsiao et al (30) found that 50% of S1 cells increased their activity with attention. One of the differences between the two studies was that the animals in the Hsaoi et al experiment were given an active distractor task (to detect the dimming of a visual stimulus) in the no attention condition.

The importance of this difference in design is highlighted by a PET study which compared S1 activation in conditions of attended touch, unattended touch and active distraction from touch (39). The following conditions were used:

1. *Unattended touch:* Vibrotactile stimuli were delivered to the fingertips but subjects were not required to attend to the stimulation.
2. *Attended touch:* The same stimulation was provided and subjects were instructed to detect changes in stimulus frequency, pressure or sweeping pattern (no such changes actually occurred).
3. *Active distraction from touch:* Subjects received the same vibrotactile stimulation but were required to perform a concurrent mental arithmetic task.

All conditions produced robust activation of S1. No significant differences in S1 activation were seen between unattended (condition 1) and attended (condition 2) touch. However, attended touch did produce significantly more S1 activation than the distraction condition (condition 3). This supports the idea that active distraction helps in the detection of attentional modulation of S1. However, it is important to note that there was a tendency for a greater blood flow increase from rest baseline to the attention condition (33%) than from rest to the unattended touch condition (27%) (cf 20% from rest to active distraction condition) but this difference did not reach significance. So it is not that distraction is necessarily different from 'no attention', but more that the addition of a distracting task allows the experimenter more control over the subject's attentional focus. This reduces the chance of the subject attending to the touch in spite of instructions not to and can reduce inter-subject variability and therefore increase the chances of detecting an effect.

Taken together the above studies suggest that attentional modulation can occur in S1, and that the likelihood of detecting such modulation increases when the subject is distracted from the touch stimulus in a controlled way during non-attention conditions.

The question still remains as to whether attentional modulation occurs to *different degrees* at different levels of the somatosensory processing hierarchy. As well as studying cellular responses in S1, Hsiao et al (30) also investigated responses in S2. They found that 80% of recorded S2 cells changed their activity with attention, compared to 50% in S1. This suggests that S2 is subject to greater attentional modulation than S1.

A number of human imaging experiments have compared the magnitude of attentional effects in S2 and S1. Using MEG, Mima et al (1998) asked subjects to perform a rare stimulus detection task (34). Subjects were given repetitive electrical stimulation of the median nerve. Stimuli could be either strong or weak. One stimulus type occurred 90% of the time and the other type occurred 10% of the time (in one experiment the strong stimulus was rare and in a second experiment the weak stimulus was rare). In an "active attention" condition subjects were told to mentally count the rare stimuli. In an ignore condition subjects watched a video and were not required to attend to the touch stimuli. Early responses (20–60ms) to touch stimuli that occurred over the left central area were thought to originate in S1. Later responses (100-200ms) which were maximal over bilateral temporal-parietal areas were assumed to come from S2. All responses were affected by stimulus intensity as expected. Both S1 and S2 showed response increases with stimulus deviance in both tasks, suggesting that activity in both areas is affected by reflexive or pre-attentive processes. Voluntary or active

attentional processes were examined by comparing MEG responses between the two tasks. This comparison showed that only S2 showed differential responses between the two tasks, with greater response seen to the touch stimuli when they were attended.

A recent PET study by Burton et al also explored the differential effects of attention on primary and secondary somatosensory areas (37). In a selective attention condition subjects had to detect a change in stimulus roughness or duration. In a divided attention condition subjects were instructed to detect a change in either attribute. In a control condition subjects were given the same touch stimuli but instructed to ignore them and perform a distracting counting task. In somatosensory regions (including S1 and S2) no differences were found between blood flow responses to selective and divided attention tasks. Comparing attention tasks to the distraction condition revealed a network of somatosensory areas modulated by attention. Foci within S1 showed some increase with attention but these did not reach significance with the most stringent statistical criteria. Decreases in S1 activity were seen when comparing passive stimulation conditions to rest (see below). In contralateral S2 significant increases were seen with attention and these increases were significantly greater than those seen in S1. A trend for attention-related increases was seen in ipsilateral S2 but did not reach significance. These data are consistent with those of Hsaoi et al (30) in suggesting that selective attention modulates S2 activation more than S1. Burton et al (37) suggest that S2 might actually influence S1 activity via a descending control path.

However, a recent fMRI study by Johansen-Berg et al (38) found significant attentional modulation of both S1 and S2. Subjects were presented with both visual and touch stimuli. In attention conditions they were instructed to detect either the visual or the touch stimuli. The maximum signal change for each task versus unstimulated rest was measured within anatomically defined regions of interest. Attended touch produced a greater maximum signal change than unattended touch in contralateral S1 and S2. In line with the findings of Burton et al (37) non-significant trends for an attentional increase were also observed in ipsilateral S2 as well as the insula. However, in contrast to Burton et al's (37) study, no evidence was found for greater modulation in S2. In fact six out of nine subjects showed a larger maximum signal change in S1 than S2, though this difference was not significant. This finding is more in line with reports of attentional modulation in the auditory system where a recent study reported greater modulation of primary than secondary auditory cortex (86). Interestingly, both the auditory study and the touch study of Johansen-Berg et al used a regions of interest analysis approach. Johansen-Berg et al found that a commonly-used group analysis procedure did not detect attentional modulation in S1 in their data and suggest that this could be due to the smaller physical size, and greater variability of S1 responses compared to S2. Burton et al (37) also comment that these factors affect the cross-validation methods they use.

Comparing attentional effects in S1 and S2 helps to determine how early in the somatosensory processing system modulation occurs. To address this question it is also relevant to ask where *within* S1 attentional effects can be seen. The major projections of somatosensory information from the mammalian ventroposterior thalamus are sent to layer IV of S1. From here the information is relayed to other layers within S1 and then on to S2 and other regions of somatosensory association cortex. The electrophysiological study of Hyvarinen et al (31) found that 16% of recorded S1 cells increased their activity with attention. Most of these cells were located in area 1 and were minimal in area 3b/3a, where the thalamic input is more direct (87). They were also located mainly in layers I, II and VI rather than layer IV where the thalamic inputs are received. This suggests that there is a hierarchy to attentional effects within S1. However, this study was perhaps limited in sensitivity by the lack of a distraction task in the control condition. Moreover, small attentional effects have been reported to occur as early as the thalamus in the PET study by Burton et al (37) discussed earlier.

6. POTENTIAL MECHANISMS OF ATTENTIONAL SELECTION

Many of the electrophysiological and brain imaging studies of tactile attention look for *increases* in neural activity as a correlate of attention (see section 5.2). However, attentional selection might also operate by decreasing signals evoked by irrelevant stimuli. A PET study by Drevets et al (36) looked at blood flow changes when different body locations were attended within the somatosensory modality. This study found that the only changes in S1 activation associated with anticipation of a sensory stimulus were decreases in areas outside the representation of the skin areas of expected stimulation. For example when subjects were required to count stimuli to the fingertips (no such stimuli were actually delivered) there was a decrease in blood flow to the areas of S1 representing the face. Drevets et al therefore suggest a model of selective attention to touch in which "potential signal enhancement may rely on generalized suppression of background activity". In the visual system a number of studies have reported suppresive effect of attention in extrastriate areas (88, 89) and inferotemporal cortex (90). It is possible that both a gain in the signal evoked by the attended stimulus, and a damping down of distracting stimuli contribute to effective attentional selection. This would suggest that different populations of neurons are modulated in different directions. This is consistent with Hsiao et al's (30) finding in SII where 58% of cells increased their activity with attention and 22% showed a decrease in activity and with a study by Burton et al (91) which reported suppression and enhancement attentional effects in S2 at different stages of a trial.

Insight into the potential mechanism for attentional selection was provided by a recent electrophysiological study of S2 responses in monkeys (92). Three monkeys were trained to perform tactile and visual tasks and to switch between modalities when instructed. Pairs of S2 cells were recorded and firing

synchronicity during the tactile discrimination task was compared to that elicited by the same touch stimuli whilst the monkeys performed a distracting visual task. The three monkeys tested performed slightly different tactile tasks. In the monkey performing the most difficult task, 35% of recorded S2 cell pairs showed a change in firing synchronicity (independent of any changes in firing rate) relative to the control task. Of these cells, 80% showed an increase in synchronicity and 20% showed a decrease relative to control. A computational model of attentional selection has shown that changes in synchronicity can change the efficacy of a representation and thus could underlie attentional selection (93). The electrophysiological study by Steinmetz et al (92) tests the neuronal plausibility of this model and supports the intriguing possibility that changes in synchronicity, which would lead to changes in synaptic efficacy, could form the basis of attentional selection in the somatosensory system.

7. MODULATION OF TACTILE ATTENTION BY VISION

All the above studies have investigated selective attention purely within the touch modality. However, in normal experience, we use combined information from different senses to facilitate the processing of relevant stimuli (94). This final section will therefore briefly review some of the literature where visual orienting has been used to facilitate the detection of a tactile stimulus (Note these studies describe modulation of a tactile stimulus by the visual modality rather than crossmodal integration of combinations of sensory modalities. For a more detailed review of the multisensory integration literature see Spence this edition). A number of studies have shown that orienting the eyes to a body site facilitates perception of touch (eg 44). This facilitation is observed even when subjects cannot see the body site being stimulated, i.e. orienting while blindfolded or in complete darkness (41). Other studies have shown that whereas purely strategic tactile orienting failed to facilitate RT (c.f. 10), visual orienting to the stimulated site facilitated all reaction times (9). Until recently it was largely unknown, however, whether vision itself facilitates the sense of touch because visual orienting was always confounded with proprioceptive orienting. That is, when subjects view a body site, they invariably orient the eyes and head towards the body site. A study by Tipper et al.(40), dissociated vision and proprioception by having subjects look at their hand (vision and proprioception), look at a video image of their hand on a monitor (vision only) or orient towards their covered hand (proprioception only). This study demonstrated that vision did indeed influence tactile perception, even without proprioceptive orienting. These behavioral studies highlight the fact that the neural representations of different sensory modalities must be capable of being flexibly realigned. For example, bimodal cells in the putamen respond both to tactile stimulation of the hand and to visual stimuli in receptive fields around the hand (45). Importantly, the visual receptive fields appear to be locked to the somatosensory fields: when the hand is moved to a new locus, the visual receptive field moves with it. The use of effective connectivity analysis techniques in

fMRI has demonstrated that these effects are not just mediated by multimodal brain structures but that touch can influence visual cortex directly via back-projections from multimodal parietal areas providing another explanation for the effects of one modality on another in spatial attention (95).

8. CONCLUSIONS

Selective attention can facilitate tactile processing (10). However, there are certain types of tactile information that can be processed just as effectively without attention (11,12,43). There is evidence for attentional effects at multiple stages of tactile processing both from behavioural studies (28) and from neuronal studies (29-39). Although selective attention has often been shown to correlate with a gain in neuronal signal evoked by the attended stimulus (29-35, 36-39), effective selection might also depend on a reduction in the signal evoked by distractor stimuli (36).

Future studies of tactile attention will benefit from combining the elegant paradigms of traditional cognitive psychology with the powerful techniques of modern cognitive neuroscience. Potentially fruitful areas for future research include the role of attention in other aspects of somatosensation, such as pain processing. For example, some recent brain imaging studies have demonstrated the neural correlates of effective distraction from pain (96-99). Also of interest are disorders of tactile attention, such as tactile extinction (100, 101). Finally, one area in which the somatosensory system has been frequently used as a model system is in the study of brain plasticity (102). Recent studies have shown that attention to touch can play a powerful role in cortical plasticity (103, 104). Therefore, selective attention to touch not only modulates ongoing processing but also has longer lasting effects on cortical representations. This deserves further study as it has potential therapeutic relevance for adaptive human brain plasticity after injury.

9. ACKNOWLEDGEMENTS

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