Predictive attenuation in the perception of touch

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The ability to distinguish sensations resulting from our own actions from those with an external cause is a fundamental aspect of human behaviour. This distinction is in some cases reflected directly in perception: for example, tickling oneself produces a less intense sensation than being tickled by someone else. In this chapter we review the evidence for a general process of sensory filtering that attenuates self-generated tactile sensation. This process depends upon a temporally-precise prediction of the sensory consequences of one's actions. We demonstrate experimentally that tactile attenuation specifically affects self-generated sensory input, leaving unchanged externally-generated sensations in the same part of the body. The level of attenuation does not vary with stimulus intensity, but rather consists of a constant subtraction in the perceived intensity of the self-generated stimulus. However, the level of attenuation can be reduced by introducing a spatial separation between the active effector and the body part in which the touch is felt. This suggests that tactile attenuation is modulated by the degree to which the context of the action is consistent with self-generation. We discuss these findings with reference to the proposed purpose of sensory attenuation as a means of enhancing the salience of unexpected external events.

Discriminating between self- and externally-generated sensation

Whenever we move, speak or otherwise perform an action the resulting changes to our body and the environment are detected by our sensory systems. Under normal circumstances we recognise these sensations as the consequences of our actions and are able to distinguish them from similar sensations that are generated externally. We are unlikely to mistake the sound of another person talking for our own voice, and we have no difficulty distinguishing between movements we make ourselves and movements that are passively applied to our body by external forces. This ability to perceive our own actions as distinct from other people's is an important part of our perception of ourselves as a single unified self, capable of willed action, and is probably crucial to our functioning as a social animal. The ability to discriminate between self- and externally-generated sensory input is also thought to play a role in some of the more fundamental functions of our sensory and motor systems.

The earliest evidence for such a role came from the investigation of eye movements. When we move our eye the image of the world on our retina also moves, and yet we do not perceive the world to move. This is not simply because we have an expectation that the world will remain stable: as Descartes observed in his Treatise of Man (1664), tapping on the side of the eye with a fingertip generates an illusion of motion in the opposite direction, exactly as one would expect to occur during an eye movement. In the nineteenth century, inspired by Descartes' observations, Helmholtz (1867) proposed that during normal eye movements the expected shift in the retinal image is compensated for in perception according to the 'effort of will' required to generate the movement. A century later, two separate studies both published in the same year proposed a model for this compensation (Sperry, 1950; von Holst and Mittelstaedt, 1950). According to von Holst's 'principle of reafference', when the motor areas of the brain generate a motor command signal to move the eyes they also send a copy of the command to the visual areas. This 'efference copy' is used to generate a prediction of the change to the visual input that will result from the eye movement (termed the 'corollary discharge' by Sperry). This predicted shift in the visual input is then reversed and applied to the actual visual input at an early stage of processing, cancelling the real shift in the retinal image with the result that a stable percept of the world is maintained.

The illusory movement observed by Descartes, Helmholtz and others when tapping on the side of the eye has a clear interpretation under von Holst’s model: the pressure applied by the finger causes a movement of the eye, but because this movement is not generated by the motor areas controlling the eye muscles an appropriate efference copy is not sent to the visual areas and the resulting retinal shift is not compensated for. As a result the world appears to move in the opposite direction to the applied force.

Subsequent research has confirmed a role for efference copy in visual perception (e.g. Mach, 1885; Kornmuller, 1930; Mack and Bachant, 1969; Stevens et al., 1976) although a number of findings suggest that it may be only one of several mechanisms involved in maintaining visual stability (Bridgeman et al., 1975; Matin et al., 1982; Grusser et al., 1987; Pelz and Hayhoe, 1995). Nonetheless, the principle proposed by von Holst and Sperry of predicting the sensory consequences of action has been highly influential. Modern formulations of this theory (illustrated in Figure 1) include a forward model: an internal representation of the body and environment that is used to predict the consequences of a motor command (Jordan and Rumelhart, 1992; Miall and Wolpert, 1996).

The predictions generated by forward models also have a number of other proposed uses within sensory and motor systems. A prediction of the way in which a motor command will change the state of the body and the environment is thought to underlie anticipatory motor control: for example, maintaining posture (Gahery and Massion, 1981; Massion, 1992) and generating appropriate grip forces when manipulating objects (Johansson and Cole, 1992; Flanagan and Wing, 1997). A prediction of the sensory feedback resulting from a motor command may not only underlie perceptual stability as in Von Holst’s model, but also be used in mental simulation (Sirigu et al., 1996), in context estimation, and to compensate for inaccuracies and delays in sensory feedback (for a review see Davidson and Wolpert, 2005).

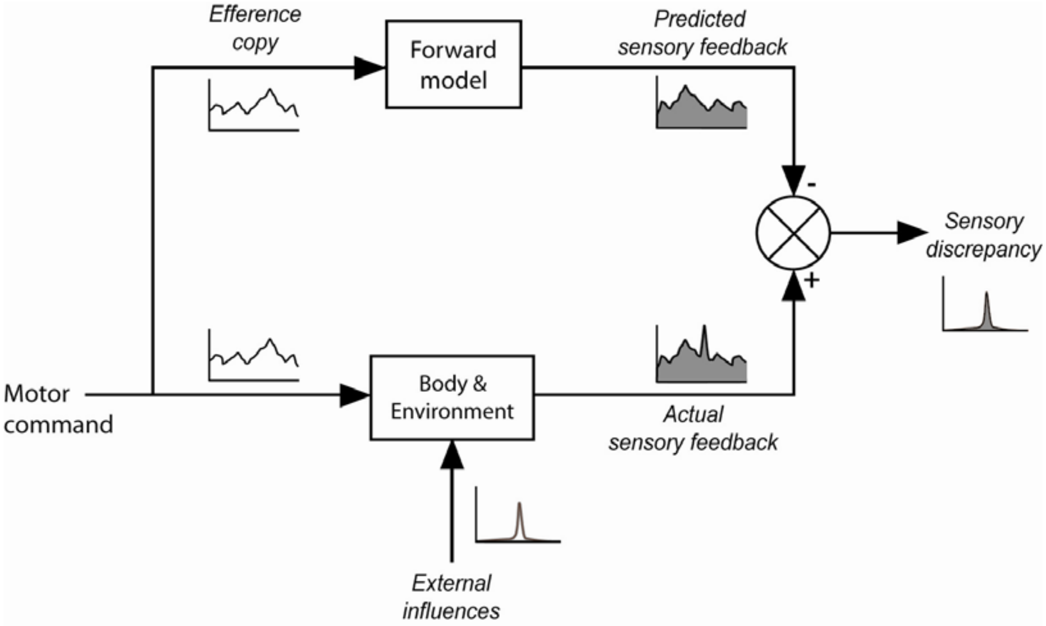

Figure 1 Distinguishing between one's own actions and external events. On the basis of efference copy, a forward model predicts the sensory feedback that will result from a planned action. The actual sensory feedback will reflect the sum of self- and externally-generated changes to the body and environment. Subtracting the predicted from the actual sensory input reveals an estimate of the sensory feedback due to external influences.

Sensory cancellation of tactile sensation

As well as maintaining perceptual stability, it has been suggested that a cancellation mechanism of the kind illustrated in Figure 1 could also filter sensory input in order to help detect unexpected changes in our environment. By subtracting a proportion of the predicted sensory input from the actual input at an early stage of processing, self-generated sensations could be attenuated, thereby enhancing the salience of unexpected external events. An everyday example of such attenuation may be found in the perception of tickle. It is a common experience that it is hard to tickle oneself, and empirical studies have confirmed that a self-generated tickle is perceived as less intense than an identical stimulus imposed externally (Weiskrantz et al., 1971; Claxton, 1975; Blakemore et al., 1998b).

Several recent studies have shown that this phenomenon is not limited to tickling, but applies to the sense of touch in general. In a study by Shergill et al. (2003), a constant force was applied to a subject's finger by a torque motor; subjects were then instructed to reproduce the force they had just felt by pressing with a finger of the other hand. Subjects consistently overestimated the force required (Figure 2, filled circles), implying that the sensation of force in the passive finger was perceived as substantially weaker when it was self-generated than when it was externally applied.

This effect is not simply due to a failure of memory: the same subjects accurately reproduced the target force when they controlled the torque motor output with a joystick (Figure 2, empty circles). In this situation the active hand is not generating the force directly, but instead the movement of the hand is translated into a force via the torque motor. A study investigating the control of grip force (Blakemore et al., 1998a) has shown that in this unusual situation predictive mechanisms are not employed. When one hand pushes on an object gripped in the other hand a precise anticipatory modulation of grip force is seen. However, when the force on the gripped object is instead controlled indirectly via a joystick, grip force modulation ceases to be predictive. In Shergill et al. (2003), the absence of attenuation when subjects reproduced the target force via the joystick is consistent with a similar failure of prediction.

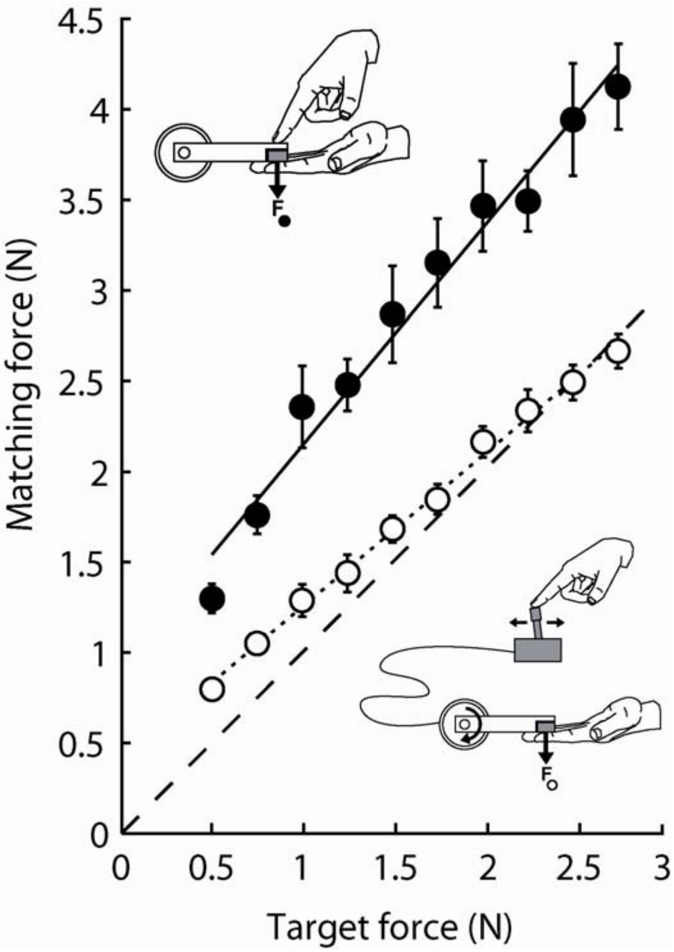

Figure 2 Matching force generated by subjects instructed to reproduce a target force applied to their index finger, either directly by pressing with the index finger of the other hand (filled circles, solid line) or indirectly via a joystick (empty circles, dotted line). Error bars indicate ±1 S.E. across subjects. Perfect performance is indicated by the dashed line. Adapted with permission from Shergill et al (2003).

Sensory prediction deficits in schizophrenia

The force-matching task described above has subsequently been used to test sensory prediction in patients with schizophrenia. As discussed, one role of sensory prediction may be to identify movements as either self- or externally-generated. If the predicted sensory input associated with a movement matches the actual sensory input, the movement is labelled as one's own. However, if the predicted and actual sensory inputs are discordant, as when one's arm is passively moved by someone else, the movement is labelled as externally-generated.

If the mechanism that predicts the sensory consequences of action was dysfunctional and produced inaccurate predictions, this could cause the misattribution of self-generated actions as externally-generated (Feinberg, 1978; Frith, 1992; Frith et al., 2000). Many patients with schizophrenia demonstrate just such a deficit, in which self-generated actions are experienced as being under outside control or self-generated speech is misperceived as an auditory hallucination (Schneider, 1959).

Shergill et al. (2005) used the force-matching task to directly test the hypothesis that patients with schizophrenia are defective in predicting the sensory consequences of their actions. Patients reproduced external forces substantially more accurately than age-matched control subjects (Figure 3), implying that the normal attenuation of the self-generated sensation was reduced in the schizophrenic patients. This study therefore provides strong evidence for a dysfunctional predictive mechanism in schizophrenia. As discussed above, efference copy signals can be used to generate both sensory and state predictions. State predictions are responsible for anticipatory motor control, which does not appear to be affected in schizophrenia (e.g. Delevoye-Turrell et al., 2003). The deficit therefore seems to be specific to the sensory prediction of the consequences of action, as it is this sensory prediction that is implicated in both sensory attenuation and identification of self-action.

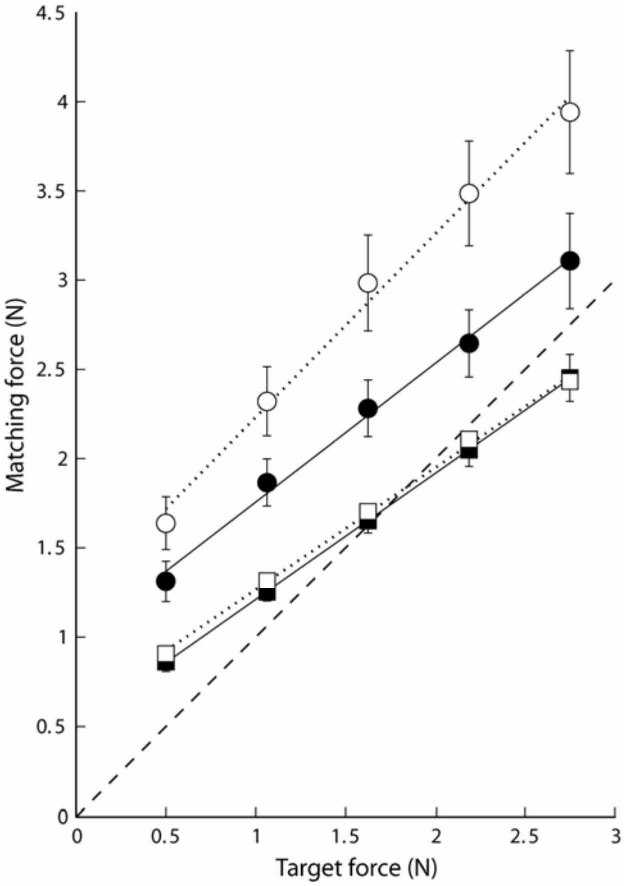

Figure 3 Matching force generated using the right index finger (circles) and joystick (squares) as a function of the externally-generated target force, for patients (filled shapes) and healthy volunteers (empty shapes). Error bars indicate ±1 SE across subjects. Dashed line represents perfect performance. Adapted with permission from Shergill et al (2005).

Tactile attenuation is the result of a temporally-tuned predictive mechanism

The mechanism of tactile attenuation has been further investigated by two studies which examined the perception of self-generated taps made by one finger on another. In Bays et al. (2005), subjects used their right index finger to tap a force sensor mounted above, but not in contact with, their left index finger. When a motor generated a tap on the left finger synchronous with the right tap, simulating contact between the fingers, the sensation of force in the left finger was attenuated compared to the same tap experienced during rest. By delaying or advancing the left tap relative to the active right tap, the time-course of this attenuation was mapped out, revealing a roughly symmetrical and relatively broad period of attenuation centred on the precise time at which the action would normally cause a tactile sensation (Figure 4 A).

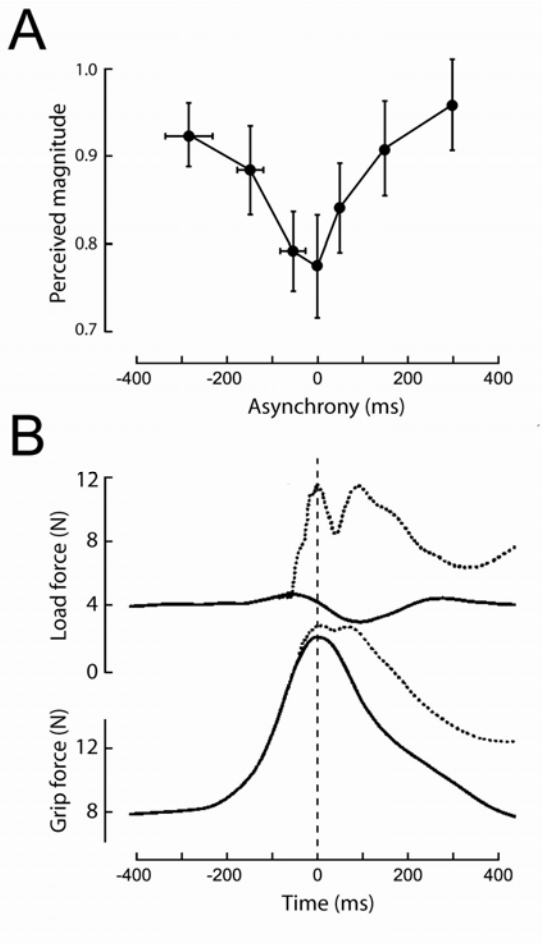

Figure 4 (A) Perceived magnitude of a tap made by the right index finger on the left as a function of the asynchrony between right finger contact and the tap on the left finger. Positive asynchrony indicates that right finger contact occurs first (i.e. the tap is delayed). Perceived magnitude was assessed by comparison with a reference tap delivered at rest. Adapted with permission from Bays et al. (2005). (B) Anticipatory modulation of grip force when dropping a ball into a grasped cup. Average load force (top) and grip force (bottom) on trials when the ball lands in the cup (dotted line) or is prevented from doing so (solid line). Abscissa shows time relative to the first peak in the mean load force due to impact (dashed line). Adapted with permission from Johansson and Westling (1988).

There are interesting parallels between the results of this study and the findings of a grip force study which also investigated force pulses (Johansson and Westling, 1988). In this previous study, subjects dropped a ball from one hand into a cup supported in a precision grip by the other hand. The initial impact of the ball in the cup generated a brief force pulse similar to the taps used as test stimuli in the current study (dotted line, Figure 4 B top). To prevent the cup from slipping out of their grasp as a result of the impact, subjects increased their grip force around the time of contact. Occasionally, the experimenter prevented the dropped ball from hitting the cup, revealing a purely anticipatory component of the grip force modulation. The time-course of this grip force increase (solid line, Figure 4 B bottom) bears a number of similarities to the time-course of attenuation seen in the current study: it has a similar temporal width, is roughly symmetrical, and is centred on the expected time of the initial force peak. These similarities are consistent with the hypothesis that tactile attenuation, like grip force modulation, depends on a prediction of the consequences of action generated by a forward model. In both cases the time profile is considerably broader than the actual duration of the force pulse. This could reflect inaccuracy or uncertainty of the internal model in predicting the time of the contact event, or a ‘safety margin’ built into the attenuation and grip force systems to allow for the possibility of a prediction error.

While the results of the psychophysical studies of attenuation described above are consistent with a predictive mechanism, they are equally consistent with a reconstructive or postdictive mechanism. A postdictive mechanism is one in which the percept of a sensory event is constructed from sensory information received around the time of the event (Dennett and Kinsbourne, 1992; Eagleman and Sejnowski, 2000; Rao et al., 2001). In this mechanism the original sensory input is available for a period after the event and its processing can depend substantially on other events that occur in close temporal proximity. Bays et al. (2006) found strong evidence to suggest that attenuation of self-generated tactile sensation results from a predictive, not postdictive, mechanism. When one finger made a tapping movement above a finger of the other hand, sensation in the passive finger was attenuated only when contact was expected between the fingers. Furthermore, the level of attenuation observed when contact was expected was the same whether or not the contact actually occurred. These results are inconsistent with a postdictive mechanism, which would have access to the actual sensory feedback in determining the level of attenuation, and hence confirm that tactile attenuation results from a prediction of the sensory consequences of action.

Here we conduct two new experiments to examine in more detail the mechanism underlying tactile attenuation. In addition we perform a meta-analysis of data from a number of studies that have used the force-matching task.

Experiment 1: Spatial and Magnitude Influences on Attenuation

A previous study of predictive motor control has shown that accurate prediction requires a natural correspondence between actions and their sensory consequences (Blakemore et al., 1998a). Two robot arms were used to simulate holding an object between the hands. As with a real object, when subjects tried to move the object with their left hand it caused a force to be transmitted to the right hand. Subjects generated an anticipatory increase in grip force in the right hand to prevent the object from slipping. For the simulation of a real object to be complete, force feedback must in turn be transmitted back to the left hand, resisting its movement. When the experimenters changed the gain of this force feedback, making the context less consistent with a real object, the anticipatory grip-force response was diminished. This suggests that the motor prediction underlying grip-force modulation depends on a realistic relationship between force input and output. Similarly, predictive tactile attenuation may require a realistic correspondence between force-generation and sensation.

To investigate this possibility, we conducted an experiment in which subjects reproduced target forces applied to their finger by pressing through a virtual object, simulated by two torque motors. This allowed the force generated by the active right finger to be dissociated from the force delivered to the passive left finger. We used this dissociation firstly to manipulate the spatial co-alignment between active and passive fingers. If predictive attenuation requires a realistic spatial correspondence between force input and output, introducing a horizontal separation between the fingers should decrease the level of attenuation observed in the matching task. Secondly, we manipulated the gain: doubling or halving the force transmitted from the active finger to the passive finger. If predictive attenuation requires that the force generated by the active finger be equivalent to the force experienced in the passive finger, adjusting the gain will reduce the level of attenuation.

Methods

After providing written informed consent 16 right-handed subjects (9 male, 7 female, aged 18-40) participated in the experiment. The experimental protocol was approved by a local ethics committee. Each subject rested his or her left index finger in a moulded support. A force sensor (Nano-17 6-axis F/T sensor, ATI Inc.) rested on the tip of the finger at the end of a lever attached to a torque motor (Maxon Motors UK, Model RE35; geared in ratio 1:4.8). The motor was fitted with a rotary optical encoder (Incremental Encoders Direct Ltd, Model SA40). To start each trial the torque motor applied a constant target force to the tip of the subject's index finger for 3 s. Following an auditory go-signal, subjects were required to reproduce the force they had just felt by pressing with the index finger of the other hand. After 3 s an auditory stop-signal was given to end the trial. Each subject completed five consecutive experimental conditions in a pseudorandom order, each consisting of fifty trials: ten trials each of five target forces in the range 1 N to 3 N.

Subjects generated the matching force on their left index finger indirectly, via a virtual link between two torque motors. Condition 1 was designed to simulate the direct generation of force as closely as possible. In order to produce the matching force, subjects pressed with their right index finger on a second force sensor situated directly above the first (Figure 5 A). This force (recorded online at 1000 Hz and smoothed with a 15 point mean filter) was transmitted to the left index finger by the lower torque motor. Because the surface of the fingertip yields under pressure, applying a force led to a small downward deflection of the lower lever, which was recorded by the rotary encoder fitted to the lower torque motor. In order to maintain an accurate simulation of a virtual object between the fingers, the upper torque motor adjusted the position of the upper force sensor online so as to maintain a constant vertical distance between the force sensors. It was previously explained to subjects that there would be no physical object between the fingers but that forces they produced would be transmitted to the other finger via the computer.

Conditions 2 and 3 were identical to condition 1 except that the upper torque motor was re-positioned, so that during force generation the left and right fingertips were separated laterally by a distance of 10 cm (condition 2) or 30 cm (condition 3). Conditions 4 and 5 were again identical to condition 1 except that now we adjusted the gain relationship between the fingers, such that a 1 N force applied by the right finger resulted in a 0.5 N (condition 5) or a 2 N (condition 6) force on the left finger.

The matching force level generated on the passive finger was calculated for each trial by taking the mean force recorded by the lower force sensor between 2000 and 2500 ms after the go-signal.

Results

In order to investigate some of the parameters that might affect sensory attenuation, in this experiment we created a dissociation between force input and output. The control condition (condition 1) simulated as closely as possible direct force-generation by the right index finger on the left, as in Shergill et al. (2003). As in the previous study, subjects applied substantially more force than was required to reproduce the target force (Figure 5 B, empty circles). This greater matching force was perceived by subjects as equal to the target force because a proportion of the self-generated sensation was attenuated.

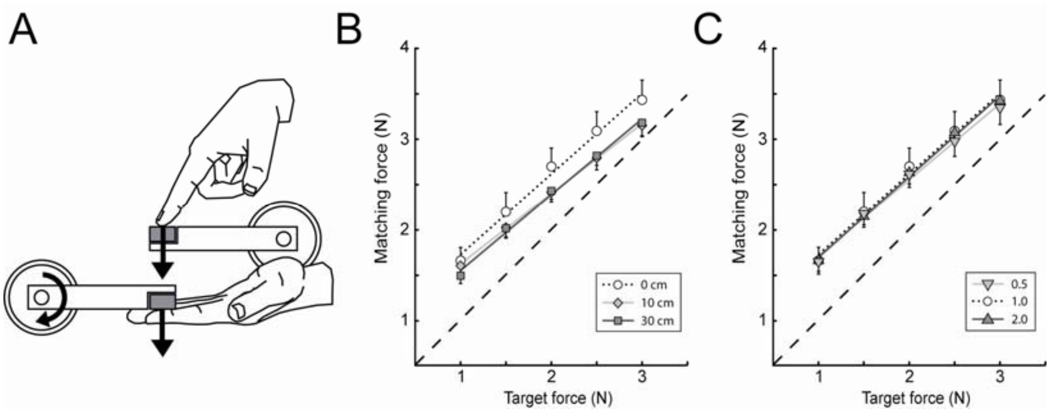

Figure 5 (A) Schematic of the experimental apparatus. Forces applied to the upper force sensor were transmitted with a variable gain to the left index finger via the lower torque motor. The upper torque motor could be moved in a direction lateral to the subject to introduce a spatial separation between the active and passive fingers. (B) Mean matching force generated by subjects with lateral separations between active and passive fingers of 0 cm (empty circles), 10 cm (diamonds) and 30 cm (squares). (C) Mean matching force generated by subjects with gains of 0.5 (downward triangles), 1.0 (empty circles), and 2.0 (upward triangles). Error bars indicate ±1 SE across subjects. Dashed line represents perfect performance.

Having created a dissociation between force input and output we were able to investigate the effect of spatial separation on attenuation. Introducing a 10 or 30 cm lateral separation between the active right and passive left fingers resulted in a reduction in the matching force level compared to the control condition, implying a reduced level of attenuation (Figure 5 B, filled shapes). A two-way ANOVA (separation distance x target force) revealed a significant effect of separation on matching force level ($F_{2,30} = 5.5$, $p = 0.009$). Post-hoc tests found no significant differences between the 10 and 30 cm separations ($t_{15} = 0.17$, $p = 0.87$) but significant differences of both from the no separation condition ($t_{15} > 2.5$, $p < 0.023$). However, subjects still significantly over-estimated the matching force required at both 10 and 30 cm separations ($t_{15} > 3.66$, $p < 0.003$), implying that attenuation was not entirely abolished.

The effect on attenuation of varying the gain relationship between the fingers is shown in Figure 5 C. In three conditions the gain was adjusted such that each newton of force applied by the right finger resulted in a 0.5 N, 1 N, or 2 N force on the left finger. A two-way ANOVA (gain x target force) revealed no significant effect of gain on matching force level ($F_{2,30} = 0.23$, $p = 0.79$).

Discussion

It has been suggested that the attenuation of self-generated sensation described in this chapter may have evolved in order to increase the salience of externally-generated sensation. To be effective therefore the underlying mechanism must be able to correctly identify when two parts of the body are interacting and apply attenuation only in such situations. This judgement is likely to be based on a range of factors, some of which we have attempted to identify in Experiment 1. In order to do this we simulated normal force-generation using a virtual link between two torque motors. Substantial attenuation was still observed even though subjects were made aware that there was no physical object between the fingers. However, when we introduced a lateral spatial separation between the fingers, the level of sensory attenuation was reduced. This suggests that a spatial co-alignment between force production and sensation may be one of the factors by which sensations are identified as self-generated. When force production and sensation are not aligned it reduces the confidence with which the sensation can be identified as self- rather than externally-generated and so less attenuation is applied. Although infrequent, spatial misalignments in force of the size examined in this study can occur during manipulation of large objects, and this may explain why the attenuation is reduced but not abolished.

Probably the clearest evidence that two parts of the body are interacting is a precise correspondence between the force generated by one body-part and the force felt in the other at the same moment. Consistent with this, it has been shown that introducing a temporal asynchrony between activity and tactile sensation reduces sensory attenuation (Blakemore et al., 1999; Bays et al., 2005). However, in this study we have demonstrated that altering the gain relationship between the fingers does not affect the level of attenuation. Specifically, doubling or halving the force transmitted from the active finger to the passive finger did not alter the extent to which sensation in the passive finger was attenuated. This result suggests that while temporal correlation between force-generation and sensation may be required to elicit sensory attenuation, an equal magnitude of force does not appear to be important. This is perhaps to be expected: when one digit applies a force on another through an object, the relationship between the force applied and the resulting sensory input can vary substantially depending on the shape and consistency of the object, the surface area in contact with the passive digit, and the angle at which the active digit meets the surface.

The amount by which sensation in the passive finger was attenuated did not vary between the different gain conditions despite substantial differences in the force generated by the active finger. We have suggested that sensory attenuation may result from a cancellation process, in which a proportion of the predicted sensory input is removed from the actual input. If this is the case, the current finding suggests that the predictive mechanism must be capable of rapidly adapting to new gain relationships between motor output and sensory input in order to continue generating an accurate prediction. Alternatively it may be that sensory attenuation results from a gating process, in which sensory sites receiving self-generated input are identified and a fixed attenuation is applied to all sensory input from those sites.

Experiment 2: Is tactile attenuation the result of a gating or a cancellation mechanism?

During active movement of a digit or limb, the ability to detect small cutaneous stimuli is reduced in the moving body part (Angel and Malenka, 1982; Chapman et al., 1987) as is the perceived intensity of suprathreshold stimuli (Milne et al., 1988). This suppression or 'gating' of tactile input begins prior to movement onset and indeed prior to muscle activation as measured by EMG (Williams et al., 1998), suggesting a mechanism based on efference copy (although see Williams and Chapman, 2002, for a discussion of the possible role of backward masking). The theory that sensory gating can be triggered by descending signals from motor planning areas is supported by a recent study by Voss et al. (2006). Pulses of transcranial magnetic stimulation (TMS) over primary motor cortex were used to delay planned finger movements at the motor output stage. Sensory suppression of cutaneous stimuli was observed at the intended time of movement, despite this being substantially prior to the actual onset of the movement.

While movement-related gating filters out sensations resulting from voluntary movement, it also removes externally-generated sensations that are unrelated to the movement. By attenuating the sense of touch in parts of the body which expect self-input, this mechanism may enhance the relative salience of external stimuli elsewhere on the body. However, sensory gating cannot assist in detecting external tactile stimuli against a background of self-generated sensation. An example of a situation in which this is relevant is reading Braille, in which unpredictable tactile stimuli (the Braille dots) must be detected against a self-generated background stimulation caused by pressing one's finger to the paper and moving it across the page.

In order to assess whether the tactile attenuation demonstrated in the force-matching paradigm reflects a gating or a cancellation process, we examined the perception of an electrical cutaneous stimulus delivered to a finger receiving a self-applied pressure. If the attenuation of the self-generated force is the result of a non-specific sensory suppression similar to movement-related gating then the perceived intensity of the electrical stimulus should also be attenuated. In contrast, a cancellation mechanism should affect only the self-generated force and not the externally-generated electrical stimulus.

Methods

10 right-handed subjects (4 male, 6 female, aged 20-31) participated in the experiment. As in the force-matching experiments, each subject rested his or her left index finger in a support beneath a force sensor at the end of a lever attached to a torque motor. The perceived intensity of brief cutaneous stimuli delivered to the finger was assessed while constant forces were applied to it through the force sensor. On alternating trials forces were either externally applied by the torque motor or self-applied by the subject pressing with the index finger of the other hand. Each subject completed 8 trials under each of these conditions at each of three levels of applied force (1 N, 2N and 3 N, in a pseudorandom order). In the self-generated condition the target force and the currently applied force were displayed as horizontal bars on a computer monitor: subjects were instructed to press on their finger through the force sensor so as to maintain the bars at the same vertical position on the screen.

During each trial, brief electrical cutaneous pulses were delivered simultaneously to the tip of the left index finger and to a second reference site on the body. The electrical stimuli were generated by an electrical nerve stimulator (Stanmore stimulator, research device designed and developed by the medical physics department, UCL, London, UK) using adhesive electrode pads (Red Dot, 3M Healthcare), with the anode at the fingertip. All subjects reported that the sensation of the cutaneous pulses in the left index finger was localised at the tip, beneath the force sensor. The reference site was either the tip of the ring finger of the left hand (5 subjects) or the left ankle (5 subjects). The magnitude of the reference pulse was fixed for each subject at a comfortable level between 150% and 200% of the detection threshold (determined prior to the experiment), whereas stimulus magnitude in the index finger was varied.

Following each stimulation, subjects verbally reported at which location the cutaneous pulse had felt stronger. The perceived intensity of the cutaneous stimuli in the index finger relative to the reference site was assessed by finding the point of subjective equality (PSE): the stimulus magnitude in the index finger that was perceived as equal to the reference stimulus. Prior to the experiment, a baseline PSE was obtained over 40 pulse pairs with no force applied to the finger. During the experiment, five pulse pairs were applied sequentially on each trial, giving a total of 40 responses for each condition and force level.

The PSE was obtained using an adaptive logistic regression procedure, as follows. After each response, the stimulus magnitude and subject's response were pooled with the data from all previous stimulations under the same condition and force level. The pooled data were fitted online with a logistic function, according to a maximum-likelihood procedure. The next stimulus intensity for that condition and force level was then chosen from a uniform random distribution bounded by the 1% and 99% points on the fitted logistic curve. This procedure limits the sampling range to stimulus intensities that will be most informative in estimating the PSE. The PSE is given by the 50% point on the logistic curve: the stimulus intensity at which the pulse in the left index finger is perceptually equal to the reference pulse and hence the subject is equally likely to make either response.

If attenuation of self-generated force is the result of a gating process then it will also attenuate externally-generated sensations that occur in the same part of the body at the same time. The perceived intensity of the electrical stimuli in the left index finger will therefore be reduced when a self-generated force is applied to it. This will be observed as an increase in the PSE in the self-generated condition compared to the externally-generated condition. In contrast, if attenuation results from a cancellation process it will affect only the self-generated force and not the externally-generated electrical stimulus. In this case we will see no difference in PSE between conditions.

Results

Points of subjective equality estimated for each condition and force level are plotted in Figure 6, as a percentage of the baseline PSE for each subject. The perceived intensity of the cutaneous stimulation in the finger, as measured by the PSE, did not change significantly from baseline when forces were applied to the finger, either when the force was externally-generated by the torque motor (empty circles) or self-generated by the subject (filled circles; paired t-tests: $t_9 < 0.61$, $p > 0.55$). A mixed model ANOVA (condition x reference site x force level) of the normalised PSE revealed no significant effect of condition ($F_{1,8} = 0.16$, $p = 0.70$), reference site ($F_{1,8} = 0.19$, $p = 0.67$), or force level ($F_{2,16} = 0.84$, $p = 0.45$), and no significant interactions ($p > 0.57$).

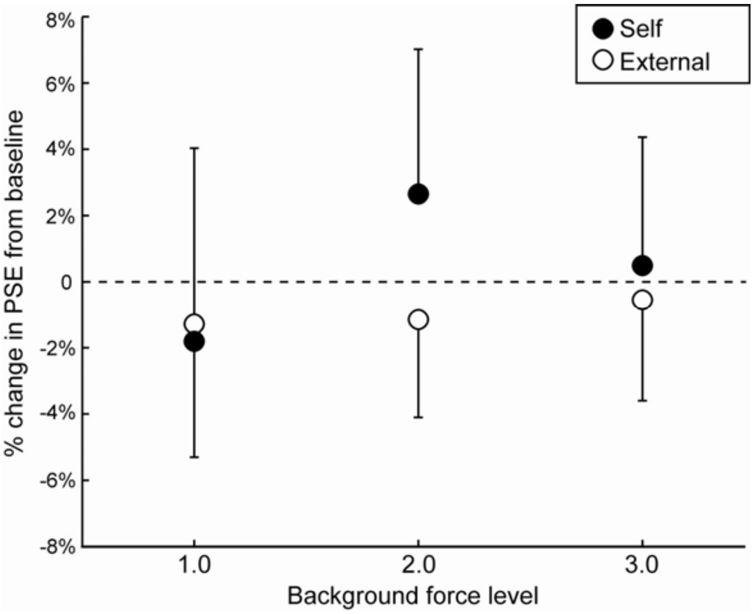

Figure 6 Perceived intensity of electrical stimuli in the index finger as a function of background force level, with an externally-applied force (empty circles) or a self-generated force (filled circles). Perceived intensity is expressed as a percentage change in the point of subjective equality from a condition in which no force was applied.

Discussion

The studies described in this chapter have shown that self-generated tactile stimulation is attenuated in comparison to identical external stimulation. This could result from a gating process similar to the mechanism that attenuates tactile sensation in a moving body part. Movement-related gating involves a general suppression of all tactile input from the active effector, with the result that stimuli unrelated to the movement, such as electrical cutaneous stimuli, are also attenuated. For example, a recent study by Voss et al (2006), using an estimation technique identical to that described here, found that active movement of a stimulated finger increased PSE by 169% (28% SE).

In contrast, we observed no attenuation of electrical stimuli during application of a self-generated force: the mean increase in PSE when a self-generated force was applied to the stimulated finger was less than 1% (3.5% SE). This suggests that the tactile attenuation investigated in this chapter is not due to a non-specific gating mechanism. Rather, these results are consistent with the action of a cancellation mechanism, which selectively attenuates only sensations that are predictable on the basis of the motor command signal.

A meta-analysis of results from the force-matching task

Since the force-matching task was first described in Shergill et al (2003), we have conducted many experiments involving variations on that simple task. In the majority of these experiments at least one experimental condition was identical to the ‘direct’ condition in the original study, in that the subject reproduced a range of target forces applied to his or her resting left index finger by pressing directly with the finger of the other hand. A total of 107 subjects, consisting of participants in the studies described in this chapter and a number of unpublished pilot experiments, completed a block of 40 or more trials of this basic force-matching task, differing only in the range of target forces tested. This presents the opportunity to conduct a meta-analysis with enhanced statistical power, allowing us to accurately estimate the amount by which self-generated sensation is attenuated and to what extent attenuation varies between individuals.

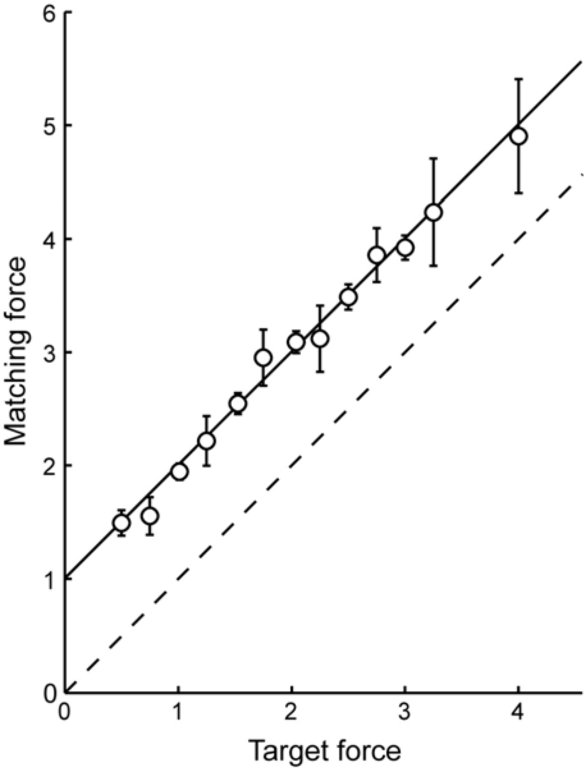

Figure 7. Mean performance of 107 subjects on the force-matching task described in Shergill et al (2003). Subject-generated matching force as a function of externally-generated target force (mean ± SE across subjects). Dashed line represents perfect performance. Solid line indicates the average line of best fit assuming a constant difference between matching and target force for each subject. Each subject was tested on between 5 and 10 target forces over the course of 40 to 80 trials.

Figure 7 shows the average matching force generated by all 107 subjects as a function of target force. As expected, subjects produced an exaggerated matching force at all levels of the target force tested, implying that the sensation of the self-generated matching force was attenuated so as to make it perceptually equal to the smaller target force. The results of the first force-matching study (Shergill et al, 2003) suggested that the difference between matching and target forces might involve a change in slope as well as intercept. However, in this much larger data set (which includes the previous results) it appears that the amount by which the matched force exceeds the target force (the 'excess force') is approximately constant for all target forces. A linear regression analysis revealed a significant intercept ($t_{106} = 12.0$, $p < 0.001$) but a slope parameter that did not differ significantly from unity ($t_{106} = 1.32$, $p = 0.19$).

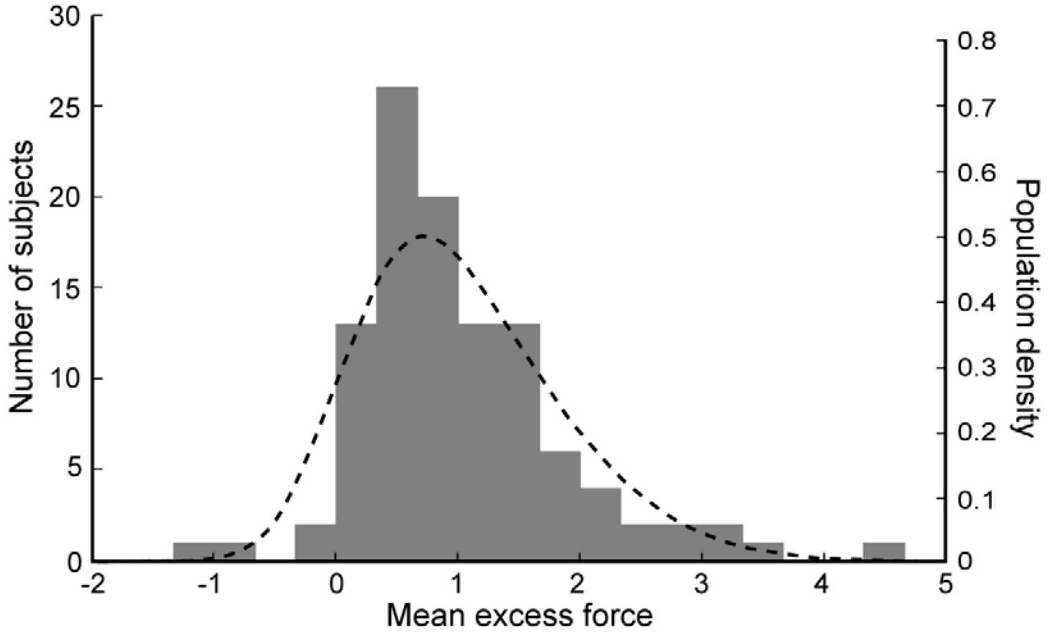

Figure 8. Histogram of the mean difference between matching and target forces across a sample of 107 subjects. Dotted line indicates the skew-normal distribution that best fits the data.

Figure 8 displays the variation in mean excess force across subjects. The data were well fit by a normal distribution (Kolmogorov-Smirnoff test, $p = 0.12$) with a positive skew (skewness = 1.16). The mean excess force was 1.00 N (s.d. 0.87 N). Although a small number of subjects showed no or very weak attenuation (11% of sample produced mean excess force <0.2 N), there does not appear to be any substantial bimodality to the distribution, and so the performance of these subjects is best explained by natural variation around the population mean. Only 4 subjects produced matching forces on average less than the target force.

In summary, the results of this meta-analysis suggest that the sensation of self-generated force is attenuated by a fixed amount, on average equivalent to a 1 N reduction in the perceived force. However, there is no a priori reason to believe that a constant difference in force measured on a newton scale corresponds to a constant subtraction in the perceived magnitude of the sensation. For example, it may be that the difference in perceived intensity between a 3 N and a 2 N force is smaller than the difference between a 2 N and a 1 N force. If this is the case, the fixed level of attenuation we have observed (1 N at all force levels) would actually reflect an attenuation in perceived intensity that varies with force level.

We therefore tested the perception of the constant forces used in the force-matching experiment in a group of 10 subjects (5 male, 5 female, aged 22-32) using open magnitude scaling. Forces in the range 1 to 7 N were presented to subjects in the same way as target forces in the force-matching task. Subjects were instructed to rate the intensity of each stimulus with a number (no particular scale was specified). Each subject's responses were subsequently scaled to the range 0 to 1 so that means across subjects could be calculated. Results are shown in Figure 9.

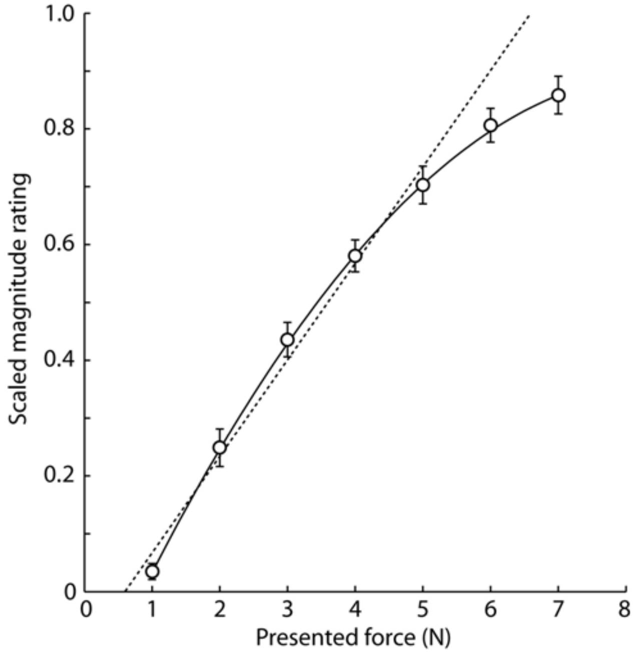

Figure 9. Perceived magnitude of constant forces applied to the fingertip. Mean ± SE rating shown, with a second-order polynomial fit for all forces (solid line) and a line of best fit for forces in the range 1-5 N (dotted line).

Subjects' gave forces separated by 1 N significantly different intensity ratings throughout the tested range ($t_9 > 3.0$, $p < 0.02$) implying that the 1 N attenuation observed on average in the matching task is large enough to produce perceptible differences in the intensity of self- and externally-generated forces. The magnitude rating was found to be approximately linearly related to the force in newtons over the range 1 to 5 N (dotted line in Figure 9), although the rated intensity began to saturate at higher force levels and a significantly better fit was achieved overall by a second-order polynomial ($t_9 = 7.9$, $p < 0.001$; solid line).

As the magnitude rating is roughly linearly related to force over the range tested in the force-matching task, we can conclude that the constant excess force observed in that task results from an approximately constant subtraction in the perceived intensity of the self-generated force.

General discussion

Self-generated tactile stimulation is perceived as weaker than the same stimulus applied by an external source. This phenomenon has been demonstrated, using a range of techniques, in the sensation of tickle (Weiskrantz et al., 1971; Blakemore et al., 1999), constant pressure (Shergill et al., 2003), and brief taps (Bays et al., 2005). The underlying mechanism may be similar to the cancellation model proposed by von Holst (1950) and Sperry (1950) to account for the stability of the visual scene during eye movements. According to this model, the expected sensory input is predicted on the basis of efference copy and subtracted from the actual sensory input at an early stage of processing. Our investigations have confirmed that tactile attenuation depends on a prediction of contact between parts of the body (Bays et al., 2006) that is precise in terms of both time (Bays et al., 2005) and location (Blakemore et al., 1999).

Clearly in tactile attenuation the predicted input is not subtracted in its entirety; otherwise we would not be able to feel our own touch at all. In this chapter we have found evidence to suggest that the quantity of sensation subtracted from self-generated touch is constant, in the sense that it does not vary with the intensity of the self-generated input. This explains both the constant excess force produced at different target force levels in the force-matching task, and the fact that artificially changing the gain between force input and output does not affect performance in that task. Note that this result does not contradict our finding in Experiment 2 that tactile attenuation specifically affects self-generated forces. A gating mechanism, such as movement-related suppression, that does not discriminate between self- and externally-generated sensation may nonetheless attenuate the sensory input in a way that varies with stimulus intensity. Similarly, a cancellation mechanism that specifically affects self-generated input may nonetheless attenuate all self-generated input equally, irrespective of intensity. This appears to be the case for tactile attenuation.

We have found that the level of attenuation can be altered by introducing a spatial misalignment between force production and sensation. This suggests that tactile attenuation is modulated by the degree to which the current context is consistent with self-generation. Spatial co-alignment of force is likely to be just one of many factors that interact in determining the level of attenuation. In Experiment 1, in order to limit our investigation to the single factor of spatial separation, we ensured that subjects were always aware (and could see) that there was no real object between their hands: only the tactile characteristics of an object were simulated. It is possible that the effects of spatial misalignment we observed might not have been found if the visual cues associated with a real object had also been present, or if the subjects had been blindfolded and led to believe they were interacting with a real object. A further question concerns adaptation: given sufficient interaction with the virtual object under a spatial misalignment, would the consistency of the relationship between force input and output eventually cause attenuation to return to normal levels? To date we have found no evidence for this kind of adaptation in tactile attenuation, although a comparable effect has been observed in grip-force modulation (Witney and Wolpert, 2003).

As discussed previously in this chapter, theoretical models of sensory prediction include a forward model, an internal representation of the body and environment that is used to transform planned motor commands into predicted sensory consequences. This forward model cannot be fixed, but rather its parameters must be updated whenever the environment in which we are operating changes. From this viewpoint, the modulation of tactile attenuation by a factor such as spatial co-alignment indicates that this factor is taken into account in determining the correct parameters of the forward model. Precisely how these parameters are updated is currently unknown, but according to one proposal, the MOSAIC model (Haruno et al., 2001), predictions made by multiple competing forward models are compared to sensory feedback, and the forward model with the smallest prediction error is selected to represent the current context. This model has the theoretical advantage that it can be extended to describe certain aspects of social interaction: a system of competing forward models that attempts to predict the observed behaviour of other people could potentially underlie action imitation and even theory of mind (Wolpert et al., 2003). However, if we are indeed able to predict the sensory consequences of another person's action this does not appear to lead to sensory attenuation. Shergill et al. (2003) performed an experiment in which subjects took it in turns to press on each other's fingers, with the instruction to each reproduce the last force they had felt. The result was a rapid escalation of force, suggesting that while the forces subjects applied themselves were attenuated, the forces applied to them by the other participant were not.

It has been suggested that the purpose of sensory attenuation is to enhance the salience of unexpected external events. Consistent with this proposal, in this chapter we have shown that tactile attenuation specifically affects self-generated input, leaving unchanged externally-generated sensations in the same part of the body. However, despite its theoretical appeal, there is currently no direct evidence to support the salience hypothesis. While it is clear that attenuation takes place, fundamental questions as to its purpose remain to be answered.

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