

# Gating of vibrotactile detection during visually guided bimanual reaches

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**Abstract** It is far more difficult to detect a small tactile stimulation on a finger that is moving compared to when it is static. This suppression of tactile information during motion, known as tactile gating, has been examined in some detail during single-joint movements. However, the existence and time course of this gating has yet to be examined during visually guided multi-joint reaches, where sensory feedback may be paramount. The current study demonstrated that neurologically intact humans are unable to detect a small vibratory stimulus on one of their index fingers during a bimanual reach toward visual targets. By parametrically altering the delay between the visual target onset and the vibration, it was demonstrated that this gating was even apparent before participants started moving. A follow up experiment using electromyography indicated that gating was likely to occur even before muscle activity had taken place. This unique demonstration of tactile gating during a task reliant on visual feedback supports the notion this phenomenon is due to a central command, rather than a

masking of sensory signals by afferent processing during movement.

**Keywords** Tactile gating · Bimanual reaching · Multisensory integration · Perception and action

## Introduction

When a distal appendage is moved, it is more difficult to detect tactile sensation on the moving body part, in comparison to baseline (or resting) levels (Chapman et al. 1987; Williams et al. 1998). This reduction in sensation when changing from static to active seems counterintuitive—the functional purpose of reducing sensation when it is more likely to be utilized is far from clear. One possibility is that tactile gating is centrally generated, reducing self-generated inputs in order to emphasize external (and probably more important) haptic stimuli. However, the vast majority of tactile gating research has been with tasks where haptic information is unlikely to have been utilized at all.

Tactile gating in the digits has been the subject of recent studies aimed at determining the underlying cause of this counterintuitive failure to detect near-threshold somatosensory input during a movement. Following initial observations that sub-threshold cortical stimulation of the motor cortex (i.e., without muscle activation) reduced the amplitude of the evoked response in the somatosensory cortex of monkeys (Jiang et al. 1990), recent findings have indicated that the actual execution of the movement may not even be necessary for tactile gating to occur. Voss et al. (2006) demonstrated equivalent levels of sensory suppression even when movement was no longer imminent, using transcranial magnetic stimulation to delay the onset of a movement. Similarly, tactile gating has been shown to occur in the

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period immediately following a cognitively inhibited motor response (Walsh and Haggard 2007).

In fact, the expectation to move (i.e., the ‘predictive’ component) appears to be necessary for tactile gating to occur. Bays et al. (2006) undertook an experiment which required individuals to elicit brief tactile sensations on their left hand with a switch that was operated by their right hand, and judge its relative strength. When the right hand operated the switch, a substantial reduction in ability to detect the tactile stimuli occurred (i.e., tactile gating). However, on trials where the right hand’s role in this task was invalidated (by quickly moving the switch away from the hand), equivalent levels of gating were apparent. Similar conclusions can be drawn from work in which preparatory movement cues are given to the left or right hand. Voss et al. (2008) were able to remove any preparation-based sensory suppression on an un-cued hand, by reducing the predictability of a movement cue to a non-useful level (i.e., 50% accurate). That is, gating only occurred when there was an expectation to move. Furthermore, when the right hand was cued more than the left hand, it showed higher levels of gating, even when the left hand made the actual movement.

However, despite the weight of evidence suggesting that tactile gating is due to movement preparation, its mechanisms are still under some debate. Williams and Chapman (2002) have shown that tactile sensation is attenuated when the finger is passively moved by another individual. Thus, even in the absence of a motor plan, some level of tactile gating occurs, either through ‘postdictive’ cancellation (i.e., the system predicts that the events would occur simultaneously, and reduces their perceived magnitude), or peripheral masking of sensation through afferent feedback.

Despite the growing number of studies examining tactile gating, the interpretations of their findings are limited by the motor tasks used to elicit the suppression. The suppression of tactile information associated with action has only been reported for simple single-joint movements of a limb or digit (e.g., Voss et al. 2006, 2008). While this simple paradigm allows for the careful experimental control of the actual movement and its efferent consequences, it is difficult to generalize any potential feedforward or feedback-related gating to other classes of movement. For example, the relative impact of sensory gating remains unclear for visually guided manual reaching—a task which requires complex planning of trajectories and the real-time integration of peripheral somatosensory cues and vision. At least one study has even shown the direct utility of tactile feedback, independent from proprioceptive and visual inputs, in guiding accurate goal-directed manual reaching behavior (Rao and Gordon 2001).

A simple prediction would be that sensory gating will be absent or attenuated during multi-joint reaches, due to the

relative importance of feedback for target acquisition in comparison to the single-joint movements in previous tactile gating paradigms, which do not require precise manual localization. Alternately, the mechanism underlying tactile gating may be independent of the level of feedback required for a movement. If this were the case, a substantial amount of tactile gating would occur despite relevance of this information in visually guided aiming. A feedback-independent (i.e., related to efference, rather than afference) explanation of tactile gating would predict a substantially earlier onset of gating, that may even coincide with the motor command itself, prior to movement onset (Williams et al. 1998).

The aim of this study was simple—to determine if the tactile gating evident during single-joint movements extends to actions with more complexity and ecological validity. Importantly, will the sensory input relevant to task completion (i.e. touch) be selectively gated out? To raise the levels of efferent and afferent movement complexity above those of single-joint movements (e.g., Williams et al. 1998), tactile detection was examined during multi-joint goal-directed bimanual reaches. The use of multiple joints and both hands for the task vastly increases the degrees of freedom (i.e., possible ‘routes’ to goal completion, in terms of muscle activation), thus raising the planning demands of the reach. Furthermore, coordination of the limbs is common in goal-directed action, and is thus arguably more ecologically valid than single-joint movements or multi-joint unimanual reaches alone. For example, the non-dominant hand often serves to define a frame of reference from which the dominant hand can function (Guiard 1987), and many tasks that are conventionally considered as unimanual can be re-classified as bimanual tasks with different attentional demands (consider the example of the non-dominant hand’s role in manipulating the paper on which the dominant hand writes).

In the current task, participants were required to report whether a vibrotactile target occurred on the left or right hand during bimanual reaches. This two alternative forced choice response methodology has been utilized successfully in previous gating research (e.g., Voss et al. 2008). Instead of comparing detection thresholds across different conditions, the crucial manipulation was the time at which the vibrotactile target occurred, relative to the bimanual reach itself. The vibration therefore was programmed to occur coincident with, or shortly after, the visual target onset (i.e., during reaction time), or at later time-points when the movement had commenced. If tactile gating manifests during visually guided bimanual reaches, participants’ ability to detect which hand the vibration occurred on would be expected to fall to chance (i.e., the detection threshold will increase compared to resting levels). If any gating in this task is related to efferent, rather than afferent

sources, then this drop in detection may even occur prior to movement onset (Williams et al. 1998). Alternatively, if gating is related to an overloading of feedback mechanisms during movement (Williams and Chapman 2002) then the highest levels of gating should occur later in the reach.

## Materials and methods

### Participants

Fourteen neurologically intact staff and students (13 right-handed and 1 left handed, determined by writing hand) from the University of Aberdeen were tested (3 male, mean age = 26.8 years, SD = 4.9). All participants were naïve to the purpose of the experiment and had normal or corrected to normal vision. Participants gave informed consent prior to testing and all procedures were approved by the local ethics committee.

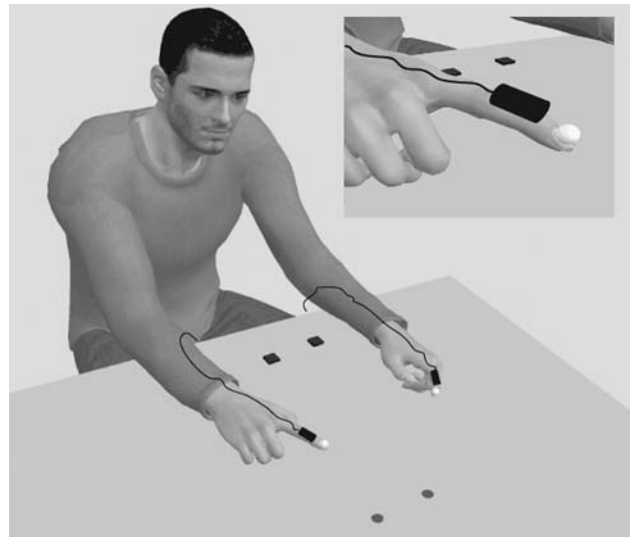
### Apparatus

A horizontal light emitting diode (LED) grid and PC software were used to deliver the green central fixation ( $7.5 \text{ cd/m}^2$ ) and red target stimuli ( $6.5 \text{ cd/m}^2$ ), both of which had a diameter of 10 mm. Small, custom built plastic cylinders (20 mm long and 13 mm in diameter) containing a 4 mm motor that rotated a small eccentric weight on its shaft at 180 Hz (1 mm amplitude) were attached to the top of each participant's index fingers to deliver the vibration. It was ensured that the vibrations were readily detectable to all participants at rest, prior to the start of each testing session.

Kinematic data were extrapolated from the movements of two small infrared reflective markers attached to the index fingers of the participants. These markers were recorded for 2-s by a 3-camera ProReflex analysis system (Qualysis Inc.) at 240 Hz. The cameras' relative positions were calibrated prior to each testing session.

### Procedure

Participants sat on a height adjustable chair in front of an LED grid atop a table surface with their index fingers on pre-defined 'home' points (18 cm apart, located on either side of the body midline at the proximal edge of the target board) and performed bimanual reaches to target pairs. Following a verbal pre-cue ("Ready..."), a fixation light appeared for a random duration (700–1,000 ms), and was then extinguished at the same time as the onset of two targets, which remained visible for 400 ms. Target appearance was the imperative cue indicating to the participants that they were to reach "as quickly and accurately as possible" with both hands to the targets, with full vision of both

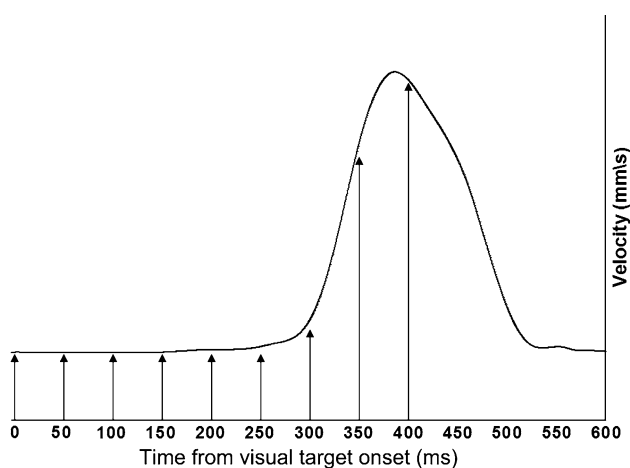


**Fig. 1** Schematic detailing of the positioning of the experimental setup (vibrotactile motors and kinematic recording markers) and target layout during a trial

throughout the lift. There were two possible locations (one more medial, one more lateral) for the target pairs in this study, to provide some spatial uncertainty to the reaching task. The required bimanual reach to either location consisted of symmetrical ipsilateral reaches away from the body in a forward direction (with the left hand reaching to the target on the left side of the board, and the right hand reaching to the target on the right side of the board—see the example trial presented in Fig. 1). Participants were told not to slide their fingers along the table surface to the location of the targets (i.e., the reach required movement in all three dimensions) or to correct their reaches upon making contact with the target board. Participants were also told to maintain their end positions until signaled to return to the home points (~1s after landing).

A 50 ms long vibration was applied to either the left or right index finger, after a variable delay from the visual target onset. These delay epochs ranged from 0 ms (i.e., at the same time as the visual target onset) to 400 ms in 50 ms intervals. Thus, on some trials the vibration would occur on one of the hands during the participant's reaction time and on other trials during the bimanual reach itself (Fig. 2). There were 20 trials per 50 ms delay epoch (i.e., 20 trials with a delay of 0 ms, 20 trials with a delay of 50 ms, etc.), and 20 catch trials, where no vibratory stimulus was delivered (200 trials in total). Pseudo-random target and vibratory epoch orders were generated for each participant.

After the reach was completed (i.e., with fingers touching the locations of the targets), but before the return to the home locations, participants were required to verbally inform the experimenter of which finger was vibrated. If they were unsure, participants were required to guess



**Fig. 2** Each *arrow* signifies the various delay epochs of the vibrations plotted relative to visual target onset (0 ms), on a single example velocity profile. Each vibration lasted for 50 ms. In our sample, reaction time typically fell between 200 and 300 ms (see Table 1). For analysis of the perceptual data, epochs were re-plotted relative to reaction time rather than target onset

(i.e., a two alternative forced choice task). No indication of when the vibration occurred was required. Participants were told that some trials would not include a vibration, but were given no information about the relative proportions of trials to catch trials. Further, participants were given no information regarding the accuracy of their perceptual reports. The vibratory motors were counterbalanced between subjects, and within subject (i.e., the motors were swapped between the hands halfway through each experimental session) in case the motors ran at subtly different strengths. The entire procedure took approximately 40 min to complete.

#### Data reduction and analyses

##### *Movement data*

The start of the 2-s kinematic records was concurrent with target onset and thus provided reaction time and movement duration. In order to retrieve these measures, in addition to spatial endpoint, displacement data were filtered offline with a second-order dual-pass Butterworth filter with a low-pass cutoff frequency of 15 Hz. Instantaneous velocities were obtained by differentiating the data with a 5-point central finite difference algorithm. Movement onset was defined as the first frame in which resultant (i.e., 3D) velocity exceeded 50 mm/s for ten consecutive frames. Similarly, movement offset was defined as the first of ten consecutive frames in which velocity was less than 50 mm/s. It was necessary to determine if the presence of a vibration at a particular time point affected the movement in any adverse way. Therefore, the relevant movement parameters (reaction time, movement duration, endpoint spatial variability and

position) were examined using a  $9$  (delay epoch between visual target onset and vibration)  $\times 2$  (hand) repeated measures analysis of variance. Significant effects/interactions were explored using simple main effects with a Bonferroni correction for multiple comparisons (overall  $\alpha = 0.05$ ).

##### *Perceptual data*

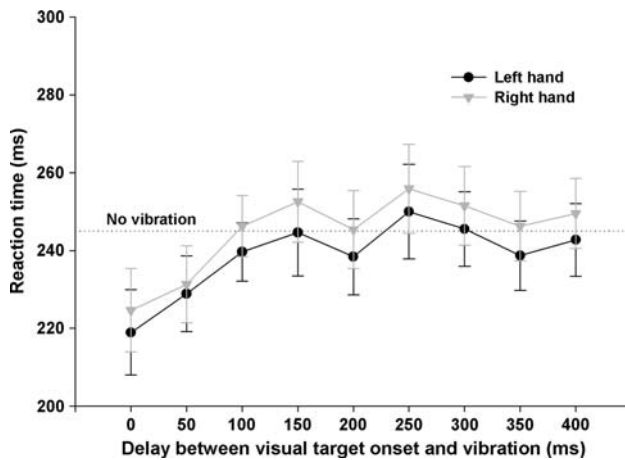
Participant's perceptual responses (i.e., which hand they felt the vibration on) were plotted relative to their overall mean time of movement onset, rather than visual target onset. This normalization allowed us to more directly examine the movement's effect on tactile detection, in addition to accounting for between-subject variability in reaction time. These responses were recorded, scored, and then normalized to 50 ms epoch bins, relative to each participant's mean reaction time. As there were insufficient trials to build a reliable function for each limb, these normalized scores were collapsed across hand to give measures of the % correct detection at the various epochs. These scores were then fit with a standard 4-parameter logistic curve in SigmaPlot (Systat Software Inc.). The time point at which the slope was steepest in each individual's curve (i.e., highest rate of change) was designated as the onset of tactile gating.

The data within these individual curves were binned in 50 ms gradations, with the mean from each bin yielding the data for the inferential statistics. These normalization and binning procedures resulted in the removal of the outer vibratory epoch bins, due to individual differences in mean reaction time (i.e., participants with longer reaction times inevitably had fewer vibrations during movement time), leaving a total of seven bins for comparison (200–150 ms before movement onset, 150–100 ms before movement onset, etc.). The tactile gating across the various epochs was examined with a univariate analysis of variance with seven levels of the epoch factor. Significant effects were explored using  $t$  tests with a Bonferroni correction for multiple comparisons (overall  $\alpha = 0.05$ ).

## Results and discussion

##### *Kinematic data*

Overall, participants demonstrated a small but significant left hand reaction time advantage when the data were examined across all vibratory epochs (239 vs. 245 ms;  $F(1,13) = 6.86$ ,  $P < 0.05$ ). The analysis of reaction time also yielded a main effect of delay [ $F(8,104) = 6.87$ ,  $P < 0.001$ ], characterized by a general facilitation participant's responses during earlier delay epochs (see Fig. 3). These effects did not interact with one another ( $P > 0.2$ ).



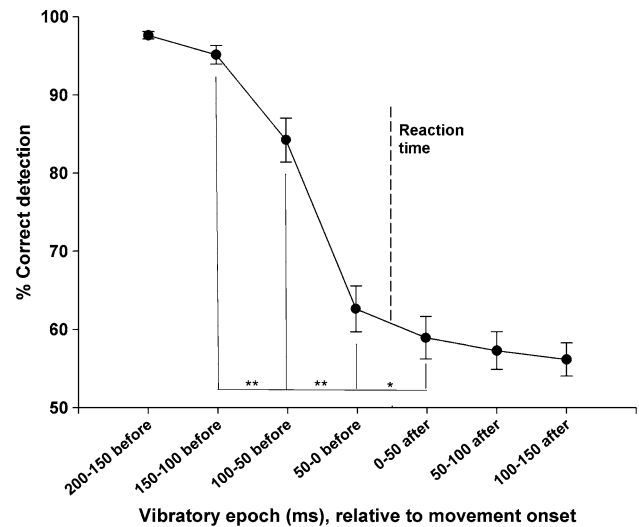
**Fig. 3** Reaction times for both hands across the vibratory delay epochs, relative to visual target onset for the 14 participants. Error bars show SEM

The movement duration of the right hand was shorter than that of the left hand across all vibratory epochs [360 vs. 368 ms;  $F(1,13) = 5.52$ ,  $P < 0.05$ ). However, there was no main effect of delay ( $P > 0.7$ ) or interaction between hand and delay ( $P > 0.9$ ) in terms of movement duration. Finally, there were no main effects or interactions related to the hand or delay epoch in terms of signed or unsigned endpoint position or variability (all  $P$  values  $> 0.2$ ).

#### Perceptual data

Statistical analyses of the perceptual data revealed a substantial reduction in the detection rates of the vibrations as a function of epoch ( $F(6,91) = 67.18$ ,  $P < 0.001$ ). This drop in detection rate is clearly evident in Fig. 4, and provides clear evidence of tactile gating during visually guided reaches. To examine the locus of this main effect, each normalized vibratory epoch in Fig. 4 was directly compared to the neighboring epoch (six tests, requiring a  $P$  value of 0.0083 to achieve significance following corrections). Significant differences between the perceptual reports for consecutive blocks were found between all the consecutive blocks except the first, and final two comparisons (full statistics reported in Table 1, and shown on Fig. 4). It can be extrapolated from Table 1 and Fig. 4 that the largest drop in detection occurred between 100 and 50 ms before reaction time with 50–0 ms before reaction time epochs. As basing conclusion only on mean data can be misleading, and does not explicitly address the question of detection (i.e., chance success) we examined individual's pattern of gating. A similar pattern of tactile gating was consistently seen across the entire sample (Fig. 5). Visual inspection of the data showed no consistent asymmetries in detection rates between the hands.

The individual logistic curve plots in Fig. 5 highlight this sharp drop in detection rates of tactile stimulation,



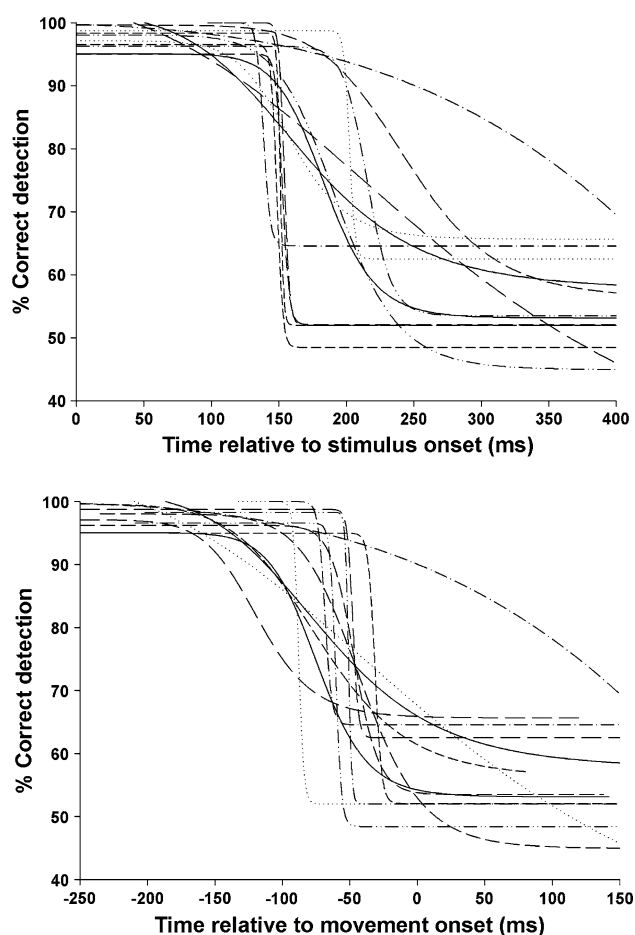
**Fig. 4** Detection of the vibration at various epochs, re-plotted (i.e., normalized) relative to reaction time for the 14 participants. Asterisk shows a significant difference between adjacent epochs with  $P < 0.05$ ; double asterisk shows significant differences with  $P < 0.01$  (full statistics reported in Table 1). Error bars show SEM

**Table 1** The mean difference in the perceptual reports between neighboring epochs, relative to movement onset, and associated post hoc analyses of the data

Comparison between epochs (ms, relative to movement onset)	Mean reduction in detection (%)	Paired $t$ test
200–150 before with 150–100 before	2.5	$t(13) = 2.61$ , $P = 0.02$ (NS)
150–100 before with 100–50 before	10.9	$t(13) = 4.28$ , $P = 0.001$ **
100–50 before with 50–0 before	21.6	$t(13) = 5.89$ , $P < 0.001$ **
50–0 before with 0–50 after	3.7	$t(13) = 3.33$ , $P = 0.005$ *
0–50 after with 50–100 after	1.6	$t(13) = 2.28$ , $P = 0.04$ (NS)
50–100 after with 100–150 after	1.1	$t(13) = 1.72$ , $P = 0.11$ (NS)

Significant difference between adjacent epochs with \* $P < 0.05$ ; significant differences with \*\* $P < 0.01$  following corrections for multiple comparisons (uncorrected  $P$  values reported within the table)

which is characteristic of the tactile gating shown in single-joint movement tasks. By recording the time point of the steepest slope (i.e., highest rate of change—a reasonably conservative estimate of gating onset, commonly used in psychophysics; Gescheider 1997) for each individual, it was determined that tactile gating occurred prior to movement onset in the vast majority of the sample (all except for a single participant; Table 2). This tactile gating preceded



**Fig. 5** The logistic curves plotted to the ‘percentage correct detection rates’ for the individual participants. All participants showed evidence of gating, with either a gradual onset of over 50 ms (the curves) or an abrupt onset of less than 50 ms (the step functions). The *top graph* shows the curves relative to stimulus onset and the bottom shows the same curves relative to reaction time. Gating onset was taken to be the point of the steepest slope in detection rates relative to reaction time (*lower graph*)

movement onset by an average of 55 ms [ $t(13) = 5.96$ ,  $P < 0.001$ ]. Although this time between gating onset is reaction time is somewhat shorter than may be inferred from the planned comparisons above (where significant differences occurred in the second comparison in Fig. 4), we feel that more conservative analyses will only serve to strengthen our findings. Furthermore, the times of gating onset and movement onset were strongly correlated with one another [ $r(14) = 0.629$ ,  $P < 0.05$ ], suggesting a relationship between the two time-points.

The findings from the current work indicate that tactile gating occurs a brief period before actual movement onset. It is therefore likely that the gating was time-locked to some other temporal event that we did not have access to with our kinematic records. The time course of the gating appears to be consistent with common values for neuromechanical delay (e.g., Cavanagh and Komi 1979). Neuromechanical

**Table 2** Individual’s mean reaction times and gating onset (the highest rate of change in the detection plots), relative to the reaction time

P	Reaction time (ms $\pm$ SD)	Gating onset, relative to movement onset
1	258 $\pm$ 22	76 ms prior
2	242 $\pm$ 23	87 ms prior
3	318 $\pm$ 36	63 ms prior
4	202 $\pm$ 32	50 ms prior
5	250 $\pm$ 26	48 ms prior
6	250 $\pm$ 29	37 ms after
7	235 $\pm$ 25	48 ms prior
8	237 $\pm$ 21	67 ms prior
9	252 $\pm$ 22	40 ms prior
10	184 $\pm$ 23	33 ms prior
11	209 $\pm$ 28	60 ms prior
12	277 $\pm$ 16	121 ms prior
13	207 $\pm$ 23	68 ms prior
14	262 $\pm$ 21	48 ms prior
Mean	242 $\pm$ 25	55 ms prior

delay (often called ‘motor time’), is the delay between muscular activation and movement onset—the time taken for the muscle to generate enough inertia to actually move the limb (Viitasalo and Komi 1981). The concordance between our data and earlier reported values of motor time provides a tentative indication that the sensory suppression is not merely coincident with, but a functional consequence of the preparation of the movement itself.

In order to support this claim we must first determine the motor time in a movement similar to the type or reach that participants performed in the main experiment. To gain our own estimate of motor time (verifying the apparent synchronicity of the sensory gating with the onset of muscle activity), we took electromyography (EMG) readings from a variety of muscles that participants would have utilized when completing the bimanual reach. We predicted that reaches of this sort would have a neuromechanical delay (reaction time subtracted from the EMG onset time) that was consistent with previous work (Cavanagh and Komi 1979), and approximately equal to the delay between reaction time and gating onset from the current work (55 ms). The 41 ms value that we determined for motor time (full details of the experimental protocol are reported in the supplementary materials), support this conclusion.

## General discussion

The aim of the current study was to determine the existence and time course of tactile gating during complex visually

guided multi-joint reaches. To examine tactile sensitivity during this class of movement, participants performed bimanual reaches to target pairs while receiving a vibrotactile stimulation at various time-points after the visual target onset. The task in the first experiment was simply to complete the movement as quickly and as accurately as possible, and verbally report the hand which had been vibrated.

Before discussion of the detection data, certain aspects of the reaching kinematics in this task must be addressed. The left hand had a shorter reaction time than the right hand, consistent with other research examining bimanual reaching with high frequency kinematic recordings of the hands (e.g., Buckingham and Carey 2009). These asymmetries merely highlight that participants were not having their reaching performance obviously affected by the vibration detection task. However, one unanticipated feature of the kinematic data was that the reaction times were shorter in the earlier delay epochs than the later ones. That is, when a vibration occurred at the same time, or close to, the onset of the visual target, participants reacted approximately 30 ms faster than during the trials without vibrations. This shortened reaction time is likely a result of the multi-modal excitation of seeing the target and feeling the vibration concurrently (Nickerson 1974). Importantly, following this initial facilitation of movement onset (i.e., with intervals of  $\leq 50$  ms) values stabilized to those observed in the absence of vibration (shown by the reference line in Fig. 3).

The presence of a strong tactile gating effect was ubiquitous—all participants appear to have reduced levels of tactile sensitivity during movement (Fig. 5). Closer inspection of the data showed that this sensory suppression occurred an average of 55 ms prior to movement onset. This demonstration of tactile suppression during a multi-joint, goal-directed movement is unique in both the sensory gating and motor-control literatures. As the tactile gating consistently preceded movement onset in this task (main study), and muscle activity (see supplementary materials) the sensory suppression is unlikely to be a peripheral consequence of the movement itself, as any reafferent sources would at this point be minimal. Of course, determining the actual timing of the sensory suppression in each participant is limited by the fact that we were unable to tailor the vibratory stimuli to each participant's detection thresholds. However, as participant's rates of detection showed the predicted, consistent drop from ceiling to chance levels, we do not feel that this limitation brings our conclusions into question. Further, these conclusions are consistent with earlier studies which noted a reduction in the levels of somatosensory evoked potentials (Jiang et al. 1990) and psychophysical detection (Williams et al. 1998) at similar time-points before movement onset in tasks that required single-joint movements. At first glance, these findings appear to add further weight to the importance of forward modeling (i.e., the relative

contributions of predictive controls of movements vs. sensory feedback, see Wolpert and Flanagan 2001) in goal-directed manual aiming. However, before this conclusion can be accepted, various competing explanations for the suppression must be considered.

The findings of the current work are difficult to integrate with studies showing tactile gating during passive movement (i.e., where a central command is not a prerequisite to movement, see Williams and Chapman 2002). These studies often invoke a 'backward masking', or 'postdictive cancellation' explanation, where suppression is caused by the concurrent sensation of other events (rather than being predicted by efferent information). However, considering that bimanual reaches are considerably more variable in terms of reaction time and other kinematic measures (see Ohtsuki 1994 for review) than the single-joint tasks employed in previous studies, any postdictive effects are, if anything, likely to be less in the current task than in previous work. Furthermore, while any masking effects of afferent processing may contribute to tactile gating during movement, these influences cannot explain the gating prior to movement onset seen in the current work.

Another plausible explanation may be that the gating of tactile sensation during bimanual reaching is merely a consequence of dividing attention between two competing sources of information. Recent studies have examined multimodal attentional competition, by extending the visual dominance effect (known as the 'Colavita effect') into the tactile domain. In an elegant series of experiments, Hartcher-O'Brien et al. (2006) demonstrated that when visual and tactile targets are displayed concurrently humans tend to ignore the tactile stimulus while still detecting the visual stimulus. This Colavita effect may underlie some portion of the tactile gating in the current (visually guided) task. For example, during the preparation and execution phases of a reaching movement, the weighting of the visual system may be increased, thus reducing the levels of tactile sensitivity. To fully rule out this explanation, trials with no vision would have to be compared to trials with full vision (only the latter are present in the current study). Of course, while attentional demands are a crucial factor in any detection task, attention can be discounted as a primary factor in the current findings simply because there was no evidence of a dual-task trade off in the movement task (i.e., reaction time did not suffer in the presence of vibratory cues). In fact, participants reacted substantially faster when they received the tactile cue in close temporal proximity to the visual onset cue.

It would be intuitive to imagine that global sensory input is utilized to complete computationally complex multi-joint goal-directed reaches. Conversely, the current work provides a unique demonstration of the suppression of task relevant (Rao and Gordon 2001; although see Flanagan et al.

2006 for an alternative view) inputs to an action with end-point precision requirements, prior to movement onset. Yet, despite the link between movement preparation and sensory suppression shown in this study, tactile feedback may still play an unconscious role guiding successful reaching behavior. Clearly, there are some conceptual similarities between the tactile suppression demonstrated during the goal-directed manual reaches of the current study, and the visual suppression used in the early demonstrations of an apparent dissociation between vision for perception and vision for action (Goodale and Milner 1992). If a similar distinction exists between haptics for perception and haptics for action, it is feasible that the motor system can make use of tactile information that is not consciously perceived (Dijkerman and de Haan 2007). Such a dissociation may be demonstrable using tactile gating, in a similar way to the online corrections of a reaching hand, made to targets perturbed during the suppressed period of a saccadic eye movement (Goodale et al. 1986).

Tactile perception performs several functions, some of which have a direct influence on goal-directed action. For example, when grasping and lifting a novel object haptic perception of the surface friction and compliance allow the grip and load forces to be automatically re-scaled online (Gordon et al. 1991), even when visual information of the objects mass is unreliable (Flanagan and Beltzner 2000). Thus, tactile perception must still be accessed in some way when it is necessary to determine the success of the initial force predictions during an object lift. This example of tactile perception influencing action contrasts with situations where haptics must be used to accurately perceive the material of a goal object (Klatzky and Lederman 2007), in the absence of visual information. The current experimental task does not fit comfortably into either of these categories, and it is unclear what level of gating would occur during these perceptual or object lifting tasks. Further research is necessary to determine whether these more functional tasks (in terms of tactile utility) suffer from the sensory attenuation seen in the current work.

In conclusion, the current experiment demonstrated that tactile gating is present during, and prior to, visually guided aiming movements—the first demonstration of this phenomenon where the sensory input is task relevant. The timecourse of the gating indicates that the phenomenon may have central, rather than peripheral, attentional or postdictive origins. Future work will build on this paradigm, to build a more comprehensive model describing the nature and neuronal mechanisms of fascinating sensory suppression during a visually guided task.

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## References

- Bays PM, Flanagan JR, Wolpert DM (2006) Attenuation of self-generated tactile sensations is predictive, not postdictive. *PLoS Biol* 4:e28
- Buckingham G, Carey DP (2009) Rightward biases during bimanual reaching. *Exp Brain Res* 194:197–206
- Cavanagh PR, Komi PV (1979) Electromechanical delay in human skeletal muscle under concentric and eccentric contractions. *Eur J Appl Physiol* 42:159–163
- Chapman CE, Bushnell MC, Miron D, Duncan GH, Lund JP (1987) Sensory perception during movement in man. *Exp Brain Res* 68:516–524
- Dijkerman HC, de Haan EHF (2007) Somatosensory processes subserving perception and action. *Behav Brain Sci* 30:189–239
- Flanagan JR, Beltzner MA (2000) Independence of perceptual and sensorimotor predictions in the size-weight illusion. *Nat Neurosci* 3:737–741
- Flanagan JR, Bowman MC, Johansson RS (2006) Control strategies in object manipulation tasks. *Exp Brain Res* 16:1–10
- Gescheider G (1997) *Psychophysics: the fundamentals*, 3rd edn. Lawrence Erlbaum Associates, NJ
- Goodale MA, Milner AD (1992) Separate visual pathways for perception and action. *Trends Neurosci* 15:20–25
- Goodale MA, Pellison D, Prablanc C (1986) Large adjustments in visually guided reaching do not depend on vision of the hand or perception of target displacement. *Nature* 320:748–750
- Gordon AM, Forssberg H, Johansson RS, Westling G (1991) Integration of sensory information during the programming of precision grip: comments on the contributions of size cues. *Exp Brain Res* 85:226–229
- Guiard Y (1987) Asymmetric division of labour in human skilled bimanual action: the kinematic chain as a model. *J Mot Behav* 19:486–517
- Hartcher-O'Brien J, Gallace A, Krings B, Koppen C, Spence C (2006) When vision 'extinguishes' touch in neurologically-normal people: extending the Colavita visual dominance effect. *Exp Brain Res* 186:643–658
- Jiang W, Chapman CE, Lamarre Y (1990) Modulation of somatosensory evoked responses in the primary somatosensory cortex produced by intracortical microstimulation of the motor cortex in the monkey. *Exp Brain Res* 80:333–344
- Klatzky RL, Lederman SL (2007) Do intention and exploration modulate the pathways to haptic object identification? *Behav Brain Sci* 30:213–214
- Nickerson RS (1974) Intersensory facilitation of reaction time. *Psychol Rev* 80:489–509
- Ohtsuki T (1994) Change in strength, speed, and reaction time induced by simultaneous bilateral muscle activity. In: Swinnen SP, Heuer H, Massion J, Cesaer P (eds) *Interlimb coordination: neural dynamical and cognitive constraints*. Academic press, NY, pp 259–274
- Rao AK, Gordon AM (2001) Contribution of tactile information to accuracy in pointing movements. *Exp Brain Res* 138:438–445
- Viitasalo J, Komi P (1981) Interrelationships between electromyographic, mechanical, muscle structure and reflex time measurements in man. *Acta Physiol Scand* 111:97–103

- Voss M, Ingram JN, Haggard P, Wolpert DM (2006) Sensorimotor attenuation by central motor command signals in the absence of movement. *Nat Neurosci* 19:26–27
- Voss M, Ingram JN, Wolpert DM, Haggard P (2008) Mere expectation to move causes attenuation of sensory signals. *PLoS ONE* 3:e2866. doi:[10.1371/journal.pone.0002866](https://doi.org/10.1371/journal.pone.0002866)
- Walsh E, Haggard P (2007) The internal structure of stopping revealed by a sensory detection task. *Exp Brain Res* 183:405–410
- Williams SR, Chapman CE (2002) Time course and magnitude of movement-related gating of tactile detection in humans III. Effect of motor tasks. *J Neurophysiol* 88:1968–1979
- Williams SR, Shenasa J, Chapman CE (1998) Time course and magnitude of movement-related gating of tactile detection in humans. I. Importance of stimulus location. *J Neurophysiol* 79:947–963
- Wolpert DM, Flanagan JR (2001) Motor prediction. *Curr Biol* 18:R729–R732