A continuous vibration-based virtual tactile motion across fingertips

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Abstract

Motion is one of the fundamental qualities not only of vision, but also of touch. Manipulation and exploration of objects involves different forms of movement between the skin and objects. A different form of tactile motion from remote sources is through substrate vibrations, and is present in arthropods such as insects and spiders, enabling them to localise approaching preys and predators. Here, we quantify the extent to humans perceive tactile motion based on vibrations sensed by fingertips. We employed a novel stimulation paradigm in which a pair of vibrations (100 Hz) with sinusoidal envelopes (0.5 cycle/s) and various phase differences between the two vibrations were delivered to two fingertips. The phase difference between the vibrations generated perception of a virtual motion across the fingertips. The findings suggest that human tactile system possesses the sensory channel for detection of motion through substrate vibrations, which is fundamentally different from tactile motion mechanisms during active surface exploration. We propose two potential neural computations underlying processing this form of motion; one based on phase difference or time delay detection, and the second based on temporal order and interval duration processing.

Introduction

Motion is a fundamental quality of sensory input. In vision, despite diverse evolutionary trajectories across different species, from insects and cephalopods to vertebrates, sensory systems have evolved and converged to principally similar mechanisms of motion processing [1, 2]. However, motion is a hallmark not only of vision but also of the tactile sensory system, and has considerable behavioural relevance to animals and humans. Manipulation and handling of objects, as well as haptic exploration of surfaces involves motion between surfaces and the skin [3]. For instance, discerning the roughness and smoothness of textures, and identifying objects' material (e.g. metal vs wood) requires palpation of fingers over the surfaces. To identify the shape of an object, we follow its contours, edges and corners with our fingers. Reading Braille is through moving fingertips from left to right across the sequence of raised dots. Additionally, processing tactile motion is integral to fine and accurate coordination of hands and digits during manipulation of objects [4, 5]. Despite the crucial role of motion in tactile perception, its computational and perceptual bases are poorly understood.

There are two sources of information for tactile motion in the literature [5, 6]: (i) the sequence of activation of mechanoreceptors and afferents representing different parts of the skin as object contours or surface moves over the skin (for instance, an insect crawling on the skin), and (ii) skin stretches caused by friction between the skin and

object (e.g. palpation of fingertips across a texture). At the level of periphery, slowly adapting type 1 afferents (SA1) convey high acuity spatial information about the position of contact between object and skin [4, 7, 8]. Thus, the spatio-temporal pattern of activity in a population of SA1 afferents with spatially-distributed receptive fields over the skin provides a channel of information about the direction and speed of motion over the skin with an acuity comparable to that of human subjects [8]. Similar spatiotemporal patterns of activity in rapidly adapting type 1 (RA1) afferents, though to a lesser extent, is thought to contribute to encoding of motion, due to their relatively small size of receptive fields [8]. In contrast, slowly adapting type 2 (SA2) afferents respond to skin stretches. Motion in different directions stretches the skin in different ways [9], hence, activating SA2 afferents differently, providing information about the direction of the motion [10].

Here, I investigate a third form of tactile motion across gaps between human's major tactile sensing organs: fingers. Finger pads and in particular fingertips possess one of the highest density of tactile mechnoreceptors in mammalian and human body [11]. Humans actively collect information and interact with the surrounding environment through their fingers [3]. This form of motion relies on the asynchrony between the contentious streams of vibro-tactile input to two or more fingertips, analogous to detecting and localising mates, preys or predators in arthropods such as in chelicerae, by sensing substrate vibrations with their appendages [12]. The spatial extent of this form of motion spans beyond the the area of contacts and the body. Additionally, as shown later, processing this form of motion does not require the spacial acuity of SA1 and RA1 afferents. The present study confirms this by generating the perception of motion using vibro-tactile stimuli which are known to activate RA2 afferents (with Pacinian corpuscle endings), and applying the stimulus to whole fingertip areas.

Materials and methods

Assume a point source e.g. a mobile phone on a table that generates the vibration $A_0 \sin(2\pi f_c t)$, where A_0 and f_c denote the amplitude and frequency of vibration, respectively. As the vibration travels through the medium – for instance, a table – in from of a plane wave, due to dissipation, scattering and absorption of its energy in the medium, the intensity of the wave amplitude attenuates with distance. The profile of attenuation with distance is usually exponential with the following form:

$$A(d) = A_0 \exp(-\gamma d), \tag{1}$$

where γ denotes the attenuation coefficient that depends on the medium and the frequency of the vibration, and d denotes the distance. Accordingly, movement of the point source relative to at any given distant point causes changes in the received amplitude of the vibration. The changes are proportional to the radial component of the velocity of movement. In the special case of a periodic movement of the source with a frequency of $f \ll f_c$, the corresponding change in the momentarily amplitude (the envelope) of the vibration at a remote point with distance $d(t)$ is periodic with frequency of f and equals:

$$A(t + t_0) = A_0 \exp(-\gamma d(t)) \sin(2\pi (f_c + \Delta f) t), \tag{2}$$

where t_0 denotes the delay corresponding to the time that the wave travels the distance d, and Δf denotes the instantaneous shift in the frequency due to Doppler effect. Both parameters depend on the speed of wave propagation through the medium which is determined by the stiffness and density of the material. For instance, the wave propagation speed in stainless steel is about 5790 ms^{-1} and in hard wood about 3960

ms^{-1}. In practice, for distances within the range of a meter or less, t_0 is negligible and in the range of a fraction of a millisecond or some nanoseconds delay, hardly detectable by human subjects. Assuming a slow motion velocity of the source compared to speed of the wave, and with $f \ll f_c$, the Doppler effect is negligible. Therefore, hereafter, I assume $t_0, \Delta f \approx 0$.

By positioning a touch sensor (e.g. fingertips) on a remote point (hereafter, referred to as the 'touch point'), one may estimate the direction of movement along the radial axis (towards to away from the touch point) based on the relative changes in the envelope of the received vibration over time. However, this information is insufficient to determine the tangential component of the motion. To obtain the sufficient information to determine the motion trajectory, two or more touch points at various locations are required (see Fig 1).

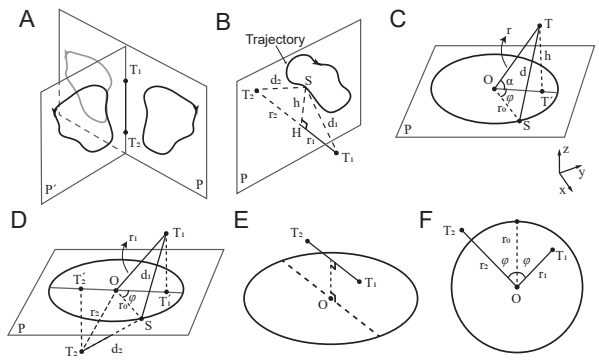

Fig 1. Detecting the motion of a remote vibrating source through patterns of vibrations sensed at two touch points. A, T_1 and T_2 denote the two touch points. The trajectory on plane P' is the rotation of trajectory on plane P around the touch axis T_1T_2. The grey closed curve is the reflection of the trajectory over the touch axis T_1T_2. B, For any arbitrary trajectory on the plane P, when T_1T_2 is ortogonal to P, the vibrations from source S received at T_1 and T_2 are in-phase. r_1 and r_2 represent the distance of T_1 and T_2 from P respectively. d_1 and d_2 denote the distance between the source S, and T_1 and T_2 respectively. d_1 and d_2 vary as S moves along the trajectory. C, A circular trajectory with radius r_0, centred at O. T' denotes the projection of touch point T on P. h, r and d denote the distance of T from P, O and S, respectively. α denotes the angle between OT and OT'. D, d_1 and d_2 denote the distance between the source S, and T_1 and T_2 respectively. d_1 and d_2 vary as S moves along the trajectory. r_1 and r_2 denote the distance between O, and T_1 and T_2 respectively. E, An example of out-of-phase vibrations, when the projection of axis T_1T_2 (dashed line) passes through O. F, the two-dimensional geometry. All other conversions as in D.

Motion direction identification by two touch points

Utilising two touch points (denoted by T_1 and T_2) provides necessary information to determine moment-by-moment location of a vibrating point source in 2D, based on the envelope of the vibration at the two touch points. In 2D, there are, however, two possible trajectories associated with the vibration patterns received at two touch points; these two possible trajectories are the mirror of each other relative to the line passing through the two touch points (hereafter, referred to as touch-point axis, Fig 1A). With two touch points, it is impossible to distinguish on which of the two trajectories the source is moving. In 3D, there is ambiguity about the trajectory of the motion

component tangential to the cylinder centred around this axis. Any trajectories that are the rotation of each other about the touch-point axis are indistinguishable (Fig 1A). Hence, there are infinite number of trajectories that create an identical pattern of vibrations at the two touch points.

In-phase vibrations

As mentioned earlier, a periodic motion with cyclic trajectory with the frequency of f results in a periodic vibration pattern in the touch points. When the changes in the envelope at one touch point with time – or equivalently with the distance, or phase in a cycle – is proportional or is a transformation of instantaneous changes in the other touch point under any arbitrary strictly increasing odd function, the two waveforms increase or decrease together and are said to be in the same phase (in-phase). For instance, when the trajectory is on a plane perpendicular to the touch-point axis, as shown in 1B, the closest (or farthest) point on the trajectory to either touch point is identical. The instantaneous change in the received vibration amplitude at each touch point is:

$$\frac{d}{dt}A_i\left(t\right) = A_0\frac{d}{dt}\exp\left(-\gamma d_i\left(t\right)\right) = A_0\frac{d}{dt}\exp\left(-\gamma\sqrt{r_i^2+h^2\left(t\right)}\right) \tag{3}$$

$$= -\gamma A_0\frac{h\left(t\right)}{\sqrt{r_i^2+h^2\left(t\right)}}\exp\left(-\gamma\sqrt{r_i^2+h^2\left(t\right)}\right)\frac{dh}{dt} \tag{4}$$

where A_i denotes the instantaneous envelope of the received vibration at the touch point T_i (for $i = 1, 2$), $h\left(t\right)$ denotes the distance of each point on the trajectory from the touch-point axis, and r_i denotes the distance of touch point i from the trajectory plane. Eq. 4 indicates that the envelope of the vibrations sensed at two touch points change monotonically in the same manner with the distance h from the touch-point axis. Therefore, the envelope of the vibrations are at the same phase. With some mathematical steps, one may show

$$A_2\left(t\right) = A_0\exp\left(-\sqrt{\gamma^2\left(r_2^2-r_1^2\right)+\ln^2\frac{A_1}{A_0}}\right), \tag{5}$$

which is a strictly increasing function of A_1, indicating A_1 and A_2 are in-phase.

Out-of-phase vibrations

Two waveforms are completely out-of-phase when there is a π phase difference between them. This corresponds to when the changes in the envelope at one touch point is reversely proportional or transformed version of instantaneous changes in the other wave under an arbitrary strictly increasing odd function. Thus, the envelope of one touch point increases as the other one decreases, and vice versa. This is equivalent to a bistable motion; for half of the cycle, the motion is perceived in one direction, and for the other half, in the opposite direction. An example of out-of-phase situation is depicted in Fig 1D and E.

Circular motion of a vibrating source

For motion on a circular trajectory of radius r_0 with velocity v (Fig 1C), the frequency of motion is $f = \frac{v}{2\pi r_0}$. The amplitude of received vibration at the point T with coordinates (φ, r) in polar coordinates, at time instance t is

$$A\left(t\right) = A_0\exp\left(-\gamma\sqrt{r^2+r_0^2-2rr_0\cos\left(2\pi ft-\varphi\right)}\right)\sin\left(2\pi f_c t\right) \tag{6}$$

The envelope of the vibration is the periodic function $A_0 \exp\left(-\gamma\sqrt{r^2 + r_0^2 - 2rr_0\cos(2\pi ft - \varphi)}\right)$ oscillating between the maximum and minimum levels of $A_0 \exp(-\gamma(r + r_0))$ and $A_0 \exp(-\gamma|r - r_0|)$, respectively, with the frequency of f. In three dimensional case, Eq. 6 changes to:

$$A(t) = A_0 \exp\left(-\gamma\sqrt{r^2 + r_0^2 - 2rr_0\cos\alpha\cos(2\pi ft - \varphi)}\right)\sin(2\pi f_c t), \tag{7}$$

where $\left(\frac{\pi}{2} - \alpha\right)$ corresponds to the inclination angle of the spherical coordinates for the touch point relative to the centre of the trajectory (Fig 1C).

Let P denote the plane of circular trajectory. Assume the projection of the two touch points (T_1 and T_2) on the plane P (denoted by T_1' and T_2', respectively) and the centre of the circular trajectory, denoted by O, are aligned and on a straight line (Fig 1D). When O is located between T_1' and T_2', the envelope of the vibrations at the two touch points are out of phase. Inversely, when O is located outside the line segment $T_1'T_2'$, the envelope of the vibrations at the two touch points are in-phase.

Without loss of generality, let the coordinates of the two touch points be (θ_1, φ, r_1) and $(\theta_2, -\varphi, r_2)$, respectively. From Eq 7, the envelope of the vibrations at these two points have a phase difference of $\Delta\varphi = 2\varphi$.

Here, for simplicity, the focus is on the condition where the centre of circular motion is on the perpendicular bisector of the line segment between the two touch points, i.e. $r_1 = r_2$. This allows better visualisation of the envelopes of the vibrations, as they have identical range due to equidistant position of the centre of motion relative to the touch points. This is also in accordance with the experimental procedure (see below) and its corresponding two-dimensional geometry.

Experimental procedure

Participants

Twelve undergraduate students (age 20–24 years; one left-handed; 4 female) from Monash University participate in this experiment. Subjects provided signed, informed consent before participating in the experiment. All experimental procedures were approved by Monash University Human Research Ethics Committee (MUHREC). The study was carried out in accordance with the approved guidelines.

Vibro-tactile stimulation

To simulate the movement of a remote (vibrating) stimulus, two vibrations were delivered simultaneously to the tips of the index and middle fingers of each subject's right hand (Fig 2A). The vibrations were sinusoidal with a base frequency of $f_c = 100Hz$, and sinusoidal envelope frequency of 0.5 Hz (Fig 2B). These parameters were chosen according to a pilot experiment to generate a reliable perception of the vibration envelope and the motion. Vibrations were generated by a set of solenoids (4 Ω, 1 Watt, diameter of 12 mm full-range speakers, as shown in Fig 2B) connected to the audio output of a PC, controlled by a custom-written script in MATLAB (MathWorks Inc., Natick), and at a sampling rate of 192 kHz.

We used sinusoidal envelopes, as this pattern constitutes one of the most fundamental functions in the nature and mathematics. Every periodic function can be represented as the sum of sinusoidal functions, known as the Fourier series. Among period functions, sine is the only that retains its shape when added to another sine function of same frequency, and arbitrary phase and amplitude. Sinusoids occur often in nature, including wind waves, sound waves, and light waves. The auditory system in

mammals recognises sinusoids as tones because sinusoid is a representation of a single frequency with no harmonics. Sinusoidal envelopes entail a motion with acceleration rather than constant speed motion, similar to that of a spring-mass or pendulum motion.

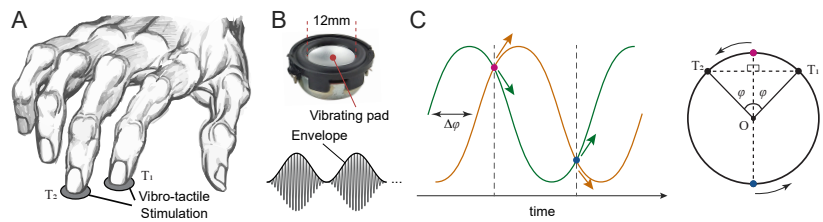

Fig 2. Motion direction discrimination task. A, The index and middle fingers of the right hand were stimulated using a pair of solenoid stimulators (upper panel, B) that delivered amplitude modulated vibrations (lower panel, B). C, The envelope of the vibrations, on each trial, had a phase difference $\Delta\varphi$. The onset of the vibrations were at one of the two points at which the amplitude of the vibrations were identical (indicated by the dashed lines).

For a specific phase difference of $\Delta\varphi$, the two vibrations were

$$A_1(t) = \frac{A_0}{2}\left(1+\sin\left(2\pi f t+\frac{\Delta\varphi}{2}\right)\right)\sin\left(2\pi f_c t\right), \tag{8}$$

$$A_2(t) = \frac{A_0}{2}\left(1+\sin\left(2\pi f t-\frac{\Delta\varphi}{2}\right)\right)\sin\left(2\pi f_c t\right). \tag{9}$$

In order to eliminate any effect of difference in the initial amplitude of vibrations on the responses, the onset of the two vibrations were at a point where the two vibrations had equal envelope. For the non-zero phase difference $\Delta\varphi$, in each cycle, there are exactly two points at which the two vibrations are equal in their amplitude: $t_0 = \frac{1}{4f}$ and $\frac{3}{4f}$, with the corresponding envelope amplitudes of $\frac{A_0}{2}\left(1+\cos\left(\pm\frac{\Delta\varphi}{2}\right)\right)$ and $\frac{A_0}{2}\left(1-\cos\left(\pm\frac{\Delta\varphi}{2}\right)\right)$, respectively (Fig 2C). As the cosine function is even, its value remains unchanged with the sign of its argument. At either initial point, the derivative of envelopes of the two vibrations are opposite of each other. The changes in the envelope of the vibrations for one of the initial points is consistent with the dominant direction of the motion, and for the other initial point, it is consistent with the opposite direction. For each trial, one of the two initial values was randomly selected with equal probability of $\frac{1}{2}$. As a result, across trials, the initial values of the vibrations provide no predictive cue about the direction of the motion.

Motion direction discrimination task

The participants performed a discrete-trial two alternative forced-choice (2-AFC) direction discrimination task. The subjects were instructed to maintain their hand and fingertips positions to their best throughout on the vibrating pads (Fig 2) the experimental session. The experiment was self-paced, with all responses via keyboard. In each trial, two vibrations with a phase difference pseudo-randomly selected from values of 0, $\pm\frac{\pi}{6}$, $\pm\frac{\pi}{3}$, $\pm\frac{\pi}{2}$, and π (rads), – equivalently, 0, ±30°, ±60°, ±90°and 180°– with a maximum duration of 6 s (3 cycles of 0.5 Hz envelope) were delivered simultaneously to the two fingertips. Subjects reported the perceived direction of the

motion by pressing either left or right arrow key on a keyboard positioned in front of them using their left hand. Subjects were free to respond at any time during or after the stimulation onset, with no response timeout imposed. Subjects, then, scored their level of confidence about their judgement by pressing one of the "1" to "5" keys. The "1" key corresponded to the lowest level of confidence (no confidence at all), and the "5" key corresponded to 100% confidence with no doubt about the judgement. The self-reported confidence ratings were normalised between 0 to 100%.

Results and Discussion

The vibration patterns from the movement of a remote stimulus when sensed at two distinct points have a phase difference providing information about the trajectory of the motion (Fig 1). Is the phase difference information read out through the tactile system to generate a perception of motion? To answer this question, I stimulated fingertips with vibration patterns that simulate a virtual motion, and quantified the extent to which these vibration patterns generate a tactile motion perception in a 2-AFC motion direction discrimination task. On each trials, two continuous vibrations, each of which composed of an amplitude modulated 100 Hz carrier vibration by a sine wave envelope at 0.5 Hz, were delivered to two fingertips (the index and the middle finger of the right hand, see Fig 2). The envelope of the two vibrations had varying phase differences relative to each other. The perceived direction of the motion depended on the phase difference between the two vibrations, as characterised by the average psychometric curve representing the proportion of left vs. right responses as a function of the phase difference (Fig 3A).

The accuracy with which the participants discriminated the direction of the motion for each phase difference (e.g. $\pm 30°$) was quantified in terms of the proportion of correct responses according to the sign of phase difference. The discrimination performance as a function of the phase difference exhibited an inverted U shape (Fig 3B), peaking at phase differences between 60–90°, and chance level discrimination performance for phase differences of 0 and 180°.

Controlled difficulty by phase difference

The discrimination accuracy at phase differences close to zero and $\pm 180°$is lower than those between 60–90°(Fig 3B). Consistently, the level of confidence about the judgements exhibits a similar trend (Fig 3C), indicating less certain judgements were on average less accurate, and their corresponding response time was longer (Fig 3D). These findings indicate that the level of difficulty of the task can be manipulated by the phase difference between the two vibrations.

The phase difference and not the amplitude difference generates the motion perception

There are two plausible mechanisms that may account for the perception of tactile motion direction: (i) through the phase difference between the two signals, and (ii) through the amplitude difference between the two signals. Our stimulation paradigm allows to verify the contribution of each factor separately; For the phase difference of $\pm 180°$, the discrimination performance, by definition, is at the chance level (0.5). This is because the vibrations with $+180°$ phase difference are identical to those of $-180°$ phase difference. This was further verified in the data, as shown in Fig 3A & B. However, for the $\pm 180°$phase difference, when one signal is at its peak, the other signal is at its trough and vice versa, leading to maximum difference between the two signals

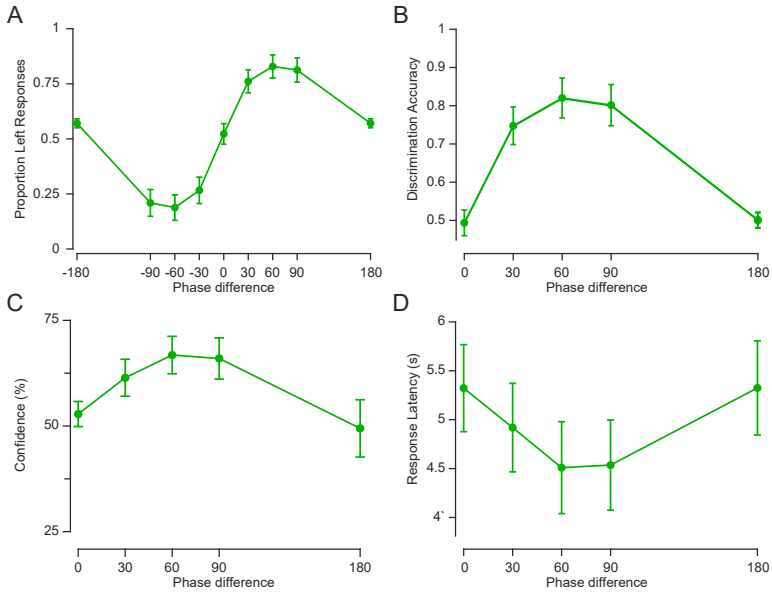

Fig 3. Behavioural characteristic functions and psychometrics. A, Psychometric curves in term of the choice likelihood (proportion of left responses) as a function of phase difference, averaged across subjects ($n = 12$). B, The discrimination accuracy in terms of the proportion of correct responses, averaged across subjects. For 0 and 180°phase differences, the responses in a pseudo-random manner labelled as either correct or incorrect. C, the average confidence level scores as a function of phase difference. D, The median response latency (time interval between stimulus onset and response), averaged across subjects as a function of phase difference. All error bars represent the standard error of the mean (SEM).

compared to other phase differences. Therefore, the information about the amplitude difference of the vibrations is maximum at ±180° phase difference. accordingly, any contribution of the amplitude difference to tactile motion perception is expected to be maximal for the ±180° phase difference. A mechanism based on amplitude difference predicts a consistent direction of perceived motion across trials. However, the choice likelihood at 180°(Fig 3A) does not support this motif. Another possibility is a mechanism based on amplitude difference results in a consistent direction of perceived motion within a trial. However, due to the bistable nature of 180°phase difference, the perception varies across trials as in Fig 3A. In this scenario, at the level of individual trials, the subjects perceive strong tactile motion, leading to high confidence scores. While the direction of perceived motion varies from trial to trial, the confidence scores are predicted to be high. The analysis of the confidence, on the contrary, revealed otherwise; on average, across subjects, the confidence score for 180° phase difference was 49.4%±6.8% (mean ± SEM, $n = 12$), less than that for other stimuli, including 0° phase difference (or equivalently, the zero amplitude difference, 52.8%±3.0%, see Fig 3C). Consistently, the response latency for 180° phase difference, on average, was higher than that of other stimuli, and almost identical to 0° phase difference (5.32±0.48 s vs. 5.32±0.44 s, Fig 3D). These finding reveal that the amplitude difference of the two signals does not create the tactile motion perception.

Recency vs primacy: the effect of initial phase on perception

The initial point of the stimulation was the moment at which the two vibrations had identical envelope amplitude (see Fig 2C). This corresponds to the points equidistant from the touch points, i.e. the intersections of the trajectory and the bisector of the touch points. On a circular trajectory, there are two points, half of the cycle (or equivalently ±180°) away from each other, at which the amplitude of vibrations at the two touch points are equal (see Methods section and Fig 2C). The directions of virtual movement within the cycle at these two points are opposite of each other (arrows in Fig 2C). In a primacy accumulation of evidence, the initial direction of the virtual motion has a higher weight in the perceived direction and influences the perceptual judgement, especially for shorter response latencies. For those trials where the initial phase corresponds to the opposite direction of the correct response, primacy is more likely to generate incorrect choice. In contrast, a recency evidence accumulation, where early evidence is under-weighed, predicts a higher proportion of correct responses.

To verify the extent to which perceptual judgements about the direction of virtual tactile motion is based on primacy or recency evidence accumulation, I quantified the psychometric curves for either initial phase condition, separately. Comparing the psychometric curves for the two initial stimulation conditions (the initial direction, Fig 4A) shows the initial condition had a small effect on perceptual judgements for ±30, ±60 and ±90°phase differences (all conditions $< 3.7\%$), implying little effect on the discrimination accuracy of subjects. The initial condition of the stimulus, however, exhibited a 24.1% bias effect on the choice likelihood for the bistable ±180°condition; an initial right-ward direction induced a bias towards left choices 24.1% more than the initial right-ward direction. Similar trend as that of ±180°was observed for 0°: an initial right-ward direction increased left choices by 9.4%. These results are inconsistent with primacy scheme, suggesting the initial segment of the trajectory does not account for perception and perceptual decisions.

To further verify this, the response latencies for each initial condition were compared. Decisions on account of primacy accumulation predicts a faster latency for a specific motion direction (e.g. towards left) when the initial phase in congruent compared to incongruent initial phase. This is due to higher weight of the earlier segments of stimulus (vibration pairs) which in the congruent condition draws the accumulated evidence towards the decision threshold. While in the incongruent condition, it pulls the accumulated evidence away from the decision threshold. As the decision is not influenced (see above, Fig 4A), the time to reach the threshold in congruent condition is predicted to be faster. In contrast to the prediction based on primacy, the response latency for positive phase differences (i.e. the left direction) for congruent condition (the left initial direction, marked in green, Fig 4B) was longer compared to that for incongruent condition (the right initial direction, marked in amber, Fig 4B). Similarly, the response latency for negative phase differences (i.e. the right direction) for congruent condition (the right initial direction) was longer compared to that for incongruent condition (the left initial direction). This confirms that the primacy scheme does not explain the data. Does this mean that the accumulation of evidence is based on a recency scheme? This is a difficult question to answer with the present data. The short answer is, not necessarily. Then how can these findings be explained? The next subsection investigates another attribute of the stimulation that explains the data: the initial amplitude of the vibrations envelopes.

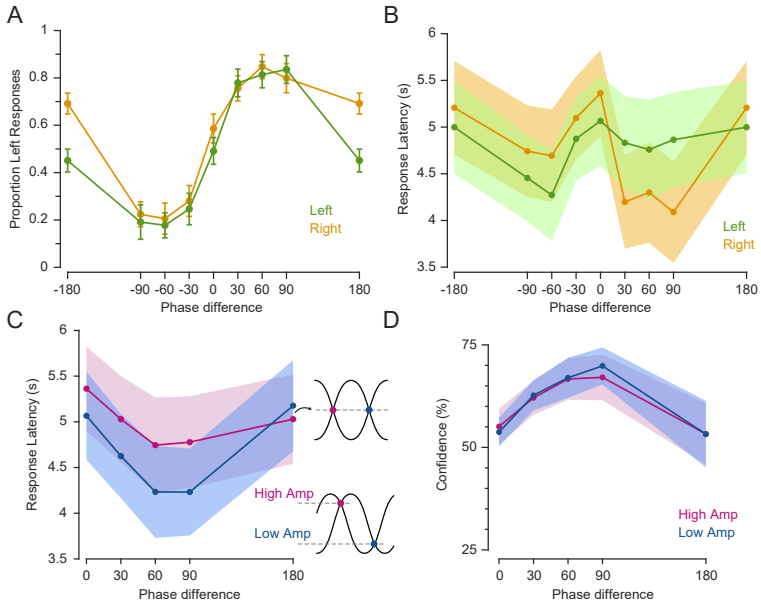

Fig 4. Effect of initial direction and amplitude. A, Psychometric curves for leftward (green) and rightward (amber) initial direction of motion along the trajectory. B, The median response latency as a function of phase difference, averaged across subjects ($n = 12$). C, As in B, but for high initial amplitude (red) and low initial amplitude (blue). The insets depict the envelopes of vibrations and corresponding initial amplitudes. D, The average self-reported confidence scores as a function of phase difference for each initial condition. Error bars and shaded areas represent the standard error of the mean (SEM).

Higher initial amplitude of vibrations delays perceptual judgements without affecting the perception

As the congruency of the initial condition with the direction of the motion does not explain the response latency, I tested the extent to which the difference in the initial amplitude determines response latency. In addition to difference in their direction of changes (the derivatives of the vibration envelopes, arrows in Fig 2C), the amplitude of the envelopes at the two initial points are different; The high-amplitude initial condition corresponds to the point on the trajectory closer to the touch points (congruent direction, see (Fig 4C inset). Inversely, the low-amplitude initial condition corresponds to the farther point on the trajectory to the touch points (Fig 2C).

Fig 4C demonstrates that when the initial amplitude of the envelopes is higher, the response latency is also longer. For the ±180°phase difference, either initial amplitudes are identical (see Fig 4C inset). Consistently, the difference between the response latencies for the two initial conditions is small. This implies that the interaction of the task difficulty (in terms of the phase difference) and the initial amplitude determines the response latency. The subjects skip the initial high amplitude segment of the stimulation, thus perceptual judgements for the high amplitude initial conditions take longer. Additionally, a higher initial amplitude is associated with a abrupt onset of stimulus distracting or masking the direction of motion. However, over the time course of stimulation (6 s) subjects accumulate sufficient evidence for judgements, and hence, the abrupt onset of stimulus does not affect the perception (and psychometric curves), and the level of confidence (Fig 4D).

Conclusion

The present study employs a novel vibro-tactile stimulation protocol to generate the perception of a continuous tactile motion. This was achieved with a minimum number of two vibrations, each of which is an amplitude modulation of a 100 Hz carrier vibration (Fig 2B). The phase difference between the two amplitude modulated vibrations generates perception of a continuous tactile motion. The direction of the vibration-induced motion depends on the phase difference between the pair of vibrations, and not the low level attributes of vibrations such as their amplitude and frequency. The perception of this form of motion was independent of the initial amplitude and phase of the envelopes (Fig 4A). Instead, the initial amplitude of the vibration affected the reaction time of the subjects (Fig 4B & C).

A major challenge in somatosensory neuroscience is to generate precisely controlled stimuli with unique sensation on every trial. Particularly in experiments involving freely moving animals, the trial-to-trial and moment-by-moment variations in the behaviour of animal causes variations in the quality of contact between the stimulator and skin, hence affecting the sensory responses. In human psychophysics, due to the elastic nature of the skin tissue, identical tactile stimuli with little variability in the quality of contact including variability in pressure, skin stretches and tensions, may activate different types of mechanoreceptors, activating parallel pathways and producing different sensations which in turn may confound the experimental results [3]. Here, we developed a stimulation paradigm relying on vibration sensation, where the basic attributes of individual vibrations such as their amplitude and frequency do not determine the perception of high-level attributes of the stimulus (phase difference). Thus, this stimulation paradigm provides an ideal framework for studying tactile sensory processing and perception.

Key to the perception of this form of tactile motion is detecting changes in the amplitude of vibrations, and then processing these complex patterns in to extract information about the instantaneous location of vibration source. Arachnids such as spiders, approximately 700 million years apart from vertebrates in evolution, possess such mechanisms to identify preys based on complex vibration patterns [12]. In mammalian glabrous skin, two types of rapidly adapting mechanoreceptors, Meissner's and Pacinian corpuscles are sensitive to vibrations [13–17]. Pacinian corpuscles are thought to constitute a substrate of vibrotactile pitch perception in mice and humans [18–21]. Similar perceptual principle was observed in whisker-mediated vibro-tactile perception in rats [22], matching the way neurons in the whisker area of primary somatosensory cortex (S1) encode combination of the frequency and amplitude of vibrations (for a review see [23]). We have previously showed that rodents, with training, have the sensory capacity to compare amplitude and frequency of two simultaneous vibrations delivered to whiskers on either mystacial pads [22–24]. This potentially provides the capacity to extract spatial information about moving objects and animals from patterns of vibrations that are generated and propagate through solid substrates.

Potential underlying neural computations

Here, I propose to potential class of computations for vibro-tactile motion perception. The phase difference between two signals in frequency domain is equivalent to temporal lag in the time domain. Thus, the first class of computations are based on the concept of Reichardt detectors [1, 25], however operating on the vibration signals to estimate the equivalent time delay between two vibrations. Conceptually, this method is based on cross-correlation analysis in the realm of signal processing. In the time domain, an estimate of the time delay between the two vibrations is the time lag at which the

cross-correlation function is maximum. Least square estimation error method and in special cases, maximum likelihood method are equivalent to cross-correlation methods [26]. In the frequency domain, the phase difference between the two signals is the phase of the derivative of the cross-spectrum function at zero. The frequency and time domain analyses are dual and related to each other. These operations and computations are linear and hence, simple neural network architectures can compute time/phase difference based on cross-correlation and spectral methods are plausible.

The second method to detect vibro-tactile motion is based on interval and order discrimination of reference points such as peaks of envelope of vibrations. The temporal order of certain reference points such as peaks of the two envelopes provide information about the direction of the motion. The subjects identify the moment each vibration envelope is at its peak, and compare it against the peaks of the other vibration. The order of those peaks with minimum interval duration determines the direction. This computation explains the longer response latency for the high amplitude initial condition compared to the low amplitude initial condition (Fig 4C). According to this model, subjects wait to detect peaks with shortest interval. For a phase difference of $\Delta\varphi$, the first set of peaks with short interval, for the high amplitude initial condition are at $\frac{1}{f} \mp \frac{\Delta\varphi}{4\pi f}$, and for the low amplitude initial condition are at $\frac{1}{2f} \mp \frac{\Delta\varphi}{4\pi f}$ which is half a cycle, i.e. $\frac{1}{2f}$ earlier. This is compatible with shorter response latencies for the low amplitude initial condition. Additionally, over the 6s duration of the stimulation (i.e. 3 cycles), there are two occurrences of peaks with short interval between them for the high amplitude initial condition, while the number of short-interval peaks for the low amplitude initial condition is three. Thus, based on this model, there is more evidence available for the low amplitude initial condition compared to the high amplitude initial condition. This suggests either up to two intervals, on average, are enough to trigger a response, or alternatively, the prediction is more confident decisions with higher accuracy for the low amplitude initial condition. The latter, however, is not consistent with the results (Fig 4D). Further studies are required to elucidate the computations and any underlying neuronal mechanisms of vibration-based motion perception.

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