

# Coherent delta-band oscillations between cortical areas correlate with decision making

Verónica Nácher<sup>a</sup>, Anders Ledberg<sup>b</sup>, Gustavo Deco<sup>b,c</sup>, and Ranulfo Romo<sup>a,d,1</sup>

<sup>a</sup>Instituto de Fisiología Celular-Neurociencias, Universidad Nacional Autónoma de México, 04510 Mexico D.F., Mexico; <sup>b</sup>Center of Brain and Cognition, Department of Information and Communication Technologies, Universitat Pompeu Fabra, 08018 Barcelona, Spain; <sup>c</sup>Institució Catalana de Recerca i Estudis Avançats, Passeig Lluís Companys, 2308010 Barcelona, Spain; and <sup>d</sup>El Colegio Nacional, 06020 Mexico D.F., Mexico

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**Coherent oscillations in the theta-to-gamma frequency range have been proposed as a mechanism that coordinates neural activity in large-scale cortical networks in sensory, motor, and cognitive tasks. Whether this mechanism also involves coherent oscillations at delta frequencies (1–4 Hz) is not known. Rather, delta oscillations have been associated with slow-wave sleep. Here, we show coherent oscillations in the delta frequency band between parietal and frontal cortices during the decision-making component of a somatosensory discrimination task. Importantly, the magnitude of this delta-band coherence is modulated by the different decision alternatives. Furthermore, during control conditions not requiring decision making, delta-band coherences are typically much reduced. Our work indicates an important role for synchronous activity in the delta frequency band when large-scale, distant cortical networks coordinate their neural activity during decision making.**

synchrony | low-frequency rhythm | brain circuits

**S**tudies of the neural correlates of decision making in behaving monkeys have mainly been based on the analysis of firing rate patterns of neurons in individual cortical circuits, recorded one by one in succession, while trained monkeys perform sensory, motor, and cognitive tasks (1–3). These studies showed that the neuronal activities distributed across parietal and frontal lobe cortices correlate with processes that lead to decision making (4–7). However, how these spatially distant, cortical circuits coordinate their activities into a unified functional network during decision making remains poorly understood.

It has been proposed that coherent oscillations of neuronal activities constitute a putative dynamical mechanism for mediating the interaction between different subsets of brain areas (8–11). Simultaneous recording from multiple intracortical areas in monkeys showed that the coherent higher frequency (beta and gamma bands) oscillations are linked to a broad variety of cognitive functions (12–18). Cortical oscillations at lower frequencies (theta and alpha bands) have also been discussed in terms of long-range integrative processes (19, 20). In fact, recent evidence showed theta-band coupling between visual area V4 and prefrontal cortex during short-term memory (21) and among the rat prefrontal cortex, ventral tegmental area, and hippocampus during working memory (22). It remains, however, probing whether coherent delta-band oscillations play a functional role in the interaction between cortical circuits. Delta-band oscillations are typically associated with slow-wave sleep (SWS; ref. 23), but an important question is whether delta-band oscillations during SWS and waking states represent the same underlying phenomenon (24). Recent findings associated delta-band oscillations in individual cortical areas with attention (25). In monkey primary visual cortex (26) and human motor cortex (27), delta-band oscillations entrain to the rhythm of external sensory events in an attention-dependent manner.

Here, we examined whether coherent oscillations coordinate the activity of five simultaneously recorded cortical areas in the monkey performing a somatosensory discrimination task (7). We specifically focused on whether coherent delta-band oscillations

play a significant functional role in linking cortical circuits during decision making.

## Results

We analyzed coherence for frequencies between 1 and 45 Hz from local field potentials (LFPs) simultaneously recorded from five cortical areas in a trained monkey performing a somatosensory discrimination task (7) (*Materials and Methods*). In this task (Fig. 1A), the monkey discriminates the difference in frequency between two mechanical vibrations delivered sequentially to one fingertip. Crucially, the monkey must hold the first stimulus frequency (f1) in working memory, must compare the second stimulus frequency (f2) to the memory trace of f1 to form a decision of whether  $f2 > f1$  or  $f2 < f1$ , and must postpone the decision report until a sensory cue triggers the motor report. The monkey was trained to perform the task up to its psychophysical threshold (Fig. 1B and C).

During each recording session, up to seven microelectrodes were individually inserted in each of the five cortical areas for simultaneous recordings of the LFPs and the activity of single neurons during the task. The selected cortical areas were the primary somatosensory cortex (S1), secondary somatosensory cortex (S2), medial premotor cortex [MPC; the MPC areas of both hemispheres were not simultaneously recorded (*Materials and Methods*)], dorsal premotor cortex (DPC), and primary motor cortex (M1) (Fig. 1D). We based this selection on the previously described responses of single neurons from these cortical areas associated with different components of the somatosensory discrimination task (7). Examples of the raw simultaneously recorded LFPs during the discrimination task are shown in Fig. 1E and Fig. S1.

**Cortical Coherence Dynamics During the Discrimination Task.** Next, to investigate low oscillatory (1–8 Hz) synchrony between LFPs from pairs of simultaneously recorded cortical areas during the task, we estimated the coherence between LFPs in short sliding windows (*Materials and Method*). Coherence is a measure of phase and amplitude consistency between two signals as a function of

## Significance

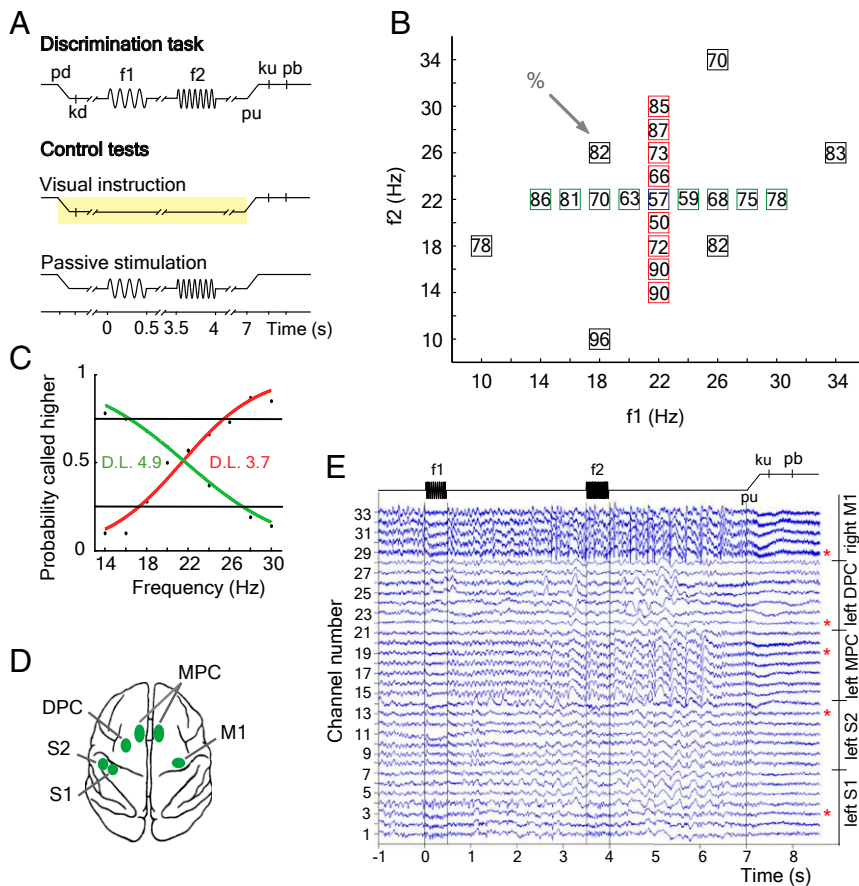
Delta oscillations have been largely associated with slow-wave sleep and anesthesia, when no conscious functions take place during these states. However, our study demonstrates that coherent delta-band oscillations reflect the linkage between distant parietal and frontal cortical circuits during decision making. Thus, these findings open an avenue for investigating whether the activity between distant cortical circuits oscillates in the delta frequency range during other cognitive functions.

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<sup>1</sup>To whom correspondence should be addressed. E-mail: rromo@ifc.unam.mx.

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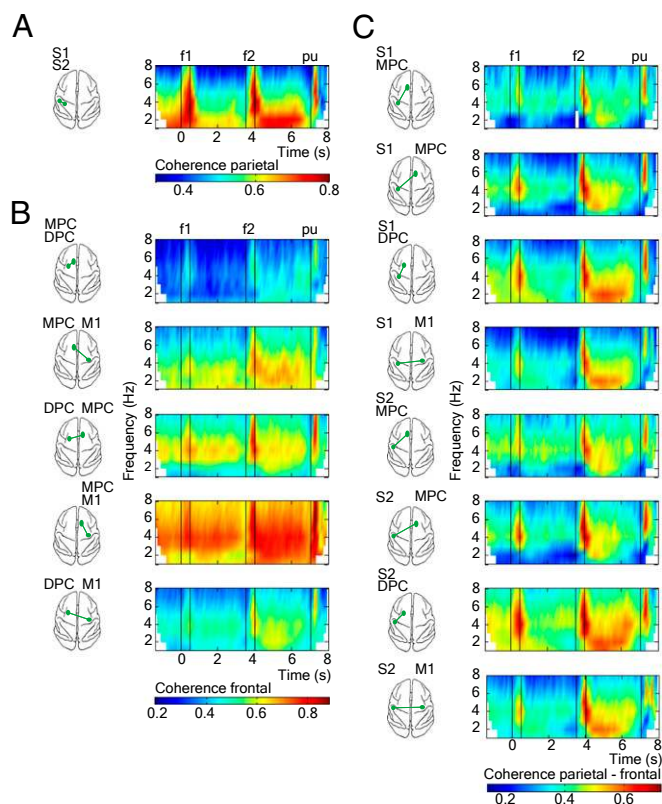


**Fig. 1.** Somatosensory discrimination task and cortical recording sites. (A) Sequence of events during the discrimination task and control tests (f1, first stimulus; f2, second stimulus; kd, key down; ku, key up; pb, push button; pd, probe down; pu, probe up; *Materials and Methods*). (B) Stimulus set during recordings. Each box indicates a (f1, f2) frequency stimulus pair. The numbers inside the box indicate overall percentage of correct trials for each (f1, f2) stimulus pair. (C) Psychophysical performance when f1 was maintained fixed at 22 Hz and f2 was variable (red curve), and when f2 was fixed at 22 Hz and f1 was variable (green curve). D.L., animal's discrimination threshold in hertz. (D) Top view of the monkey brain and the cortical areas recorded (green spots). (E) Raw local field potentials simultaneously recorded during the discrimination task. We illustrate one single trial in one example recording session. LFPs are aligned to the f1 stimulus onset. For analysis purposes, we selected only one channel in each cortical area (red asterisks). Channel selection varied across sessions.

frequency, and coherence values ranges between 0 (no consistent relationship between the two signals) and 1 (a constant relationship). We note that a significant coherence between two cortical LFPs can result if the two areas receive similar external inputs or if the two areas are interconnected and communicate with each other (or a combination of these possibilities). We obtained a total of 14 parietal, frontal, and parietal-frontal interareal comparisons (*Materials and Method*). Time frequency maps of coherence for all pairs of areas revealed significant modulations in the low frequency range (1–8 Hz, Fig. 2; 1–45 Hz, Fig. S2) during the task. The low frequency range oscillations (delta, 1–4 Hz; theta, 4–8 Hz) between sensory areas in the parietal lobe (S1 and S2) showed stronger coherence modulations during the stimulation periods and the delays immediately afterward (Fig. 2A). Motor areas in the frontal lobe showed low frequency range coherence modulations throughout the task, but delta-band coherence was strongest during the delay period between the end of f2 and the cue that triggers the motor response (pu; i.e., postponed decision period, Fig. 2B). This elevated delta-band coherence during the postponed decision period was also observed between the cortical areas located in the parietal and frontal lobes (Fig. 2C). Thus, a pattern of delta-band synchronization varying in magnitude and time course for all pairs of cortical areas was observed during the postponed decision period. The synchronous delta oscillations in these cortical recorded areas are clearly present in the raw data (Fig. 1E and Fig. S1).

**Delta Coherence Is Modulated by Decision Making.** A fundamental question is whether the observed coherent oscillations between spatially segregated cortical areas are directly associated with the decision-making process of this task. To answer this question, we selected hit trials in which  $f_2$  is equal to 22 Hz. In this case,  $f_2$  (22

Hz) can be judged higher or lower depending on the variable f1 frequency. This selection allows us to discard effects due to the different f2 stimulus frequencies. Next, we computed coherences separately for trials corresponding to the two possible responses ( $f2 > f1$  and  $f2 < f1$ ) and subtracted the resulting coherence spectrograms (Fig. S3). To assess the statistical significance of these coherence differences, we performed a cluster-based non-parametric randomization test (*Materials and Methods*). This analysis identified the pairs of cortical areas showing significant coherence differences (Fig. 3A). For each time-frequency plot of coherence differences (Fig. 3B), we detected all connected time-frequency points above a threshold value and used the size of these clusters as the test statistic. The significant clusters are shown in red in Fig. 3C. Clusters spanned from f2 to reaction time period (~500 ms after the pu) in delta and theta frequency bands. For each cortical area pair, we obtained the frequency values that best corresponded to the location of the significant clusters (the maximum length of the horizontal cluster dimension shown as red lines in Fig. 3C). Coherence for the two groups of trials ( $f2 > f1$  and  $f2 < f1$ ) as a function of time (Fig. 3D) revealed significant coherence differences during the postponed decision period, when the frequency values are in delta frequency range (2–3 Hz, red values in Fig. 3C). The consistency of these coherence differences across recording sessions are shown in Fig. S4. We next investigated whether these coherence differences are restricted to the delta band or whether they were also present in the theta frequency range (5–8 Hz). Fig. S5 shows that there were no significant coherence differences at theta frequency during the postponed decision period. However, significant coherence differences at theta frequency were found during the 500 ms immediately after pu (i.e., reaction time period). However, the time at which the monkey releases its hand from the key after the pu cue is



**Fig. 2.** Cortical coherence dynamics during the discrimination task (1–8 Hz). (A) Parietal pair areas. (B) Frontal pair areas. (C) Parieto-frontal pair areas. Time-frequency plots show averaged LFP-LFP coherence over all sessions ( $n = 18$ ) for simultaneously recorded cortical pairs. Coherence was calculated for hit trials by using an adaptive window that decreases in length with increased frequency in 100-ms consecutive window steps (note the boundary effects for lower frequencies). We show significant coherence results up to 8 Hz ( $P < 0.05$ , nonparametric randomization test; *Materials and Methods*). White time frequency points outside boundary effects indicate that coherence is not significant. Black vertical lines depict time task events: presentation of the first stimulus (0–0.5 s), presentation of the second stimulus (3.5–4 s), and probe up event (7 s).

variable, and we cannot discard a possible movement effect in the coherence differences found during this task period.

To test whether delta-band coherence differences are explained by differences in power in the same frequency band, we applied the same cluster-based analysis for power in each recorded area. The parietal areas (S1 and S2) displayed differences in this frequency range at 2 Hz, but none of the frontal lobe areas recorded from the right hemisphere (MPC and M1) showed significant power differences for delta band as a function of the animal's decision (Fig. S6). However, significant beta-band (13–30 Hz) power differences were found for right MPC and right M1 recorded areas during the postponed decision period, results that have been reported (28). Significant beta-band clusters observed during the f1 period for S1 and S2 areas are likely due to stimulus entrainment.

**Delta Coherence Is Context Dependent.** To further test whether delta-band coherences are directly associated with decision making, we also analyzed coherence in two control tasks: passive stimulation and visual instruction (Fig. 1A, *Middle* and *Bottom*; *Materials and Methods*). During passive stimulation, the same stimuli used during the discrimination task were delivered to the fingertip, but the monkey was not requested to perform the task. During visual instruction, the trials proceeded exactly as in the discrimination task,

but the stimuli were not delivered to the skin and the movements were guided by visual cues present from the start of the trial. In this last condition, it is not possible for the monkey to elaborate a decision based on the evaluation of somatosensory information, but the same movements as in discrimination task were executed for reward. Compared with the discrimination task, both control conditions had reduced delta-band coherence, in particular during the postponed decision period (Fig. 4). To test whether this reduced coherence was caused by the fewer number of trials during control tasks ( $n = 30$ ), we repeated the coherence analysis by selecting 30 random hit trials during the discrimination task (Fig. 4B). Similar coherence results were found compared with those results obtained during the discrimination task in which all hit trials were selected (Fig. 2). Fig. 4E shows the coherence differences among the three tasks during the postponed decision period. Quantification of these differences during the postponed decision period revealed that the magnitude of delta-band coherence in the discrimination task is significantly higher compared with both control sets (Table S1). Moreover, we explored coherence differences between  $f2 > f1$  and  $f2 < f1$  groups of trials by using the same cluster-based randomization test for the pairs of cortical areas as we did in the discrimination task (Fig. 3). There were no significant coherence differences in the frequency range studied (1–8 Hz) during the whole time task, neither for the visual instruction (Fig. S7B and C), nor for the passive stimulation (Fig. S7D and E). Thus, under control conditions, delta-band coherences differences did not depend on the animal's decision report.

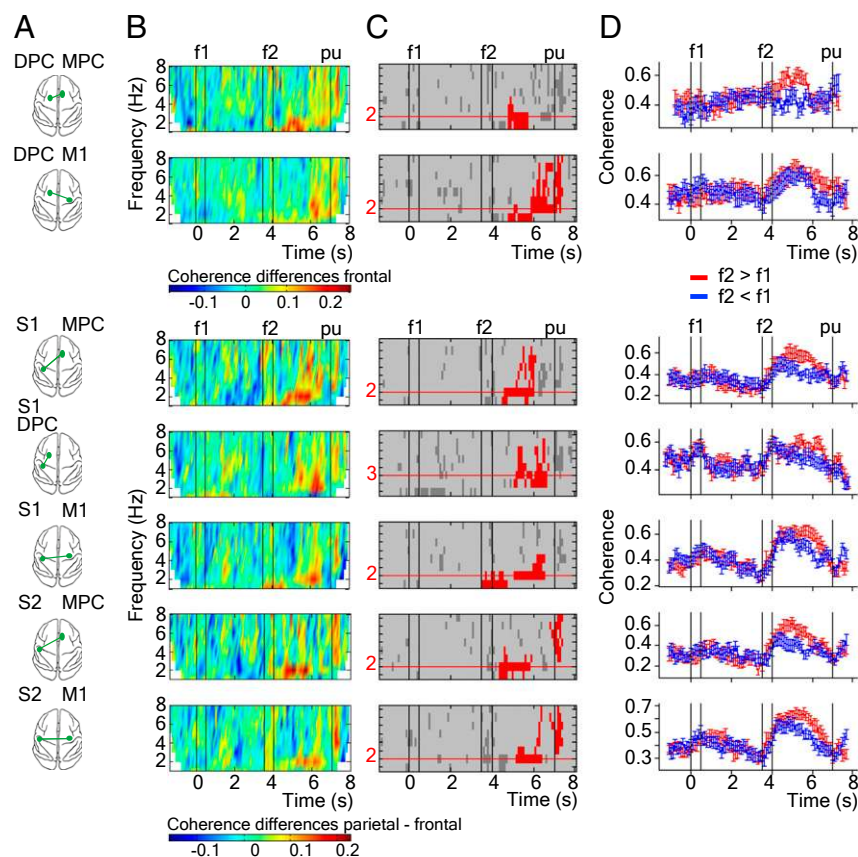
**Spike-Field Synchrony.** To investigate whether the synchronous delta-band oscillations of the LFPs influence computations in the local neuronal circuits, we next made spike-triggered averages (STAs) of the LFPs (*Materials and Methods*). In many cases, STAs exhibited a strong oscillatory patterning in the frequency range of 1–3 Hz, indicating that temporal patterning of single neuron discharges were correlated with the phase of delta-band LFPs (Fig. S8). This result suggests that synchronized delta-band activity could coordinate the spiking activity of neurons in widespread cortical areas. Moreover, STAs were also modulated by the different decision alternatives (Fig. S8D), showing that the synchronization between spike times and LFPs carry decision related information.

## Discussion

Our findings demonstrate that the simultaneously recorded activity from parietal and frontal cortical areas is synchronized in the delta-band frequency range during decision making. This synchronization is widespread, modulated by the different decision alternatives and context specific. Interestingly, these patterns of synchronization are prevalent for interactions between the sensory areas (S1 and S2) located in the left parietal lobe (contralateral to the stimulated finger) and the motor areas (MPC and M1) located in the right frontal lobe (contralateral to the responding hand/arm). Thus, this synchrony could facilitate the communication between the left and right hemisphere during decision making. However, further analysis is required to show whether this interaction is so.

It is worth mentioning that previous studies in which simultaneous recordings from multiple cortical areas were made, the functional role of delta-band was not explored. One possibility is that delta oscillations are hard to detect if the relevant task periods are of shorter duration ( $<1$  s). The long postponed delay period (3 s) of our task allowed for the studying of delta-band oscillations. Another possibility is that delta oscillations have been considered of little functional relevance in cognition because they are consistently observed in SWS and during general anesthesia (23, 29). There is no definitive evidence regarding the origin of delta activity in the brain, but several studies place the site of waking delta-band generation in the anterior medial





**Fig. 3.** Significant coherence differences between  $f_2 > f_1$  and  $f_2 < f_1$  for groups of hit trials in which the  $f_2$  stimulus frequency is equal to 22 Hz. (A) Schematic view of the cortical pairs from which coherence is calculated (green spots). (B) Time-frequency plots of the coherence differences between both groups of trials (Fig. S3B). (C) Time-frequency plots showing the clusters where there are coherence differences between  $f_2 > f_1$  minus  $f_2 < f_1$  groups of trials. Only significant clusters are plotted in red color ( $P < 0.05$ , two-sided test; Materials and Methods). Horizontal red lines indicate the frequency values where the significant cluster has the maximum length. (D) Time course of coherence for each group of trials at frequency values (horizontal red lines). Error bars correspond to SEM ( $\pm 2$ ) over recording sessions ( $n = 18$ ). Black vertical lines depict time task events: presentation of the first stimulus (0–0.5 s), presentation of the second stimulus (3.5–4 s), and probe up event (7 s).

frontal cortex (30, 31). Moreover, recordings in waking animals show the existence of delta-band oscillations in the nucleus accumbens (32) and dopamine neurons of the ventral tegmental area (33), structures that are part of the brain reward system. These observations, together with those reported in attentional tasks (25–27), show that delta-band oscillations occurring in individual brain areas play a role in cognitive functions. Our results show that distant cortical circuits are linked in the delta-frequency band during decision making. However, whether the activity between distant cortical circuits oscillates in the delta frequency range during other cognitive functions is an open question.

## Materials and Methods

This study was performed on one adult male monkey (*Macaca mulatta*), weighing 12 kg. All procedures followed the guidelines of the National Institutes of Health and Society for Neuroscience. Protocols were approved by the Institutional Animal Care and Use Committee of the Instituto de Fisiología Celular.

**Discrimination Task.** The paradigm used here has been described (34, 35). The monkey sat on a primate chair with its head fixed in an isolated, sound-proof room. The right hand was restricted through a half-cast and kept in a palm-up position. The left hand operated an immovable key (elbow at  $\sim 90^\circ$ ), and two push buttons were in front of the animal, 25 cm away from the shoulder and at eye level. The centers of the switches were located 7 and 10.5 cm to the left of the midsagittal plane. In all trials, the monkey first placed the left hand and later projected to one of the two switches. Stimuli were delivered to the skin of the distal segment of one digit of the right, restrained hand, via a computer-controlled stimulator (2 mm round tip; BME Systems). The initial probe indentation was 500  $\mu\text{m}$ . Vibrotactile stimuli were trains of short mechanical pulses. Each of these pulses consisted of a single-cycle sinusoid lasting 20 ms. Stimulus amplitudes were adjusted to equal subjective intensities; for example, 71  $\mu\text{m}$  at 12 Hz and 51  $\mu\text{m}$  at 34 Hz (a decrease of  $\sim 1.4\%$  per Hz). During discrimination trials (Fig. 1A), the mechanical probe was lowered (probe down; pd), indenting the glabrous skin of one digit of the hand; the monkey placed its free hand on an immovable key (key down; kd); after a variable prestimulus delay (0.5–3 s) the probe

oscillated vertically at the frequency of the first stimulus ( $f_1$ ); after a fixed delay (3 s), a second mechanical vibration was delivered at the second stimulus ( $f_2$ ) frequency; after another fixed delay (3 s) the probe is lifted off from the skin (probe up; pu); the monkey released the key (ku) and pressed either a lateral or a medial push button (pb) to indicate whether  $f_2$  was of higher or lower frequency than  $f_1$ , respectively. The monkey was rewarded with a drop of liquid for correct discriminations. Performance was quantified through psychometric techniques (Fig. 1B and C).

**Control Tests. Visual instruction.** Trials during the visual instruction begin exactly as described in the discrimination task, but when the probe touched the skin, one of the push buttons was illuminated. The monkey had to respond by holding the immovable key until the light was turned off and the probe was lifted off from the skin, which triggers the hand/arm movement. The monkey was rewarded for pressing the previously illuminated push button (100% correct responses). Note that in this condition, the vibratory stimuli are absent. The yellow box in Fig. 1A represents the time in which one of the push buttons remained illuminated.

**Passive stimulation.** During this condition, the monkey was trained to maintain its free arm motionless during the trial (Fig. 1A). Stimuli were delivered to the fingertip and the animal remained alert by being rewarded with drops of liquid at different times, but no motor response with the free hand was required.

**Recording.** Data acquisition, amplification, and filtering were described in detail (36). In brief, LFPs and the activity of single neurons were simultaneously recorded with an array of seven independent, movable micro-electrodes (1–1.5 M $\Omega$ ) inserted in each of five cortical areas. Electrodes within an area were spaced 305 or 500  $\mu\text{m}$  apart (37). Spike sorting was performed manually on-line, and single neurons were selected if they responded to any of the different components of the discrimination task (7, 36). The cortical areas were the S1, S2, MPC, DPC, and M1 (Fig. 1D). Recordings in S1, S2, and DPC were made in the hemisphere contralateral to the stimulated hand (left hemisphere), and in M1 contralateral to the responding hand/arm (right hemisphere). Recordings in MPC were made either in the hemisphere contralateral or ipsilateral to the responding arm in different sessions ( $n = 11$  and  $n = 7$ , respectively). MPC areas were not



intervals of 1 s each. The first 500 ms after the end of the second stimulus and the last 500 ms before the probe up event were not included in the analysis to prevent phase locking between spikes and LFPs due to stimulus and movement-related activity. STAs were calculated by averaging LFP segments  $\pm 1$  s around every spike recorded in correct hit trials. To characterize the variability of the STA results, the same analysis was applied to "surrogate data" where the order between LFP trials and spike trials were randomly permuted. For each recorded cell, we made 100 such permutations (shown as gray curves in the background of Fig. S8 B and C). To explore STA modulations as a function of the animal's decision, the STA analysis was done separately for  $f_2 > f_1$  and  $f_2 < f_1$  groups of hit trials in which the  $f_2$  stimulus frequency was equal to 22 Hz (Fig. S8D).

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