Cortical topography of intracortical inhibition influences the speed of decision making

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The neocortex contains orderly topographic maps; however, their functional role remains controversial. Theoretical studies have suggested a role in minimizing computational costs, whereas empirical studies have focused on spatial localization. Using a tactile multiple-choice reaction time (RT) task before and after the induction of perceptual learning through repetitive sensory stimulation, we extend the framework of cortical topographies by demonstrating that the topographic arrangement of intracortical inhibition contributes to the speed of human perceptual decision-making processes. RTs differ among fingers, displaying an inverted U-shaped function. Simulations using neural fields show the inverted U-shaped RT distribution as an emergent consequence of lateral inhibition. Weakening inhibition through learning shortens RTs, which is modeled through topographically reorganized inhibition. Whereas changes in decision making are often regarded as an outcome of higher cortical areas, our data show that the spatial layout of interaction processes within representational maps contributes to selection and decision-making processes.

computational neuroscience | plasticity | cortical reorganization

The mammalian neocortex contains orderly topographic maps of receptor surfaces that emerge early during ontogenetic development (1, 2). However, the functional meaning and relevance of the topographical arrangement are still debated (1–5). There is agreement that topographic mapping is instrumental in minimizing computational costs by keeping the length of axonal and dendritic wiring low, thereby contributing to the compactness of the neural circuitry (1, 6–8). On the other hand, experimental studies have focused on the extent and size of topographic maps, thereby exploring how and where physical stimuli and their attributes are localized and represented in the brain. Cortical lateral interaction seems to play a crucial role in the integration of information from remote skin portions, which is required for localization and discrimination (9–11), contour integration, as well as contextual influences by surrounding elements (12, 13). Accordingly, cortical processing is modulated by nonlinear interactions through range-dependent intracortical excitation and inhibition. The mean-field approach has been shown to provide an adequate and elegant way to model the collective properties of large numbers of interacting neurons (14–16).

Decision making has been discussed in the context of contributions of frontal and prefrontal cortical areas (17–20). Our study provides an extension of the framework of cortical topographies by demonstrating through a combination of psychophysics, plasticity, and modeling that the speed of perceptual decision making is modulated by the topographic layout of intracortical interactions within early sensory cortical areas. We used a tactile multiple-choice reaction time (RT) task that requires selecting a given finger out of all 10 fingers on both hands (Fig. 1) (21). RTs strongly differ among individual fingers, displaying an inverted U-shaped function in which the RTs for the middle fingers of each hand are significantly slower than those of other fingers.

To address the role of altered topographic maps in the speed of perceptual decision making, we induced plastic changes to the cortical hand representation by applying a so-called tactile coactivation protocol (22–24). Coactivation is a form of repetitive sensory stimulation based on the induction of presumably Hebbian learning mechanisms (24–26). Coactivation has been shown to expand cortical finger representation (27, 28) and to reduce intracortical inhibition, as indicated by reduced paired-pulse inhibition (29). Here we found that after coactivating the middle finger, its RTs were significantly shortened, resulting in the near disappearance of the inverted U-shaped distribution.

To model the underlying processes at the neuronal population level, we used neural fields with different groups of neurons coding for different fingers embedded in a topographic representation, which interact through a Mexican hat-type interaction characterized by recurrent excitation and lateral inhibition (14, 15). Simulations show the inverted U-shaped distribution of RTs as an emergent consequence of lateral inhibition within cortical representational maps. By weakening the strength of inhibition, our model accounts for cortical map expansion and behavioral changes by replicating the shortening of RTs. Our model thereby attributes both the emergence of the inverted U-shaped distribution and its modification through learning to different levels of topographically organized lateral inhibition. Although the role of cortical topographies for spatial localization is straightforward, these findings provide evidence that interaction processes within cortical maps are crucial for selection processes and functions related to decision making.

Results

Reaction Time Performance at Baseline. RTs differed for individual fingers [repeated-measures (rm) ANOVA, post hoc Scheffé; $P < 0.001$; Fig. 2*A*] under the 10-choice condition. RTs for the middle fingers (d3) of each hand were significantly slower than for the thumb (d1), index finger (d2), and little finger (d5) (all $P < 0.001$), but not d4 ($P = 0.307$). RTs were also slower, overall, for the left than the right hand ($P = 0.005$).

Under dual-choice conditions (left d3 vs. right d5, or right d3 vs. left d5), RTs did not differ for d3 and d5 (rmANOVA, post hoc Scheffé; $P = 0.868$ for left d5 vs. right d3, $P = 0.336$ for right d3 vs. left d5; Fig. 2*C*). Overall, following Hick's law (1952), RTs of both d3 and d5 were faster under the dual-choice than the 10-choice condition ($P < 0.0001$). Therefore, the observed slowing of d3 under the 10-choice condition is specific to the process of selecting from among all 10 fingers. We also used a five-choice

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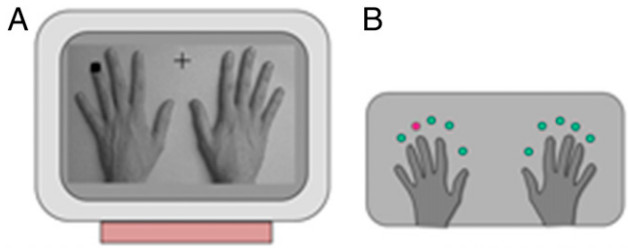

Fig. 1. Experimental setup. Images of both hands were displayed on a screen in front of the subjects, and on any given trial the finger to be selected was marked (*A*). Responses were given via a hand-shaped 10-button keyboard (*B*).

task, where five fingers of one hand were randomly selected and subjects had to respond with the corresponding fingers. This condition revealed a similar inverted U-shaped RT distribution with short RTs for d1 and d5 and the longest RTs for d3.

Reaction Time Performance After Tactile Coactivation. Perception and behavior are not only subject to improvement through training but similarly through repetitive sensory stimulation. Coactivation is a form of repetitive stimulation, which follows the idea of Hebbian learning: Synchronous neural activity, necessary to drive plastic changes, is evoked by tactile "co"-activation of the skin. Several studies have shown that after a few hours of coactivation, tactile discrimination abilities were improved (22, 23, 25, 27–29). To provide further evidence for the Hebbian nature of coactivation, we used a modified version of the coactivation protocol consisting of a single, small stimulation site instead of one large area. This protocol lacking coactivation evoked no effects, neither perceptually nor in cortical maps (28). The lack of effects implies that spatial summation requirements indicative of cooperative processes need to be fulfilled to drive behavioral changes. Although it appears conceivable that coactivation induces changes of synaptic transmission, the nature of the underlying mechanisms so far remains unknown.

Coactivation applied for 3 h to right d3 had a major impact on RTs (Fig. 2*B*). Again, differences between fingers were significant both for the right (rmANOVA, post hoc Scheffé; $P < 0.001$) and left hand ($P < 0.001$). Pre/post differences were significant (rmANOVA) for the right ($P < 0.001$) and left hand ($P < 0.001$). On the coactivated right hand, interaction between differences for fingers and pre/post differences was significant ($P = 0.011$), indicating a different gain, that is, a different amount of shortening of RTs for individual fingers. Such a differential shortening was not observed for the noncoactivated, left hand, where RTs of individual fingers were reduced by about the same amount (Fig. 2*D*).

To scrutinize the specific influence of coactivation and to separate it from the general influence of improvement by practicing the task, we compared the gains of individual fingers for different conditions (Fig. 2*D*). Differences between fingers of the noncoactivated left hand did not reach significance (rmANOVA; $P = 0.776$). In contrast, gains of individual fingers differed significantly on the coactivated right hand ($P < 0.001$). Post hoc Scheffé tests revealed that the gain of the coactivated d3 was larger than the gain of all other fingers ($0.002 < P < 0.032$; contrasts for all other fingers were not significant), indicating that the amount of coactivation-induced learning was larger for d3 than for all remaining fingers. These findings were further substantiated by data from the control group (no coactivation), which did not show differences in gain between fingers, although a general but small improvement was observed on all fingers (Fig. S1 and *SI Methods*).

The observation of shorter RTs of the left fingers after right finger coactivation, and of the fingers of both hands after retesting without coactivation (control group; *SI Methods*), can in principle be due to practice or to coactivation itself. In the latter case, coactivation must be assumed to exert contralateral effects. However, the shortening of RTs for the left fingers after coactivating right d3 was small compared with the effects seen on the coactivated d3 (Fig. 2 *C* and *D*). A similar RT shortening was observed in the control group that received no coactivation ("sham" stimulation; Fig. S1). Moreover, in recent experiments on changes in tactile acuity after coactivating fingers of the right, dominant hand, measurable changes of acuity of the left, nonstimulated hand had never been observed (22, 23, 25–29), which argues for a substantial locality of coactivation-induced changes and supports the view that after repeated testing, RT effects are due to practice.

Moreover, the speeding up of RTs after coactivation was specific to the 10-choice condition (Fig. 2*C*). For dual-choice tasks, when testing left d3 versus right d5, and right d3 versus left d5, we found no significant differences (rmANOVA) between pre- and postconditions ($P = 0.251$), and interactions between differences for fingers and pre/post differences also did not reach significance ($P = 0.905$). Even more importantly, in the dual-choice task for the coactivated right d3, no significant difference (rmANOVA) for pre- versus postconditions ($P = 0.391$) and no significant interaction between differences for fingers and pre/post differences were found ($P = 0.623$) when right d3 was tested against left d5.

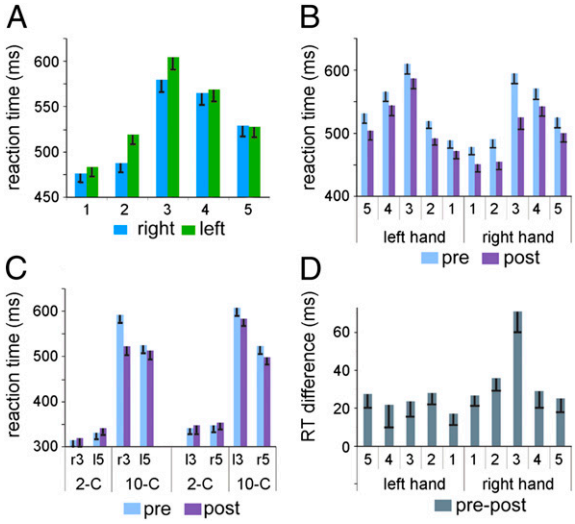

Fig. 2. Effects of coactivation on RTs: experimental findings. (*A*) Mean (±SE) RTs for all fingers (digits 1–5) of the left (green) and right (blue) hand. RTs differ among fingers, with d3 being slowest and d1 and d5 being fastest ($P < 0.001$). The left hand exhibits slower RTs than the right hand ($P = 0.005$). (*B*) Mean (±SE) RTs of all fingers (digits 1–5) of the left and right hand before (light blue) and after (magenta) coactivation. RTs on right d3 were significantly faster after application of coactivaton ($P < 0.001$). (*C*) Comparison of mean RTs (±SE) for right d3 (r3) and left d5 (l5) as well as left d3 (l3) and right d5 (r5) in a dual-choice (2-C) and 10-choice task (10-C) before (light blue) and after (magenta) coactivation. RTs did not differ for d3 and d5 under the dual-choice condition, but slowed substantially under the 10-choice condition, particularly for d3. Speeding-up of RT after coactivation was restricted to the right-hand, coactivated d3. (*D*) Mean (±SE) pre/post RT differences for all fingers (digits 1–5) of the left and right hands. Although all fingers had slightly faster RTs under the post condition, only right-hand d3 showed a significant speeding up ($0.002 < P < 0.032$).

Model: Baseline Performance. We constructed a model in which the fingers were represented in a topographical map. A number of mathematical approaches to information processing in such maps exist (14, 15). To model cortical representations of separate fingers, we used a one-dimensional cut through the cortical

surface such that the representations of different fingers were aligned along this one-dimensional neural field, with different sites of the neural field representing different fingers (Fig. 3 *A* and *B*; for details, see *SI Methods*). The sizes of the cortical representations in the model were chosen to be in accordance with empirical data regarding the dimensions of cortical finger representations (30). In accordance with empirical data from human individuals, the representations of the fingers of the left hand were made slightly smaller than those of the right hand (31). Within the neural field, different neurons interact by distance-dependent interaction (15) with local excitation (equivalent to recurrent self-excitation) and longer-range inhibition (Mexican hat-type interaction) (schematically illustrated in Fig. 3 *A* and *B*). To model competition across all fingers of both hands, inhibition decays for increasingly larger distances but never approaches zero. The involvement of different neural field sites coding for different neurons depends on two factors: their activation level, which is determined by the stimulus input (modeled as Gaussian distributions of activation) (32), and the baseline activity of these field sites (Fig. 3 *A* and *B*). The baseline activity was considered inhomogeneous such that different field sites have different baseline activities, which may vary depending on various factors such as task involvement (33, 34), the probability of responses to be made (33), and memory traces of previous responses (35). Effectively, the influence of these factors corresponds to target input in spiking mean-field and network models (36, 37), variation of the threshold (38–40) in sequential sampling (41) and diffusion models (42, 43), or leaky competing accumulator models (44) as the distance to threshold decreases.

In the 10-choice task, the baseline activity of the neurons coding for all fingers was high (Fig. 3*B*), causing them to contribute strongly to interaction. Because inhibition is distance-dependent, a specific pattern occurs: d3 of each hand is within the strong inhibitory range of both neighboring d2 and d4, yet to a lesser extent inhibited by d1 and d5. In contrast, d1 and d5 are only inhibited strongly by d2 and d4; they are inhibited more weakly by d2 and d3 (Fig. 3*B*). The global inhibition that decays for increasingly larger distances but never approaches zero ensures competition across all fingers, so that only one finger can respond at any given time.

RTs were modeled as time to threshold until activation of neurons coding for specific fingers reached a predefined threshold. Modeling RTs showed that inhibition within the neural field produced an inverted U-shaped pattern, with d3 of each hand being slowest and d1 and d5 being fastest, in accordance with behavioral data (Fig. 4*D*). In addition, the slightly smaller representation of the left hand made inhibition more pronounced for decisions with the left than the right hand, leading to longer RTs for left-hand reactions in general, again in accordance with empirical data (Fig. 4*D*).

In contrast, only two fingers are strongly involved in task processing in the dual-choice task. Therefore, in the model, the baseline activity of only two fingers makes them strongly involved in processing (Fig. 4*C*). Simulations of RTs not only dramatically decreased RTs as a replication of Hick's law but also made the difference between left d3 versus right d5, or right d3 versus left d5, disappear due to the lack of mutual inhibition, which is

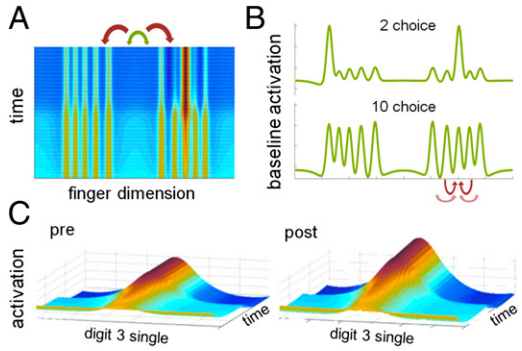

Fig. 3. One-dimensional model of cortical finger representations. (*A*) We model a one-dimensional cut through the cortical surface, with the representations of the different fingers aligned along this one-dimensional neural field. Activations develop continuously over time under the influence of baseline activation [yellow indicates higher baseline activation than average (blue)], stimulus inputs (higher activation after stimulus onset indicated by red), and interactions within the field [Mexican-hat interaction, schematically indicated by green (excitation) and red (inhibition) arrows]. In addition to the distance-dependent inhibition depicted here, a weak global inhibition component was used to provide completion across all fingers, so that only one finger can answer at any given time. (*B*) Under the 10-choice condition (*Lower*), all 10 fingers have high baseline levels of activation. D3 is within the inhibitory range of d1, d2, d4, and d5 (red arrows; transparency indicates strength of inhibition), whereas d1 (correspondingly d5) is only within inhibitory range of d2 and d3. Under the dual-choice condition (*Upper*), only d3 of one hand and d5 of the other hand have high baseline activation. (*C*) Weakening of inhibition for right-hand d3 to account for the influence of coactivation leads to higher levels of activation if d3 is selected, incorporating the effect of coactivation on the enlargement of the cortical finger representation (28).

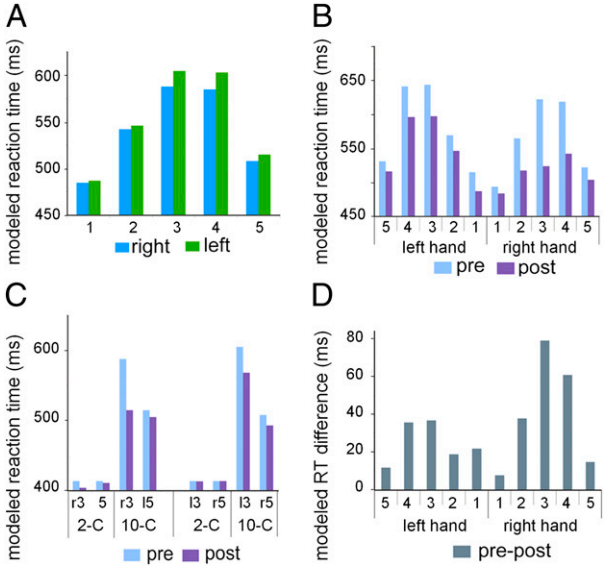

Fig. 4. Modeling RTs before and after coactivation. (*A*) Modeling RTs demonstrates that inhibition within the neural field (Fig. 3 *A* and *B*) produces an inverted U-shaped pattern, with d3 of each hand being slowest and d1 and d5 being fastest, both in accordance with behavioral data. The smaller representation of the left hand (green) results in a stronger inhibition being more pronounced for decisions with the left than the right hand (blue), lengthening reaction times for the left hand. (*B*) Comparison of simulated RTs before (light blue) and after (magenta) coactivation. Decreasing inhibition weakly for all fingers (to account for general task learning) and strongly for right d3 (to account for coactivation-induced effects) leads to an overall decrease in simulated RTs, with the difference strongest for right-hand d3. (*C*) Under dual-choice conditions (2-C), simulated RTs did not differ for d3 and d5, but show several-fold slowing under the 10-choice condition (10-C) (light blue bars). Simulated RTs under the dual-choice condition also did not differ before (light blue) and after (magenta) coactivation, whereas only right-hand d3 (r3) exhibits substantial slowing after coactivation of this finger (blue vs. magenta bars). Simulated reaction times for the same fingers under the 10-choice condition are depicted for direct comparison. (*D*) Simulated pre/post RT differences for all fingers of the left and right hands show the largest increase in speeding for d3, aside from an unspecific but small acceleration for all fingers due to task learning.

operating in the 10-choice task (Fig. 4*C*). Our model therefore attributes the occurrence of the inverted U-shaped RT patterns to task-dependent lateral inhibition within cortical maps.

Modeling the Influence of Tactile Coactivation. Coactivation led to a decrease of cortical inhibition (29), which has been assumed to cause an expansion of the size of d3 representation (28). We therefore implemented the observation about reduced inhibition in the model by decreasing the involvement of inhibitory neurons coding for the coactivated right d3 in inhibitory interaction. Such a decrease in inhibition for d3 led to an increase in the maximum level of activation elicited, if d3 is selected in the model (Fig. 3*C*), which in turn leads to an increase in the size of cortical representation for d3. Modeling RTs showed that such a decrease in inhibition sped up RTs specifically for the coactivated right d3 (Fig. 4*B*).

Just as shown by the empirical data, speeding up of RT by simulated coactivation (Fig. 4 *B* and *D*) was restricted to the 10-choice condition, with no effects in the dual-choice task (Fig. 4*C*). Whereas for the 10-choice task all fingers contribute to the interaction, resulting in a large mutual inhibition, in the dual-choice task only two fingers contribute, resulting in a numerically smaller inhibition. The impact of coactivation is modeled by decreasing the involvement of inhibitory neurons coding for the coactivated finger. Such a decrease in inhibition for the coactivated finger led to an increase in the level of activation. Because under the dual-choice condition the two fingers compete only mildly, the advantage arising from this coactivation effect has no impact on RTs (Fig. 4 *B*–*D*). Combined with weakening the strength of inhibition, we can model the influence of coactivation-induced modification on RTs. These observations support the notion that inhibitory interaction within cortical maps plays a crucial role in perceptual decision making.

As described for the empirical data above, we similarly evaluated the effect of simulated coactivation on the left, noncoactivated hand (Fig. 4 *B* and *D*) and on a control group to separate the effect of task practice, which resulted in a general, but small, shortening of RTs (*SI Methods*). We modeled practice-induced shortening of RTs with the same concept such that inhibition for all fingers decreased. Modeling RTs under these conditions showed an overall but substantially smaller effect in keeping with the empirical data (Fig. S1).

Discussion

Investigation of choice RTs is a convenient way to study decision-making processes. We used a tactile multiple-choice RT task that requires selecting a given finger out of all 10 fingers on both hands (21). The fact that increasing the number of choices increases RT was already discovered in the 19th century (45) and was formulated into Hick's law many decades ago (46). In fact, the multiple-choice RTs we recorded were in the range of 500 ms, compared with 200 ms for dual-choice RTs. Multiple-choice RTs differed significantly across individual fingers, displaying an inverted U-shaped function in which the RTs for the middle fingers of each hand were slower by ∼100 ms. Phenomenologically, the slow response of the middle finger has been discussed in the context of a so-called end effect, bow effect, or serial order effect, which are often observed in cognitive tasks (47, 48). The substantial duration of the RTs of the middle finger is not due to mechanical or muscular constraints, as in a dual-choice task the RTs of the middle finger and the little finger are comparably short (in the range of 250 ms). Moreover, we demonstrated that the end effect almost disappears when a simple Hebbian learning protocol consisting of repetitive stimulation of the middle finger is followed, resulting in a significant speeding up of the RTs of the middle finger. Again, this learning effect was limited to a multiple-choice condition.

To explain the long RTs of the middle finger under baseline conditions as well as the selective speeding up following learning, we used neural fields to model subpopulations of neurons coding for different fingers. Key components of the modeling approach include number of choices (multichoice vs. dual-choice tasks) and inhibition among these choices. Importantly, this inhibition is characterized by a specific spatial structure that arises as a consequence of the topographic mapping of the finger in cortical space. Choices between neighboring fingers inhibit each other more strongly than those between more distant fingers because their cortical representations are closer to each other. Because lateral inhibition is constrained by the cortical distance between fingers, we observe a graded effect in which inhibitory effects are larger for neighboring but weaker for more distant fingers. Therefore, in our simulations, the inverted U-shaped RT distribution is the result of lateral inhibition processes within the cortical map of the fingers.

RT models have been extensively studied on a behavioral level, relying on accumulation of information over time, or on diffusion processes by single counters or units with one unit representing one choice (see reviews in refs. 39 and 40). Often, RT models are neurally inspired by incorporating concepts such as mutual inhibition for two-choice (44, 49) and multichoice tasks (50). Our approach, as well as that in ref. 36 and recently in ref. 16, uses neural fields in which single choices are explicitly represented by populations of neurons. Recently, it was shown that models implementing multineuron representations for each choice were able to flexibly switch between different numbers of choice alternatives without changes in network parameters or inputs, which supersedes top-down regulation to deal with changes in the number of choices (37). In such a network, its capacity to code for many choices is positively correlated with the number of neurons representing individual choices, which adds to its physiological plausibility.

Our experiments included both dual-choice and multichoice conditions. In the model, the neural field spans the representation of all 10 fingers. Whether one specific site (coding for one particular finger) is involved in computational processing depends on inputs added to the field. By choosing inputs corresponding to the current task situation (multi- vs. dual-choice), the field can account for both behavioral tasks.

Inhibition among choices is an important component of many models (36, 44) that accounts for the increase in RT with increasing numbers of choices. Often, models incorporate inhibition without implementing a specific metric or spatial structure. In this case, inhibition acts as a global component where one response option inhibits all others (32, 44, 50). Other models assign a metric to the interaction among choices characterized by a given distance. Such a distance can correspond to distance in feature space (36) or to distance in response space (34), but does not explicitly connect to cortical space (i.e., the closeness of representation in cortical coordinates).

Directly linking a feature or response space to cortical representation might be advantageous when attempting to link behavior to neurophysiological data. In this respect, our experiments provide a unique design: The response space, which is defined as the different response options spread across all fingers of each hand, is directly linked to representational maps in the somatosensory cortex (i.e., cortical space). Therefore, the response options between fingers are mapped onto distance in cortical coordinates. This relationship is based on the topographic mapping of the body surface onto cortical space, which in the case of finger representations displays a remarkable order (9, 10, 30, 31). A second crucial prerequisite comes from the observation that interaction within the cortical map is spatially structured, consistent with the Mexican-hat component used in our model (10, 51). By using distance-dependent cortical interaction, we explicitly connect behavioral space to corresponding cortical map dimensions, which enables our model to account for distance-specific effects of RT data, thereby extending the potential functional role of cortical maps.

Selecting a finger in a 10-choice RT task can be seen as a fairly simple form of decision making. U-shaped effects on RTs are well-established for visual stimuli, and even for higher-level cognitive stimulus spaces (47, 52). It remains an interesting question as to whether cognitive spaces may be mapped onto coordinates of cortical representation comparable to our approach, which take advantage of the close relationship between response space and cortical space: Using feature space instead of response space opens the possibility of linking the end effect to cortical topographies and thus the layout of lateral inhibition. An even more challenging question is how the form of perceptual decision making studied here might generalize to more sophisticated forms as in neuroeconomics (53). It has recently been suggested that embodied cognition might also play a role in economics (54), which would open a way to link very abstract levels of decision making to basic sensorimotor processing.

A second major component of our approach was to extend the framework of decision making within cortical topographies to learning processes. RTs can be sped up through perceptual learning (55) but also through constraints arising from specific behavioral traits such as action video game playing (56). The speed of decision making in both our empirical and computational data was influenced not only by distance and number of choices but also by plastic changes of cortical maps. The speed of decision making was substantially affected after coactivation of the middle finger, as indicated by a significant decrease of RTs of the stimulated middle finger under the multiple-choice condition.

Using neuroimaging and electrical source localization, coactivation has been shown to lead to an increase in the size of the cortical representation of the fingers used for coactivation. Linear correlation analysis revealed significant relationships between cortical map changes and the parallel improvement in two-point discrimination abilities (23, 27, 28). A similar result was obtained for changes in cortical excitability: After coactivation, paired-pulse inhibition was reduced, and the amount of suppression was positively correlated with the individual gain in performance (29). These findings have been taken as an argument that the neural changes reflect changes in cortical processing causally related to the processing of tactile information. Although effects of coactivation on tactile perception are well-established (25), our results here provide evidence for an influence of such learning protocols on the speed of perceptual decision making.

There are many modeling approaches to account for reorganization in adults, and there is agreement that the balance between excitation and inhibition is a key factor. In a simulated cortical network of lateral excitation and inhibition, the model could reproduce experimentally observed receptive field expansions following cortical lesion when parameters were set to an inhibition-dominant scheme (57). In a recurrent network model of excitatory and inhibitory units, strengthening inhibitory to excitatory connections along with excitatory to excitatory connections could capture reorganization of receptive fields after amputation as well as sharpening of cortical responses, as observed behaviorally after training (58).

In our model, lateral inhibition plays a central role, which was motivated by experimental and theoretical observations. First, recording neural responses in rat somatosensory cortex before and after coactivation of the paws revealed no changes in response amplitudes (59), which has been interpreted as a lack of increased excitation. Data from human subjects have shown that following coactivation, paired-pulse inhibition was reduced whereas response amplitudes of the first response remained unchanged (29). Such a pattern of changes is a signature of reduced intracortical inhibition with no or only minor impact on thalamocortical transmission. Also, altered excitation is unlikely to account for reduced paired-pulse inhibition, as GABAergic mechanisms are involved in mediating paired-pulse inhibition. Finally, to explain improvement of two-point discrimination in parallel with impaired localization performance, both observed experimentally after coactivation, we have used a mean-field approach similar to that used here (60). Decreasing lateral inhibitory interaction resulted in bimodal activation for distances that before coactivation evoked only single peaks, whereas for localization, reduced inhibition permitted more fluctuation of peak position, thus deteriorating localization (60).

In our model, the learning-reduced inhibition speeds up the model's RTs for the corresponding finger. Therefore, our computational results imply an important role for interaction within cortical maps for the speed of decision making, and also highlight the importance of this interaction for transmitting plastic changes in cortical maps and cortical topography into behavior.

Although topographic cortical maps have been recognized as a ubiquitous organizational principle, their functional role is still debated (1, 2). Our results suggest a crucial involvement of interaction processes that are organized within the cortical topography in the computation of the speed of perceptual decision making. This implication extends beyond the functional roles suggested so far, such as a facilitation of perception by suppression of nearby distracters (61), or a facilitation mediating a smooth perception of moving stimuli (8, 62, 63).

Methods

Subjects. Thirty-seven right-handed subjects with normal or corrected-to-normal vision were tested. Coactivation was applied in 22 subjects (15 additional subjects served as the control, repeating the task without coactivation; *SI Methods*). The study was approved by the local Ethics Committee of the Ruhr-University Bochum and was performed in accordance with the Declaration of Helsinki; all subjects gave their written informed consent.

Reaction Time Measurements. We measured multiple- and dual-choice RTs in a finger selection visuo-tactile task adopted from ref. 21. An image of both hands was displayed on a monitor and one finger was selected by a visual marker. Subjects had to press the key corresponding to the selected finger on a hand-shaped 10-button keyboard (Fig. 1 and *SI Methods*).

Coactivation. Repetitive tactile stimulation was applied for 3 h to the tip of the right middle finger (22, 23, 25, 27–28) (*SI Methods*).

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