

# Sensory integration across space and in time for decision making in the somatosensory system of rodents

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**Environment is represented in the brain by a neural code that is a result of the spatiotemporal pattern of incoming sensory information. Sensory neurons encode inputs across space and in time such that activity of a given cell inhibits the ability of near-simultaneously arriving sensory stimuli to excite the cell. At the behavioral level, consequences of such suppression are unknown. We investigated the contribution of spatially distributed, near-simultaneous sensory inputs to decision making in a whisker-dependent learning task. Mice learned the task with a single whisker or multiple whiskers alike. Both groups of mice had similar learning curves and final success rates. However, multiple-whisker animals had faster response times than single-whisker mice, requiring only about half the time to perform the task successfully. The results show that spatially distributed sensory inputs in a highly redundant sensory environment improve speed but not accuracy of the decisions made during simple sensory detection. Suppression of the near-simultaneous sensory inputs could, therefore, act to reduce the sensory redundancy.**

sensory deprivation | whiskers | tactile learning | cortex

Sensory neurons with their spatially localized, topographically organized receptive fields represent the external world in a spatiotemporally restricted manner. Although spatial encoding of the sensory information is based on the identity of the receptor being activated, the temporal encoding is a function of the timing of the receptor activation (1). During sensory stimulus perception, both processes take place concurrently to encode “what” information is available “where” within the array of sensory receptors. Previous studies in the somatosensory system showed that when multiple sensory receptors are near-simultaneously (less than  $\approx 80$  ms) occupied to encode sensory information, stimulus-evoked activity is integrated sublinearly (2–9). Such nonlinear interaction between sensory inputs is not unique to the somatosensory modality (10, 11); nonetheless, its contribution to sensory perception and decision making is unknown. We have addressed these questions in the whisker system of the mouse.

Whiskers with their varying length and orderly placements in rows and arcs constitute a 3D sensory array. As the animal palpates an object, located at some distance in front, whiskers contact the object in an order determined by their position within the “whisker grid.” Those rostral whiskers long enough to reach the object collect the sensory information before more caudally located ones with a latency ( $< 40$  ms; ref. 12) proportional to the distance between them and the speed of whisking. Although sensory integration within a row is temporal in nature, within an arc the integration is primarily spatial because of largely simultaneous deflection of whiskers in a given column. The integration of the sensory information on this array is performed in many stages of the somatosensory axis (2, 3, 6, 7) and has been shown to modulate the expression of plasticity (13–17). Moreover, the cortical readout of the incoming sensory information is necessary for active sensation (18–20) and has been suggested to be depressing with increasing number of

simultaneously deflected whiskers (5) and with single-whisker (SW) deflections delivered with short delays (6, 8, 21). Considering the predominantly suppressive interaction between different whisker deflections across the whisker pad and time, it could be argued that because of the reduction in stimulus-evoked response after the first whisker deflection, secondary whisker deflections should minimally contribute to the performance of the animal.

We tested this hypothesis by training mice with a SW or multiple whiskers (MW) on a whisker-dependent learning task. The results showed that overall success of the mice in this sensory-motor task is predominantly determined by a SW’s input, and allowing mice to integrate sensory information across the whisker pad improves speed but not accuracy of the tactile (haptic) decision making.

## Results

**Increased Sensory Input Does Not Improve Success Rate on a Decision-Making Task.** We studied the tactile decision-making process on the gap-crossing (GC) task [supporting information (SI) Fig. 5]. In this task mice are trained to locate a target platform and jump onto it to receive a reward. Mice ( $n = 7$ ) with a SW intact (right-D2) learned the task in  $< 80$  trials [Fig. 1a; mean gap-distance (GD) difference between the first and eighth bin ( $\Delta M_{GD1-8} = 2.9$  cm;  $t(6) = 7.6$ ;  $P < 0.0001$ ; Holm–Sidak]. Additional training on the task did not improve the maximum GD at which mice gap-crossed [ $\Delta M_{GD8-20} = 0.4$  cm;  $t(6) = 1$ ;  $P > 0.2$ ].

Increasing the number of whiskers available to collect sensory information did not improve the overall performance of the mice [ $F(1,12) = 0.3$ ;  $P > 0.3$ ; ANOVA]. Mice trained with all of their whiskers intact (MW;  $n = 7$ ) started [ $\Delta M_{GD}SW-MW = 0.8$  cm;  $t(12) = 1.6$ ;  $P > 0.1$ ] and completed [ $\Delta M_{GD}SW-MW = 0.7$  cm;  $t(12) = 0.9$ ;  $P = 0.372$ ] their training with a performance similar to SW mice. However, MW mice learned the task in  $< 40$  trials [ $\Delta M_{GD1-4} = 3.9$  cm;  $t(6) = 8.5$ ;  $P < 0.0001$ ], significantly faster than SW mice [ $F(19,190) = 1.9$ ;  $P = 0.016$ ]. Continued training on the task did not improve the maximum distance MW mice could gap-cross [ $\Delta M_{GD4-20} = 0.2$  cm;  $t(6) = 0.3$ ;  $P = 0.764$ ].

The two groups differed from each other [Fig. 1B;  $F(13, 156) = 2.2$ ,  $P = 0.011$ ] in that mice with MW performed with higher probability of GC ( $P_{GC}$ ) in larger GDs (at 6 cm,  $t(12) = 2.4$ ; at 6.5 cm,  $t(12) = 2.8$ ; at 7 cm,  $t(12) = 2.5$ ,  $P < 0.05$ ].

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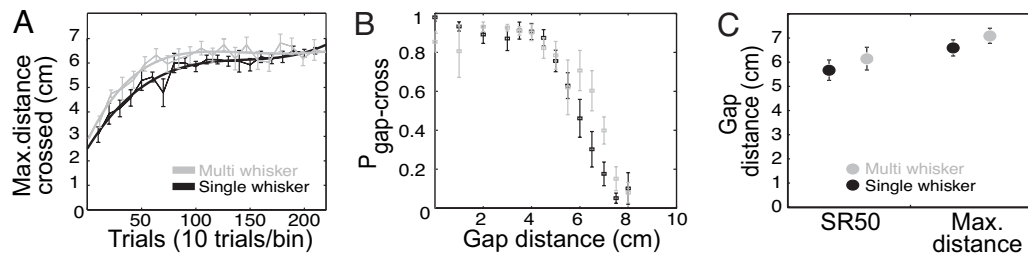
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Abbreviations: MW, multiple whiskers; SW, single whisker; GC, gap crossing; GD, gap distance;  $P_{GC}$ , probability of GC; LDA, linear discriminant analysis.

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**Fig. 1.** Mice trained with all of their whiskers intact (MW; gray traces) and a SW (black) learn the GC paradigm. (A) Learning in the task is defined as the increased GD successfully crossed with an increasing number of training trials. (B)  $P_{GC}$  as a function of GD is used to quantify the GC accuracy across distances. (C) Overall success in the task can be measured by using GD at 50% success rate (SR50) and maximum distance crossed.

However, this difference was not caused by a performance deficit of the mice with SW. Rather it reflected the delay in reaching the asymptote in the learning curve, as  $P_{GC}$  comparisons across GDs for those last 10 training trials were similar across the SW and MW mice [SI Fig. 6; 6 cm,  $t(12) = 0.1$ ; 6.5 cm,  $t(12) = 0.2$ ; 7 cm,  $t(12) = 0.1$ ;  $P > 0.8$ ].

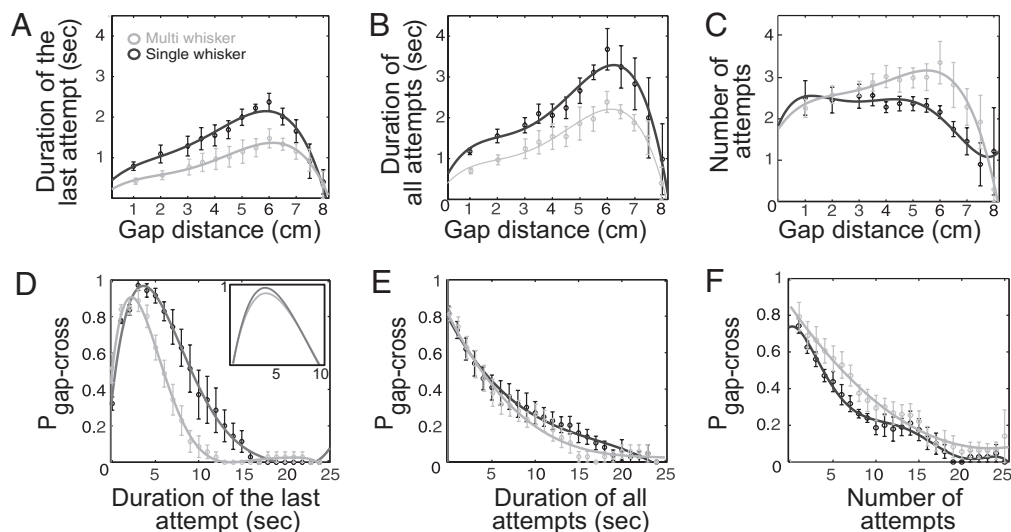
To compare the performance of the mice on the task independent from the extent of the training, we calculated the GD at which mice achieved 90%, 50%, and 10% success rates after interpolating the  $P_{GC}$  across GDs (Fig. 1C). These psychometric functions showed that SW mice performed the task with 90% success rate ( $90.5 \pm 14.9\%$ ) when the GD was  $<4.5$  cm. With increasing GD, the success rate decreased [ $F(1,13) = 46.2$ ;  $P < 0.001$ ], falling to 50% success at  $6 \pm 1$  cm (mean  $\pm$  SD) and  $<10\%$  at  $7 \pm 0.5$  cm (Fig. 1C). Training mice with MW did not improve these statistics. MW mice crossed with an  $89 \pm 16\%$  success rate at distances  $<4.5$  cm. Their success rate dropped to 50% at  $6 \pm 1$  cm [MW vs. SW;  $t(12) = 0.8$ ;  $P > 0.4$ ] and  $<10\%$  at  $7 \pm 0.6$  cm (MW vs. SW;  $P > 0.1$ ; Mann-Whitney rank sum test). These results suggest that increasing the number of touch receptors to perform the GC task enables mice to acquire the task quicker without affecting the probability of the successful GC.

**Increased Sensory Input Reduces the Duration of Sensory Integration Before Decision Making.** One of the determinants of decision making is the integration of sensory information collected

before reaching a decision (22–24). To quantify the contribution of spatially distributed, near-simultaneous sensory input to sensory integration, we studied the duration of exploration of the target platform before successful GC during the last attempt ( $T_{last}$ ) and across all attempts ( $T_{all}$ ) within a trial. Regardless of the variable studied, both SW and MW varied the duration of sampling according to GD [Fig. 2A;  $F(1,13) = 15.3$ ;  $P < 0.001$ ]. SW mice explored the target platform most briefly at the smallest (0 cm;  $305 \pm 70$  ms) and largest (8 cm;  $404 \pm 300$  ms) GDs [ $\Delta T_{last}$  at 0–8 cm (the difference of the duration of the last attempt at 0 and 8 cm) =  $98.8$  ms;  $t(6) = 0.4$ ;  $P > 0.6$ ]. As the distance increased  $T_{last}$  increased in parallel, reaching  $2,372 \pm 215$  ms at 6 cm [ $\Delta T_{last}$  at 6–0 cm =  $2,067$  ms;  $t(6) = 7.9$ ;  $P < 0.001$ ] before decreasing to  $914 \pm 423$  ms at 7.5 cm (see SI Fig. 7 for  $T$  scores,  $P$  values, and difference of means for the pairwise comparisons between GDs).

Mice trained with MW showed a similar exploration pattern.  $T_{last}$  at 0 ( $196 \pm 97$  ms) and 8 ( $331 \pm 330$  ms) cm were the fastest response times across GDs. As the distance was enlarged  $T_{last}$  increased, reaching  $1,473 \pm 235$  ms at 6 cm [ $\Delta T_{last}$  at 6–0 cm =  $1,278$  ms;  $t(6) = 4.9$ ;  $P < 0.005$ ;  $\Delta T_{last}$  at 6–8 cm =  $1,143$  ms;  $t(6) = 4.4$ ;  $P < 0.005$ ]. As in the SW mice,  $T_{last}$  gradually decreased at distances  $>6$  cm [e.g., at 7.5 cm,  $939 \pm 268$ ;  $\Delta T_{last}$  at 6–7.5 cm =  $534$  ms;  $t(6) = 2$ ;  $P = 0.043$ ].

Although the temporal pattern of exploration was similar



**Fig. 2.** MW training reduces the latency to gap-cross. (A and B) Duration of exploration at the last attempt before successful gap-cross (A) and across all attempts within a trial (B) were inversely correlated with the number of whiskers. (C) The number of attempts per GD did not significantly differ with the number of whiskers available during training. (D)  $P_{GC}$  as a function of the duration of the last attempt was used to calculate the temporal limits of sensory information integration. This duration was significantly prolonged during the SW training. (Inset) The  $P_{GC}$  distribution of MW mice normalized to the decay phase of the  $P_{GC}$  of SW mice. (E and F)  $P_{GC}$  across experimental groups as a function of the duration of all attempts (E) and number of attempts (F) were unaltered by the number of whiskers used in the training. See SI Tables 1 and 2 for the details of polynomial fits.

across the two groups, mice with MW required less time to explore the gap before crossing [ $F(1,12) = 6.5$ ;  $P = 0.025$ ]. Multiple pairwise comparisons across GDs showed that the difference in the sampling was most prominent at distances where animals preferentially use their whiskers ( $\approx 5.5 < X < \approx 8$  cm) to perform the task. At 6 cm, for example, mice with SW required on average 899 ms longer to gap-cross successfully [ $t(12) = 2.8$ ;  $P < 0.05$ ]. At those GDs  $\approx 6$  cm, mice with MW were still quicker to perform the task [SW vs. MW;  $\Delta T_{\text{last}}$  at 5.5 cm = 979 ms;  $t(12) = 3$ ;  $P < 0.05$  and  $\Delta T_{\text{last}}$  at 6.5 cm = 685 ms;  $t(12) = 2.1$ ;  $P < 0.039$ ] although the two groups required similar duration of exploration at the largest distances [ $\Delta T_{\text{last}}$  at 7.5 cm = 25.2 ms;  $t(12) = 0.1$ ;  $P < 0.9$  and  $\Delta T_{\text{last}}$  at 8 cm = 73.3 ms;  $t(12) = 0.2$ ;  $P < 0.8$ ].

**Duration of Sensory Integration Across Attempts Within a Trial Is Reduced by Increased Sensory Input.** Incoming sensory information is integrated to reach a decision; however, the temporal limits of this integration in whisker-dependent learning paradigms are unknown. To question whether integrating information improved the performance on the task, we repeated the analysis described above, but this time using the duration of sampling within a trial across all attempts ( $T_{\text{all}}$ ) in SW and MW mice.

The general pattern of exploration across all attempts was similar to the exploration pattern at the last attempt (Fig. 2B): short exploratory times sufficed at the minimum (0 cm) and maximum (8 cm) GDs, although  $T_{\text{all}}$  increased with GD between 0 and 6 cm, reaching a maximum at 6 cm before decreasing to a near minimum at 8 cm (SI Fig. 7). Mice with SW required significantly longer exploration than MW mice [ $F(1,12) = 6.6$ ;  $P = 0.025$ ]. Pairwise comparisons of  $T_{\text{all}}$  across GD between SW and MW mice showed that the difference was most prominent at  $6 \pm 0.5$  cm. Mice with SW required  $\approx 58\%$  [ $3,113 \pm 179$  vs.  $1,970 \pm 301$  ms;  $\Delta T_{\text{all}}$  at 5.5 cm = 1,143 ms;  $t(156) = 2.1$ ;  $P < 0.05$ ] more time to perform the task at 5.5 cm. With increasing GD the difference between the groups reduced minimally [e.g., 6.5 cm;  $3,245 \pm 519$  vs.  $2,146 \pm 173$  ms;  $\Delta T_{\text{all}}$  at 6.5 cm = 1,099 ms;  $t(156) = 2$ ;  $P < 0.05$ ].

One possible reason for the increased duration of exploration by SW mice could have been an increased number of visits to the gap ( $N_{\text{attempt}}$ ). However, comparisons (Fig. 2C) of  $N_{\text{attempt}}$  between SW and MW mice showed that the groups were statistically similar to each other [ $F(1,12) = 2.5$ ;  $P > 0.1$ ]. The only variable significantly affected  $N_{\text{attempt}}$  was the GD, as both SW and MW mice required an average of  $\approx 2.5$  visits at small GDs, which ultimately reduced to  $\approx 1$  visit at large distances [ $F(1,13) = 6.4$ ;  $P < 0.01$ ].

**Increased Number of Whiskers in Training Shortens the Temporal Window of Sensory Integration.** One of the conclusions derived from the analyses above is that mice with SW were about half as fast as the MW mice to successfully perform the task. To question whether this reduced reaction time represents a lengthening of the sensory integration time window or just a temporal shift, we quantified the limits of the integration window from the  $P_{\text{GC}}$  as a function of  $T_{\text{last}}$  (Fig. 2D) and defined as the onset and offset of the probability distributions' half-width.

Mice with MW, compared with SW mice, had an earlier onset [ $764 \pm 205$  vs.  $1,382 \pm 64$  ms;  $t(7) = 69$ ;  $P = 0.038$ ] and offset [ $7,095 \pm 571$  vs.  $10,952 \pm 948$  ms;  $t(12) = 3.5$ ;  $P = 0.004$ ] for sensory integration, resulting in a shorter integration window [ $6,331 \pm 465$  vs.  $9,570 \pm 959$  ms;  $t(12) = 3.04$ ;  $P < 0.05$ ] for sensory information before decision making. This reduction was further ported by the overlapping modes of the two distributions after normalizing the  $P_{\text{GC}}$  distribution of MW mice to the decay phase of the  $P_{\text{GC}}$  of SW mice [Fig. 2D Inset; before normalization modes of  $P_{\text{GC}}$  distributions: SW,  $4.6 \pm 0.6$ ; MW,  $3.3 \pm 0.4$ ;  $T = 40$ ;  $P > 0.1$ ]. These results suggest that changes in the temporal

limits of the sensory integration period with SW training reflect a genuine increased duration of the temporal window for sensory integration after restricted sensory input. This difference between SW and MW mice was not observed if  $T_{\text{all}}$  [Fig. 2E;  $F(1,24) = 0.4$ ;  $P > 0.9$ ] or  $N_{\text{attempt}}$  were considered [Fig. 2F;  $F(1,24) = 0.3$ ;  $P > 0.9$ ].

**Ability to Discriminate Between GDs Does Not Require MW.** Successful GC requires animals (i) to make a judgment about the GD and (ii) to prepare a motor execution plan specific to that particular distance for landing onto the target platform. Therefore, discriminating GDs should be an integral part of the decision making on this task.

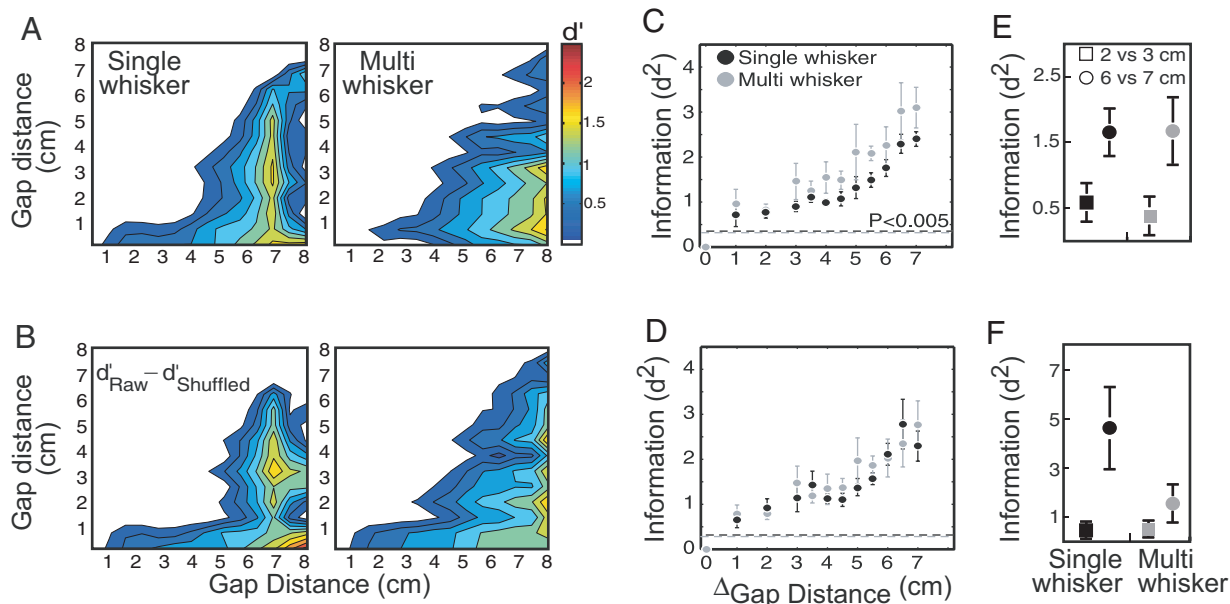
To compute the discriminability indices ( $d'$ ; ref. 25) across the GDs, we combined the data within SW and MW mice across GDs and calculated the pairwise shuffle corrected  $d'$  based on  $T_{\text{last}}$ ,  $T_{\text{all}}$  (Fig. 3 A–C), and  $N_{\text{attempt}}$  (SI Fig. 8). Among these variables, temporal measurements of exploration had significantly better discriminability power than  $N_{\text{attempt}}$ . For both  $T_{\text{last}}$  and  $T_{\text{all}}$ , the  $d'$  increased as the distance between reference GDs ( $\Delta_{\text{GD}}$ ) increased. To quantify this dependency of the  $d'$  on the  $\Delta_{\text{GD}}$ , we calculated the information in  $d'$  across experimental groups and GDs.

In both SW and MW mice, the discriminability of GDs increased in proportion to the absolute difference between GDs to be discriminated. The  $d'$  of GDs as calculated from  $T_{\text{last}}$  showed that an ideal observer can reliably discriminate GDs as small as 1 cm by using the information available in the  $T_{\text{last}}$  [SW vs. chance,  $0.7 \pm 0.2$  vs.  $0.2 \pm 0.02$ ,  $H(1) = 7.5$ ;  $P = 0.004$ ; MW vs. chance,  $1 \pm 0.3$  vs.  $0.2 \pm 0.01$ ,  $H(1) = 7.5$ ;  $P = 0.004$ ]. As the  $\Delta_{\text{GD}}$  increased, information in  $T_{\text{last}}$  doubled by 5 cm [SW at 1 cm vs. 5 cm:  $0.7 \pm 0.2$  vs.  $1.3 \pm 0.2$ ,  $t(11) = 2.2$ ,  $P < 0.05$ ; MW at 1 cm vs. 5 cm:  $1 \pm 0.3$  vs.  $2.1 \pm 0.4$ ,  $t(11) = 3.0$ ,  $P < 0.05$ ] and tripled by 6 cm (Fig. 3C).

If mice integrated sensory information across multiple attempts within a given trial, the discriminability of GDs would be expected to improve in some proportion to the additional incoming sensory information. Therefore, we next calculated the discriminability index for  $T_{\text{all}}$ . As in  $d'$  measures based on the  $T_{\text{last}}$ , the discriminability of GDs was significantly above the chance level already at 1 cm of  $\Delta_{\text{GD}}$  [SW vs. chance,  $0.6 \pm 0.2$  vs.  $0.2 \pm 0.02$ ,  $H(1) = 8.3$ ;  $P = 0.002$ ; MW vs. chance,  $0.8 \pm 0.2$  vs.  $0.2 \pm 0.01$ ,  $T = 69$ ;  $P = 0.04$ ]. Compared with  $T_{\text{last}}$ , integrating information across multiple epochs of exploration at the gap did not improve the discriminability of the GDs either for SW mice ( $0.6 \pm 0.2$  vs.  $0.7 \pm 0.2$ ,  $T = 52.5$ ;  $P = 0.949$ ) or MW mice [ $1 \pm 0.3$  vs.  $0.8 \pm 0.2$ ,  $t(12) = 0.5$ ;  $P = 0.652$ ]. The discriminability based on  $T_{\text{all}}$  doubled by  $\Delta_{\text{GD}} = 3.5$  cm for mice with SW ( $0.6 \pm 0.2$  vs.  $1.3 \pm 0.3$ ,  $T = 8.3$ ;  $P = 0.035$ ) and by 3 cm for MW mice [ $0.8 \pm 0.2$  vs.  $1.5 \pm 0.4$ ,  $t(6) = 3.7$ ;  $P = 0.011$ ] before tripling at 5.5 (SW) to 6.0 (MW) cm compared with the information available at 1 cm  $\Delta_{\text{GD}}$  (Fig. 3D).

To examine whether there were other parameters of animal activity that could carry information about the discriminability of GDs, we repeated the same analysis on  $N_{\text{attempt}}$  (SI Fig. 8). This variable performed poorly in the analysis. Although  $d'$  calculated from  $N_{\text{attempt}}$  differed from the statistical chance level [SW:  $F(11,132) = 6.6$ ,  $P < 0.001$ ; MW:  $F(11,132) = 4.5$ ,  $P < 0.001$ ], the information in  $d'$  reached significance only after 6 cm of  $\Delta_{\text{GD}}$  [SW:  $t(6) = 3.2$ ,  $P = 0.002$ ; MW:  $t(6) = 3.7$ ,  $P < 0.001$ ] regardless of the number of whiskers used during training [ $F(1,12) = 0.01$ ,  $P = 0.918$ ].

At different GDs, mice use various sources of sensory information to perform the task. At distances  $> 5$  cm, mice exclusively rely on inputs from whiskers, and at smaller distances they collect information by using tactile receptors in the skin and around the nose, together with whiskers. Therefore sensory information collected at different distances could carry distinct information



**Fig. 3.** Increased number of whiskers during GC training does not improve GD discriminability. (A and B) Shuffle-corrected  $d'$  indices calculated for the duration (sec) of the last attempt (A) and all attempts within a trial (B) show that GD discrimination based on sensory exploration does not depend on the number of whiskers available during exploration. (C and D) Information ( $d^2$ ) measurements on duration of the last attempt (C) and all attempts in a trial (D) show that discriminability of GDs is improved as the distance between them ( $\Delta_{GD}$ ) increased. Dashed lines indicate the significance at  $P < 0.005$ . (E and F) The discriminability of GDs based on duration of last attempt (E) and all attempts (F) depends on the actual GD.

about the distance of the target platform. To test this hypothesis, we calculated the information in the  $d'$  for the same  $\Delta_{GD}$  of 1 cm at two different ranges, 2–3 and 6–7 cm. Regardless of the number of whiskers the mice used during training ( $T = 20$ ,  $P = 0.262$ ), information in the  $d'$  increased several-fold for larger GDs [SW (2–3 vs. 6–7 cm):  $0.6 \pm 0.3$  vs.  $1.7 \pm 0.1$ ,  $t(6) = 2.1$ ,  $P = 0.06$ ; MW (2–3 vs. 6–7 cm):  $0.4 \pm 0.2$  vs.  $1.7 \pm 0.5$ ,  $T = 59$ ,  $P = 0.014$ ] as calculated from  $T_{last}$  (Fig. 3E). Integrating the information across all attempts did not radically change these results [Fig. 3F; SW (2–3 vs. 6–7 cm):  $0.4 \pm 0.2$  vs.  $4.7 \pm 2.1$ ,  $T = 26$ ,  $P = 0.04$ ; MW (2–3 vs. 6–7 cm):  $0.6 \pm 0.1$  vs.  $1.5 \pm 0.4$ ,  $T = 59$ ,  $P = 0.014$ ].

The difference in the information across large and small GDs for the same  $\Delta_{GD}$  suggest that tactile information collected at “whisker” distances has more predictive power about the discriminability of GDs than the information gathered at short “nose” distances. However, these results cannot determine whether the residual information at nose distances is large enough to discriminate GDs with accuracy better than chance. We, therefore, compared the information at short distances with shuffled data. Results showed that discrimination measurements based on  $T_{last}$  [SW (2–3 vs. chance):  $0.6 \pm 0.3$  vs.  $0.2 \pm 0.02$ ,  $T = 47$ ,  $P = 0.535$ ; MW (2–3 vs. chance):  $0.4 \pm 0.2$  vs.  $0.2 \pm 0.01$ ,  $T = 61$ ,  $P = 0.318$ ] and  $T_{all}$  [SW (2–3 vs. chance):  $0.4 \pm 0.2$  vs.  $0.2 \pm 0.02$ ,  $T = 38$ ,  $P = 0.073$ ; MW (2–3 vs. chance):  $0.6 \pm 0.1$  vs.  $0.2 \pm 0.01$ ,  $T = 38$ ,  $P = 0.073$ ] at short distances do not carry significantly more information than predicted by chance. These results identify the whisker input as the principal tactile information used to discriminate GDs.

**Comparable Accuracy of GD Prediction by SW and MW.** Results of the previous analysis showed that mice can discriminate GDs as small as 1 cm by using their whiskers based on the information they collect during the last attempt before GC and across all attempts within a single trial. However, the accuracy of this prediction about the size of the GD (i.e., location of the target platform) is unknown. We studied this psychometric function

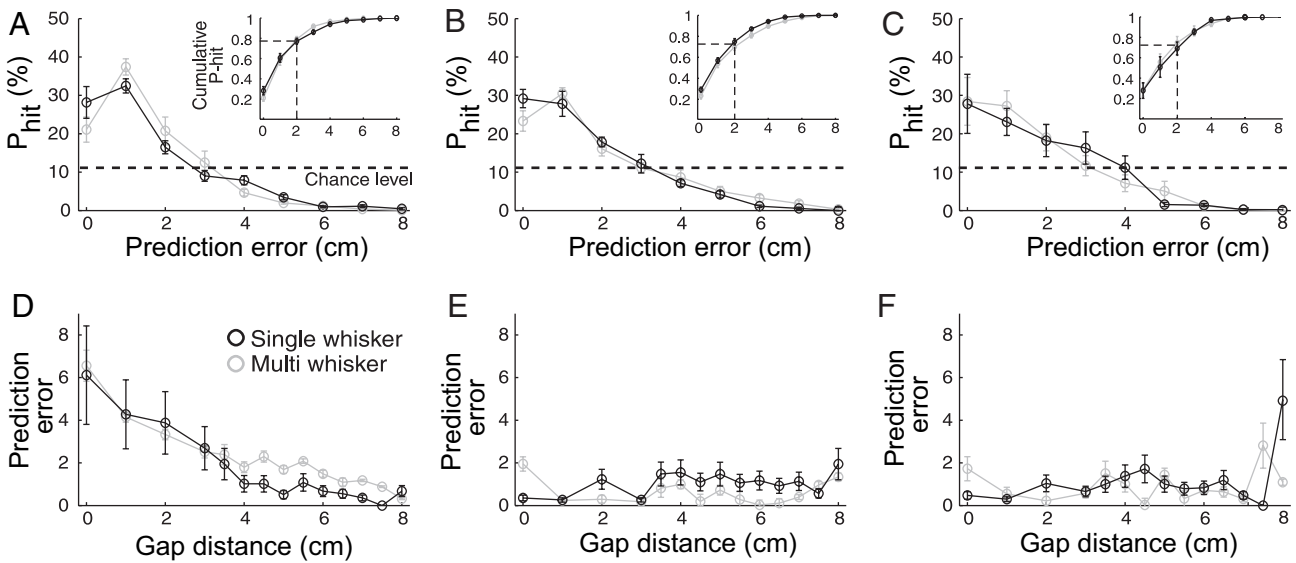
during SW and MW training by using linear discriminant analysis (LDA).

Among the independent variables examined,  $T_{last}$  had the best likelihood of successful GD prediction. An ideal observer, using LDA, could correctly predict ( $P_{hit}$ ) the GD at  $\approx 21 \pm 1.2\%$  of the MW training trials by observing only  $T_{last}$  (Fig. 4A). If errors were allowed, the performance of the observer increased to  $37 \pm 0.1\%$  at 1 cm [vs. chance (shuffled) data,  $F(8,96) = 14$ ,  $P < 0.001$ ] and decreased back to  $21 \pm 1.3\%$  at 2 cm ( $P < 0.001$ ) of prediction error, reaching a sum of  $79 \pm 1\%$  for those predictions with an accuracy of  $\leq 2$  cm ( $P = 0.01$ ). Allowing error rate to further increase to 8 cm reduced the  $P_{hit}$  from  $12 \pm 0.1\%$  at 3 cm to  $1 \pm 0.002\%$  and  $0\%$  at 6 and 8 cm, respectively, all significantly insignificant compared with the chance level of  $P_{hit}$ . These results suggest that an observer can reliably predict the GD  $79 \pm 0.1\%$  of the time with an accuracy of  $\leq 2$  cm by observing only the duration of the last trial before decision making during MW training.

Training mice with SW did not alter these statistics. An ideal observer, using LDA, could correctly predict the GD at  $28 \pm 1.6\%$  ( $\Delta P_{hit} = 7\%$ ,  $P < 0.001$  vs. MW) of the trials by observing  $T_{last}$ .  $P_{hit}$  improved with increasing error rates reaching a sum of  $77 \pm 0.1\%$  for predictions with an accuracy of  $\leq 2$  cm [ $T(1) = 430.5$ ,  $P = 0.61$  vs. MW].

To determine whether the  $P_{hit}$  differs across GDs, we computed the average prediction error ( $\Delta_{PE}$ ) as a function of GDs (see *Materials and Methods*). This analysis showed that accuracy of GD predictions based on  $T_{last}$  increased with increasing GDs [Fig. 4B;  $F(1,8) = 105.5$ ;  $P < 0.001$ ] from  $6.3 \pm 2.1$  cm error rate at 0 cm to  $0.5 \pm 0.2$  cm at 8 cm, suggesting that sensory information collected at large distances has more power for predicting actual GDs. The number of whiskers available during training significantly affected  $\Delta_{PE}$  [ $F(1, 8) = 15.9$ ;  $P < 0.001$ ].  $T_{last}$  of SW mice more accurately predicted the GD compared with MW mice, albeit only at distances between 4.5 and 6 cm ( $\Delta_{PE} = 1-1.3$ ;  $P < 0.005$ ).

When sensory information collected across attempts was considered  $P_{hit}$  was limited to  $29 \pm 2.4\%$  for the predictions



**Fig. 4.** Increased number of whiskers during GC training does not improve accuracy of GD predictions based on duration of sensory exploration. (A–C) Probability of correct prediction ( $P_{hit}$ ) as a function of the prediction error shows that GD predictions based on the duration of the last attempt (A), duration of all attempts (B), and duration of the last attempt during successful trials (C) are significantly above the chance level for those error rates  $\leq 2$  cm. The average chance level is calculated from the shuffled distribution of GDs and is identical for those animals trained with SW (black traces) and MW (gray traces). (Insets) Cumulative  $P_{hit}$  as a function of prediction error. (D–F) Distribution of the prediction errors in respect to GD for calculations based on duration of the last attempt (D), duration of all attempts across all trials (E), and duration of the last attempt during successful trials (F).

based on  $T_{all}$  of SW mice (Fig. 4C), significantly better than  $23 \pm 1\%$  correct predictions relying on the  $T_{all}$  of MW mice [ $\Delta P_{hit}$  at 0 cm = 5.8;  $t(13) = 6.8$ ;  $P < 0.001$ ]. As before, statistically significant predictions had an error  $\leq 2$  cm. Within this margin,  $T_{all}$  of mice with SW had a success rate of  $75 \pm 1\%$  and  $T_{all}$  of MW predicted  $70 \pm 1\%$  of the GDs correctly [ $F(1,12) = 8.4$ ,  $P = 0.013$ ]. Compared with predictions based on  $T_{last}$ , inclusion of the exploration duration across all attempts within a trial did not significantly affect the accuracy of predictions of SW data [ $F(1,8) = 2.007$ ;  $P = 0.182$ ] but worsen those of MW data [ $F(1,8) = 34.9$ ;  $P < 0.001$ ].

Accuracy of  $P_{hit}$  depends on the GDs. To determine whether increasing the duration of sensory integration significantly modulates this dependency, we repeated the analysis across GDs. Compared with the predictions based on  $T_{last}$ ,  $T_{all}$  had significantly better accuracy, especially at small GDs [Fig. 4D; SW:  $F(1,13) = 85.4$ ,  $P < 0.001$ ; MW:  $F(1,13) = 19.7$ ,  $P < 0.001$ ]. Across GDs, MW data had a smaller error rate ( $0.77 \pm 0.1$ ) than SW data [ $1.08 \pm 0.1$ ;  $F(1,13) = 12.3$ ;  $P = 0.004$ ].

Next, we repeated these analyses on  $P_{hit}$  and average prediction error rate across GDs by using duration of exploration only before successful GC (Fig. 4E and F). The results showed that when successful trials were considered the probability of correct GD prediction was similar to the successful and failed trials combined for the SW data [ $28 \pm 3\%$  vs.  $28 \pm 2\%$ ;  $t(6) = 0.2$ ;  $P = 0.843$ ] but higher for the MW data [ $21 \pm 1$  vs.  $28 \pm 2$ ;  $t(6) = 3.2$ ;  $P = 0.018$ ]. Compared with predictions with an accuracy  $\leq 2$  cm and based on  $T_{last}$  before successful and failure trials combined, these values represent a significant reduction in  $P_{hit}$  based on SW data [ $77 \pm 1\%$  vs.  $70 \pm 2\%$ ;  $t(6) = 5$ ;  $P = 0.002$ ] but just a tendency for MW data [ $79 \pm 1\%$  vs.  $75 \pm 3\%$ ;  $t(6) = 1.6$ ;  $P = 0.17$ ]. The accuracy of predictions as a function of GD increased when only successful trials were considered [ $F(1,8) = 32.8$ ;  $P < 0.001$ ]. This improved accuracy, however, was limited to short ( $< 4$  cm) GDs [e.g.,  $\Delta P_{PE}$  at 0 cm = 5.2;  $t(6) = 15.2$ ;  $P < 0.001$ ;  $\Delta P_{PE}$  at 3 cm = 1.9;  $t = 5.509$ ;  $P < 0.001$ ] and did not affect the average prediction error rate at GDs between 4 and 7 cm [e.g.,  $\Delta P_{PE}$  at 4 cm = 0.179;  $t(6) = 0.5$ ;  $P = 0.604$ ;  $\Delta P_{PE}$  at 7 cm = 0.352;

$t = 1$ ;  $P = 0.309$ ]. At the largest distances, relying solely on  $T_{last}$  at the successful trials significantly impaired the accuracy of predictions [ $\Delta P_{PE}$  at 7.5 cm = 0.964;  $t(6) = 2.8$ ;  $P < 0.05$ ;  $\Delta P_{PE}$  at 8 cm = 2.532;  $t(6) = 7.3$ ;  $P < 0.05$ ]. The number of intact whiskers during training did not alter these statistics [SW vs. MW;  $F(1,12) = 0.04$ ;  $P = 0.851$ ].

## Discussion

We studied the function of sensory integration across space and in time on a tactile decision-making paradigm. This so-called GC task is a binary sensory-motor task where the subject is required to locate a platform by using tactile inputs to receive a reward. The modality of the tactile input depends on the distance of the target platform to the subject. At short distances ( $< 5$  cm) mice use whiskers and other touch receptors around the nose. At longer distances ( $\approx 5 < X < 8$  cm) they solely rely on the information from whiskers (20). Mice trained with all of their whiskers intact required 0.3 (8 cm) to 1.5 (6 cm) s of exploration before successfully crossing onto the target platform at whisker distances. However, mice do not necessarily need MW to succeed in this task. Animals with all but one of whose whiskers clipped learned the task as well as the mice trained with MW, yet they required a longer sensory exploration time [0.4 (8 cm) to 2.4 (6 cm) s] before decision making. Independent from the number of whiskers used in the task, the mice were able to discriminate GDs as small as 1 cm based on the sensory evidence they collected before decision making. The accuracy of their estimate did not depend on the number of whiskers, as both groups of animals trained with SW or MW could correctly predict distances at 75–80% of the trials with an accuracy of  $\leq 2$  cm if they relied solely on the sensory information collected before decision making.

Studies in humans and monkeys suggest that “evidence” in favor of or against a decision is collected across the array of sensory receptors and over time before reaching a decision (22–24). We show here in mice that the duration of sensory integration is inversely correlated with the number of receptors available to collect sensory data such that with increasing number of sensory inputs the latency to decision decreases.

One primary finding of the experiments reported is that mice could discriminate between distances with high accuracy by using their whiskers. Studying the neural mechanisms underlying such fine distance discrimination ideally requires simultaneous chronic imaging of the sensory input on whiskers and neural activity along the somatosensory axis. However, recent acute electrophysiological recordings combined with controlled whisker deflections along the length of whiskers showed that the radial distance of the whisker contact can be encoded by the ensemble action potential rate of the neurons in the trigeminal ganglion such that with increasing distance between the deflection point and the stub of the whiskers the number of stimulus-evoked action potentials decreases (26). This reduction in the action potential rate when the animal receives the tactile information closer to the tip of the whisker could also explain the observations that within the whisker range on the GC task the likelihood of successful GC reduces with increased GD.

The principal conclusion derived from the results reported is that increasing the number of near-simultaneously deflected whiskers does not improve the asymptotic probability of success in decision making but reduces the duration of sensory integration required to make a decision. Previous electrophysiological recordings and optical imaging experiments in the primary somatosensory cortex showed that increasing the number of near-simultaneously deflected whisker reduces the excitation in the network in a way that those secondary whisker deflections contribute minimally to the overall representation of the train of whisker deflections (2–9). This sublinear summation of the sensory activity across the array of whiskers and in time has temporal limits: Whisker deflections delivered with a latency less than  $\approx 50$  ms cause the most prominent sublinearity, which recovers when interwhisker deflection interval is increased to  $>80$ – $100$  ms (9, 21, 27). Considering that mice whisk at  $\approx 20$  Hz during active whisking (28), the sublinear summation of the sensory-evoked activity will be significant even across adjacent cycles of whisking.

The function of this nonlinear summation is likely to reduce redundancy in the sensory stimuli. Tactile information animals gather to perform the GC task is highly redundant. The surface, structure, and the formation of the edge of the target platform are all uniform. Moreover, the elevation of the platform along the edge is constant. Therefore any two points on the target platform where animals collect the sensory information have similar properties, and thus carry redundant and/or repeating patterns of tactile information. In such environments, reducing redundancy in the sensory information can be one of the ways to improve efficacy of sensory processing considering that reduced redundancy should boost the “channel capacity” to carry signal and augment speed of information processing (29, 30). Experiments reported here support this view as animals with MW required shorter exploration duration compared with mice

with SW to perform the task. The difference was not caused by a change in the nature of the sensory signal carried considering that there is as much information in the SW sensory input as in the MW condition and the predictive powers of the sensory information collected with SW and MW are statistically similar.

Despite failing to contribute to the accuracy of the decisions made, near-simultaneous sensory inputs significantly reduced the speed of decision making. On average across GDs, animals trained with MW performed nearly twice as fast as those animals trained with a SW. The mechanism of this faster sensory-motor transformation is unknown; however, it is unlikely to include changes in the latency of the stimulus-evoked activity in the primary somatosensory cortex (8).

Taken together, these results show that integration of the spatially distributed sensory information in time improves the speed but not accuracy of decision making and provide a functional role for sublinear summation of sensory stimuli in sensory cortices.

## Materials and Methods

Fourteen adult ( $P > 60$ ) C57BL/6 mice (Charles River, Sulzfeld, Germany) from both sexes were used according to the animal welfare guidelines of the Max-Planck Society. Mice had ad libitum access to food and water except during training and testing on the appetitively motivated GC training. The training was performed on two custom-built platforms equipped with infrared motion sensors. A custom-written software quantified the duration and frequency of sensory exploration.

**Discriminability and Information Measurements.** Ability of mice to discriminate GDs based on the sensory information collected in a given trial was quantified by using  $d'$  (25). This is a simple index, used to quantify the discriminability of two populations with equal variances and defined as the absolute difference of the mean of the two populations over the variance of the two. We calculated the  $d'$  for all combinations of GDs and shuffle-corrected these values to create a discriminability matrix.

To quantify whether SW and MW differ from each other in terms of their sensitivity to discriminate distance, we quantified the information in  $d'$  terms ( $d'^2$ ) as the ratio of the square of the difference between the two population means to the square of the variance (31).

**LDA.** We used LDA (32) to quantify how well one can predict what the GD is from the exploration time at a given trial. To do so, we first trained the LDA algorithm on 2/3 of the data with equal probability of priors, and then tested the predictions of the LDA on the rest of the data in respect to predictions based on shuffled data.

See *SI Text* for further details on materials and methods.

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