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Research

Motor–sensory convergence in object localization: a comparative study in rats and humans

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In order to identify basic aspects in the process of tactile perception, we trained rats and humans in similar object localization tasks and compared the strategies used by the two species. We found that rats integrated temporally related sensory inputs (‘temporal inputs’) from early whisk cycles with spatially related inputs (‘spatial inputs’) to align their whiskers with the objects; their perceptual reports appeared to be based primarily on this spatial alignment. In a similar manner, human subjects also integrated temporal and spatial inputs, but relied mainly on temporal inputs for object localization. These results suggest that during tactile object localization, an iterative motor–sensory process gradually converges on a stable percept of object location in both species.

Keywords: behaviour dynamics; closed feedback loops; adaptive process; video-tracking; sensory substitution; decision-making

1. INTRODUCTION

Perception, the process of grasping the environment, is an active process involving both motor and sensory variables [1–5], whereby animals actively move their sensory organs to obtain information about the environment [6–17]. Rodents, for instance, actively employ their whiskers in sweeping back-and-forth movements when exploring their surroundings [18–20]. Primates employ active eye and hand movements to scan and explore remote and nearby environments [21,22]. In fact, motion of the sensory organs (whiskers, eyes, fingers) is required for perception to occur altogether; without motion, stationary objects are not contacted and stationary visual images hardly activate photoreceptors [23–25].

In addition to a general requirement of sensor motion for perception, the specifics of sensor movements [4] may enhance the discriminative ability of observers. In turn, afferent signals have a strong influence on motor control of sensory organs [26]. These effects constitute

an iterative process, whereby perception emerges from an adaptive operation of motor–sensory loops, i.e. loops that include sensory organs (we use the term ‘motor–sensory’ rather than ‘sensory–motor’ in order to emphasize the fact that sensation of stationary objects begins with sensor motion). During such iterative processes, motor components probe the environment and sensory components convey the results of this probing [5]. In adaptive iterative processes, the motor probing is expected to gradually converge towards the perception of external objects. Whisking is an example of an iterative process, and it has been proposed that it is adaptive in the sense that the motor–sensory feedback optimizes sensory processing [27,28].

During horizontal object localization, both rats [29,30] and mice [31] actively palpate objects with their whiskers, typically across multiple whisking and contact cycles. Both trained rats and mice can localize objects along the horizontal dimension with a single whisker intact and generally do so in an active manner. In general, task performance is not degraded when all but a single whisker are removed, and may even improve in some cases [29]. This observation precludes whisker identity as a parameter required for determining horizontal location. Instead, codes based on relative temporal delays [10] or angular tuning [32] most probably contribute to horizontal encoding. Coding by time requires an accurate measurement of the moment of contact relative to a temporal reference point, such as the onset of whisker motion. During

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† Deceased 16 August 2009. The article is dedicated to our friend and colleague Maciej Pietr, for his significant contribution to this work.

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One contribution of 18 to a Theo Murphy Meeting Issue ‘Active touch sensing’.

artificial whisking in anaesthetized rats, whisker motion, contact and detach events are all reliably encoded by primary trigeminal afferents, enabling precise neuronal encoding of horizontal object location [33]. Unlike horizontal localization, however, radial localization seems to operate on different principles. Behavioural studies demonstrate that rats require multiple whiskers and neither use nor depend on active whisker movements when localizing objects along the radial dimension [34]. During artificial whisking, primary afferents vary their firing rates as contacted objects are placed at different radial locations [35], suggesting a rate code of radial object location [10]. The absence of whisker movements during radial localization in rats does not rule out adaptive processes, as head and body movements are still required to enable contact between whiskers and objects. The motor–sensory circuits, however, are likely to be different for radial and horizontal localization.

Active exploration of an environment requires dynamic interplay between motor components such as reaching and palpation, as well as sensory components such as proprioception and cutaneous sensation. Interaction with a changing environment requires an ability to adapt to these changes, which requires some means for anticipating changing conditions rather than reacting to changes in the environment through error-detecting feedback loops [36–38]. To reduce errors, the brain can learn anticipation errors in one cycle and modify the motor commands that initiate the next cycle [39–41].

To date, there is little hard evidence for iterative motor–sensory processes, partly owing to an emphasis on simple and stereotyped tasks explored in highly trained animals. Previously, we have explored haptic object localization in the rat vibrissal (whisker) system [29] and in humans [42]. Rodent whisking is a rhythmic motion in the absence of contact, and can persist uninterrupted for tens of seconds or longer. During object localization, however, whisking bouts are significantly shorter and less spectrally pure [29], leaving a brief window for observing adaptive effects (approx. three to six whisk cycles). Our human studies addressed some of the experimental limitations encountered in rodent behaviour above by developing a novel sense in humans, whereby subjects were equipped with flexible fibre rods attached to their fingertips and trained to localize vertical poles using these whisker appendages while blind and ear-folded. The fact that subjects had never previously been exposed to such a task allowed us to study adaptive behaviour during learning. In both tasks, subjects (rats and humans) achieved high levels of performance (as measured by spatial acuity). By construction, the two tasks were similar and both rats and humans employed palpating movements during performance of the task. Thus, these experiments afforded us a unique possibility to explore common aspects of an active perceptual task in two different species.

Here, we describe the dynamics of the palpation process in rats and humans in terms of motor–sensory information about the location of two objects. The task given to our rats and human subjects was a relative

localization task, where subjects had to discriminate the relative spatial location of two vertical poles, one placed on each side (right or left) of the subject. We denote relative location here by $\Delta x = x_{\text{right}} - x_{\text{left}}$, where x is the coordinate along the horizontal (posterior–anterior) axis; subjects had to report whether Δx was positive or negative. We explored two variables that have previously been proposed as likely candidates for perceptual cues underlying horizontal object localization: (i) the temporal delay between bilateral contacts (Δt), conveyed by tactile ex-afferent signals, and (ii) the angular difference between the whiskers (Δa) at the moment of first contact with one of the poles, conveyed by proprioceptive re-afferent signals (figure 1 and electronic supplementary material, movie S1).

2. MATERIAL AND METHODS

All experiments were conducted in accordance with Institutional guidelines and were approved by the Institutional review board.

(a) Behavioural data: rat

We revisited the dataset collected by Knutsen *et al.* [29]. Behavioural data of four rats successfully trained in a whisker-dependent relative object localization task were used for the behavioural analysis. In brief, the rats were water-deprived and trained through multiple stages to approach two vertical poles that were displaced relative to each other, at varying offsets, along the anterior–posterior body axis of the rat. The rats had to centre their head between the two poles and learned to palpate the objects with their whiskers in the dark, and to report the identity of the closer pole in return for a reward (water). The rats were initially trained with all whiskers intact, and later tested with either a single row or arc of whiskers and finally with only a single whisker (always the whisker located in row C and arch 2) intact on each side of the head. We tracked a total of 473 trials where the entire sequence of approach, whisker–object contact and head-retraction was recorded by a high-speed (1000 frames s^{-1} [43]) video camera. For the analysis presented here, we included a subset of 230 tracked trials, where at least three distinct movement cycles with contact occurred. Two motor–sensory variables were estimated from the whisker-tracking data: (i) Δt is the difference in time between bilateral contact onsets in each cycle and (ii) Δa is the angular difference between bilateral whiskers in the first frame of any contact (left or right) in each whisking cycle (figure 1a).

(b) Behavioural data: human

Twelve male and female human subjects were trained in a novel haptic localization task [42]. In brief, elastic polyvinyl chloride (PVC) rods were attached to the fingertips on both hands. The rods were moulded into a conical shape by heating and stretching. The diameter of each whisker changed gradually from 1.8 mm at the base to 1.2 mm at its end and their length was 34.5 cm. The rods' stiffness was slightly softer than that of a drinking straw, and they did not bend

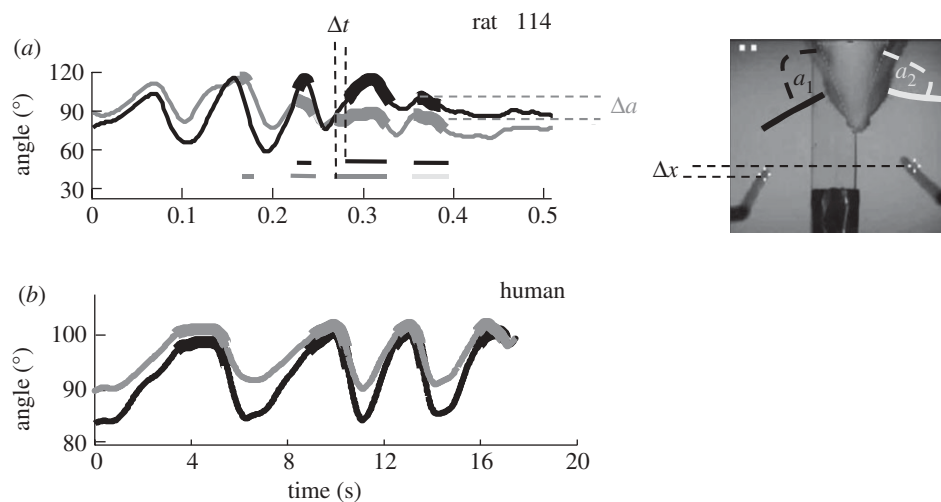


Figure 1. Examples of data collected from behaving rats and humans. (a) Rat whisking and active touch. Whisker angle as a function of time as calculated from tracked movement traces of the right (black) and left (grey) whiskers of a rat performing the bilateral localization task, using one whisker on each side of the snout. Whisker angles relative to the line that intersects the ipsilateral eye and nose (a_1 and a_2) and poles offset (Δx) are depicted in the right panel. Moments when the whisker touched the pole are marked with a bold line on the angle traces and indicated by horizontal lines below. Δt is the time difference between bilateral touch events. Δa is the bilateral angle difference at certain time point. The Δt and Δa depicted here are from different cycles. Note that the whisker that touched the poles first in the first touch became the more posterior in the last touch. (b) Human whisking and active touch. Hand angle as a function of time as calculated from traces of right (black) and left (grey) PVC whiskers attached to a human performing the bilateral localization task.

under their own weight when held horizontally. Rod displacement and applied forces were measured with accelerometers and force transducers located on the fingers. Subjects were blindfolded and seated on a chair in front of two vertical poles, one located on each side (left and right). Subjects were instructed to contact the poles only with the flexible rods and to report the closest pole. The relative horizontal offset of the poles was changed manually between trials ranging between 20 and 1 cm following the same staircase paradigm of the rats in Knutsen *et al.* [29]. After each trial, the subjects received oral feedback ('correct' or 'wrong') from the experimenter. As with the rat data, we estimated the motor–sensory variables, Δt and Δa , from the tracking of the flexible rods.

(c) Data analysis

We computed inter-variable correlations using Spearman's correlation (Statistical Toolbox, MATLAB). The average Rho was tested to be different from 0 using t -test. The ability of Δa and Δt to predict the behavioural outcome in rat trials was tested using receiver operating characteristics (ROC) analysis [44]. Briefly, we apply n thresholds (tr_1 – tr_n) to Δa or Δt and use each threshold (tr_i ; $1 \leq i \leq n$) to construct a decision criterion (e.g. 'right' if $\Delta a < tr_i$, otherwise 'left'). For each threshold, we calculate true- and false-positive rates from the subject's report according to the assumed criterion. A curve of true versus false rates in all the n thresholds (the ROC curve) is then computed and the area under this curve (AUC) is calculated. A value of $AUC = 0.5$ denotes chance level prediction (i.e. the given variable cannot predict subjects' responses for any threshold, under the assumed criterion) and $AUC = 1$ denotes full prediction (i.e. there exists a threshold tr_i for which the

given variable fully predicts subjects' responses). The probability $p(AUC > 0.5)$ was computed using confidence intervals as described in Hanley & McNeil [45]. Overall, p -values were corrected for multiple comparisons using the false discovery rate (FDR) procedure [46]. Here, $FDR = X$ means that the proportion of expected false discoveries is equal to or smaller than X .

3. RESULTS

(a) Temporal delay between bilateral contacts: rat

In trials where rats touched the poles at least three times across three different movement cycles, we measured the temporal delay between bilateral contact onsets (Δt) during the first, second and last touch events (see example in figure 1a). The correlation between Δt and the difference in the horizontal position of the poles (Δx) was calculated for each touch cycle. In figure 2a, we present the correlation coefficient (Spearman's Rho; black lines) between Δt and the difference in the horizontal position of the poles (Δx) as a function of cycle number in four individual rats that performed the task with a single whisker intact on each side of the face. In general, the correlation between Δx and Δt tended to decrease along the trial both during correct (figure 2a) and incorrect (figure 2b) trials. Interestingly, in three rats (113, 114 and 137) this correlation was negative in the last touch cycle in incorrect trials, suggesting that Δt was a source of confusion for these rats. These results indicate that while the rats coordinated the movements of bilateral whiskers at the beginning of a trial such that they were at the same angle at the same time and thus Δt was correlated with Δx , they reduced this coordination in later stages of the trial.

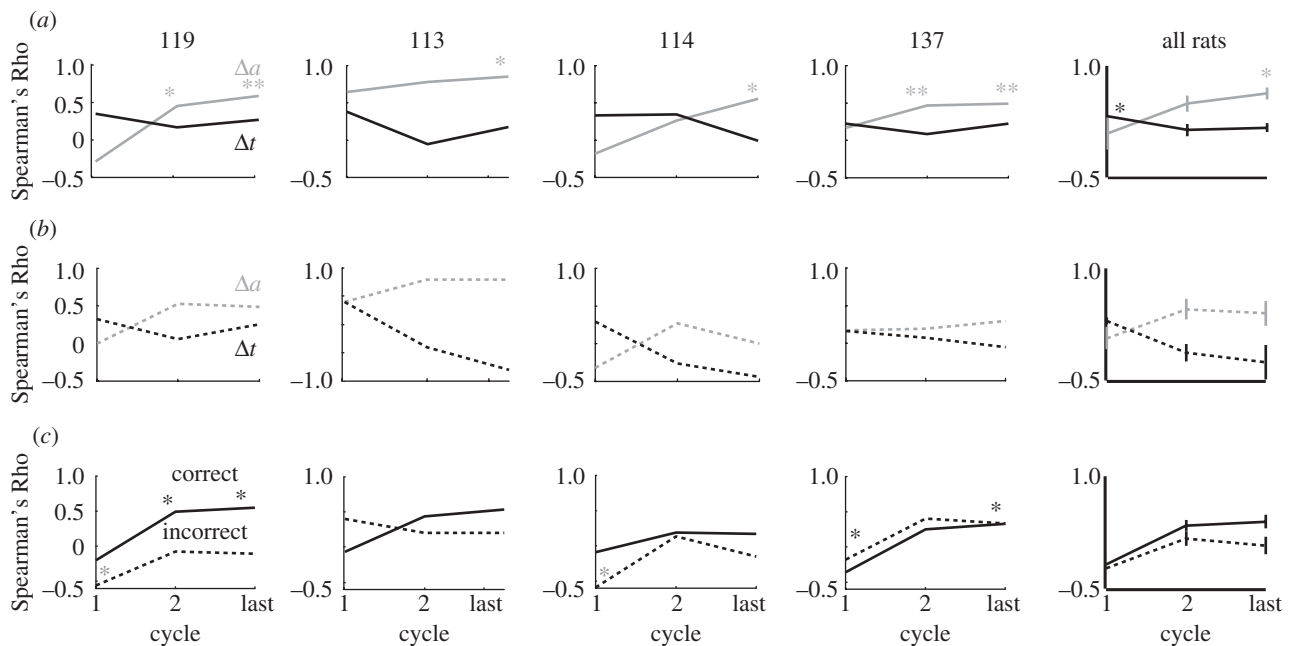


Figure 2. Correlations between Δt , Δa and Δx in rats as a function of cycle number. (a) The correlation between Δt and Δx (black) and between Δa and Δx (grey) in four individual rats in correct trials. (b) Same as in (a), for incorrect trials. (c) The correlation between Δa and Δx in the first, second and last touch, and Δt in the first touch. Correct trials (solid) and incorrect trials (dashed) are depicted. Right-most column depicts means and SEM for four rats. Stars indicate that the probability (p) that Rho (average Rho in ‘all rats’) was not equal to 0 was significant after correction for multiple comparisons (see §2): *FDR = 0.05; **FDR = 0.005.

(b) Angular difference between bilateral whiskers: rat

For the same rats and touch events, we measured the angular difference between the whiskers (Δa) at the time of the first touch (left or right) in each (contacting) cycle (figure 1a). Note that while Δa was fully correlated with Δx when both whiskers touched the poles (by definition), this was not necessarily the case when only one whisker touched a pole; Δa upon unilateral touch onset was determined by whisker coordination and not by physical constraints enforced by the stimulus. Figure 2 shows the correlation coefficients between Δa and Δx (grey lines) as a function of cycle number for correct (figure 2a) and incorrect (figure 2b) trials. In general, the correlation between Δa and Δx was weak in the first contact and increased along the trial. The increase in Δa – Δx correlation reflects the increased information about the environment that was available to the rat in a given cycle before contact.

(c) Correlation between Δa and Δt : rat

Because Δt correlated with Δx at the beginning of the trial and Δa correlated with it at later stages, it is interesting to test if initial Δt affected later Δa . Indeed, Δa in cycles 2 and onwards correlated with the Δt that was measured in the first cycle (figure 2c). Interestingly, Δa did not depend on Δt s that were measured in later cycles (data not shown). Moreover, in incorrect trials (dashed lines), the correlation between Δa and Δx was, in general, lower than that in correct trials (solid lines). Again, the correlation between Δt and Δa was caused by the predictive alignment of the whiskers before the physical contact with the pole. This finding indicates that accurate representations of Δx are developing in the rat brain during the trial.

(d) Correlation between perceptual cues and perceptual reports: rat

Correlations between Δa or Δt and the reports of the rats were estimated by the area under the ROC curve (see §2). This analysis suggests that rats based their reports mainly on Δa at the last contacting cycle (figure 3). As expected from the correlations of the sensory cues with the stimulus offset (Δx , figure 2), their correlations with rats’ reports developed along the trial. In correct trials, reports correlations with Δt decreased and those with Δa increased (figure 3a). The analysis of incorrect trials reveal opposite trends and suggests that, at least in some trials, the rats considered Δt in the last contacting cycle instead of Δa ; using Δt , however, was associated with increased error rates owing to the misalignment of the whiskers (figure 3b).

(e) Perceptual cues during human whisking

Examining Δa and Δt parameters in correct and incorrect trials in humans performing the same bilateral localization task, scaled to human size and using artificial whiskers attached to individual fingers [42] revealed correlation patterns that resembled those of the rats (figure 4a,b). The major difference, however, was that although the correlation between Δa and Δx increased along the trial, that between Δt and Δx increased as well (in correct trials, figure 4a). In addition, whereas the Δa – Δx correlation in correct trials was smaller than that in incorrect trials, the Δt – Δx correlation was higher in correct versus incorrect trials. This is consistent with our human subjects using Δt , rather than Δa , as their primary perceptual cue. Despite that, Δa became more and more correlated with the initial Δt along the trial (figure 4c). This suggests that despite the temporal strategy employed

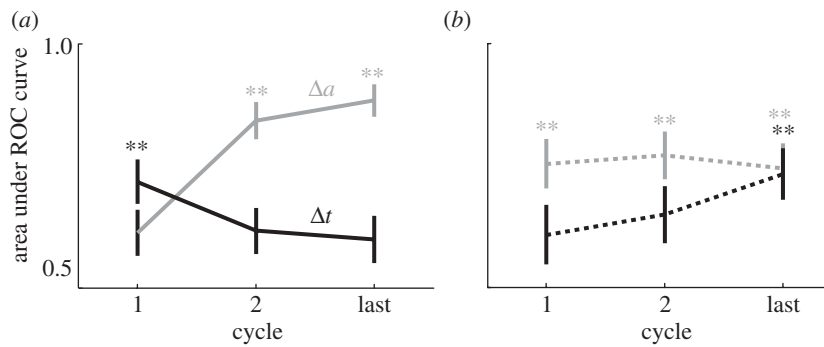


Figure 3. Estimation of the ability of Δt and Δa to predict rats' perceptual reports. Area under an ROC curve (AUC) is presented for Δt (black) and Δa (grey) in correct (a) and incorrect (b) trials. A value of AUC = 0.5 denotes chance level prediction and AUC = 1 denotes full prediction. Asterisks indicate that the probability (p) of AUC > 0.5 (chance level) was significant after correction for multiple comparisons (see §2): *FDR = 0.05; **FDR = 0.005.

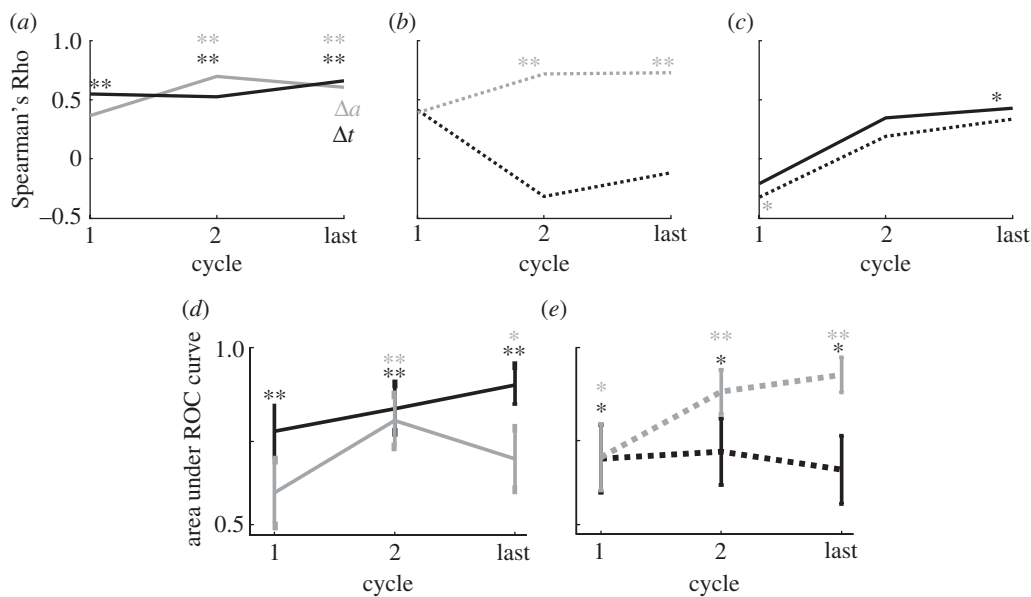


Figure 4. Correlations between Δt , Δa and Δx and their ability to predict decision in humans as a function of cycle number. (a,b) Correlations between Δt and Δx (black) and between Δa and Δx (grey) in correct and incorrect trials, respectively, for all 12 human subjects. (c) Correlation between Δa in first, second and last touch, and Δt in the first touch in correct (solid) and incorrect (dashed) trials. (d,e). Area under an ROC curve (AUC) is presented for Δt (black) and Δa (grey) in correct (d) and incorrect (e) trials. A value of AUC = 0.5 denotes chance level prediction and AUC = 1 denotes full prediction. Stars indicate that the probability (p) that Rho was not equal to 0 (in a–c) or AUC > 0.5 (for d,e) was significant after correction for multiple comparisons (see §2): *FDR = 0.05; **FDR = 0.005.

by our human subjects, they did not eliminate an apparently automatic process in which Δa represented Δx more and more accurately as the trial proceeded.

(f) Correlation between perceptual cues and perceptual reports: human

Correlations between Δa or Δt and the reports of the humans were also estimated by the area under the ROC curve (see §2). Unlike rats that based their reports on spatial (proprioceptive) cues, humans based their reports mainly on Δt at the last contacting cycle (figure 4d,e). In correct trials, reports' correlations with Δt increased between cycles (figure 4d). The analysis of incorrect trials suggests that, in some trials, the humans considered Δa in the last contacting cycle instead of Δt ; using Δa , however, was associated with increased error rates (figure 4e).

4. DISCUSSION

Here, we have demonstrated signatures of a convergence process in object localization by whisking in rats and

humans. In both rats and humans, performing the same bilateral localization task, information on pole offset (Δx) was initially higher in the bilateral temporal offset (Δt). In both rats and humans, information carried by the whiskers' angular offset (Δa) on Δx increased in successive cycles. The major difference between rats and humans was that at the end of each trial, before the perception was reported, Δa was more informative in rats, whereas Δt was more informative in humans. This is consistent with rats basing their correct reports primarily on Δa and humans on Δt . Evidence suggests that part of their errors stemmed from relying on the less-reliable variables (Δt in rats and Δa in humans). Interestingly, despite their apparently different report strategies, in both rats and humans, the correlation between initial Δt and later Δa increased monotonically along the trial, suggesting that at least part of the convergence process is automatic.

Automatic convergence processes are also supported by the behaviour of individual neurons in the

thalamus and cortex of the anaesthetized, artificially whisking rat, which exhibit stabilization dynamics [47,48]. It is assumed that once the network reached steady-state, information gain becomes low and a behaving rat would exit the mode of information accumulation and move on (or report its perception if it is involved in such a task). This is consistent with the observation that rats report their perception in this task after approximately four contacting cycles on average [29].

When an external object is continuously present, subjects usually use at least a few tenths of a second to perceive it [6,20–22,49]. Importantly, perceptual acuity usually increases with increased brain–object interaction time [49–54]. Our results suggest that such improvements result from a process in which the brain converges upon accurate perception using motor–sensory loops.

These results are consistent with perception emerging from a convergent process, which is primarily based not only on motor–sensory dynamics [55], but probably also includes local network dynamics [56,57]. During this process, motor and sensory variables gradually change until a percept emerges. The rules governing these dynamics are not yet known. Yet, in a simple task such as the horizontal localization task studied here, simple convergence dynamics that aimed at nullifying a single variable (Δt in rats or Δa in humans) could be identified. These observations encourage us to believe that the rules controlling convergence dynamics in other, more complex perceptual tasks are also traceable.

Together, these experiments show that haptic perception with whiskers is a dynamic and iterative process. Both rats and humans use iterative processes to establish stable representations of object location. Given that these representations depend critically on whisker movements, and whisker movements change from trial to trial, it is suggested that the neuronal representations converged upon in each trial are not fixed. That is, they change from trial to trial. As perceptual reports are consistent between trials, it is suggested that what determines perceptual reports are not internal neuronal representations *per se*, but rather the relationships between these representations and the motor–sensory patterns converged upon [5].

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