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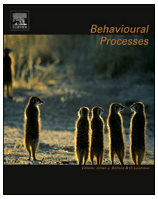

A case of visuo-auditory sensory substitution in rats

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ABSTRACT

Sensory substitution refers to a process whereby an agent, by means of a removable specialized instrumentation, becomes capable of exploiting an available sensory modality in order to perceive properties of the environment which are normally accessible by means of a different modality. We describe a situation of visual-auditory sensory substitution in the rat. Rats were placed in complete darkness, and trained to follow a virtual path whose position was signalled by a sound activated by a video-tracking device. Our hypothesis was that the rats would be able to succeed in this task of spatial navigation, following the sound contour by means of sensory-motor coupling based on seeking the sound (all-or-none) and mastering the relation between their own actions and the expected sensory feedback. Our results confirm this hypothesis and show the progressive structuring of meaningful exploratory activity, leading from the appearance of stopping behaviour when the sound is lost or acceleration when the sound is discovered, up to a veritable sensory-motor strategy which maximizes the possibilities for discovering and following the sound path. Thus, the animals seem to have developed a new form of perception which translates in particular into motor behaviour adapted to the search for sound.

1. Introduction

The term « sensory substitution » refers to a process whereby an agent, by means of a removable specialized instrumentation, becomes capable of exploiting an available sensory modality in order to perceive properties of the environment which are normally accessible by means of a different modality which is temporarily or definitively unavailable (Bach-y-Rita, 2004; Bach-Y-Rita et al., 1969; Gapenne, 2014; Lenay et al., 2003; Visell, 2009; Wall and Brewster, 2006). The key to this learning involves mastery of the relation between the actions performed by the agent and the determination of the associated sensory effects. By extension, sensory substitution offers the opportunity for observing novel forms of learning, including the spatial dimension, and thus contributes original data concerning the conditions under which such learning can occur.

The majority of studies in this area have been performed with human subjects. The near-total absence of studies on other animal species may be explained in part by the difficulty for an animal to attribute a novel meaning to an existing sensory modality. For example, sound and touch are not normally sensory modalities used for spatial reference in so-called "visual" species. However, surprising innovations in behaviour show that the capacities of animals in this domain are certainly under-estimated (Millot et al., 2014). The reason for the paucity of animal studies may therefore lie rather in the difficulty for the experimentalist to communicate a complex instruction to the animal, and in particular to put the animals in a situation where they may freely learn the instructions. Studies on new-born human infants complete the picture to the extent that they demonstrate the capacity of infants aged 2 months, thus unable to understand verbal instructions, to establish a relation between the activity of sucking on a dummy teat and synchronous auditory feedback (Rochat and Striano, 1999).

The object of the present study is to validate a situation of sensory substitution in the rat and, more specifically, to demonstrate the possibility of achieving visual-auditory substitution in order to solve a task of spatial navigation. An initial behavioral study by Strelow et al. demonstrated the possibility of using a visual-auditory sensory substitution device by three young macaque monkeys reared from birth in conditions of visual deprivation (Strelow et al., 1987). These animals were equipped with a sonar system which emitted an auditory signal containing information on the distance (pitch frequency), the spatial position (difference in stereo amplitude) as well as texture (tonal timbre frequency), which made it possible to appraise properties of the environment and objects at a distance. In particular these young animals learned to avoid obstacles in the cage where they lived, to catch hold of

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fixed or mobile objects, and to discriminate textures. More recently, two studies using neural prosthetic devices have made it possible to show that rats are capable of exploiting signals that they do not naturally perceive. Thomson, Carra & Nicolelis (2013) have shown that adult rats were able to perceive infra-red light by means of a neural prosthetic device consisting of an infra-red sensor whose activation triggered electrical stimulations in their vibrissal cortex. These animals were thus able to learn to use infra-red light emissions to localize the correct position of a reward which was previously indicated by visual light. Finally, Norimoto and Ikegaya (2015) have performed a similar study, this time by implanting a neural prosthetic device equipped with a geomagnetic compass.

These studies do not implement the original protocols which redeploy a sensory modality naturally available for the animal; the activity of the animal directly triggers an intra-cortical stimulation, and not the stimulation of an available sensory organ by means of an artificial stimulator. However, one can accept the hypothesis that the mechanism of learning is similar to that in sensory substitution. Neurobiological mechanisms underlying sensory substitution have been identified in the ferret or the cat, demonstrating the process of functional reorganization between the sensory cortices of different modalities (Rauschecker, 1995; Roe et al., 1993; Sur et al., 1988). For example, the auditory cortex of the new-born ferret can acquire functional and anatomical properties of the visual cortex when visual neuronal information is directed towards it (Sur et al., 1988).

In order to demonstrate the processes of sensory substitution at the behavioural level, we have designed a situation in which rats, in total darkness, must reach the site of a reward. In order to achieve that, the animals have learned to follow virtual paths indicated by a sound which is triggered each time the nose of the animal encroaches on the path. An essential point is that the sound employed is always the same, and therefore provides no information on the orientation or the distance of the animal with respect to the possible goals. Only the interactions of the animal with the sound flow, in particular its active exploration and its back-and-forth movements with respect to the virtual sound path, can give meaning to the sound. The spatial navigation is based on a complex interaction between locomotion and the feedback of multiple sensory signals (e.g. Arleo and Rondi-Reig, 2007; Retailleau et al., 2012). Amongst these signals, some may be termed reafferent signals generated by the movements of the navigator; these signals result from the activity of the vestibular system, receptors in the muscles and tendons, or the visual system if we consider the optical flow. Other signals, which may be termed exafferent signals (their appearance is not determined by the activity of the animal), are produced by the environment and activate the visual, olfactory, tactile or auditory senses. In either case, these signals are used in an egocentric and/or allocentric manner according to whether they contribute to a reference internal to the body of the navigator and/or with respect to a fixed point in the external environment (Retailleau et al., 2012). Research studies in animals have demonstrated the use of one or several sounds according to a fixed reference, thus showing the capacities of animals to follow a sound tropism or to integrate exafferent sound signals in a spatial context (Rossier et al., 2000; Watanabe and Yoshida, 2007). However, to our knowledge, to date there has been no demonstration of the use of a reafferent sound in rodents, which therefore represents a situation of additional interest for the study of visual-auditory sensory substitution.

On this basis, we put forward the hypothesis that the animals will be able to achieve a sensory substitution allowing them to perform a navigation by following a sound contour by means of a sensory-motor coupling based on seeking a sound and mastering a relation between their own actions and the expected auditory effects (here minimal in all-or-nothing). In this sense, we expect that there will be a progressive structuring of meaningful exploratory activity, starting with the appearance of behaviours of stopping when the sound is lost and acceleration when the sound is found again, and going on to a relevant sensory-motor strategy which maximizes the possibilities of finding and following the sound.

2. Materials and methods

2.1. Animals

9 male DA/HAN rats were used for the experiment of spatial navigation by sensory substitution. The animals were aged 50 ± 5 days at the start of the tests. The rats were kept in groups of 3 in standard animal cages with sawdust and straw. Food was freely available, whereas water was in limited supply during the period of the test. At that time, the drinking bottle was only available 2 h after passing the behavioural tests. The restriction of water to 2 h per day was introduced gradually over the course of a week. During this period, the animals were also familiarized with contact with the experimenter. Over the whole period of restriction, the state of health of the animals was regularly monitored.

The animals were lodged in a cabin which was ventilated and heated (21 °C ± 2), near to the experimental room. Light was regulated on a semi-inverted cycle (lighting starting at midnight and turned off at midday), which made it possible to test the animals during their stage of activity between 13 h and 19 h.

The research was conducted in conformity with the EU Directive 2010/63/EU concerning the protection of animals used for experimental scientific purposes.

2.2. Behavioral testing

2.2.1. General procedures

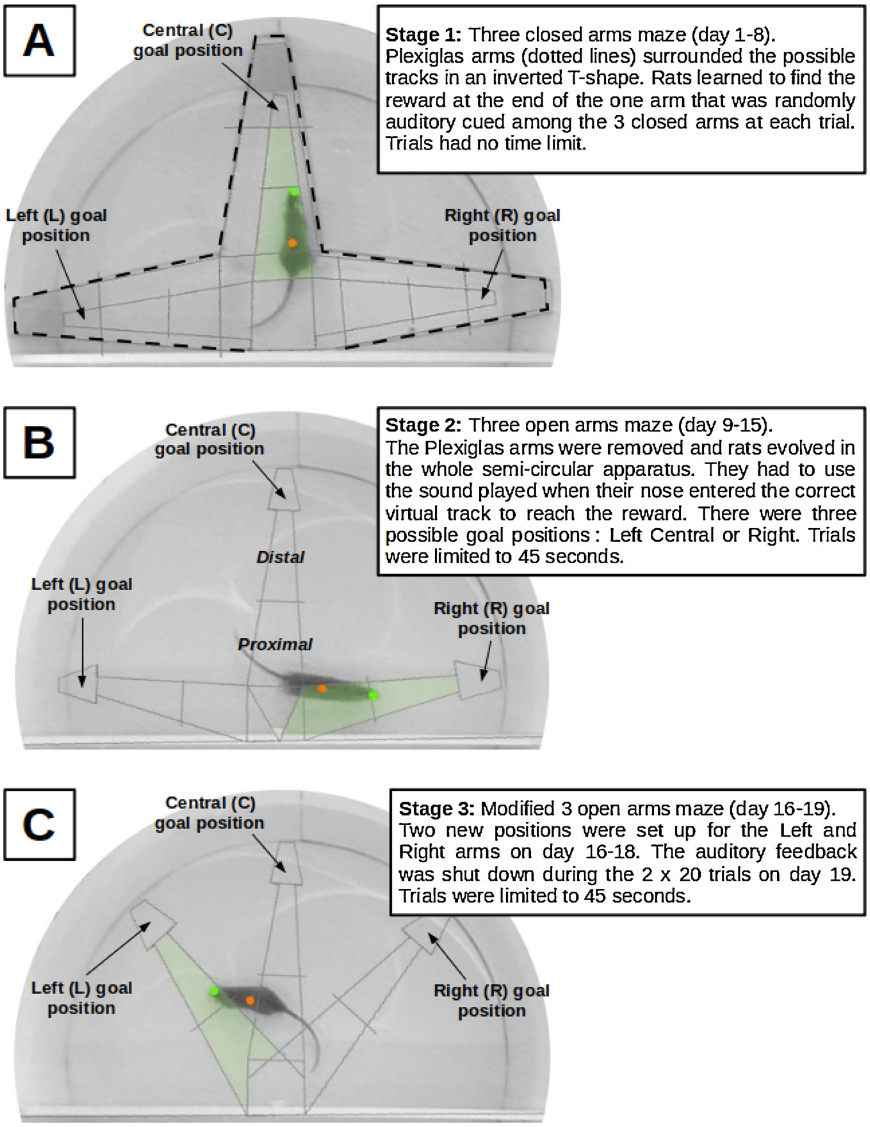
The experimental setup (Fig. 1) consisted of a semi-circular arena in ivory-coloured Lucoflex (1 m diameter / 30 cm high). The experimental room, situated in the basement, was totally dark; the ANY-maze® video-tracking device (Stoelting Co, Wood Dale, IL – version 4.89) made it possible to follow the movements of the animals under infra-red lighting by 3 projectors of 15–24 LEDs (wavelength 850 nm, Conrad, France). The darkness was measured at less than 0.1 lx by an Extech EN300 apparatus (Conrad, France) and a control experiment showed that the animals were not able to discriminate a white target from a black target (a rectangle in A4 format in each case) situated at 20–80 cm distance.

At each stage of the experiment (see details below), three virtual paths were demarcated using the ANY-maze software. As soon as the nose of the animal entered the path that was chosen by the system as the correct one for a specific trial, a continuous sound (4000 Hz, 55 dB) was played by means of the ANY-maze interface and a loudspeaker placed above the test device. When the nose of the animal entered the extremity of the correct path, referred to as the goal position, a reward of 80 μl of water was distributed at ground level by means of a metallic cannula of 0.8 mm. A new trial started each time the animal passed again by the departure zone at the intersection of the three possible virtual paths.

The experiment consisted of 3 consecutive stages (Fig. 1). Each stage consisted of 40 trials per day (2 sessions of 20 trials with an interval between sessions of at least 1 h). For each trial, the position of the correct path was defined by ANY-maze in pseudo-random manner among the three possible positions (with never more than 3 consecutive trials on the same path) by the ANY-maze software. The correct position for a specific trial was Left (L), Central (C) or Right (R).

2.2.2. Stage 1 – three closed arms maze

Stage 1 lasted 8 days (day 1 to day 8). During this stage, the virtual paths were enclosed, 2 cm from their limits, by Plexiglass arms (Fig. 1A). For each trial, the rats started at the centre of the apparatus and had to reach the extremity of the arm indicated by the sound stimulus in order to obtain the liquid reward. A new trial started when the animal returned to the centre. The trials in stage 1 did not have a time



Stage 1: Three closed arms maze (day 1-8). Plexiglas arms (dotted lines) surrounded the possible tracks in an inverted T-shape. Rats learned to find the reward at the end of the one arm that was randomly auditory cued among the 3 closed arms at each trial. Trials had no time limit.

Stage 2: Three open arms maze (day 9-15). The Plexiglas arms were removed and rats evolved in the whole semi-circular apparatus. They had to use the sound played when their nose entered the correct virtual track to reach the reward. There were three possible goal positions : Left Central or Right. Trials were limited to 45 seconds.

Stage 3: Modified 3 open arms maze (day 16-19). Two new positions were set up for the Left and Right arms on day 16-18. The auditory feedback was shut down during the 2 x 20 trials on day 19. Trials were limited to 45 seconds.

Fig. 1. Illustration of the experimental setup and the configuration of the paths: (A) Stage 1: 3 paths in closed format; (B) Stage 2: 3 paths in open format; (C) Stage 3: 3 paths of which 2 are new, in open format. Each path is divided into a proximal part, close to the zone of departure, and a distal part close to the goal (reward) position. In all stages, the goal position was chosen pseudo-randomly at each new trial. The green colour shows the path that was auditory cued by the system for a possible goal position: e.g. Central (in A), Right (in B) or Left (in C).

limit. However, when an animal remained immobile for more than 10 min, the session was interrupted and the mean parameters calculated on the basis of the trials computed during the day.

2.2.3. *Stage 2 – three open arms maze*

Stage 2 lasted 7 days (day 9 to day 15). The Plexiglass arms were removed and the animals could move freely over the whole semi-circular arena, while the position of the virtual paths remained identical to stage 1 (Fig. 1B). In order to avoid as far as possible deviant search strategies (e.g. the animal goes straight to different reward points and verifies each time whether or not there is a sound in the proximity), and to force the animals to use the sound flow, the reward was only delivered if the animal first traversed the proximal part of the sound track (*proximal* in Fig. 1B) before the distal part (*distal* in Fig. 1B) and finally the reward position (*goal* in Fig. 1B). The duration of each trial was now limited to 45 s.

2.2.4. *Stage 3 – modified three open arms maze*

Stage 3 lasted 4 days (day 16 to day 19). On the first 3 days, the rats had to generalize their learning to a new configuration of the paths (Fig. 1C). Now, the left and right paths were moved to an oblique position with respect to the central path which was unchanged. On day 19, the test conditions were strictly the same, except that the sound feedback was no longer played when the nose of the animal entered the correct path. This situation allowed us to obtain a good control on the influence of the sound in guiding the animal in the maze. Each of these trials was also limited to 45 s.

2.3. *Data recording*

Quantitative and qualitative measures were made for all 3 test stages. The quantitative parameters were measured with the help of the video-tracking ANY-maze software, whereas the qualitative parameters were observed and counted on the basis of the video recordings of the sequences of video-tracking.

During stage 1, the animals moved in a maze with 3 arms. The goal was to demonstrate the beginning of an active search for the sound, and the use of the sound in order to reach the position of the reward. We therefore measured quantitative parameters such as the distance covered to succeed a trial, or the number of errors per trial. An error consists of entering the extremity of an arm not indexed by the sound. In addition, the mean speed in an arm indexed by the sound was measured and compared to the speed in the two paths not indexed by the sound.

The analysis of the tracking videos made it possible to describe the progression of the search strategies in the following ways: systematic entry (the animal goes systematically to the extremity of each arm entered, whether or not there is a sound); U-turn strategy (the animal systematically turns back before the extremity of an arm if there is no sound); and a combined strategy (composed of both the previous strategies). Trials where the animal succeeded directly (i.e. the first arm entered did produce a sound and the animal went to the end of that arm) were not considered here. An error was counted when an animal triggered the sound in the correct arm but then turned back before reaching the extremity.

During stages 2 and 3, the main parameter used was the percentage of trials that were successful, i.e. when the animal obtained the reward in less than 45 s. The percentage of successful trials was analysed globally but also as a function of the positioning of the arm with sound reinforcement.

As for stage 1, a qualitative analysis of the behaviour was carried out on the basis of the video recording of all trials. We counted the number of successful trials in which the rat adopted a scan strategy (*scanning*). Such a strategy was defined by reaching the goal position with sweeping movements inside/outside the sound track (Fig. 2). Alternate coding were composed of failed trials and succesfull trials with *direct* strategies (i.e. going straight to the goal position without sweeping movement) or *alternative* (e.g. activating both proximal and distal zones, then losing the soundtrack and coming back the goal zone without using the tone) and non-determined strategies.

The behaviour was also observed when the animals crossed the auditory path diagonally. Thus we noted the number of reorientations which were relevant from a spatial point of view (i.e. centrifuge: moving towards the goal), compared to the inverse redirections (i.e. centripetal: towards the point of departure). This latter parameter was designed to analyse whether the animals also integrated spatial information about the setup, the possible position of the rewards and their position, in addition to information related to the presence or absence of the sound.

2.4. Statistical analyses

On account of the non-normality of the distribution of a large number of variables, the quantitative analyses were performed using the Friedman ANOVA (repeated measure/learning sessions). Pairwise comparisons were calculated with the Wilcoxon signed-rank test. The Holm method was used for P value adjustment in case of multiple comparisons. For qualitative data, Chi^2 tests were used to compare the proportions of the different strategies employed.

Effect sizes were calculated as W = χ^2_w / (sample size x number of measurement per subject − 1) for a Friedman ANOVA and as r = Z standardised value of the Wilcoxon test / square root of (n1 + n2) in the case of a Wilcoxon signed-rank test.

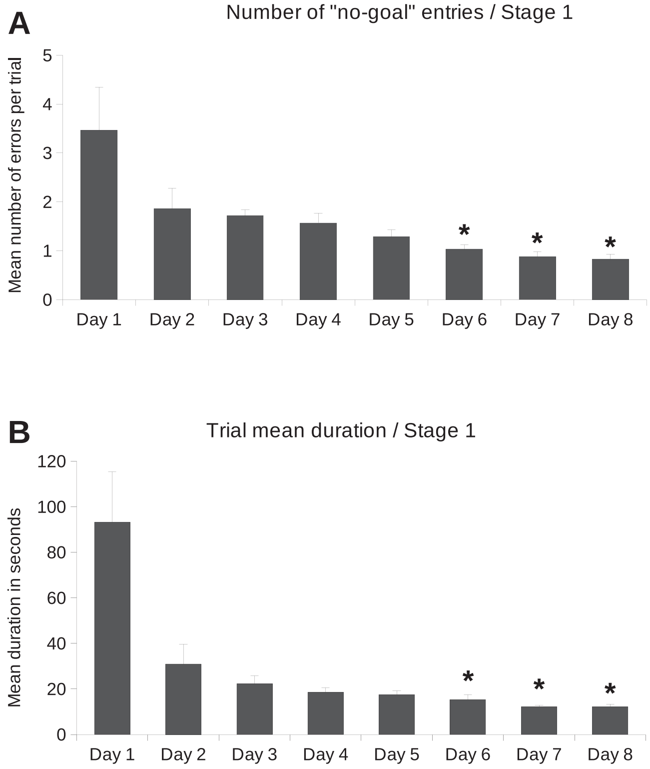


Fig. 3. Mean number of entries into the non-goal zone (A), and mean duration of a trial (B), for each day of stage 1. The data are presented as mean + SEM. Statistics: multiple comparisons by Friedman ANOVA; * p < 0,05 by comparison with Day 1.

3. Results

3.1. Stage 1

During the first stage of the study, the animals were exposed to maze with 3 arms, in total darkness. The number of errors (i.e. the number of entries into a goal area not indexed by the sound) is shown in Fig. 3A; it decreased significantly over the days of the trials (χ^2_w = 42.26, df = 7; p < 0.001 | Effect size W = 0,67). Post-hoc tests show that the difference compared to day 1 was significant on days 6, 7 and 8 (p < 0.05 | Effect size r = 0,63 for the day 1 *vs.* day 8 comparison). The analysis of the mean time required to complete a trial (Fig. 3B) also shows a significant lowering over the course of the days of

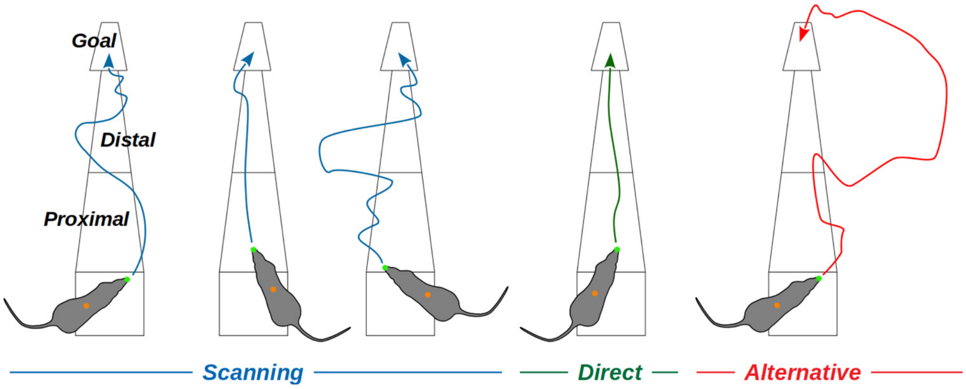


Fig. 2. Illustration of the strategies in stages 2 and 3: scanning was defined by reaching the goal position with sweeping movements inside/outside the sound track (blue); a direct strategy consisted in going straight to the goal position without sweeping movement (green); an alternative strategy was counted when the rat activated both proximal and distal zones, then lost the soundtrack and came back the goal zone without using the tone.

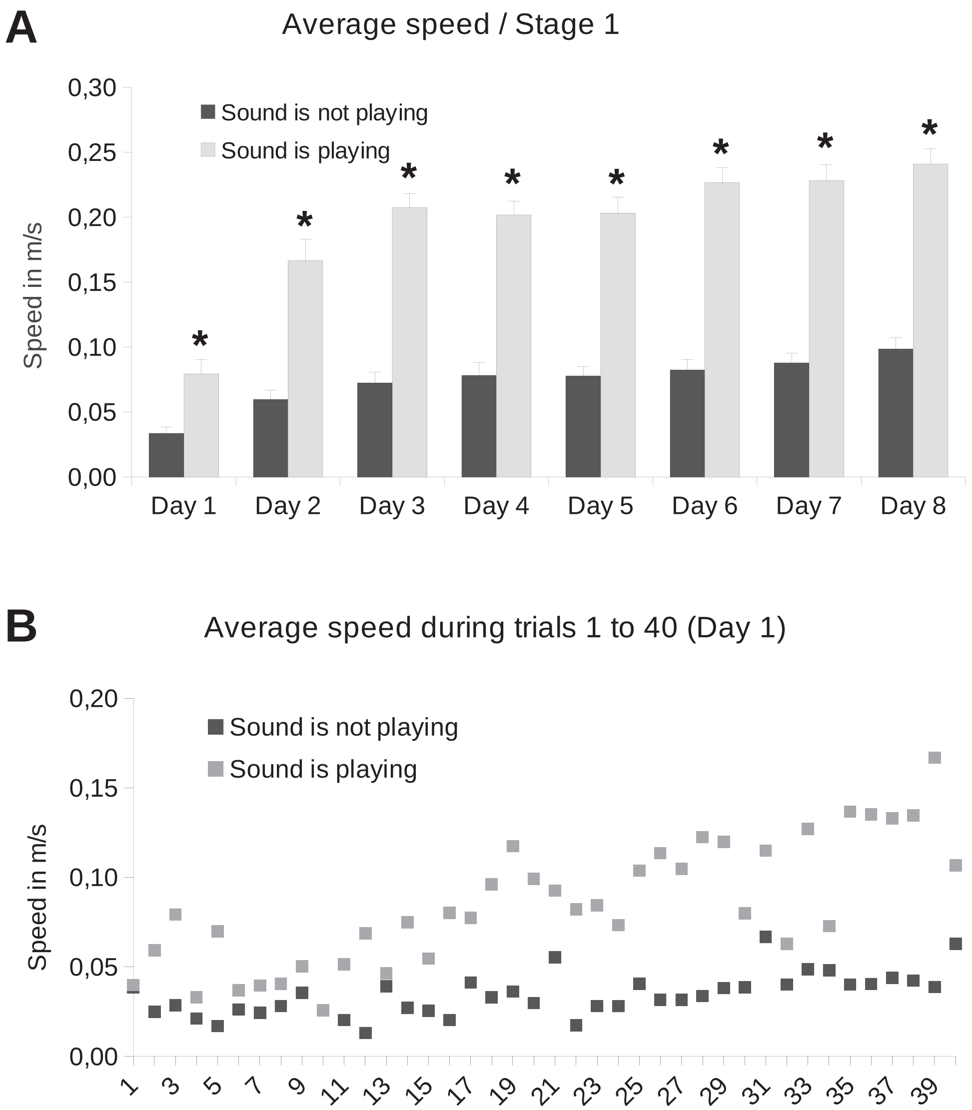


Fig. 4. Global comparison over the course of stage 1 (A), then detailed comparison within Day 1 (B), of the mean speed on the path indexed by the sound compared to the mean speed in the two paths non-indexed by the sound. Statistics: Wilcoxon, * $p < 0,05$ for intraday comparisons (sound is not playing vs. sound is playing).

the trials ($\chi^2_w = 51.44$, df = 7 ; $p < 0.001$ | Effect size W = 0.82) and significant differences between days 1 and days 6, 7 and 8 (p at least < 0.05 | Effect size r = 0,63 for the day 1 *vs.* day 8 comparison).

Analysis of the speeds of movement of the animals over the course of stage 1 (Fig. 4A) shows a significant increase in speed when the sound is playing ($\chi^2_w = 35.59$, df = 7 ; $p < 0.001$ | Effect size W = 0.56) but also when the sound is not playing ($\chi^2_w = 40.30$, df = 7 ; $p < 0.001$ | Effect size W = 0.56). The speed of movement when sound is playing is significantly greater on days 3, 6, 7 and 8 compared to day 1 (p at least < 0.05 | Effect size r = 0,63 for the day 1 *vs.* day 8 comparison), and the speed without sound is significantly greater from day 4 onwards compared to day 1 (p at least < 0.05 | Effect size r = 0,63 for the day 1 *vs.* day 8 comparison). However, two-by-two comparisons show, for each day of stage 1, that the speed of movement in the paths indexed by sound is greater than in paths not indexed by the sound (Wilcoxon; p at least < 0.05 | Effect size r = 0,63 for the comparison on day 8). Detailed analysis of the speed per trial shows that this difference appears towards the 10th trial and more clearly from the 20th trial of the first day (Fig. 4B).

The detailed analysis of the strategies adopted by the animals on day 1 and day 8 shows a clear change of their behaviour (Fig. 5). The number of trials with a strategy of systematically entering the goal zone whether or not the sound is playing decreases between day 1 and day 8, although the difference is barely significant statistically (p = 0.053). The number of trials that are successful with a strategy of systematically making a U-turn in a path with no sound, or with at least one U-turn (Combined), increases ($p < 0.001$ each time). The number of errors, corresponding to U-turns made in a path where the sound is playing, decreases from day 1 to day 8 ($p < 0.001$).

3.2. Stage 2

During the second stage of the test, from day 9 to day 15 of the experiment, the Plexiglass arms were removed and the animals behaved in an open semi-circular environment. As shown in Fig. 6A, the percentage of successful trials increased from 55% on the day 9 to 94% on day 15 ($\chi^2_w = 47.90$, df = 7 ; $p < 0.001$ | Effect size W = 0,89). Post-hoc comparisons indicate that the improvement with respect to day 9 is significant from day 11 onwards (p at least < 0.05 | Effect size r = 0,63 for the day 9 *vs.* day 15 comparison).

A detailed analysis of the successful trials shows that it is mainly trials on the left and right arms which are successful on day 9 (Fig. 6B). However, the percentage of successful trials when the reward is in the centre does increase significantly ($\chi^2_w = 44.56$, df = 7 ; $p < 0.001$ |

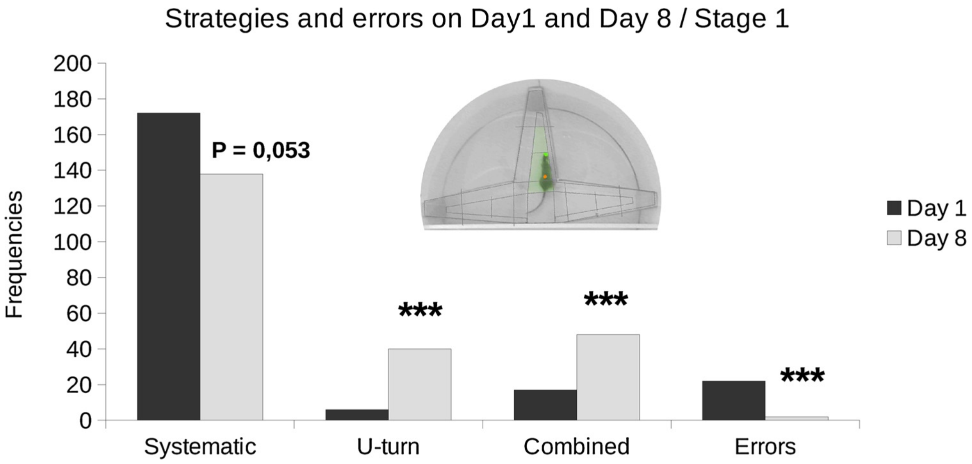


Fig. 5. Evolution of the search strategies over the course of stage 1. Systematic: the animal goes systematically to the extremity of each arm entered, whether or not there is a sound; U-Turn strategy: the animal systematically turns back before the extremity of an arm if there is no sound; combined strategy: both the previous strategies are used in a trial; error: when an animal triggers the sound in the correct arm but then turns back before reaching the extremity. Statistics: Chi-squared, $p < 0,001$ for the comparison between Day 1 and Day 8.

Effect size W = 0,83), and on day 15 the differences between trials on the right or left compared to the centre are no longer significant, whereas they were on the previous days ($p < 0.05$ | Effect size r = 0,63 for both comparisons on day 9).

Analysis of the number of successful trials involving a scanning strategy shows an increase between the first day (Day 9) and the last day (Day 15) of stage 2 (Fig. 8, left). Similarly, the number of trajectories bent towards the goal zone after encountering the sound increases between day 9 and day 15, passing from 9 to 30 occurrences ($\chi^2 = 11.31$, df = 1; $p < 0.001$). On the same days, the number of trajectories bent towards the zone of departure is not enough to be analysed (2 observations on day 9 and one observation of day 15). The

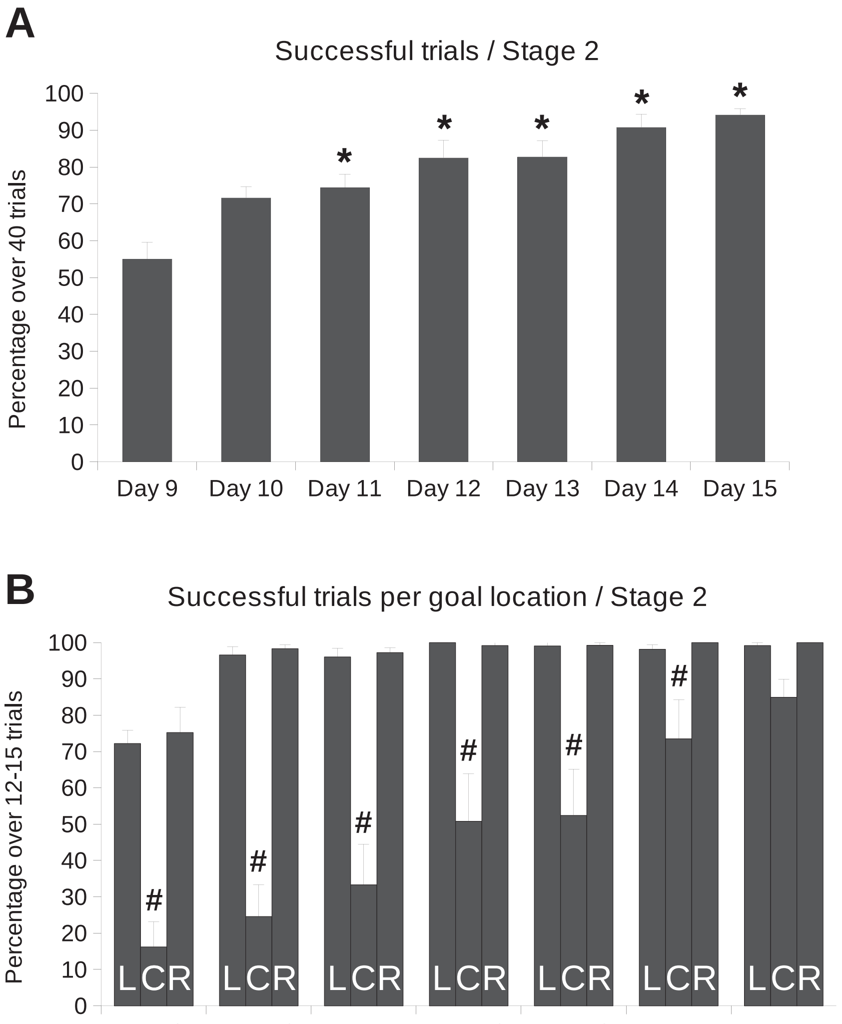


Fig. 6. A) Mean percentage of successful trials per day (40 trials) in stage 2. Statistics: multiple comparison, * $p < 0,05$ in comparison with Day 9. B) Mean percentage of successful trials according to the rewarded path (Left: L ; Center: C ; Right: R). Statistics: Wilcoxon, # $p < 0,05$ in comparison with the left and right paths. The data are presented as mean + SEM.

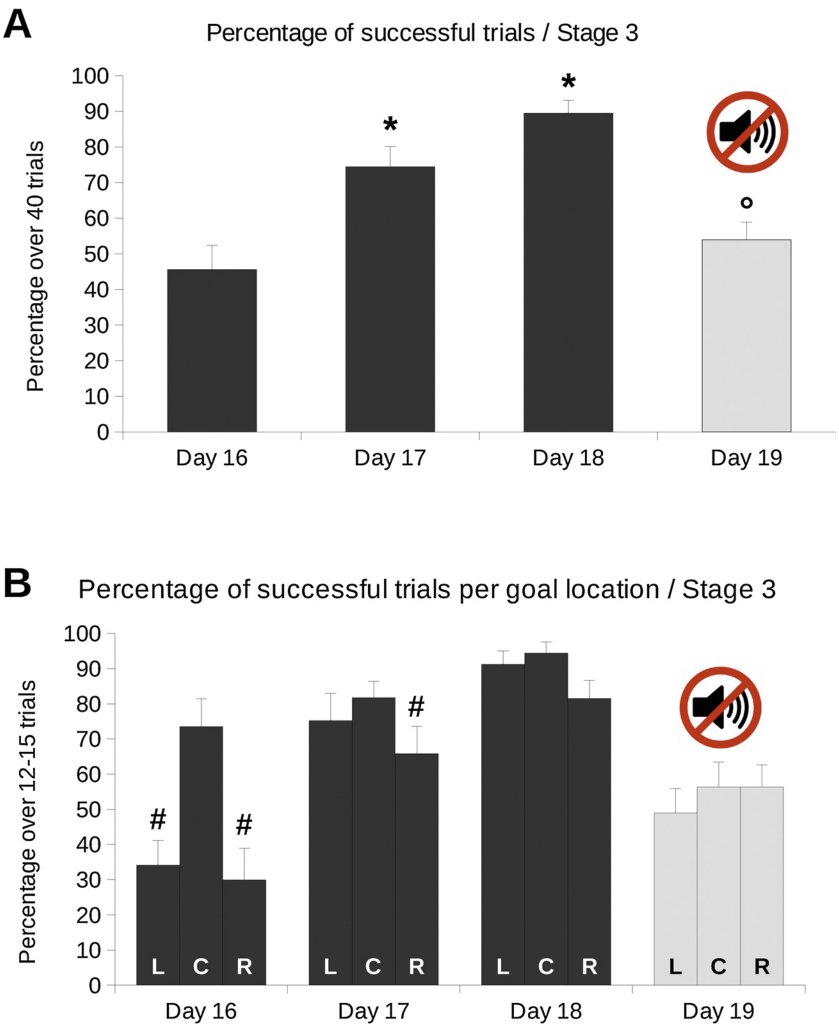


Fig. 7. A) Mean percentage of successful trials per day (40 trials) in stage 3. Statistics: Wilcoxon test, * $p < 0,05$ in comparison with Day 16; ° $p < 0,05$ in comparison with Day 18. B) Mean percentage + SEM of successful trials according to the rewarded path (Left : L, Center : C or Right : R). Statistics: Wilcoxon test, # $p < 0,05$ compared to the central path. The data are presented as mean + SEM.

number of inflexions towards the goal zone is greater than the number bent towards the departure zone for day 15 ($\chi^2 = 27.12$, df = 1; $p < 0.001$).

3.3. Stage 3

On the first day of stage 3 (day 16), with two new oblique tracks, the mean number of successful trials is 45.55% (Fig. 7A). It increases to 74,45% on day 17 and then to 89.45% on day 18 ($\chi^2_w = 15.94$, df = 7 ; $p < 0.001$ | Effect size W = 0,89). Both percentage at day 17 and day 18 are significantly higher than on day 16 ($p < 0,05$ | Effect size r = 0,63 on both comparisons). Again, the detailed analysis of successful trials shows that there is a difference between the central path, unchanged with respect to stage 2, and the two new oblique paths (Fig. 7B). On day 16, the percentage of successful trials is better on the central path than on the left ($p < 0.05$ | Effect size r = 0,63) and right ($p < 0.05$ | Effect size r = 0,60) paths. On day 17 the difference is still present between the central path and the path on the right ($p < 0.05$), and there is no longer a significant difference between the 3 paths on day 18.

On day 19, during the 40 trials without tone, the mean number of successful trials falls back to 53.9% (Fig. 7A). This performance is less good than that obtained on day 18 ($p < 0.05$ | Effect size r = 0,63) but is not significantly different from that on day 16. The analysis of percentage success rate per path in this condition does not show any difference between the 3 paths (Fig. 7B).

The analysis of trials which were successful due to a scanning strategy shows an increase between day 16 and day 18 ($\chi^2 = 31.98$, df = 1; $p < 0.001$) (Fig. 8 right). On day 19, when the sound feedback is cut, the number of trials successful due to a scanning strategy falls back to the value of day 16, thus creating a significant difference compared to the previous day ($\chi^2 = 39.87$, df = 1; $p < 0.001$).

The number of trajectories bent towards the goal zone after encountering the sound increases from 40 to 68 between days 16 and 18 ($\chi^2 = 7.25$, df = 1; $p < 0.01$). At the same time, the number of trajectories bent towards the zone of departure passes from 8 to 3 occurrences. Whether it be on day 16 or on day 18, the number of inflexions towards the goal zone is each time greater than the number of inflexions towards the departure zone.

4. Discussion

Our study has made it possible to validate a behavioural task for the study of sensory substitution in the rat comparable to that achieved in experiments with human subjects. Our results do indeed show that rats are capable of following a virtual path by means of minimal auditory information (the sound delivered is identical whatever the absolute or relative position of the animal with respect to the point of reward), in

Fig. 8. Number of successful trials with a scanning strategy (defined as reaching the goal position with sweeping movements inside/outside the sound track) in stages 2 and 3. Statistics: Chi-squared, *** $p < 0,001$ for comparisons between Day 15 and Day 9, and between Day 18 and Day 16. °°° $p < 0,001$ for the comparison between Day 19 and Day 18.

order to localize the position in space of a reward. In conformity with the theoretical framework of sensory substitution, also known as perceptual suppleance (Lenay et al., 2003), the animals seem to have developed a new form of perception which corresponds in particular to a locomotion and behaviours adapted to the search for sound.

The learning accomplished in the course of our study comprises several stages which make it possible to bring the animals progressively to succeed in the final task. The point is that contrary to a task with adult human subjects, in the present case it is not possible to convey explicitly the instructions and the mode of functioning of the sensory substitution device. It is important to note this point because it is known that in experiments conducted with humans, the explanation of the situation by means of verbal instructions is an important condition for the true development of a sensory substitution (Auvray et al., 2005; Epstein et al., 1986). In the course of the first stage of the test, the animals discovered the experimental setup, the possibility of obtaining a reward by moving to the extremity of the arms, and the sound which is triggered in certain conditions. Quite rapidly, they associate the sound and the reward and modify their behavior in the presence of the sound. Initially that results in moving faster when the sound is present. Later, the entries in the extremities of arms which are not rewarded decrease – the animals make a U-turn before arriving at the end of the arm – and one observes the development of behaviors where the animals test for the presence of sound or not at the entry to the arms. From this moment on, the animals are already behaving as though they are seeking the sound which, even absent, has become an important element in their exploratory activity. At this stage, the data obtained show that the animals do not content themselves with simply responding to stimuli from the environment, but that they actively seek them. We consider that here we have provided objective behavioral elements which bear witness to agency in the animal, and which constitute the premises for putting in place an effective exploratory strategy (Buhrmann and Paolo, 2015). This point, described in the literature on humans, thus corroborates the interpretation which can be given of the work of Jékely et al. (2008) on orientation and locomotion towards light even in primitive forms of life such as zooplankton, to the effect that locomotion serves first and foremost to seek relevant sensory returns.

During the subsequent stages of the study in an open environment, still in complete darkness, we have shown that the mechanism of sensory substitution is inscribed in a multi-sensoriality that the animal must manage. In the conditions of the stage 2, we observe that initially the animals have good performances on the left and right paths, which border on the edge of the arena, but fail to find the central path when that is the path with the reward. This confirms the preponderance of the tactile modality in learning in rodents (Roohbakhsh et al., 2016). However, over the days and since the tactile sense loses its relevance in the situation of search in an open arena, the animals adapt their exploration with a view to exploiting the sound in order to guide their movements. Thus we observe that the number of trials which are successful in the centre increases. In the course of stage 3; the animals are able to generalize the process of sensory substitution to new positions of the lateral left and right paths which are oblique with respect to the central path. Their mastery of the determination of the occurrence of sounds as a function of their actions thus allows them to improve their performances in just a single day.

Finally, when the possibility of sensory substitution is suppressed by extinguishing the loud-speaker during the 40 trials of day 19, that causes a decrease in the performances of the animals. The same effect is found in other studies in the literature. When the sound feedback of the sonar system which equipped the young macaques was cut, the animals were no longer able to explore their environment, to grasp objects or to discriminate textures (Strelow et al., 1987). It was exactly the same for studies where the cortical stimulation in response to the activation of an infra-red captor (Thomson et al., 2013) or a geomagnetic compass (Norimoto and Ikegaya, 2015) was cut.

However, the animals do succeed a substantial number of trials in this control stage. This shows that the performance of the animals did not rest solely on the possibility of a sensory substitution. The animals also made use of idiothetic indications stemming from the configuration of the arena (i.e. one part flat and one part semi-circular; materialized positions of possible points of reward; centrifugal orientation of possible paths). This hypothesis is confirmed by the majority of centrifugal orientations taken by the animals after having crossed the virtual path, and thus having heard then lost the sound. This result is important since it lends support to the idea that a sensory substitution is never limited to a single sensory modality; *ad minima,* and as a function of the movements of the animal necessary to trigger the production of sound signals, proprioception is systematically involved. The work of Thomson et al. (2013) is no exception in this regard, since the rats in this study perceive new « visual » information (i.e. in the infra-red range) but continue to see in the spectrum of visible light (in particular the 3 possible positions of the rewards). These animals thus manage a co-occurrence of two sorts of signals, one natural and the other artificial. An extension of this work could have consisted in testing the animals in complete darkness, and to analyze in detail their movements to demonstrate strong coupling between their orientation and the capture of the infra-red signals.

In the work of Norimoto and Ikegaya (2015) the animals also perform in the dark, but move in a maze with walls that it is possible to touch, unlike the open space proposed in our study. In addition, in the studies of Thomson et al. (2013) and Norimoto and Ikegaya (2015), the direction to be taken is indicated by the sensory feedback since the latter is only provided when the animal is in the correct orientation. Our task is more complex in this respect; here, the sound does not carry any indication about direction, and only becomes meaningful through the interactions of the animal with the virtual path and in particular successively entering and leaving the path. In this respect, our study demonstrates the possibility of minimalist sensory substitution in animals, which has been shown for humans by means of the TACTOS device (Rovira et al., 2014; Ziat et al., 2007) or The vOICe device (Auvray et al., 2007; Meijer, 1992). This aspect of our work must however be qualified. The paths to be followed are both straight and oriented in centrifugal fashion with respect to the centre and the point of departure for the trials. However, the paths are conical and one does observe micro-scanning behaviours towards the end of the path, which indicates that the animals do not rely solely on a form of integration of the trajectory.

A final aspect concerns the very long duration required for the acquisition of our task. In this, our study rejoins that of Thomson et al. (2013) where the animals also performed numerous sessions, using a visual stage and then a “blind” stage with only infra-red light available. In the case of Norimoto and Ikegaya (2015), the animals learned to navigate in a setup which “frames” the movements, as in stage 1 of our study. These 3 studies show the complexity of the learning not only of the sensory substitution itself, but also its mobilization for a given task, and this without the possibility of providing verbal instructions concerning either the technical aspect of the situation or appropriate strategies for learning. Everything must be discovered progressively by the animal. We tried putting the animals immediately in the final situation (i.e. stage 3), and found that they were incapable of succeeding in the task even after a large number of trials (data not shown). In the situation set up by Strelow et al. (1987), the animals seem to have adopted the setup more rapidly but were continually exposed to the sensory substitution device. In our experiment, and in those of Thomson et al. (2013) or Norimoto and Ikegaya (2015), the rats were only exposed for several minutes per day to the sensory substitution. Doubtless, a protocol with continuous exposure would make it possible to improve the duration of learning (Remmelink et al., 2015). On the other hand, it is also possible that a species of primate, such as the macaque, would be faster at this sort of learning than the rat, because less specialized on the sensory level and more apt for multimodal transfers.

5. Conclusion

In conclusion, by means of a novel and integrated experimental situation, our work supports the idea that a functional sensory substitution, similar to that observed in humans, is possible in rodents. The qualitative analyses of this behavioural study have also made it possible to affirm the agency of the learning process, which strengthens the proximity with behaviours observed in humans. The robustness of the results augurs well for the possibility of studying in finer detail the conditions for sensory-motor coupling and the underlying cerebral plasticity. However, we consider that it would also be appropriate to consolidate these findings by proposing to the animals a more complex situation, where the number of trajectories would be greater and multi-oriented, in a larger circular space, and containing a single point of reward situated in the centre. This progress of the experimental protocol would make it possible to appreciate the capacity for generalization in the rat.

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