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TUTORIAL

Beyond sensory substitution—learning the sixth sense

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Abstract

Rapid advances in neuroscience have sparked numerous efforts to study the neural correlate of consciousness. Prominent subjects include higher sensory area, distributed assemblies bound by synchronization of neuronal activity and neurons in specific cortical laminae. In contrast, it has been suggested that the quality of sensory awareness is determined by systematic change of afferent signals resulting from behaviour and knowledge thereof. Support for such skill-based theories of perception is provided by experiments on sensory substitution. Here, we pursue this line of thought and create new sensorimotor contingencies and, hence, a new quality of perception. Adult subjects received orientation information, obtained by a magnetic compass, via vibrotactile stimulation around the waist. After six weeks of training we evaluated integration of the new input by a battery of tests. The results indicate that the sensory information provided by the belt (1) is processed and boosts performance, (2) if inconsistent with other sensory signals leads to variable performance, (3) does interact with the vestibular nystagmus and (4) in half of the experimental subjects leads to qualitative changes of sensory experience. These data support the hypothesis that new sensorimotor contingencies can be learned and integrated into behaviour and affect perceptual experience.

(Some figures in this article are in colour only in the electronic version)

1. Introduction

Is perceptual awareness in the brain? Recent years have seen numerous efforts to pinpoint the neural correlate of consciousness (Crick and Koch 1998, Chalmers 2002, Crick and Koch 2003). These studies try to identify relevant neuronal structures and the type of activity giving rise to conscious perception. The role of primary sensory areas versus higher sensory areas has been the focus of many studies investigating binocular rivalry (Leopold and Logothetis 1999). Although primary sensory areas are intensively studied, their contribution to perceptual awareness is highly controversial (Tong 2003). Furthermore, a number of arguments have been put forward that the relevant neuronal structures reside in higher cortical areas (Crick and Koch 1998, Logothetis and Schall 1989). This highlights the alternative that non-sensory cortical areas might serve a decisive role in perception.

A problem relating to theories based solely on a neuronal correlate of consciousness is the emergence of different qualities of perception pertaining to different sensory modalities. Once physical events are transduced to neuronal activity by peripheral sensory organs, the information on the quality of peripheral events seems to be lost. Why should the activity of neurons in different areas give rise to qualitatively different perceptual events? In contrast to these theories, O’Regan and Noë (2001) suggest that perception is not established by the activation of specific brain structures, but by a lawful connection of perception and action. The qualitative difference between two modalities is neither a result of the site of sensory processing in the cortex, nor the differences inherent in the neural code. Instead, it is a result of the difference in structural invariants of the change of sensory input resulting from action. Modalities are different because these sensorimotor dependencies are different for each sensory organ and stimulus source. The immense plasticity of the brain (Kaas 1991, Elbert *et al* 1995) enables it to extract these dependencies. Hence, the quality of sensory awareness is determined by the systematic changes of afferent signals resulting from behaviour, called sensorimotor contingencies (O'Regan and Noë 2001).

Let us consider the example of sensorimotor contingencies in vision: the human retina is inhomogeneous due to the blind spot and an irregular distribution of rods and cones. Yet, our perception of the visual world neither features inhomogenous colour distribution nor holes due to occlusion or lack of photoreceptors in the retina. Looking at a straight line while moving towards it produces a very different pattern of photoreceptive activation than moving the eyes along the same line. Yet, we perceive the two lines to be identical. Sensorimotor contingencies connect these distinct patterns of activation to the motor actions that produce them. Moving towards a straight line causes the area of the retinal activation to expand in a certain manner. The pattern of activation remains constant when moving one's gaze along the line. Rules coupling neuronal activation and action do not suffer from the aforementioned imperfections of the retina. Combining rules like the two described earlier, also account for the phenomenon that the two populations of activities are perceived to be the same line.

Inspiration and support for skill-based theories of perception have been provided by experiments on sensory substitution. Sensory substitution, originating from experimental sensory prosthetics, deals with devices replacing one (possibly defective) modality by providing the input via another modality. Bach-y-Rita has pioneered the transformation of visual stimuli to haptic information in normal and blind subjects (Bach-y-Rita *et al* 1969, Bach-y-Rita 1972). A device transformed images captured by a video-camera into vibrotactile information transmitted to the skin on the back of the subject. Blind subjects utilizing this sensory substitution device were able to use the visual information in a purposeful and goal-directed manner. Furthermore, the subjective quality of this artificial visual perception was different from anything the blind subjects had experienced before, and visual objects were found to be located in the external space instead of on the skin (Bach-y-Rita 2003). However, this change in perception only occurs when subjects are allowed to actively manipulate the camera, exploring their surroundings in a natural manner (Bach-y-Rita 1972, 2004). These findings support the idea that a sensory modality is a particular way of actively exploring the environment. If this is the case, and a modality is constituted by a set of laws connecting action to a change in sensory input, then a modality is not bound to a particular sensory apparatus (Hurley and Noë 2003, Noë 2004).

Visual sensory substitution experiments, however, face two fundamental problems. Firstly, the information rates typically handled by the visual system far exceed those of the somatosensory system. Thus, it cannot be expected that perception created by a sensory substitution device resembles the normal visual modality to a large extent. Secondly, even in blind subjects, the visual cortex may be involved in processing signals relayed by a sensory substitution device. Braille reading activates the primary visual cortex in blind subjects (Sadato *et al* 1996, 1998, Wittenberg *et al* 2004). Hence, it is difficult with this experimental approach to differentiate between neural and skill-based theories of perceptual awareness. Nevertheless, skill-based theories suggest that it is possible to create perceptual experiences by imposing sensorimotor contingencies of the visual domain on to somatosensory signals. In these initial explorations a number of similar devices have been developed and tested, yielding similar results (Meijer 1992, Bach-y-Rita *et al* 1998, 2003, Hanneton *et al* 1999, Arno *et al* 2001, Lenay *et al* 2001, Bach-y-Rita and Kercel 2003, Bach-y-Rita 2004).

Let us presume firstly that the differences in sensorimotor contingencies constitute the qualitative differences between modalities and, secondly, that the brain is generic and plastic (Ramachandran 1993). Consequently, providing access to a novel set of sensorimotor contingencies, not supplied by any other sensory apparatus, will give rise to a qualitatively new perceptual experience, thus creating a new modality.

In order to investigate this hypothesis experimentally, we had to first find a sensory domain differing sufficiently from the existing human modalities to be describable by a new set of sensorimotor contingencies and then provide the subjects with an artificial means to access and use the information from this new domain. We did so by constructing a belt enabling its user to infer his orientation relative to magnetic north via vibrotactile stimulation.

That way, the person wearing the belt is provided with permanent input about his direction relative to the earth's magnetic field. Even though the existence of magnetic senses in certain animals shows that this information can be useful (Ritz *et al* 2002, Meyer *et al* 2004, Mora *et al* 2004, Mouritsen and Ritz 2005), in humans there is no indication of a natural sensory organ providing this kind of information. As this sensory domain differs sufficiently from existing human modalities to be describable by a new set of sensorimotor contingencies, the present device establishes not sensory substitution, but direct sensory enhancement.

Providing information on the environment not covered by an existing sensory organ raises many questions. Would this information be utilizable for behaviour when normal sensory information is diminished and under natural conditions? Would it take conscious effort to use it, or would it allow for subcognitive use? What would be its subjective quality? We formalize these questions in four hypotheses:

- *Weak integration hypothesis.* The sensory information provided by the belt can be processed and improves performance in some tasks.
- *Strong integration hypothesis.* Information on orientation of the belt is firmly integrated in human perception and sensory signals of the belt, inconsistent with sensory inputs provided by the other modalities produce measurable responses.

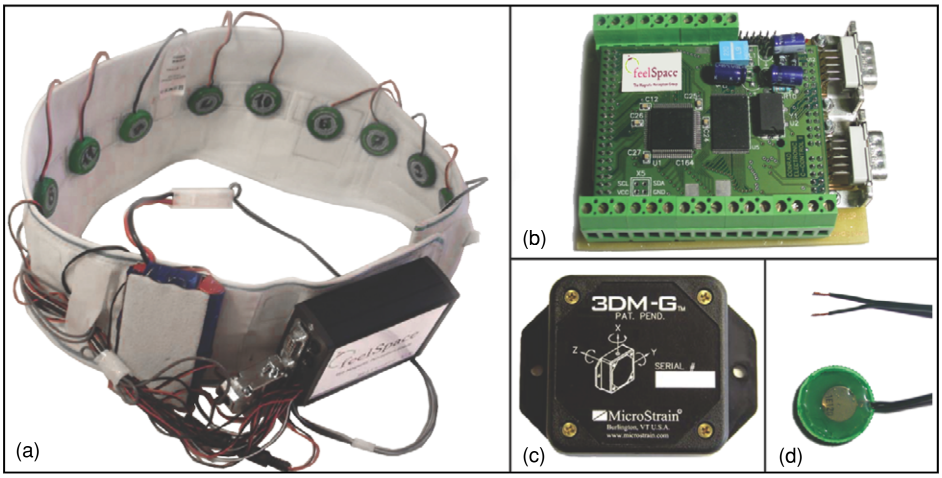

Figure 1. The feelSpace belt device. (a) The black box in front contains the main control unit (b) in which the 3DM-G compass (c) is plugged. The free socket optionally connects the belt to a PC. The (green) caps contain 13 vibrators (d). The (blue) pack on the left is the battery pack. The compass and the vibrators are attached to the belt by Velcro® fasteners.

- *Subcognitive processing hypothesis.* Sensory information provided by the belt can be processed at least partly without attention.
- *New modality hypothesis.* Mastery of the belt-imposed sensorimotor contingencies results in qualitatively new perceptual experiences.

In what follows, we describe four sets of experiments designed to investigate these hypothesis. After 6 weeks of training we evaluated performance and perception by a battery of tests, including outdoor orientation tasks, navigation in a virtual environment, nystagmography, posturography and subjective reports. These experiments investigate to what extent new sensorimotor contingencies can be learned and integrated into behaviour and whether the newly acquired sensory information has a profound effect on perceptual experience.

2. Methods

2.1. The belt

We developed a device that delivers global orientation information as vibrotactile stimulation to the user (figure 1). It maps directional information measured by a compass via a control unit to a set of vibrators by activating the element pointing north.

The device should provide reliable orientation information over a period of several weeks in a continuous manner. Therefore, we designed it as a belt worn around the waist. It measures the orientation of the trunk around the body's main axis. Arm, leg or head movements are often independent of the body's main axis and do not influence the orientation measurement. Also, the torso is an area where the restraints in daily movements caused by the device are minimal, while the spatial resolution for sensitivity of vibration is satisfactory (Cholewiak 2004). We equipped the belt with a power supply, compass, a control unit and 13 vibrating miniature motors attached to the inside of the belt, which provide the tactile stimulation onto the torso's perimeter. The compass feeds information about the direction of north to a microprocessor based control unit, which in turn activates the vibratory element that is directed towards north.

The belt had to be suited for all day long usage over several weeks and wearing comfort and skin friendliness were important aspects. We used an orthopaedic rib fracture belt as the basis, which is designed for long-term usage. It is made of skin-friendly material that is comfortable to wear, flexible but nevertheless stable, as it should support the body. The material's firmness allowed us to attach all components on to this basis and to have reliable, fixed places on the skin especially for the vibrators.

To support comfort and ease of use, the information provided by the compass needs to be as accurate, fast and reliable as possible. Hence the hardware needs to cope with sudden changes in motion velocity and direction associated with the kinetics of human motion. We tested and compared several compass systems. The MicroStrain's DM-G compass provides a tilt range of 360° over all three motion axes. Combining gyroscopes, accelerometers, and magnetic sensors, it compensates for the shortcomings of each individual sensor and gives an excellent estimate of orientation. Fortunately, this model had already been successfully tested when tried on the human body (Churchill 2004). The compass attached to a subject's knee while walking, jumping and rising from a chair can cope with bodily movements as well as magnetic disturbances in everyday environment. Thus, the MicroStrain's DM-G compass provides the information most adequately.

The control unit mapping the information from the compass to the vibrators is mounted on a circuit board that provides additional components for interfacing with power supply, vibrators and serial connections. In a pilot study, we observed that the beat of several vibrators active simultaneously is annoying for the subjects. Therefore we decided to activate only one vibrator at a time. If the person wearing the belt turns clockwise, the site of stimulation jumps to a vibrator located in counter-clockwise direction. The subjects can sense the direction of north through a vibration on the waist. According to previous psychophysical experiments discrimination thresholds for vibration in different body areas are quite diverse, and detection thresholds of vibration are not equally good on every position (Cholewiak 2004). Nevertheless, our objective was to use as many vibrators as possible to make the switching between adjacent stimulation sites appear nearly continuous. This is approximately achieved with a design of 13 vibrators distributed evenly around the waist. Although the delay time of the compass is low, the latency in vibration of the element pointing north is just noticeable. This was mainly due to the small rotation motors of the vibrators that need some time to get active. Furthermore, the unit can be interfaced from a PC. This additional feature was used in some of our experiments (on virtual environment and physiological tests) to provide wrong belt information or to simulate a virtual north.

The power supply was designed to provide sufficient power for a continuous operation of more than 10 hours. This is achieved by an array of standard 1.2V NiMH rechargeable batteries.

2.2. *Subjects*

Four experimental subjects and four controls participated in the study. Their ages ranged from 20 to 43 years, and in each group there was one female and three male participants. One of the experimental subjects is an author of this paper, which is not desirable for scientific reasons. However, as the experiments are of an exploratory nature, it is not possible to completely characterize and exclude potential adverse effects on the experimental subjects beforehand. Therefore, for ethical reasons, it seemed advisable to include an expert subject and to perform this project in part as a self-experiment. A pilot study with a first generation sensory enhancement device and follow-up experiments, which are currently in progress, are mentioned in the discussion section. Behavioural and physiological tests took place before and after a training period of 6 weeks.

2.3. *Training*

The training period began immediately after the pre-training tests and consisted of two parts: experimental subjects were required to wear the belt during waking hours over the entire training period. Both experimental subjects and controls had to exert at least 90 min of outdoor activity each day. To give additional behavioural relevance to the information provided by the belt, subjects and controls engaged in a weekly outdoor training. It consisted of simple pointing tasks. Participants had to stand at a starting position in an empty area facing a clearly visible reference point, in this case a camera tripod. Afterwards they were blindfolded and began to move around, following the verbal instructions of a supervisor. Instructions were in the form: ‘Turn 45° to the left, now walk 10 steps.’ The numbers of instructions in each run varied, leading to different complexities of runs. After each run, subjects were asked to point to the direction of the reference point they faced in the beginning. Then they were allowed to remove the blindfold to see how they had performed. These training sessions lasted for about half an hour per person per session.

2.4. *Experiments*

The experiments included several different conditions. In the normal operation mode the belt vibrates towards north consistently (correct belt information, CI). As a control we always tested the performance with the belt switched off (no belt information, NI). In two of the experiments described below, the signals provided by the belt were modified, so that it provided inconsistent information (wrong belt information, WI).

3. Outdoor navigation tasks

3.1. *Introduction*

To test whether the information provided by the belt can be used effectively (*weak integration hypothesis*) and to quantify the navigational skills of our subjects, we employed outdoor navigation tasks, which were conducted once before and once after the training period. The weak integration hypothesis predicts that experimental subjects should show improved performance in the orientation tasks when using the belt. This difference in performance should be significantly larger than in the control group.

A well-known method for quantification of navigational skills is homing tasks: a blindfolded subject is guided to a point in space (the so-called home point) and is asked to memorize its location. Afterwards, the subject is led along the edges of shapes of varying complexity and is then asked to return to its home point using the shortest possible route.

Homing tasks can be performed in allothetic (navigating according to salient landmarks) or in idiothetic mode (relying on one’s own recent displacements in space). As we were aiming at idiothetic orientation, our task was designed accordingly and the subjects were blindfolded (Stepankova 2003).

3.2. *Methods*

In a large and empty university courtyard, polygonal shapes of varying complexity were drawn on the ground. We used three-sided, four-sided and five-sided polygons (two of each, see figure 2 for some exemplary shapes).

There were two experimental conditions: correct belt information (CI) and no belt information (NI). In the CI condition the belt was consistently vibrating towards the north. In the NI condition the belt was switched off. CI and NI trials occurred in alternating order to balance the learning effects.

The blindfolded subjects were unaware of the shape of the polygons and were led by the experimenter over the whole polygon but the last edge. Arriving at the last vertex of the polygon, the subjects were asked to home in on their starting position along a direct path. The ideal route would be the edge connecting the first vertex (home) to the last vertex of the polygon. In the case of a triangular shape, for example, the subject was led over two sides, and the third side would

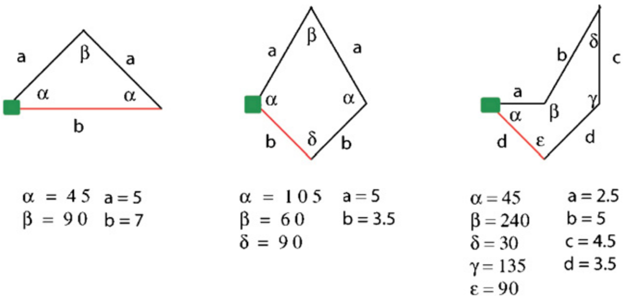

Figure 2. Shapes in the outdoor homing tasks: the (green) rectangle denotes the starting point, i.e. the 'home'. The trajectory is clockwise starting from the home. The light (red) side of the shapes depicts the ideal homing vector. The Greek letters denote the angles in degrees, the roman letters, the length of the side in meters.

be the ideal homing vector. We measured the distance between the actual and recalled starting points, and the angular deviation between the performed and ideal homing vectors.

3.3. Results

Measurements of distance and angular error were highly correlated. Therefore, we only report the results on the angular deviation. Furthermore, results in the six shapes were similar enough to collapse the measurements in order to increase the number of trials. Significance was tested using the signed rank test.

We investigated whether the mean error for each subject changed after training with the belt, and if there was an effect of the experimental condition (CI versus NI conditions). For statistical comparisons we also collapsed the subjects in each group.

Before training there was no performance difference between experimental and control subjects, regardless of whether the belt was switched on or not ($p > 0.05$). Neither for experimental nor for control subjects, the condition of the belt (CI or NI) changed performance levels. After training, the same comparisons between CI and NI revealed identical results for the controls. Apparently, the weekly training did not change the performance in either of the belt conditions for the control group ($p > 0.05$). For the subjects who were trained with the belt, a comparison of NI and CI conditions showed fewer errors in the CI condition than errors in NI condition ($p < 0.05$). Their performance improved when provided with correct belt information (figure 3).

This was not due to a decrease in performance in NI condition, since there was no statistical difference between pre-training and post-training NI trials ($p > 0.05$). Additionally, experimental subjects were better than any other control subject, as long as their belt was switched on.

3.4. Discussion

We investigated the subjects' performance in outdoor navigation tasks. Our analysis revealed that for experimental subjects the error decreased only when their belt was switched on. This led to a superior performance compared to that of the control group.

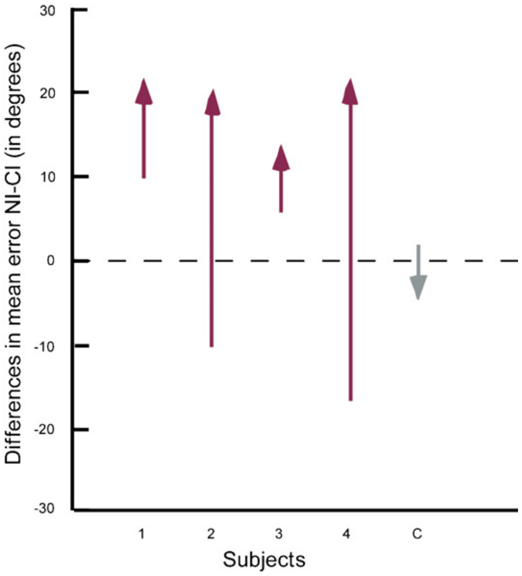

Figure 3. This graph depicts the difference between CI and NI conditions. The mean error for all shapes in the NI condition is subtracted from the CI condition. The arrows depict the development of performance before versus after training. Their direction indicates these two points in time. The dark (red) arrows refer to single subjects. The grey arrow is the mean of control subjects' performance. Note that after training, this difference becomes positive for experimental subjects.

In outdoor environments, factors such as heterogeneous distribution of light intensity, localized sounds or wind direction may be used as landmarks and thus change the purely idiothetic navigation mode. However, in our design each CI-trial was followed by a NI-trial—hence, these external factors should have been nearly identical.

There were no differences in performance before training—the performance of the two groups was similar, and the belt information did not make a difference for neither of them. We have shown that the direction information provided by the belt can be used effectively after training. We succeeded in quantifying the effects of the belt on navigational skills. Thus, we confirmed our hypothesis that the sensory information provided by the belt can be processed, and training improves performance.

4. Navigation in a virtual reality environment

4.1. Introduction

In this paper we investigate the interaction of the information supplied by the belt with normal sensory signals, in particular visual information. Thus, this experiment is geared to address the strong integration hypothesis.

As an experimental paradigm, we selected a typical orientation task of every day life, like finding a place in an urban environment. In the real world the benefit of the information supplied by the belt on navigation in such an environment is difficult to measure in a controlled way. The multitude of spatial cues and the typically large timescale of navigation in real world environments allow ample influence of cognitive analysis. In a virtual environment, in contrast, we can overcome these problems by isolating the effect of the belt from additional cues that influence navigation performance. Furthermore, we can design a time competitive task in which cognitive reasoning is limited. Therefore, a virtual environment offers important advantages to investigate the integration of information provided by the belt in a navigation task. Here we design a time competitive task in which the participants have to navigate within a complex environment. During the task we provide information of a virtual north to the belt while other spatial cues are well controlled. Furthermore, we can generate conditions in which the belt provides misleading heading information. In this condition the vibration of the belt does not reflect the actual rotation of the subject in the virtual world. By comparing the subject's performance in different conditions—with correct belt information (CI), with wrong belt information (WI) and without any belt information (NI)—we estimate the level of integration of the belt information.

According to the strong integration hypothesis the experimental subjects are expected to show an improved performance with correct belt information. In contrast, incongruent information by the belt is expected to decrease performance compared to baseline.

4.2. Methods

We designed a time competitive task in which the participants had to navigate within a complex environment. To achieve environments close to realistic settings the map layout was inspired by city maps of Munich and Paris. The user was not provided with any information about the maps prior to the experiment, but had to explore it while solving a task. In these environments we placed eight numbered boxes at fixed locations. The subjects had to search for these cubes and collect them in ascending order of their numbers. Thereby they encountered boxes with higher numbers that had to be collected only during a later phase of a trial. This gave the subjects the possibility to remember positions of the boxes. We measured performance by the time needed to collect all items and the total path traversed.

We implemented the virtual environment as a modified version of the first person ego-shooter Quake III Arena by ID Software. This software provided a framework for moving an agent in a virtual world with a naturalistic first person perspective. The virtual environment represented a labyrinth-like urban environment without global visual cues. No features helping in orientation were provided apart from the shape and direction of the corridors, eight numbered cubes and three different textures of wood and stone indicating three districts in the environment.

During a run, only the first person view of the agent was shown on the screen, with the number of the box that has to be collected next, displayed on top (figure 4). When a box was collected by running through it, it did not disappear, but still served as a landmark. Only the display at the top of the screen was updated. A run ends when the eighth box is collected.

Figure 4. In-game screenshot of the virtual environment on a map inspired by Munich Walls have neutral stone and wood textures. One of the boxes that have to be searched is shown in the figure. The display at the top indicates which box has to be collected next.

Keyboard and mouse controlled the movements and looking direction. The player's movements were restricted to walking forward and backward and turning left and right. Since the player cannot look up and down, the pictures appear more static. This reduces the amount of cybersickness, a sudden feeling of nausea and indisposition often experienced by participants who are unfamiliar with these kinds of computer games (LaViola 2000).

The virtual environment controlled the belt via the serial port of the PC. In the correct information trials, the belt represented the rotations of the virtual agent, i.e. it provided information about a virtual north within the game environment. In the wrong information case, the belt also yielded information about a virtual north, but in contrast to the correct information condition this direction was not fixed, but slowly rotated. The amount of this drift was 10% of the players' rotation and therefore not easily perceivable. But it resulted in unreliable information about the direction of north. During the no-belt runs the belt was switched off.

We tested the experimental subjects and controls in two sessions, one before and one after the training period. In each session we tested each participant in each condition (CI, WI, NI) on three different maps, resulting in nine trials. The subjects were informed about the condition and map in the respective trial. The order of the conditions and maps was balanced across participants, but was identical in pre- and post-training tests. Each trial lasted about 10 min until the player had found the last box. After every third trial the participants had to take a break.

4.3. Results

Averaging over subjects did not provide evidence for significant differences in the performance reached on each map. Therefore we did not differentiate between maps in the further analysis. Learning effects over trials were also negligible and we did not have to adjust the serial position of individual trials.

Utilizing the information provided by the belt, the subjects should acquire a two-dimensional (2D) representation within

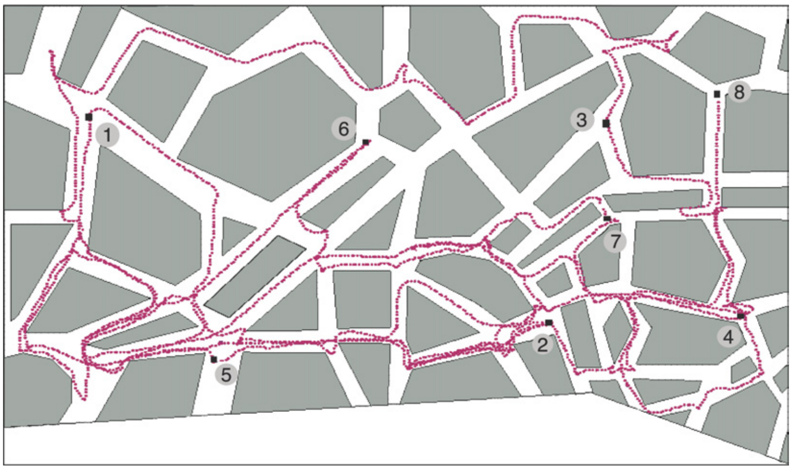

Figure 5. Trajectory of an experimental subject in a trial with correct belt information. The figure shows one of the maps that is derived from the street map of Paris. The numbers indicate the numbered boxes; the (red) dots depict the path that a subject has taken. As can be clearly been seen, the boxes are distributed in a way that the subject has to traverse boxes that he has to collect later on. The figure shows that the subject prefers some of the routes to others, orientating along local cues.

each trial. This is expected to lead to improved performance searching for higher numbered cubes. Such a change of performance within a trial varied strongly between subjects. Instead of choosing the optimal shortest path to the next cube, the players sometimes went a long way round since they seem to have used local cues for orientation (figure 5). Thus, these data do not indicate that the subjects created a 2D representation of the environment.

To compare performance in different conditions, we evaluated the time differences of runs in two conditions. To test the hypothesis that experimental subjects improved performance with correct belt information after training, we investigated the performance with no information versus correct belt information (NI–CI: The time of a CI run subtracted from the time of a NI run). The three maps yield three performance values for each subject and condition. Since the complexities of the maps are comparable we can form nine combinations of NI–CI pairs resulting in nine difference values. We observed an increase for one experimental subject (from −18.84 s to +3.5 s) and for two controls (from −16.01 s to +9.4 s and from −6.3 s to +2.5 s). These pre- and post-training differences were all significant (t-test, $p < 0.05$). Yet on an absolute level, the performance with correct belt information was not significantly better than the performance without belt, except for one control (t-test, $p < 0.05$). Thus, the trained subjects did not improve their ability to use the belt information in this paradigm (figure 6).

As the next step we tested the effect of wrong belt information on performance of experimental subjects after training.

In one subject but none of the controls we observed an increase of the mean difference WI–NI, which reached a positive absolute value in the post-training tests (t-test, $p < 0.02$). Thus, we observed a disturbing effect of incongruent information provided by the belt in only one experimental subject.

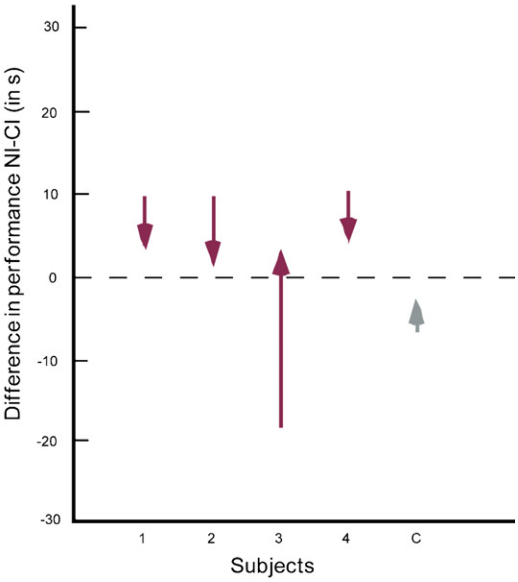

Figure 6. Performance of experimental subjects and controls in the virtual environment. On the y-axis, the difference in foraging time between NI and CI is denoted in seconds. The direction of the arrows indicates the development of performance. Dark (red) arrows refer to single subjects and the grey one is the mean of control subjects' performance. Positive values indicate improved performance with correct belt information.

4.4. Discussion

Our analysis shows significant changes in different aspects of performance in two experimental subjects and in two controls. The variability between individuals is too high to assume a general effect that distinguishes the two experimental groups. Hence, these results of this experimental paradigm do not support the strong integration hypothesis.

Why could our experimental subjects not profit from the belt information in an environment that provides very few other cues for navigation?

The participants may not have been able to form a representation of the maps or box locations during a run because of the high complexity of the map environment. This is indicated by the high variability across trials and subjects and the subjective impression of random search when looking for the next box. At the same time, this complexity is needed to encourage the usage of the belt, since the potential benefit is large. Different base performance of the participants might also result in these highly variable results, since former experience with computer games might influence performance. We applied a within-subject analysis that minimizes such a problem. Besides, our analysis did not reveal strong learning effects and even inexperienced users had no problems with the control of the game. Thus, these design issues do not explain why the experimental subjects cannot profit from the belt information.

Another important issue is the transfer of expertise acquired during training in daily life to performance in the virtual environment. In the outdoor tests reported earlier, the experimental situation was well matched to the training context. In contrast, in the virtual environment normal proprioception and visual inputs are decoupled, and the normal vestibular signals are not compatible with the information provided by the belt. Given that over many years the subjects had learned to use visual information to orientate themselves, the experience of 6 weeks training time with the belt appears rather short. Thus, it is conceivable that the conflict of normal vestibular signals and the information provided by the belt is resolved to the advantage of the visual modality. Essentially, we speculate that the experimental subjects were not able to use the information provided by the belt, as the experimental situation of the virtual environment was not close enough to the real environment experienced during the 6 weeks of training. Pressing buttons on a keyboard does involve different sensorimotor contingencies than does navigation in outdoor environment. Hence, a critical test of the strong integration hypothesis requires that information provided by different modalities are confronted in an experimental situation that matches the context of training. In either case, this experiment demonstrates that in some situations, the newly acquired sense is not on a par with the classic senses.

5. Physiological tests

5.1. Introduction

According to the subcognitive processing hypothesis the heading information provided by the belt can be firmly integrated into human perception, even in the absence of attention. Here, to circumvent effects of attention we pursue an approach excluding the influence of high-level cognitive processes. We use two techniques related to posture and orientation in space: nystagmography and posturography. The interaction of the newly acquired information by the belt with these two physiological reflexes is investigated.

Posturography investigates the influence of heading information on body sway using the Romberg test for balance testing. Nieschalk *et al* (1999) describe a prototypical body-sway experiment using similar equipment and experimental conditions. Under natural conditions vestibular and visual signals contribute to the maintenance of balance. During the measurements the belt provides information either consistent or conflicting with the visual and vestibular signals. Hence, posturography is an objective test of the integration of belt information with visual and vestibular signals in the control of balance and thus suitable to test the subcognitive processing hypothesis.

Nystagmography investigates the stabilization of visual stimuli on the retina during head rotational movements. The vestibulo-ocular reflex compensates for head rotation around the vertical axis. During head rotation in one direction, the eyes move in the opposite direction. This slow phase is followed by a rapid movement of the eyes in the direction of the head movement. This quick phase is labelled the vestibular nystagmus. In the ideal case during the slow phase the image is perfectly stabilized on the retina, while the quick phase accounts for the limited range of eye movements. However, due to the hydrodynamics of the vestibular organ, eye movements habituate during sustained rotation. In a lit environment visual information supplements the vestibular system and the habituation is largely reduced (Kandel *et al* 2000). We used nystagmography to investigate the interaction of vestibular signals with the additional information provided by the belt. The belt indicates rotations without habituation; hence the subcognitive processing hypothesis predicts an increase of eye movements during body rotation (per-rotatory nystagmus). Hence, nystagmography is an objective test of the integration of belt information with vestibular signals and suitable to test the subcognitive processing hypothesis.

Using posturography and nystagmography in this study, we investigate the interaction of vestibular and visual signals with the information supplied by the belt in experimental subjects and controls.

5.2. Methods

Posturography and nystagmography on experimental subjects and controls were performed before and after the training phase.

We applied the Romberg test to the experimental subjects and controls before and after training experiments. This test is commonly used for balance testing in clinical diagnosis. The subjects were standing with their eyes closed on a posturography—platform (‘Luzerner Messplatte’, Otopront, Hohenstein Germany) while changes in their centre of balance were continuously recorded. During posturography, subjects received information via the belt as well as by vestibular signals. Each session consisted of three conditions differing in the type of signal provided by the belt. Either the belt was switched off providing no information (NI), or the belt was interfaced with an external computer program to simulate a continuous rotation around the vertical axis and thus providing information conflicting with normal visual and vestibular signals (WI). For a quantitative comparison in each condition we measured the total length of the sway path and compared the effect of training on this measure.

Experimental and control subjects were also tested using nystagmography. Participants sat on a swivel chair (Hortmann

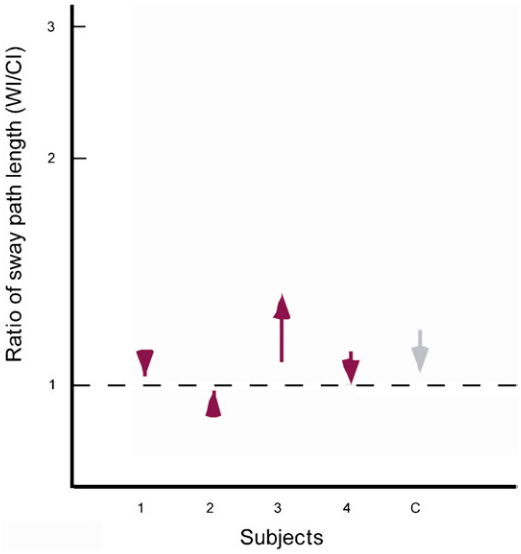

Figure 7. Sway path of the experimental subjects during posturography before and after training. Arrows indicate the tendency (dark red = individual experimental subjects, light grey = mean over controls).

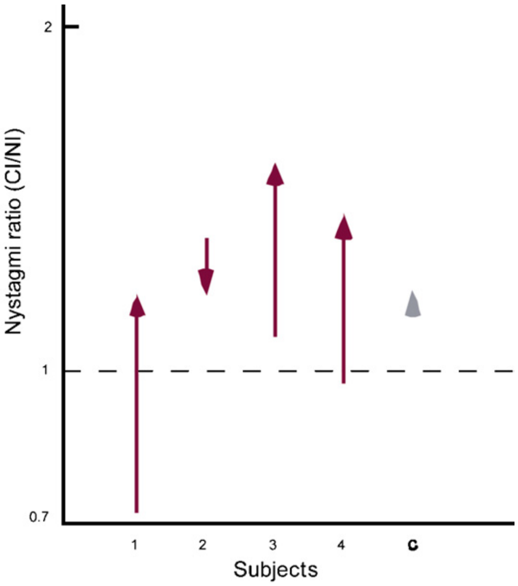

Figure 8. Per-rotatory nystagmus of the experimental subjects before and after training. Each data point indicates the logarithmic ratio of the number of fast eye movements with correct belt information and without belt information for the subjects. Positive values indicate a improved performance with belt information (dark red = individual subjects, light grey = mean over controls).

CNG) in a dimly lit room. After a short calibration procedure they closed their eyes, and the chair started to rotate. Following an acceleration phase of 30 s, the chair rotated at a constant speed clockwise for three min and then stopped abruptly. After a break of 4 min the procedure was repeated with a counter clockwise rotation. Each session consisted of two conditions; the subjects received information via the belt and vestibular signals (CI) or the belt was switched of (NI). In both cases, however, they did not receive visual information as their eyes were closed. We recorded their eye movements with the help of six electrodes placed in a standard configuration around their eyes. For a quantitative comparison we measured the number of fast eye movements occurring after the acceleration phase.

5.3. Results

We compared the length of the sway path during posturography without belt information and with conflicting information. Before training, experimental subjects and controls displayed a difference in sway path under these two conditions of about 1.6 cm ± 2.1 cm (figure 7). After training the variance of this measure increased, but reached significant difference to pre-training results in one experimental (13 cm) and one control subject only (14 cm). Hence, the measure of sway path increased after training as predicted by the subcognitive processing hypothesis in not only one of the four experimental subjects, but also in one of the controls.

We compared the per-rotatory nystagmus with belt information (CI) and without belt information (NI). Before training the experimental subjects made on average 1% more frequent fast eye movements in the CI condition than in the NI condition. This difference increased to 34% after training. This effect is, however, due to large increases in three of the four subjects and a small decline towards an equal number of fast eye movements in the fourth subject (figure 8). In contrast, in the controls no systematic effect (7% versus 8%) was observed. Thus, the number of fast eye movements increased after training as predicted by the subcognitive processing hypothesis in three of the four experimental subjects.

5.4. Discussion

Here we investigated the interaction of the newly acquired information by the belt with two physiological reflexes. Using posturography no consistent effect of training was observed in the majority of experimental subjects and controls. In a single experimental and a control subject, however, the conflicting information provided by the belt induced an increase of sway path. These data do not support the prediction of the subcognitive processing hypothesis. However, the measurements of per-rotatory nystagmus are consistent with the prediction of the subcognitive processing hypothesis in all but one experimental subject.

How can we understand the diverging results of the two types of measurements? Posturography relates primarily to the position of the centre of gravity of the body in relation to the supporting area of the feet. As a consequence, the otolith organs play a pivotal role in the maintenance of posture. In contrast, pure rotations of the trunk have a limited effect on the centre of gravity of the body. Hence, the signals supplied by the belt do not relate primarily to posture. With respect to nystagmography the situation is reversed. The vestibular information pertaining to rotation originates in the semicircular channels and has a direct influence on eye movements. This aspect relates directly to the signals conveyed by the belt. Under natural conditions the information provided by the belt is of direct relevance to the control of eye movements. Hence, the differences observed in the two physiological tests can be understood as a direct consequence of the relation of the information provided by the belt to natural behaviour and reflexes tested. Furthermore, they provide proof that even without attentive processes the newly provided information is integrated supporting the subcognitive processing hypothesis.

6. Subjective reports

6.1. Introduction

The most ambitious aim of the study was to assess the extent of changes induced by training with the belt on qualitative experience. O'Regan and Noë (2001) argue that perceptual awareness is established by mastery of sensorimotor contingencies. As a straightforward generalization we formulate the new modality hypothesis. It predicts that after sufficient experience with the signals supplied by the belt during natural behaviour, a new quality of sensory experience will emerge. The possibilities to assess these effects are limited to introspection and subjective reports. Here we evaluate the subjects' experiences by questionnaires, diaries, and through face-to-face feedback.

6.2. Methods

During the complete training interval of 6 weeks, the subjects filled out a daily questionnaire. It assessed the everyday use of the belt, controlled for eventual technical problems and health related aspects, and documented the navigational abilities and qualitative experience of space. Furthermore, after each of the weekly outdoor training sessions, interviews of subjects and controls covered all these aspects in depth. Upon completion of the training and finals tests we conducted comprehensive interviews.

6.3. Results

To report about the sensory experiences of the subjects while wearing the belt, we have to take into account the private nature of perceptual experience. Thus, these data are not suited for inter-subject comparison and statistical tests. Here we present the observations during the experiment in the style of a case report with quotations indicated in italics. The subjective reports show high variability and partly even contradictory subjective experiences.

For all experimental subjects the training period was tiring—especially in the first few days of training. For one subject this even resulted in the feeling of exhaustion and longer sleep phases. None of the four control subjects reported any change in their spatial perception. Also, two of the four experimental subjects experienced no or only minor qualitative changes in their perception of the environment. They had to concentrate to access the information provided by the belt. '*I really felt very little, but I had the feeling I was better with the belt at least at the natural-environment orientation tests. At places where I am often, I know immediately where north is.*' This points at the possibility to use the information provided by the belt when the subject concentrates on it and processes it consciously. '*The belt is annoying—for me it is uncomfortable, and the vibration is too loud such that I have problems to concentrate.*' For those two subjects, the stimulation was perceived as tactile sensation, and the vibration was even perceived as disturbing at times.

'*Subjectively, I couldn't feel the difference between the virtual environment test trials with incoherent, with coherent and without belt information.*' For one subject the vibration was hardly noticeable, such that it was not recognized when the belt was accidentally switched off. Thus, he could not use the information effectively in all situations.

In great contrast, the other two subjects reported profound changes in their subjective experiences. Yet they did not perceive a local magnetic field. Instead, these subjects described that the input from the belt reflected properties of the environment rather than being simply tactile stimulation: '*It was different from mere tactile stimulation because the belt mediated a spatial feeling.*' This feeling was present in everyday situations: '*I was intuitively aware of the direction of my home or of my office. For example, I would wait in line in the cafeteria and spontaneously think: I'm living over there.*' These subjects also showed improved orientation performance and higher awareness of the spatial relations between different locations while wearing the belt. They had a feeling of an ordered environment, which was guided by the subjective experience of the space in which '*reference points are intuitively present and help a lot in navigating around and understanding relations between places*'. Unexpectedly, magnetic north had no special status, but spatial perception related always to landmarks. The actual spatial context was felt as being massively enlarged, and spatial relationships could be memorized effortlessly. Both subjects report effects on memory of places, landmarks and orientation. For one of the subjects, the effect on memory was most impressing as he could easily memorize new spatial context, e.g. when visiting a city, without concentrating on the processing. One subject travelled to foreign cities with the belt and reported: '*The orientation in the cities was interesting. After coming back, I could retrieve the relative orientation of all places, rooms and buildings, even if I did not pay attention while I was actually there.*' Further, both explain that their navigation was no longer based on a graphical representation but on a 2D representation. The navigation along a sequence of local cues was replaced by a global orientation. They explained that the access to the information provided by the belt did not require attention: '*During the first two weeks, I had to concentrate on it; afterwards, it was intuitive. I could even imagine the arrangement of places and rooms where I sometimes stay. Interestingly, when I take off the belt at night I still feel the vibration: When I turn to the other side, the vibration is moving too—this is a fascinating feeling!*' These two subjects did not need to put effort in using the information, but rather after some time it was natural to gather additional information on the environment and to use it.

These two subjects that reported a change in perception had difficulties to grasp what exactly changed. Articulating the perceptual quality they accessed and the qualitative experience arising from the different kind of spatial perception was hard. The observer got the impression that they lack concepts for what happens, such that they could only use metaphors and comparisons to come closer to an explanation. Interestingly, for one subject the effects during training were noticeable but not overly impressive. Only after he stopped wearing the belt was the full amount of induced changes apparent: '*After removing the belt, my living space shrank quickly: the world appeared smaller and more chaotic because relative positions to places beyond the visual horizon were rather unorderly*.' However, the other subject did not experience such a fast change in his spatial perception after removing the belt. For him, the effects that had been there before, just disappeared slowly—just the cognitively acquired knowledge on relations and positions remained. For both subjects the effects were completely lost after some time, and remembering and describing the perceptual quality was difficult at that time. The difficulty to explain to others what they felt resembled the former problem to explain the difference in experience they felt during the phase of wearing the belt. Indeed, it was much easier to talk about changes in perception between experimental subjects, than to communicate it to naïve controls.

6.4. Discussion

There are variable results in the subjective experience during the training period. The four subjects experienced the processing of the information provided by the belt rather differently.

The subjective reports by two of the experimental subjects did not indicate a change of perception. These two could not report the difference in their perceptions going beyond the ongoing tactile stimulation. Here, motivational factors as well as wearing comfort might play a role. One of the subjects in whose case little changes occurred had difficulties adjusting the belt for wearing comfort and was just happy once the six weeks of training were over.

On the other hand, two of the experimental subjects reported profound changes in perceptual awareness. Interestingly, these were the two subjects who were making the most active use of the belt-information, who improved their performance in outdoor orientation tasks, and showed consistent effects in nystagmography. Furthermore, the perception of space changed in two subjects and in one additional subject who was not in the original experimental group (Nagel *et al* unpublished observations). Results of the additional subject point at a different change in experience than of those reported above. Interestingly, this subject did not feel the kind of ordering of the space and the relative order between areas and landmarks. Rather, she reported that she arranged everything according to north during the time when wearing the belt. That is, she developed a feeling of where north is and sorted landmarks and directions relative to north. Further, this subject reported feeling dizziness and being irritated when she stopped wearing the belt. For a few days, spatial relations were different for her than during wearing the belt.

The results presented in this study give a mixed picture. On one hand the variability between the subjects is large. In part we can only speculate about the reasons for this and cannot present a recipe that guarantees changes in the quality of perception of individual subjects. On the other hand, the results give proof that training new sensorimotor contingencies can induce qualitative changes in perception. This is even more remarkable, as all subjects were adults and way past critical periods where e.g. binocular fusion (Hubel *et al* 1977) or native language acquisition (Kim *et al* 1997) is supposed to occur. Furthermore, the subjects reporting changes of spatial perception also had consistent results in the objective tests reported above. Thus, these subjects intimately integrated the information provided by the belt. The subjects reported a qualitative new experience, which had arisen during the period of intensive training and usage of the belt leading to integration in their daily lives.

As our results do not point at the formation of a primary modality because our subjects did not experience a local magnetic field, we rather assume that the qualitative change in perception gives evidence for modifications of a meta-modality. This secondary modality is informed by various modalities such as vision, audition and proprioception, all of them being involved in natural spatial perception.

7. Discussion

Inspired by sensory substitution and skill-based theories of perception, we set out to explore the integration of qualitatively new information based on a new set of sensorimotor contingencies. Adult subjects are continuously provided with information about their orientation in space, via vibrotactile stimulation. We formalize the potential consequences for performance and perception in a set of four hypotheses (see introduction). Here we relate the results obtained in outdoor orientation tasks, navigation in a virtual environment, nystagmography, posturography and subjective reports to these hypotheses.

- *Weak integration hypothesis.* Due to the general formulation of this hypothesis—sensory information provided by the belt can be processed—all experiments may bear on this question. The most direct evidence, however, is supplied by the outdoor orientation tasks. The context of this task was close to natural behaviour and a significant difference between experimental subjects and controls is observed. This demonstrates that training with the belt can improve performance supporting the weak integration hypothesis.
- *Strong integration hypothesis.* If the orientation information is inconsistent with normal sensory signals from other modalities, the effects are highly variable. For example, during the navigation task in the virtual environment the information provided by the belt has to compete with visual information and is in conflict with normal vestibular signals. The results of this experiment show limitations of utilizing the

newly acquired information in complex situations with multimodal information. Thus, given the constraints of the present experiment (regarding belt, training time and experimental context) we can presently not support the strong integration hypothesis.

- *Subcognitive processing hypothesis.* The physiological tests were designed to minimize the effect of attention and high-level cognitive reasoning. Under these conditions some of the tests, and we argue the relevant ones, demonstrated systematic effects of the information provided by the belt on physiological reflexes. These data support the subcognitive processing hypothesis.
- *New modality hypothesis.* In two of the four experimental subjects, profound changes of sensory experience occurred. This provides proof of concept that sensory experiences may be learned and are compatible with skill-based theories of perception. Furthermore, it lends support to the new modality hypothesis.

Remarkably, in no case are subjects reported to perceive a local magnetic field. Strictly speaking, the changes in perception indicate not a genuinely new modality, but modification of the meta-modality of spatial perception. The term 'meta-modality' is used to reflect the fact that normal spatial perception is fuelled by visual, auditory and somatosensory information. The ability to infer spatial information from these pooled 'primary' modalities may have thwarted our objective to create a completely new sensory modality. Instead, the acquired sensorimotor contingencies lead to a transformation of this already existing meta-modality.

During evolution, animals like humans acquired senses that are most helpful for their survival. Introducing a new sensory modality may require it to be behaviourally relevant. The ability to sense local distortions of magnetic fields is of questionable behavioural relevance. However, magnetic senses are widely used for navigation in the animal kingdom. There is evidence that disruption of the magnetic field changes the homing behaviour in pigeons (Keeton 1971). In a recent study, Mora *et al* (2004) have shown that pigeons make use of magnetic particles in their beaks to sense magnetic fields. It is not only migrating birds that can benefit from the additional orientation information provided by the global magnetic field. For sea turtles, magnetic information becomes important once they are navigating in the open sea (Lohmann and Lohmann 1996). Lobsters that are exposed to alterations in the magnetic field are able to orient themselves back towards their caves (Boles and Lohmann 2003). According to Meyer *et al* (2004), sharks are able to sense magnetic fields as well. Magnetoreception and a pronounced sense of smell allow for exceptional navigational abilities. In humans, there is no evidence of a magnetic sense (Fildes *et al* 1984). Yet some tribes in Australia and Central America have a remarkable performance in global orientation (Levinson 2003), and humans can point to the north when they have limited other cues in displacement-release experiments (Baker 1980). This directly relates to particular properties of language used in these tribes making a well-developed sense for orientation highly relevant in daily live. For subjects living in our culture such a sense is not directly crucial for survival, but still convenient for behaviour. This is a hint that aspects of behavioural relevance do not lead to emergence of a new primary modality but favour a transformation of the meta-modality of spatial perception.

In the discussion above we might have given the impression that the present experiments favour skill-based theories of perception over neuron based theories. This, however, is not the case. In an influential article, O'Regan and Noë (2001) argue that for conscious perception sensorimotor contingencies must be learned and the knowledge applied. Such learning, however, is instantiated in the brain. Further, just like information, knowledge is defined by a recipient. Thus, the important aspect is, that no passive properties of the outside world are represented with the concomitant problem of bringing these to perceptual life, but dynamic properties related to the behaviour of the subject are coded and enacted. Theories aiming to explain perceptual consciousness face the problem of understanding how physical mechanisms can give rise to consciousness. There are numerous efforts to explain this phenomenon by finding evidence that certain specific neural states have contents that match the experiential content of the phenomenological states (Chalmers 2000). Some theorists emphasize the structural level of specific circuits of neurons, their type of activity, and their projections (Crick and Koch 1998). Others favour the dynamical systems view stressing the role of large-scale dynamical patterns and the intrinsically temporal nature of perception (Thompson and Varela 2001). Here, consciousness is understood to arise from the integrated temporal activity of large populations of neurons distributed over the whole brain (Engel *et al* 1999). Evolutionary theories apply the theory of natural selection to neuronal processes such that consciousness is an emergent property of increasingly complex and integrated neuronal groups developing, following neuronal variation and selection (Edelman 1978). Thus, the dynamic recursive signaling ('re-entry') would give rise to our conscious perceptions. Alternatively, the assumption that there are minimal patterns of activity that are sufficient to produce perceptual awareness (Kanwisher 2001, Rees *et al* 2002) is challenged by a more holistic understanding of conscious perception, doubting the direct match between neuronal and perceptual content (Noë and Thompson 2004). The perceptual experience is a temporally extended process of attentive engagement, and it is this activity that brings forth the content of experience (Noë 2004). Perceptual processes are not restricted to the brain; rather they include the nervous system, the body, and the environment (Varela *et al* 1991). Perceptual experience thus cannot be understood independent of the sensorimotor context of the subject as a whole (Thompson and Varela 2001, Varela *et al* 1991). As a consequence, the most important aspect of skill-based theories is that the brain should not be investigated in isolation, but that a full understanding will require consideration of the behavioural context including body movements of the subject as well as changes in the environment and the subject's reaction to them. This is in line with the observation of the present study, that passive stimulation by a single vibrator is not sufficient for perceptual events to arise. Thus, skill-based and neuron based theories are not contradictory as such, but emphasize different aspects, which are most probably necessary for perceptual awareness to arise.

In this study we provide evidence that newly acquired sensory information can have profound effects on performance and perceptual experience. We do not know all the parameters that led to (or prevented) the effects on performance and perception. Yet we have delivered conceptual proof that it is possible to learn new sensorimotor contingencies. Our results emphasize the importance of considering the relation to behaviour, when investigating perceptual awareness. Given that introducing new sensorimotor contingencies may create qualitatively new perceptual experiences, we recommend that when you want to know what it is like to be a bat (Nagel 1974), you should whistle for orientation and learn to fly.

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