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When Feeling Is More Important Than Seeing in Sensorimotor Adaptation

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Summary

Perception and action are based on information from multiple sensory modalities. For instance, both vision and proprioception provide information about hand position, and this information is integrated to generate a single estimate of where the hand is in space. Classically, vision has been thought to dominate this process, with the estimate of hand position relying more on vision than on proprioception [1]. However, an optimal integration model [2] that takes into account the precision of vision and proprioception predicts that the weighting of the two senses varies with direction and that the classical result should only hold for specific spatial directions. Using an adaptation paradigm, we show that, as predicted by this model, the visual-proprioceptive integration varies with direction. Variation with direction was so strong that, in the depth direction, the classical result was reversed: the estimate relies more on proprioception than on vision. These results provide evidence for statistically optimal integration of information from multiple modalities.

Introduction

When multiple sources provide information about a quantity, a single estimate of the quantity can be achieved by combining the information. For example, we can both see and feel where our hands are, and this information is integrated to generate a single estimate of where the hand is in space. The feeling of hand position is based on proprioceptive information, which we define as the ensemble of sensory information from receptors in the muscles, skin, and joints. Integration of visual and proprioceptive information has been studied extensively in experiments in which subjects view their hand through optical prisms [1, 3]. Prisms displace the visual field and therefore induce a conflict between the visual and proprioceptive signals about hand position. Such a conflict can be used in different ways to estimate the way in which visual and proprioceptive signals are combined and, specifically, the weighting given to each. For example, in prism adaptation experiments, subjects point at visual targets and proprioceptive targets before and after they adapt to prisms; the change in their pointing behavior measures the adaptation of each modality [4]. Other methods to estimate the weighting measure localization of visual, proprioceptive, and combined visual-proprioceptive targets [5, 6]. The weightings can then be derived from the responses to the combined visual-proprioceptive targets relative to the responses in the other two conditions.

The picture that emerged from such studies is that (when all visual cues are available) the estimate of hand position relies more on vision than on proprioception, sometimes expressed as “vision dominates proprioception”. The visual weights in most reports are between 0.6 and 0.8, and the proprioceptive weights are between 0.2 and 0.4 [1]. The precise values depend on the experimental conditions. For instance, the proprioceptive weight is larger when the hand is moved actively than when it is moved passively (by the experimenter), and the proprioceptive weight also increases with decreasing availability of visual cues [7]. When vision is reduced to seeing a small light on the finger in otherwise complete darkness, the proprioceptive weight can even exceed the visual weight [7, 8].

When multiple sources provide information about a quantity, and the goal is to minimize the uncertainty in the final estimate, the theoretically optimal way to combine the information is to weight each source by its precision, which is the inverse of its variance [2, 9, 10]. We will now show that the findings summarized above are consistent with this. The precision of visual and proprioceptive localization in a horizontal plane is nonuniform (shown schematically as ellipses in Figure 1), with vision being more precise in azimuth than in depth (by “in depth” we mean in the radial direction relative to the observer; “in azimuth” refers to the direction orthogonal to that) and proprioception being more precise in depth than in azimuth [11]. The shape of the visual ellipses results from the fact that it is more difficult for the visual system to judge distance than direction [12, 13]; target direction can be derived from gaze direction, whereas target distance has to be derived from less precise cues such as vergence and disparity [14, 15]. The precise shape of the visual ellipse also depends on the viewing conditions and the vertical level of the horizontal plane. The shape of the proprioceptive ellipses is mainly determined by the geometry of the arm [11]. Since proprioceptive signals are related to joint angles, uncertainty in the finger position can be understood from uncertainty in joint angles. For an almost extended arm, as shown in Figure 1, uncertainty in both the shoulder and elbow angles results in much more uncertainty in the finger position along the azimuth than in the depth direction.

Prisms induce a mismatch between vision and proprioception along the azimuth, a direction in which localization is “best” for vision and “worst” for proprio-

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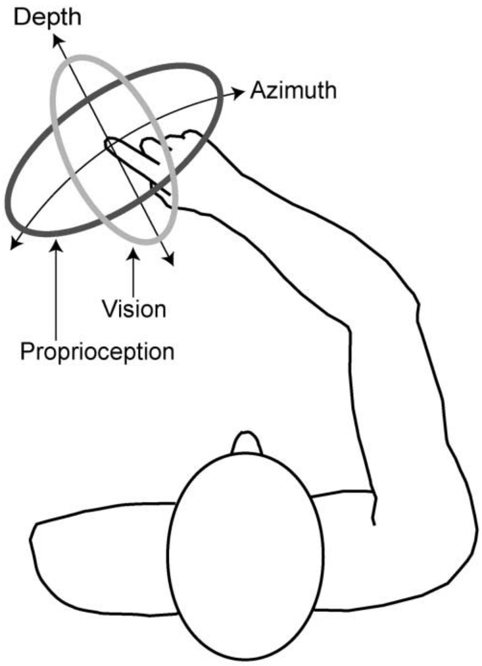

Figure 1. Direction-Dependent Precision of Visual and Proprioceptive Localization

The top view of a subject with the right hand in the area tested. Ellipses represent a schematic of the precision (not to scale) for localizing either a visual target or a proprioceptive target [11]. The narrower an ellipse in a certain direction, the more precise the localization. Note that the visual and proprioceptive ellipses are approximately orthogonal.

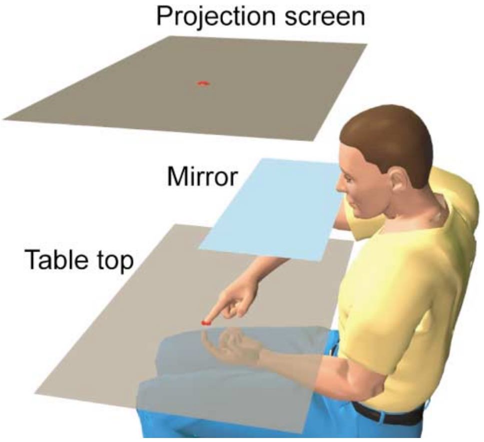

Figure 2. Experimental Setup

The subject looked in the mirror, which was positioned midway between the tabletop and the projection screen. As a result, the table was occluded, but the image of the projection screen was seen in its place. The right arm was also occluded, but the motion tracker recorded the fingertip position, which could be presented to the subject as a red circle. During adaptation, the relationship between actual hand position and red circle position was perturbed by displacing the circle either in azimuth (leftward) or in depth (forward).

ception. Therefore, the optimal integration hypothesis predicts that, as observed, the integration should rely more on vision than on proprioception. The dependence of the weights on factors such as active versus passive movement of the hand and the available visual information [7] is also consistent with the hypothesis. Proprioceptive localization is more precise after active than after passive movement [16], so the proprioceptive weight should be larger after active movement. Reducing the visual information will lead to less precise visual localization and therefore to a reduction of the visual weight.

More evidence for optimal integration has been obtained by studying two-dimensional hand localization in a horizontal plane [2]. Since the relative precision of vision and proprioception varies with direction (see Figure 1), optimal integration can no longer be described by single visual and proprioceptive weights. Instead, the whole two-dimensional precision is taken into account. The result is that the integrated estimate of hand position is predicted not to be on the straight line between the positions where it is localized on the basis of vision only and proprioception only (assuming these are different), but it will be off that line. This prediction has been confirmed experimentally [2].

Here, we explicitly test whether the weighting of vision and proprioception varies with direction. Specifically, we determine visual and proprioceptive adaptation to visual-proprioceptive mismatches in depth and in azimuth. In azimuth, vision is more precise than proprioception. In depth, however, the precision of proprioception is increased and that of vision decreased, so the integration should rely more heavily on proprioception. Our paradigm measures visual and proprioceptive adaptation rather than weights. Since the modality weighted most heavily will adapt least [9], the prediction is that proprioceptive adaptation will be smaller in depth than in azimuth.

Results and Discussion

Subjects pointed at visual and proprioceptive targets before and after they adapted to visual-proprioceptive mismatches in the setup shown in Figure 2. We measured visual and proprioceptive adaptation to mismatches in azimuth and in depth; that is, we measured how much the mean pointing responses toward visual and proprioceptive targets changed during adaptation.

Both in azimuth and in depth, our subjects showed significant visual and proprioceptive adaptation in the expected direction (for all combinations of direction and modality, $p \leq 0.01$, one-tailed t tests). Next, we examined the relative proportions of visual and proprioceptive adaptation. In accordance with previous studies [1], the ratio between proprioceptive and visual adaptation in azimuth was 67:33 (left columns in Figure 3). In contrast, in the depth direction, the ratio between proprioceptive and visual adaptation was 28:72 (right columns in Figure 3). As predicted by the optimal integration model, the proprioceptive adaptation was significantly smaller in depth than in azimuth (one-tailed paired t test: $t_{13} = 3.3$, $p < 0.003$), demonstrating direction-dependent adaptation. Moreover, in depth, the visual adaptation was significantly larger than the proprioceptive adaptation (two-

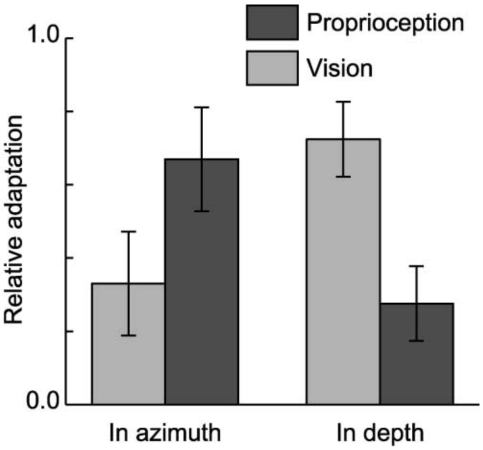

Figure 3. Relative Visual and Proprioceptive Adaptation

The bars show the mean relative adaptation across subjects, and the error bars represent standard errors.

tailed paired t test: $t_{13} = 2.19$, $p < 0.05$), indicating that in depth proprioception is weighted more heavily than vision.

Previous work [2] suggested that the weighting of vision and proprioception for hand localization could vary with direction. Here, we explicitly determined the visual and proprioceptive adaptation to visual-proprioceptive mismatches in two orthogonal directions in otherwise identical conditions, and we found different results. This shows that different weightings apply simultaneously for different directions. Moreover, we found that, in the depth direction, proprioception is weighted more heavily than vision.

An earlier study [8] had already shown that the estimate of hand position in the depth direction is not based on vision only, but it is also based on proprioception. However, no larger weighting of proprioception than vision was found, presumably because the passive positioning of the target hand led to less precise proprioceptive information than in our study. We found that, in more natural conditions, the proprioceptive weighting is larger than the visual weighting. This suggests that a larger reliance on proprioception is very common in everyday life. This is the converse of the classical view that the brain relies more on vision. That view was based on the azimuthal displacement caused by optical prisms, which turns out to be a special case.

Our results support the optimal integration model, which suggests that the brain weights the information from each modality in a way that minimizes the uncertainty in perceived position. The weights are flexible; not only do they vary with experimental conditions such as active versus passive movement, but, in a given condition, they also vary with direction. It can therefore be misleading to say that one modality dominates another; the situation is better described by flexible weighting in which the weights are optimized for the precision in a given situation. It is not clear how the brain obtains the knowledge about the direction-dependent precision; it may estimate precision directly from the noise in incoming sensory information, but it may also have learned it from experience. Multisensory areas of the brain such as the parietal lobes [17, 18] may perform the integrative computations required to achieve optimal integration.

Experimental Procedures

A total of 14 naïve subjects (6 females and 8 males) gave informed consent and participated in the study. All subjects participated in two adaptation sessions, an adaptation in azimuth and an adaptation in depth, in a counterbalanced order. Subjects sat at a large horizontal table, in a normally illuminated room, with their head supported by a chin rest (see Figure 2). A Polhemus Fastrak motion tracker was used to measure the position of the subject's right and left index fingers at 120 Hz. The targets and the feedback of the right finger position were presented as virtual images in the plane of the table. This was achieved by projecting an XGA screen with an LCD projector onto a horizontal rear projection screen suspended 51.0 cm above the table. A horizontal front-reflecting mirror was placed face up 25.5 cm above the table. Subjects had no direct view of their arm because it was covered by the mirror. The subjects viewed the reflected image of the rear projection screen by looking down at the mirror. By matching the screen-mirror distance to the mirror-table distance, all projected images appeared to be in the plane of the table (when viewed in the mirror), independent of head position. Targets were presented as 17-mm diameter yellow circles, and the finger position was indicated by a 7-mm diameter red circle (cursor spot). Using a cursor spot leads to equally precise localization of the hand as viewing the whole hand, because viewing only the fingertip and viewing the whole hand lead to the same localization precision [19]. Prior to each experiment, we calibrated the output of the Polhemus: we recorded its output over a grid of 24 points on the table and performed quadratic regression of this output to the actual grid locations.

Each session consisted of three phases: preadaptation, adaptation, and postadaptation. Each trial started with both hands in tactile starting positions (the right hand above and the left hand below the table) about 10 cm straight ahead of the subject. To avoid stereotyped movements, we used four different target positions close together. They were on the corners of an imaginary 2.5-cm square about 50 cm in front of and 10 cm to the left of the subject's body midline.

In the preadaptation phase, subjects used their left hand under the table to point to visual, proprioceptive, or both visual and proprioceptive targets. Proprioceptive targets were defined as the position of the right fingertip, which was placed on a tactile marker on the tabletop. The subject moved the right hand actively to the target; a beep confirmed when the hand had reached it. Vision was blocked by Plato (Translucent Technologies) visual occlusion spectacles from the moment the right hand began to move. In the visual target condition, the right hand remained in its starting position, and the visual target was presented at one of the four locations. In the combined visual-proprioceptive condition, the visual target was also displayed, but now the subject also had to put the right finger on the corresponding tactile marker. Full visual feedback was provided about the right finger position, shown by the cursor spot, during the movement from the starting position to the target. In all conditions, subjects pointed with their unseen left hand touching the underside of the table. No feedback was given. The endpoint of the movement was defined as the first point at which the tangential velocity dropped below 5 cm/s. At this time, another beep sounded; the subject then moved both hands to their starting positions to start the next trial. Visual feedback was provided when the hands were within 15 cm of their starting positions so that the subject could easily guide them to the starting positions. This also reduced proprioceptive drift [20]. Subjects pointed three times to each of the four targets in each condition in a pseudorandom order.

In the adaptation phase, only the visual-proprioceptive condition was presented. This phase consisted of 12 trials (3 repetitions for each target) in which a 5-cm visual perturbation was gradually introduced during the first 10 trials. Gradual introduction of the displacement [21] and concurrent vision of the hand [3] lead to more complete and quicker adaptation than immediate introduction and terminal feedback. The images of both target and finger position were displaced, either in depth (forward) or in azimuth (leftward). The image of finger position was not displaced at the starting position, but it was fully displaced at the target position. In between, the displacement increased linearly. Unlike prisms, this method allowed equivalent visual displacements in azimuth and in depth without any visual distortions. The subjects were questioned after the experiment: none of them had noticed the perturbations.

After the adaptation phase, a postadaptation phase was tested, which was identical to the preadaptation phase. The preadaptation phase of the second session was preceded by a "deadaptation" phase in which the displacement of the previous session was gradually reduced to zero (like the adaptation phase in reversed order).

We determined the change between pre- and postadaptation pointing to proprioceptive targets (ΔP) and to visual targets (ΔV). For both modalities, we calculated mean pointing errors (pooled over targets because these were very close together) and determined their difference between pre- and postadaptation along the displacement direction (with positive values denoting changes in the expected adaptation direction). Relative adaptation was calculated for proprioception as $\Delta P/(\Delta P + \Delta V)$, and, for vision, it was calculated as $\Delta V/(\Delta P + \Delta V)$.

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