Neck muscle vibration in full cues affects pointing

Sarah McIntyre
School of Psychology, University of Sydney, Sydney, NSW, Australia

Tatjana Seizova-Cajic
School of Psychology, University of Sydney, Sydney, NSW, Australia

Vibration of the dorsolateral neck stimulates proprioceptors that are normally active during head movement; this induces a visual illusion of contralateral motion and displacement of a stationary target seen against a homogenous background. The spatial constancy explanation of the illusion argues that it occurs because information about head movement is necessary for accurate egocentric localization of visual objects. Accurate egocentric localization, in turn, is necessary for the success of object-directed motor action, but previous studies failed to find evidence that vibration affects pointing toward visual targets in a normally illuminated, structured field. Our goal was to provide this evidence. Vibration lasting 12 s was applied to either side of the neck while observers (N = 11) pointed at the visual target with an unseen hand. Vibration of the right side of dorsal neck in the illuminated visual field induced a 26-mm lateral bias in pointing responses in comparison to the vibration of the left side. We conclude that the mechanism that takes into account neck proprioceptive signals also operates in full cues. The pointing bias in full cues generally co-occurred with reported stationariness of the visual target, suggesting a conflict between cues used in perception of body-centric position used to guide action, which include neck proprioception, and those used in perception of motion, for which object-relative retinal information is sufficient.

Keywords: neck proprioception, visuomotor control, multimodal, multisensory, reaching and pointing, motion illusion, human, muscle spindle, dissociation


Introduction

It is essential to understand how retinocentric information is transformed into the body-centric frame of reference to fully understand the integration of visual and motor processing. This transformation allows organisms to use visual information about external objects to accurately perform motor tasks such as reaching and pointing. This is distinct from tasks that involve making relative judgements about two stimuli in the environment, which do not require the transformation.

Transformation of retinocentric information into a body-centric frame of reference requires intersensory integration where retinal inputs are combined with inputs from other senses such as proprioception (Harris, 1994; Lackner & Levine, 1979; Roll, Roll, & Velay, 1991). Proprioception informs about the movement and position of body parts. It is required for visually guided action because it specifies the position of the eyes relative to the head and the position of the head relative to the body (in fact, a change in the position of any body part is relevant to visually guided action if it also displaces the eyes relative to the environment; see Roll et al., 1991). A turn of the head unaccounted for may result in misreaching toward an object.

The integration of visual and proprioceptive information discussed above is nonredundant. Proprioception does not inform about position of visual objects, and we do not depend on vision for information about the position of the head relative to the body. The two senses are linked in a system that requires both components to produce an output such as the position of a visual object in the body-centric frame of reference. Howard (1997) called this kind of intersensory system a nested sensory system. One can test if a sensory signal is part of a nested system for a particular task by disrupting that signal and observing the effect on task performance.

Proprioceptive signals can be disrupted using muscle vibration to investigate the role of neck proprioception in visually guided action. Vibration selectively activates muscle spindle receptors, and this induces an illusory sensation of body part movement that is consistent with the extension of that muscle (Goodwin, McCloskey, & Matthews, 1972). When applied to the dorsolateral muscles in the neck, vibration induces a visual illusion where observers perceive a stationary visual target as moving and displacing toward the hemifield contralateral to the vibration site (Biguier, Donaldson, Hein, & Jeannerod, 1988; Karnath et al., 1994; Lackner & Levine, 1979; Seizova-Cajic, Sachtler, & Curthoys, 2006; Strupp, Arbuso, Borges Pereira, Dieterich, & Brand, 1999; Taylor & McCloskey, 1991). This effect is a close relative of the oculogyral illusion, illusory motion seen as a consequence of vestibular stimulation (see Graybiel & Hupp, 1946). A parsimonious explanation of both illusions...
views them as the product of the spatial constancy mechanism usually responsible for accurate perception of position and motion in the body-centric frame of reference (Lackner & Levine, 1979). Both neck proprioception and the vestibular signals inform about head movement, and an illusory signal about this event creates an illusory end percept in vision (motion and displacement of the target).

The spatial constancy account of the vibration-induced visual illusion is robust: Similarly displacing effects can be induced by vibrating extraretinal muscles (Velay, Roll, Lenerstrand, & Roll, 1994), and the effects of neck vibration on localization generalize to the auditory domain (Lewald, Karnath, & Ehrenstein, 1999). Neck muscle vibration also induces monkeys to make systematic errors on a task in which they have been trained to make saccades to the remembered location of a target (Corneil & Andersen, 2004).

A puzzling result of vibration studies is that the illusory effect is absent or much reduced in an illuminated environment with rich visual cues. This was shown using subjective reports (Biguer et al., 1988; Velay et al., 1994), as well as quantitative measures of perceived motion (Seizova-Cajic & Sachtler, 2007, their Figure 6B). This is a great challenge to the proposed spatial constancy explanation because the rich visual context is the normal context in which sensorimotor systems operate. The spatial constancy explanation argues that neck proprioception is a necessary component of a nested sensory system concerned with body-centric position of visual targets because no other cue can indicate where the head is relative to the body (the only exception to this is when we have vision of the body itself, but we can still reach accurately if we do not see our body). If neck proprioception is necessary, as we argue, then it should not be suppressed in the normal, fully illuminated operating environment.

This was our rationale, and our goal was to provide evidence that, even in full cues, neck proprioception influences perceived body-centric position used to guide action. We used vibration of dorsal neck muscles to bias the registered head position and, with it, the perceived position of visual objects. The observer attempted to point at the visual target with an unseen hand. In the critical condition, a relatively rich visual field was presented, and the question was whether a vibration-induced proprioceptive signal would affect pointing.

### Methods

Nine naive observers and the two authors completed the experiment (one observer never experienced any horizontal illusory motion and discontinued the experiment). All participants had normal or corrected-to-normal vision.

**Vibratory stimulus**

Neck vibration was applied either to the left or to the right side of the neck. The vibrator (model: Vibraneck, Benchmed, set at 90 Hz vibration frequency) was placed on the lower dorsal neck, a few centimeters from the spine. Its location was initially determined by palpation, in an attempt to find the area where splenius capitis is most accessible, followed by the fine adjustment by trial and error, until the observer reported seeing consistent smooth motion of a visual target. If the observer reported only vertical motion, the position was adjusted further until horizontal motion was reported (but the observers were not informed about the expected direction of motion). The vibrator was then attached to the neck and held in place using medical tape and an elastic band to ensure that it was pressed firmly into the muscle. The elastic band was attached to a bar placed to the side and in front of the participant, contralateral to the vibrator.

**Visual stimuli**

Observers saw a reflection of the target, an LED, in a mirror inclined at 45°, bottom edge near (see Figure 1A). The virtual location of the LED (20° diameter) was at a distance of approximately 60 cm from the eyes, 12 cm below the eye level, and behind the mirror. Two identical LEDs were placed 37 mm apart, symmetrical around the median plane, and only one was shown in each trial. In some trials, the LED was the only source of light and no other objects or surfaces were visible. In other trials, the checkered surface (41° × 30.5°) in which the LED was embedded and the outline of the apparatus were illuminated by a desk lamp (see Figure 1B). To point at the target, the observers reached behind the nontransparent mirror and, using a stylus, made contact with the touch-sensitive graphics tablet (Intuos 12 × 18 in., Wacom). The arm and the hand were covered with a black cloth and could not be seen at any point during the trial.

**Prismatic displacement**

An important feature of the experiment was that prisms were used to displace the whole visual field variably across trials. This introduced a level of uncertainty regarding the body-centric position of the whole field including the target, although its position within the visible environment was similar from trial to trial (one of the two LED positions shown in Figure 1). We believed that this would abolish reliance on the unchanging retinal input in repeated trials and force the participant to rely on body-centric position to perform the task (see the Discussion section for more details).
When the structured visual field was shown, observers wore a pair of lightweight plastic goggles. In two thirds of the trials in which the background was visible, the goggles had a 25-diopter Fresnel prism (3M Press-On Optics) fitted to one eyepiece, resulting in the 14° contralateral displacement of the image for that eye only. Viewing was binocular, and because the other eye’s monocular direction was unchanged, the resulting change in binocular visual direction (see Ono, 1991) was approximately 7.2°. Vergence-defined distance of the stimulus also changed to 18 cm. However, egocentric distance specified by the gradient of vertical disparities (see Gillam & Lawergren, 1983; Longuet-Higgins, 1982) present in the checkered surface was not affected by goggles and indicated the real viewing distance (60 cm). The perceptual outcome of this cue conflict between vergence and vertical disparities was that the surface appeared closer as compared with nonprism trials (according to our estimate, the difference was approximately 10–12 cm).

Fresnel prisms also induced some blur in the monocular image, but it was much reduced in binocular viewing because the sharp image from the other eye dominated. Because the nature of the binocular vision is such that separate monocular images are not available for conscious inspection, the observers could not tell which eyepiece had a prism attached to it.

### Experimental conditions and procedure

Vibration was alternately applied to the left (Left) and right (Right) side of the neck to create a contralateral bias in the registered positions of both the head and the LED. A period of 8 s was used to induce the bias; on the basis of the results of previous studies (Biguer et al., 1988; Seizova-Cajic et al., 2006), we believed that this would be long enough to induce the illusion without allowing adaptation to dramatically reduce the effect. The LED was either presented in total darkness (Dark) or embedded in a structured visual field shown in Figure 1B (Light).

To prevent reliance on memory in pointing, we used two different locations of LED (LED1 and LED2) in both Dark and Light conditions, and prismatic goggles described above were used in the Light condition. There were three pairs of goggles: Left-displacing, Right-displacing, and Non-displacing (with no prism attached). The observers were not told how many goggles were used or what their properties were. The prism swapping took place in total darkness. Participants were asked to pass to the experimenter the goggles they had been wearing, and the experimenter helped them to put on a new pair.

Each observer participated in four blocks of trials: Dark–Left, Dark–Right, Light–Left, and Light–Right. Half of the participants first received vibration on the Right and then on the Left; for the other half, the order was reversed. Illumination conditions were presented to each observer in the same order for both sides of the neck, and the order of these was counterbalanced across participants. The LED and Prism conditions were presented in pseudorandom order within these blocks. Dark blocks were approximately 5 min long and Light blocks were approximately 8 min long.

In summary, if Dark and Light conditions are considered separately, the combination of the other variables listed above results in the total of 4 conditions in Dark (LED Position × Vibration Side) and 12 conditions in Light (LED Position × Vibration Side × Prismatic Displacement). Each Dark condition was repeated four times, and each Light condition was repeated twice. Participants were also given 1-min practice runs before the experimental trials.

Schematics of the temporal structure of a single trial in both Light and Dark conditions are shown in Figure 2. Each trial began with vibration in conjunction with the
visual stimulus, and the observer’s task was to look at the LED. Eight seconds after the onset of vibration, a sound indicated that the observer should point at the target. Observers were instructed to indicate the location of the target at the moment of pointing, touching the tablet twice in quick succession (the two responses were averaged). The vibration and visual stimulus continued for 4 s after the sound, giving observers sufficient time to complete their response. They then returned the hand to their lap and rested in total darkness during the 28-s intertrial interval to allow the aftereffect of vibration (Seizova-Cajic et al., 2006) to dissipate. In the Light condition, the intertrial interval was used to swap prism goggles.

At the end of the experiment, participants described what they saw and felt. They were questioned about the magnitude and direction of motion of the visual target, whether they felt any head motion, and how many LEDs in different positions they believed were used throughout the experiment.

Results

Pointing data

Neck vibration affected pointing in both conditions of illumination (Dark and Light). Figure 3 (top) shows the pointing responses of a single representative participant, D.E. He displayed a consistent pointing bias in the Right vibration condition compared to the Left vibration condition, in both darkness and light. The effect seems to be more pronounced in darkness.

Figure 3 (bottom) shows the mean pointing responses across all subjects. Vibration-induced lateral displacement was 42 mm in the Dark condition and 26 mm in the Light condition (approximately 4° and 2.5° of visual angle at 60 cm viewing distance). A 2 × 2 repeated measures ANOVA with illumination condition and vibration side as factors showed that the main effect of vibration, Right versus Left, was significant, F(1, 10) = 8.327, p = .016,
whereas the illumination condition, Dark versus Light, was not, $F(1, 10) = 0.135$, $p > .05$. There was no interaction between the two, $F(1, 10) = 2.037$, $p > .05$.

Although the difference between the Dark and Light conditions did not reach significance, 9 of 11 participants displayed a larger magnitude of deviation in darkness ($p < .05$, one-tailed binomial probability test).

The above analysis concerning vibration side and illumination was computed with the results collapsed across the other two variables—LED and prisms—because they did not interact with the critical variables. Note also that we only referred to the lateral displacement (i.e., along the $x$-axis) because that was the predicted systematic effect of vibration.

A detailed account of the effect of the LED and prismatic displacement and the relevant statistical analyses are given below separately for the Dark and Light conditions.

**Dark condition**

When pointing toward the target in darkness, the observers were sensitive to different positions of the two LEDs. Table 1 shows the responses as a function of vibration side and LED position.

A two-way repeated measures ANOVA with factors vibration side and LED was carried out on the horizontal pointing locations in darkness. As described earlier, the main effect of vibration was significant. The effect of LED was also significant, $F(1, 10) = 184.664$, $p < .001$, and there was no interaction between the two variables, $F(1, 10) = 0.032$, $p > .05$.

**Light condition**

When pointing toward the target in a structured field, the observers were sensitive to different positions of the two LEDs as well as to the prismatic displacement of the whole visual field. Table 2 shows the effect of prisms and LED position on pointing (averaged across vibration side).

A repeated measures ANOVA with factors vibration, LED, and prismatic displacement was carried out on the horizontal pointing locations. As described earlier, the main effect of vibration was significant. The main effect of LED was also significant, $F(1, 9) = 344.553$, $p < .001$, and so was the linear trend contrast for the main effect of the prism goggles, $F(1, 9) = 44.349$, $p < .001$. None of the interactions reached significance.

We carried out similar analyses on the vertical components (the $y$ coordinate) of the pointing responses and found that none of the experimental conditions had a significant effect. Group data presented in Figure 3 show a relatively high variance for the vertical component of the pointing behavior. These interindividual differences most likely arose because of the individual differences in the anatomy of the neck and small differences in vibrator placement. Depending on the exact vibrator position, in addition to the targeted muscle, splenius capitis, the sternocleidomastoid and trapezius muscles could also have been affected, resulting in vertical and horizontal illusory motion of varying magnitudes. Because our criterion for vibrator placement was the direction of horizontal motion, the vertical component of the illusion varied much more widely across individuals. However, at the individual level (see top panel of Figure 3 for a representative example), this variability is of the same order of magnitude as the horizontal one, with a mean $SD$ of 26 mm.

### Table 1

<table>
<thead>
<tr>
<th>Light condition</th>
<th>LED1</th>
<th>LED2</th>
<th>LED1</th>
<th>LED2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Left dorsal neck</td>
<td>x</td>
<td>y</td>
<td>x</td>
<td>y</td>
</tr>
<tr>
<td>x</td>
<td>42 (56)</td>
<td>90 (46)</td>
<td>0 (39)</td>
<td>49 (44)</td>
</tr>
<tr>
<td>y</td>
<td>-1 (95)</td>
<td>-1 (95)</td>
<td>0 (81)</td>
<td>1 (83)</td>
</tr>
</tbody>
</table>

Table 1. Mean pointing responses in darkness as a function of vibration side and LED position. Means are expressed as a deviation (in millimeters) from the leftmost mean response (Right vibration side condition, LED1), which was arbitrarily assigned a value of $(x, y) = (0, 0)$. Values that are enclosed in parentheses are standard deviations of the mean.

### Table 2

<table>
<thead>
<tr>
<th>Light condition</th>
<th>LED1</th>
<th>LED2</th>
<th>LED1</th>
<th>LED2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Left-displacing prism</td>
<td>x</td>
<td>y</td>
<td>x</td>
<td>y</td>
</tr>
<tr>
<td>x</td>
<td>0 (49)</td>
<td>49 (44)</td>
<td>43 (44)</td>
<td>91 (44)</td>
</tr>
<tr>
<td>y</td>
<td>0 (91)</td>
<td>7 (92)</td>
<td>11 (93)</td>
<td>12 (95)</td>
</tr>
<tr>
<td>Right-displacing prism</td>
<td>x</td>
<td>y</td>
<td>x</td>
<td>y</td>
</tr>
<tr>
<td>x</td>
<td>79 (55)</td>
<td>124 (45)</td>
<td>15 (94)</td>
<td>12 (89)</td>
</tr>
</tbody>
</table>

Table 2. Mean pointing responses in full cues as a function of prismatic displacement and LED position. Means are expressed as a deviation (in millimeters) from the leftmost mean response (Left-displacing prism, LED1), which was arbitrarily assigned a value of $(x, y) = (0, 0)$. Values that are enclosed in parentheses are standard deviations of the mean.

**Reports**

In the Dark condition, all participants reported horizontal illusory motion of the target in the predicted direction for at least one side of the neck, but the amplitude of reported motion varied widely. No participant reported clear target motion in the opposite direction to what was predicted, although five observers mentioned some oscillation.

In the Light condition, only three participants experienced any motion of the visual stimulus, but they were unsure of the direction.
Two participants reported a slight sensation of head motion but could not report the direction. A third participant reported an occasional sensation of rightward head motion in the Right vibration condition—the opposite direction from the predicted one; he was also the only participant who pointed in the opposite direction in both Dark and Light conditions, and he experienced only slight motion in darkness.

All of the participants overestimated the number of LED positions used throughout the experiment, which suggests that they did not rely on remembered positions to guide their pointing behavior.

Discussion

When pointing to the visual target during neck vibration, observers erred toward the side contralateral to the vibrated side of the neck. This pointing behavior reveals the workings of the spatial constancy mechanism that relies on neck proprioception to convert retinal input into a body-centric frame of reference. The novel finding of our study is that the error also occurred when the target was embedded in a rich visual context, as would be expected, but was not found in previous research for reasons discussed below.

Our result differs from that of Velay et al. (1994) who failed to find an effect of vibration on pointing in the structured field. They vibrated the eye muscles rather than the muscles of the neck, but this should make little difference because the constancy mechanism should take into account the proprioceptive signal from the eye just as it does the signal from the neck.

The reason our results are different, we believe, lies in the specifics of the respective experimental procedures. There was an experimental artifact in the study by Velay et al. that we avoided in ours. In their study, target position within the visual field was constant across trials, and so was the apparent position of the visual field relative to the body; under these circumstances, observers’ position relative to the target appears constant, which allows them to simply repeat the same pointing movement over and over, without reconsulting the signal from the neck that would normally influence their manual action.

In contrast to this, in our study, the prisms created an optical displacement of the whole visual field from one trial to the next, which was obvious to the observers. We also used two slightly different positions of the target within the visual field. Therefore, factors other than vibration also suggested that egocentric position of the target varied and had to be reassessed in each trial. These circumstances are more representative of everyday manual actions, and they revealed the contribution of neck proprioception to visually guided action.

Our result is also apparently inconsistent with the perceived stationariness of the target in the structured field (during vibration) that was reported by our observers, as well as in previous studies (Biguer et al., 1988; Lackner & Levine, 1979; Seizova-Cajic & Sachtler, 2007). Thus, our observers, who were influenced by vibration in their pointing, reported no target motion in full cues during vibration.

This dissociation between pointing behavior and perceived motion is consistent with other literature that shows that the visual system uses spatial information in different ways depending on the task (see Abrams & Landgraf, 1990; Bridgemen, Kirch, & Sperling, 1981; Knill, 2005; Seizova-Cajic, 2003; Smeets, Brenner, de Grave, & Cuijpers, 2002). Tasks are not best distinguished by being action or perception tasks but in terms of the frames of reference used. Neck proprioception is necessary not only for action tasks that rely on the body-centric frame of reference such as reaching but also for purely perceptual tasks that depend on the same frame of reference, such as judgments of the straight-ahead relative to the body. We predict that the latter task would also be affected by vibration in the fully structured visual field.

In contrast, the perception task in our study heavily relied on the visual context (retinal frame of reference) because it concerned target motion. Perception of motion was most likely absent during vibration due to the lack of relative motion in the rich visual field. In his classical studies on motion perception, Johansson (1978) demonstrated that a dot undergoing an elliptical motion, when seen in isolation, appears to move along an elliptical trajectory. This is consistent with its motion in the egocentric frame of reference, the only one available. However, if another dot is added, relative motion prevails and the perceived trajectory changes dramatically. Similarly, in our stimulus conditions, perceived motion of the LED seen in isolation is consistent with egocentric motion signals, from proprioceptive (including the neck) to retinal. However, in the structured visual field, where visual reference points abound, the target appears stationary because it is stationary relative to the rest of the field. In other words, the weighting of neck proprioceptive input is reduced when in conflict with another motion cue, object-relative motion. The question remains why the whole field does not appear to move relative to the observer, as it happens in the oculogyral illusion (see Graybiel & Hupp, 1946).

There is a potential source of confusion in the above theoretical analysis that we wish to clarify. As just described, in perception of motion, one can rely on the egocentric reference frame (i.e., use both proprioception and vision) or on the retinocentric reference frame (use retinal input alone). In the present case, the two are in conflict, and the winner seems to be the retinal input alone. We said in the Introduction section that cues in a nested sensory system are complementary and nonredundant; that is, they cannot be in conflict. This is not
contradictory to what we are saying here because in the present analysis, the conflict is not between the subcomponents of the nested sensory system (proprioception and retinal input) but between the output of the nested system and an independent source of information about motion (relative motion in the retinal input itself).

Conclusions

The obtained results clearly demonstrate the role of neck proprioceptive signals in the nested sensory system comprising of the retinal and proprioceptive inputs, which is drawn upon when humans perform visually guided arm movements. A consistent pointing error in the context of a structured visual field suggests that neck proprioception plays an essential role in navigation in the natural environment and that vibration-induced visual illusions are not just an artifact of laboratory environments.

Acknowledgments

This research was supported by the SESQUI grant to T.S.-C. and by internal funds of the School of Psychology, University of Sydney. We thank Nenad Petkovski for software development and Juno Kim for icon production.

Commercial relationships: none.
Corresponding author: T. Seizova-Cajic.
Email: tseizova-cajic@psy.unsw.edu.au.
Address: School of Psychology, University of New South Wales, Sydney, NSW, Australia 2052.

Footnote

Howard (1997) makes a very useful distinction between nested sensory systems and *multicue* systems. The latter type involves integration of redundant sensory inputs (cues) to produce a single outcome. If such inputs are discrepant, the question of their relative importance or weighting arises and the outcome can be described as a weighted mean. An example is the combination of vestibular and neck proprioceptive signals, which inform about the position of the head and, therefore, also about the subjective straight-ahead of visual objects (see Karnath, Sievering, & Fetter, 1994; Strupp et al., 1999). In contrast, when dealing with nested sensory systems as in the current study, the question of weighting is meaningless because each of the nested sensory signals contributes unique, nonredundant information to the system.

References


